

RESEARCH REVIEW

Snapshot isolation and isolation history challenge the analogy between mountains and islands used to understand endemism

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Abstract

Aim: Mountains and islands are both well known for their high endemism. To explain this similarity, parallels have been drawn between the insularity of “true islands” (land surrounded by water) and the isolation of habitats within mountains (so-called “mountain islands”). However, parallels rarely go much beyond the observation that mountaintops are isolated from one another, as are true islands. Here, we challenge the analogy between mountains and true islands by re-evaluating the literature, focusing on isolation (the prime mechanism underlying species endemism by restricting gene flow) from a dynamic perspective over space and time.

Framework: We base our conceptualization of “isolation” on the arguments that no biological system is completely isolated; instead, isolation has multiple spatial and temporal dimensions relating to biological and environmental processes. We distinguish four key dimensions of isolation: (a) environmental difference from surroundings; (b) geographical distance to equivalent environment [points (a) and (b) are combined as “snapshot isolation”]; (c) continuity of isolation in space and time; and (d) total time over which isolation has been present [points (c) and (d) are combined as “isolation history”]. We evaluate the importance of each dimension in different types of mountains and true islands, demonstrating that substantial differences exist in the nature of isolation between and within each type. In particular, different types differ in their initial isolation and in the dynamic trajectories they follow, with distinct phases of varying isolation that interact with species traits over time to form present-day patterns of endemism.

Conclusions: Our spatio-temporal definition of isolation suggests that the analogy between true islands and mountain islands masks important variation of isolation over long time-scales. Our understanding of endemism in isolated systems can be greatly enriched if the dynamic spatio-temporal dimensions of isolation enter models

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as explanatory variables and if these models account for the trajectories of the history of a system.

KEYWORDS

endemic species, flickering connectivity system, geological ontogeny, glacial–interglacial fluctuations, island biogeography, isolation, mountain islands, palaeoclimate, past connectivity, sky islands

Every continent, every country, and every island on the globe, offer similar problems of greater or less complexity and interest, and the time has now arrived when their solution can be attempted with some prospect of success. Many years of study of this class of subjects has convinced me that there is no short and easy method of dealing with them; because they are, in their very nature, the visible outcome and residual product of the whole past history of the earth. (Wallace, 1880)

1 | INTRODUCTION

Mountains are known for hosting about half of the biodiversity hotspots of the world (Barthlott, Rafiqpoor, Kier, & Kreft, 2005; Hoorn, Perrigo, & Antonelli, 2018; Myers, 1988; Orme et al., 2005), for their high levels of endemism (Hughes & Eastwood, 2006; Körner, 2004) and for their iconic radiations (Hughes & Atchison, 2015; Nürk et al., 2020). To explain the high concentrations of endemic species in mountain areas, parallels have long been drawn between “mountain islands” (see Glossary), which are surrounded by land, and “true islands”, defined here as islands surrounded by (oceanic) water bodies. In fact, elevation-driven isolation and consequent endemism is a common situation for many mountain species, because many taxonomic groups show maximum species richness (Heaney et al., 2016; McCain, 2005, 2009; McCain & Grytnes, 2010) and higher rates of endemism at higher elevations (Steinbauer et al., 2016). Analogies between mountain islands and true islands typically invoke high levels of isolation (e.g., Särkinen, Pennington, Lavin, Simon, & Hughes, 2012), high levels of endemism (e.g., Nogué, Rull,

& Vegas-Vilarrúbia, 2013), legacy effects of past surface areas during climate fluctuations (e.g., Van der Hammen, 1974; Simpson, 1974), geophysical dynamism (Ali, 2017; Antonelli et al., 2018) and high frequencies of *in situ* speciation (Hughes & Eastwood, 2006; Nürk et al., 2020).

Besides these commonly quoted parallels, few studies directly compare the drivers of endemism (Box 1) in mountain islands and true islands (but see Itescu, 2019; Steinbauer et al., 2016). Accordingly, comparisons of their intrinsic characteristics, including their geological ontogeny, life span, isolation characteristics and isolation history, and of the contribution of these characteristics to contemporary patterns of endemism, are uncommon. Here, we revisit the concept of isolation and its link with endemism by focusing on, and questioning, the postulate (and common assumption) that mountain islands and true islands are analogous systems. In comparing these two systems, we clarify what can be learned about islands as drivers of endemism. For convenience, we use the term “island” to refer to both mountain islands and true islands.

2 | ISOLATION AS A STATE AND A PROCESS

“Isolation” is defined in common English as “the process or fact of isolating or being isolated”, highlighting the ambiguity with respect to being a state or a process. What “being isolated” means is often biased by what humans intuitively perceive as isolated (“habitat bias”; Wiens, 1995), and this is reflected in the measures to quantify isolation (Box 2). An example is the Euclidean distance or Haversine distance between islands, which is easy to quantify and conceptualize, but may neglect ecological and evolutionary dimensions of isolation,

BOX 1 Identifying and measuring endemism

There is a key distinction between endemism (see Glossary) as the proportion of species that are endemic (here “percentage endemism”) and endemism as the number of species that are endemic (here “endemic species richness”). Herein, we focus primarily on percentage endemism. Endemism occurs at various spatial scales, from large (e.g., continents) to small (e.g., islands or mountain tops), and at different taxonomic levels, mostly from families to (sub-) species (Morrone, 2008). Accordingly, the spatial delimitation (size and shape) of an area over which to estimate endemism can be contentious but is a prerequisite for defining endemism (Crisp, Laffan, Linder, & Monro, 2001; Daru, Farooq, Antonelli, & Faurby, 2020; Guerin, Ruokolainen, & Lowe, 2015).

Two main approaches exist in the literature to identify endemism spatially: one uses geographical units as reference entities, the other a gradual range size-based approach. The first approach is binary and defines whether a species occurs only within a given entity or not (e.g., a single island, archipelago, mountain range or country) and is, therefore, often evolutionarily meaningless. According to this definition, endemism can be nested, that is, a single-island endemic is, by definition, also an archipelago endemic. In contrast, the second approach is continuous; the smaller a species' range size, the higher is its level of endemism. The sum of “endemism values” of all species in a given area results in its overall level of endemism and can be related to the geographical extent of the area (i.e., endemics–area relationships).

On a temporal scale, endemics can be separated into two groups: “neoendemic” and “palaeoendemic” (Stebbins & Major, 1965). The former describes species formed by “recent” speciation (e.g., divergence and reproductive isolation, hybridization and polyploidy in plants) that failed to disperse out of the ancestral area (Laffan & Crisp, 2003; Morrone, 2008). Palaeoendemics are usually relict species whose ranges became spatially restricted over evolutionary time-scales (Gillespie, 2009; Mishler et al., 2014) but can also have persisted by dispersing between volcanic islands while they emerge and perish (Fernández-Palacios et al., 2011). Empirically distinguishing between these alternatives is often difficult. As alternatives, various authors have proposed “phylogenetic endemism” (Mishler et al., 2014; Rosauer, Laffan, Crisp, Donnellan, & Cook, 2009) and “weighted endemism” (Crisp et al., 2001; Laffan & Crisp, 2003). Although different in their approaches to capture endemism, each endemism metric is inherently related and strongly influenced by the spatial extent at which it is studied (Daru et al., 2020).

such as intermittent gene flow (for a review of isolation indices, see Iltescu, Foufopoulos, Pafilis, & Meiri, 2020). Here, we advocate for a more sophisticated biogeographical conceptualization of “isolation” based on the arguments that: (a) no biological system is “isolated” in an absolute sense (Taylor, Fahrig, & With, 2006); and (b) isolation has multiple spatial and temporal dimensions that relate to isolating biological and environmental processes (Gillespie, Lim, & Rominger, 2020).

The effect of isolation on endemism results from multiple ecological and evolutionary processes of different intensities (Figure 1). For instance, higher levels of isolation (Figure 1, right side) are reflected in reduced levels of gene flow, resulting in the potential for allopatric speciation and genetic drift (Gillespie et al., 2012; Heaney, 2000). Isolation changes over time, modulated by changing environments, direction, continuity and intensity of vectors (wind, ocean currents and human transport) and by species traits (Gillespie & Roderick, 2002; Gillespie et al., 2020; Pepke, Irestedt, Fjeldsø, Rahbek, & Jönsson, 2019; Steinbauer, 2017). This means that through time, an island experiences different levels of isolation (Figure 1, top) and, as a result of the different processes at play (Figure 1, centre), present-day patterns of endemism carry a mix of the legacies from these processes (Figure 1, bottom). Accordingly, we define isolation of an island (i.e., island-like entity) as “a continuum of processes whose strengths vary in space and time, modulated by species traits and by environmental and geological conditions that influence the (spatial) characteristics of the island and, as a result, change the degree of gene flow”. Based on this definition, a change in isolation represents a change in how influential processes that lead to reduced (e.g., cladogenetic/allopatric speciation, genetic drift) versus increased gene flow (e.g., “dispersification”, Glossary; Moore & Donoghue, 2007; hybridization after secondary contact: Grant, 2014; Petit et al., 2003) are for the ecological and evolutionary pool of a focal species assemblage or, in this case, the percentage endemism (Figure 1). In our theoretical framework, “isolation” is always defined from the perspective of focal taxa or assemblages (Gillespie & Roderick, 2002; Wiens, 1995), which is also the case for endemism, and is best viewed as encompassing both patterns and processes. With this definition, we also embrace the complexity of patterns and processes as quantified by landscape “connectivity” in terrestrial systems (Box 2), where “isolation” is only one of several variables to quantify the spatial composition and arrangement of patches.

Building upon our redefinition of isolation, we develop a conceptual framework for mountain islands and true islands that takes into account the degree of isolation at a certain moment in time (i.e., “contemporary”), differences in isolation between species groups, and dynamic changes of isolation over time (Figure 2). The framework allows testing how these variables jointly contribute to contemporary patterns of endemism. We start by discussing the main dimensions that influence what we call “snapshot isolation”, which is the degree of isolation of mountain islands and true islands at any point in time (Figure 2a). We then address “isolation continuity”, which considers the past dynamics of isolation (Figure 2b), and the record of past

BOX 2 Isolation, connectivity, connectedness and fragmentation

The way that isolation in island biogeography has commonly been defined and used is a solely distance-based measure. “Decreased isolation”, meaning decreased distances between islands, is frequently equated with “increased connectivity” in the literature, suggesting a continuous gradient of isolation along which connectivity represents the other side of the same coin. This usage poorly represents the concept of “connectivity” as formalized originally in landscape ecology. Connectivity in a landscape as defined by Taylor et al. (1993; Glossary) was always intended to include both the physical structure and arrangement of patches and also the behaviour of organisms within the landscape in response to these physical characteristics and the surroundings. The former was described to be the “structural connectivity” (Glossary), often quantified by interpatch distances alone (e.g., straight-line distance, nearest-neighbour measures), but can also include the surface area of the patch, type of habitat and suitability of the patch for focal species [nicely summarized by the “intrapatch connectivity” within the concept of “habitat availability” or “reachability” by Pascual-Hortal & Saura (2006) and Saura & Pascual-Hortal (2007)]. “Connectedness” (Glossary) refers only to the degree of physical connection between patches. Isolation as usually defined in island biogeography is thus one aspect of structural connectivity. However, “connectivity” is not properly captured by an index of linear distances alone.

The variability in the movement and behaviour of taxa (e.g., resulting from influences of dispersal capacities and directional dispersal vectors) is represented by “functional connectivity” (Glossary). In landscape ecology, the importance of an organism-centred approach to quantification of connectivity has been much emphasized (e.g., Pearson, Turner, Gardner, & O'Neill, 1996; Saura & Rubio, 2010; Taylor et al., 2006; Wiens, 1995); this is ignored when considering only structural connectivity. The functional connectivity explains why a given arrangement of patches/islands can be perceived as being both connected and disconnected by two species with different dispersal capabilities and opportunities (Taylor et al., 2006). Thus, “connectivity” is an inherent description and integration of the landscape characteristics and the behaviour of taxa within this landscape (Tischendorf & Fahrig, 2000). Numerous connectivity indices have been developed and later on compared and reviewed by Tischendorf and Fahrig (2000) and by Saura and Pascual-Hortal (2007), who also

isolation (“isolation history”), which combines isolation continuity with the overall duration of isolation (Figure 2c). Together, current isolation and isolation history mediate the dominant isolation-related processes driving endemism (Figure 2d). We specifically discuss how endemism depends on the continuity of isolation through time and argue that the degree and dynamics of isolation differ substantially among types of mountain islands and true island systems.

3 | SNAPSHOT ISOLATION

Snapshot isolation is the degree of isolation of a location at a given point in time and consists of two main dimensions (Figure 2a): (a) the environmental difference of a location from its surroundings (“Difference_{sur}”); and (b) the effective distance from an equivalent environment (“Distance_{equiv-env}”). Here, “equivalent” means that an environment is similar enough to be within the environmental tolerance of a focal organism. Both dimensions depend on the pre-adaptations of a species, such as its environmental niche (Janzen, 1967) and dispersal ability, which could potentially evolve at the focal location. Life-history strategies of evolving clades affect success rates for colonization of islands and island-like environments (e.g., Pepke et al., 2019). Thus, the isolation of a given location varies between organisms according to the breadth of their environmental tolerance, dispersal capacity and adaptations to use existing dispersal vectors to establish in new locations (Gillespie & Roderick, 2002; Gillespie et al., 2020; Steinbauer, 2017).

3.1 | Environmental difference from surroundings (Difference_{sur})

This dimension is related to the concept of the inhospitable matrix and the patch–corridor–matrix contrast (Forman, 1995), but we question the notion of using a “habitat patch” to represent islands as units of analysis to understand species richness (also see Fahrig, 2013). Here, we assume that the difference in environmental conditions between a location and its surroundings, here termed Difference_{sur}, is sufficient to impose ecophysiological constraints on a particular species' range, such as the prevention or the inhibition of gene flow through species dispersal and establishment. Differences in environmental conditions are easiest to identify when there is a sharp transition in space between two environments, such as between land and water at the coast of true islands. In such cases, the difference is so large for most organisms that isolation is often measured simply by the distance to another landmass (See section 3.2; Itescu et al., 2020).

Although true islands are rather clear in their sharp transitions from land to water (although coastal and intertidal zones can form wide transitions), a gradient of transitions exists for islands in mountain environments, from abrupt to gradual. Sharp transitions are typically brought about by three phenomena: (a) strong abiotic environmental gradients, such as the temperature gradient along steep slopes, or sharp changes in bedrock or geomorphology; (b) forest

BOX 2 (Continued)

proposed an approach that is potentially useful for comparing mountain islands and true islands (further details in Supporting Information Appendix S1).

The concept of “fragmentation” (Glossary) has gone through a similar process of becoming increasingly diffuse and ambiguous in its usage since its original formulation [see reviews by Franklin et al. (2002) and Fahrig (2019)]. Often (mis)used in the literature as analogous to the opposite of “landscape connectivity”, originally it described only the breaking up of habitat that results in reduction of surface area, increase of patch numbers and increase of isolation, without accounting for the responses of organisms.

ecotones, such as the upper forest line (highest elevation of continuous forest), which results in abrupt changes in solar radiation and water availability, for example; and (c) boundaries of human land use. Examples of gradual transitions in “sky islands” (see Glossary), include the Madrean sky islands in North America, which feature gentle slopes and thus have blurred gradient boundaries. The table-top mountains in Venezuela, moreover, feature clear and sharp transitions. The effectiveness of environmental or land-use gradients in influencing the isolation of mountain systems varies between species.

Although clearly bounded by a water body, true islands also feature a mix of transitions, because they are often environmentally heterogeneous (e.g., large spatial variety in soils, topography and microclimates). For true islands, this results in different degrees of snapshot isolation, both within islands and between islands within a (meta-)archipelago. The Hawaiian Islands, for instance, show a high environmental heterogeneity (Seijmonsbergen, Guldenaar, & Rijsdijk, 2018). Hawai'i is the youngest island of the archipelago (c. 0.6 Myr old) and features the highest volcanic peak on an island worldwide [Mauna Kea, 4,207 m above present sea level (a.s.l.)]. Some aspects of the abiotic diversity are low attributable to the relative youth of the mountain, whereas its elevation creates high

variability in microclimatic zonation and orographic rainfall, producing a wide range of vegetation zones and, as such, represents a sky island within a true island (Steinbauer et al., 2016). In contrast, one of the oldest islands of the archipelago, Kauai (c. 5.3 Myr old; 1,598 m a.s.l.) displays high abiotic environmental variability and limited microclimatic zonation. Thus, although $\text{Difference}_{\text{sur}}$ can be characterized by a sharp boundary, this dimension is better regarded as a continuum ranging from abrupt (e.g., water and land at the coast of a true island) to gradual transitions (e.g., gentle slopes), or combinations of the two, and is applicable to a wider range of systems with island-like properties (Gillespie & Roderick, 2002).

3.2 | Effective distance from equivalent environment ($\text{Distance}_{\text{equiv-env}}$)

The geographical distance between landmasses is often the only dimension of isolation accounted for in models of island biogeography and is traditionally measured as straight-line distances to other landmasses (Itescu et al., 2020; Whittaker & Fernandez-Palacios, 2007). In simulation models, this has proved valuable to test hypotheses on the influences of distance to the mainland and island size on

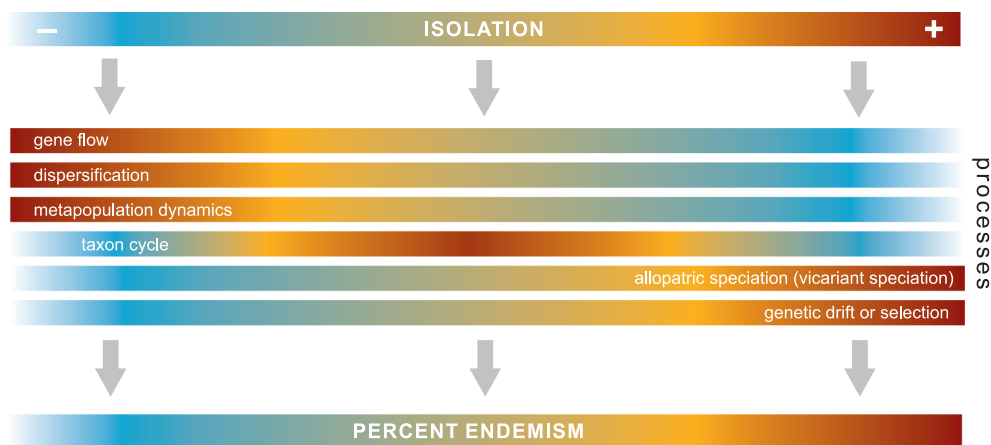


FIGURE 1 Isolation is a continuum of different processes that interact with species traits to result in particular levels of endemism. Darker/warmer and lighter/colder colours in the bars indicate high and low levels, respectively. The degree of isolation of an island or other insular system changes, often resulting in different processes influencing the species composition and thus the degree of endemism in an island. A lesser degree of isolation (left) is not a synonym for higher “connectivity” (see Box 2). Percentage endemism is the percentage of native species that are endemic. For definitions of the terms “endemism”, “taxon cycle” and “dispersification”, see Glossary

endemism (Rosindell & Phillimore, 2011). However, the effective isolation captured by measures of straight-line distances can vary between species and higher-level taxonomic groups (Gillespie & Roderick, 2002; Weigelt & Kref, 2013). Defining isolation only by

distances between landmasses ignores the role of the environmental tolerances of species or assumes that all landmasses are homogeneous. It also ignores differences between species in their ability to use existing dispersal vectors and the directionality of many vectors

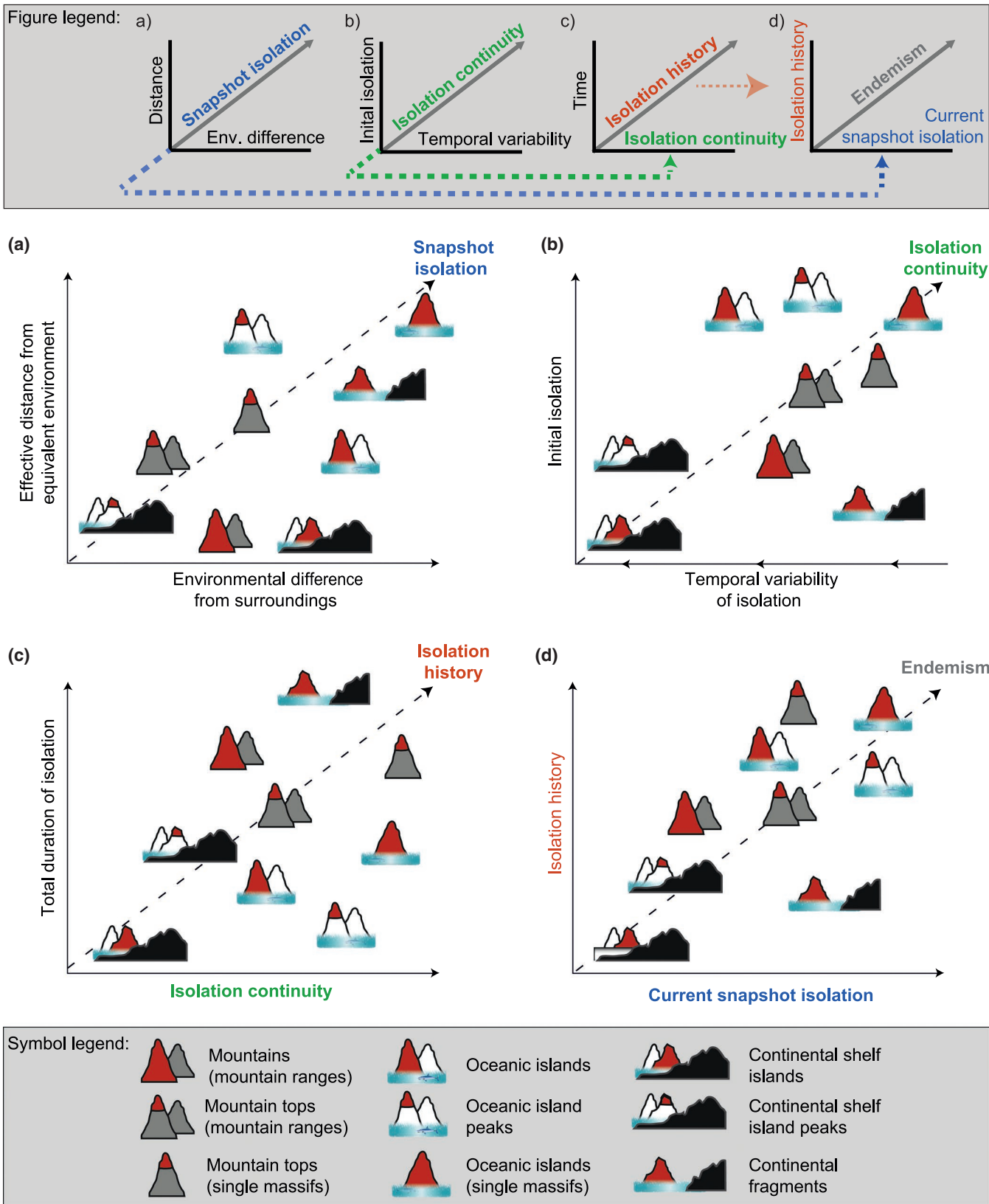


FIGURE 2 A framework for endemism in mountain islands and true islands, derived from bringing together key aspects of the overall isolation of these islands and its dynamics through time. This scheme highlights both similarities and differences between mountain islands and true islands and between different types of islands and mountains. We separate important dimensions of isolation, each of which is expected to affect the amount and nature of contemporary endemism at any given place. (a) Snapshot isolation is the degree of isolation at any given moment in time, depending on species traits. (b) Isolation continuity describes the temporal aspect of isolation in terms of its dynamics through time and the degree of isolation when the island arose. Note the reversed axis for temporal variability of isolation. (c) Isolation history considers the total duration of isolation (time) alongside isolation continuity. (d) These aspects of isolation history together shape current patterns of endemism, in conjunction with current levels of isolation of the island, which in most cases can be considered to represent the last c. 2,500 years (Lambeck et al., 2014). The considerable variation within the types of insular systems depicted is not shown; instead, each type is located according to what we suggest might be representative of that type overall and integrated across the full range of organisms. For definitions of the terms, including “oceanic islands”, “continental shelf islands” and “continental fragments”, see Glossary

(e.g., wind or water currents; biotic agents; Gillespie et al., 2012, 2020). Thus, we argue that $\text{Distance}_{\text{equiv-env}}$ is more meaningful as a species-specific measure, which can differ between co-existing species (Steinbauer et al., 2016; Steinbauer, Irl, & Beierkuhnlein, 2013; Weigelt & Kreft, 2013). The equivalent environments may be within the same island, archipelago or mountain range, or beyond.

Despite pronounced gradients, delimiting mountain islands and quantifying $\text{Distance}_{\text{equiv-env}}$ can be challenging in the absence of clear boundaries between habitats that vary in suitability for focal species (Fahrig, 2013). For “alpine islands” (Glossary), the upper forest line might serve as a simplified equivalent to the coastline of true islands in defining relatively pronounced boundaries, making it possible to use connectivity metrics that require clearly delimited units of analysis (Supporting Information Appendix S1). However, such landscape ecological measures of “connectivity” (Box 2) are rarely used in marine archipelagos (but see Cabral, Weigelt, Kissling, & Kreft, 2014). Comparing connectivity (ideally from the perspective of a focal species) between archipelagos of mountain islands and true islands (Table 1) could help in estimation of the importance of the spatial organization of islands in shaping endemism, especially when integrated over time-scales as long as the Quaternary (section 4). Additionally, the use of directional network models that take into account island age (Carvalho, Cardoso, Rigal, Triantis, & Borges, 2015) and randomized simulations to test the effect of archipelago configuration on richness in “oceanic archipelagos” (Glossary; Jöks & Pärtel, 2019) can provide additional common ground to compare mountains and true islands.

4 | ISOLATION CONTINUITY

The dimensions that define snapshot isolation are dynamic and change through time. Isolation continuity (Figure 2b) comprises two main components: (a) the temporal variability of snapshot isolation, and (b) the initial level of isolation when the island is formed. Isolation history (isolation continuity combined with the overall duration of isolation) is addressed in Section 5.

4.1 | Temporal variability of isolation

Long-term environmental changes have influenced the distribution of species and evolutionary processes globally. True islands

and mountains were formed and shaped by different geological processes that act at different temporal scales, affecting isolation through time. Generally, both mountains and islands composed of bedrock are essentially shaped by tectonic forces or volcanic activity, whereas islands composed of unconsolidated sediments (e.g., barrier islands) are formed by sedimentary processes (Ali, 2017; Molnar, 2018; see “Different types of mountains” in Supporting Information Appendix S2). Surface processes related to long-term erosion and Quaternary climate fluctuations have further reshaped the geomorphology of mountains (Antonelli et al., 2018 and references therein) and islands (e.g., Geirsdóttir, Miller, & Andrews, 2007) over time. Here, we focus on how the Quaternary (the last 2.58 Myr; Gibbard, Head, & Walker, 2010) influenced the temporal variability of isolation of islands and mountains over geologically recent times and how this variability influenced the distribution of biota and their evolution.

Although during the last c. 2,500 years, global sea level has remained relatively constant (rate of change < 0.4 m/1,000 years; Lambeck, Rouby, Purcell, Sun, & Sambridge, 2014), fluctuating sea levels during most of the Quaternary (60–100 m; Figure 3a) caused substantial changes in island isolation (Figure 4; e.g., Ali & Aitchison, 2014; Fernández-Palacios et al., 2016; Norder et al., 2018, 2019; Rijdsdijk et al., 2014; Weigelt, Steinbauer, Cabral, & Kreft, 2016). The effects of mid-to-late Quaternary sea-level stands on true islands in the Sunda Sea were depicted on maps as long ago as the first half of the 20th century (Dickerson, 1941; Molengraaff & Weber, 1919), showing massive increases in surface area as numerous islands connected (Woodruff, 2010). The Pleistocene Aggregate Island Complexes model (PAICs; Brown et al., 2013), Oscillating Geography Model (Ali & Aitchison, 2014) and Glacial-sensitive Model (Fernández-Palacios et al., 2016) all assess the influence of island isolation and “connectedness” (Glossary) by sea-level change on biota and evolutionary processes.

The magnitude of change in isolation varies with the bathymetry of true islands and with archipelago configuration (Figure 4a; Table 2; Norder et al., 2018, 2019; Voris, 2001). Higher sea levels during interglacials (Figure 3a) caused many true islands to become smaller and more isolated, whereas during glacial periods they were larger and sometimes connected to other islands or continents (Figure 4a). Some archipelagos, such as the continental islands of the Seychelles (Figure 4a), the atolls of Phoenix and Aldabra, largely submerged for a short period in the last interglacial

TABLE 1 Spatial configurations of mountain islands and true islands

Type of archipelago	Mountain island examples	True island examples
Stepping stone archipelago between two or more large surface areas	Stepping stone archipelago between mountain ranges:	Stepping stone archipelago between a large island and the mainland or between two large islands:
Isolated massif with outliers	<ul style="list-style-type: none"> • Madrean archipelago • Great Basin archipelago • Altai/Tien Shan Basin • Meso-American massifs 	<ul style="list-style-type: none"> • Archipelago Sea (Baltic Sea) • Lesser Sunda islands • Sulu archipelago • Kuril Islands (islands between Japan and Taiwan) • Lesser Antilles • Tuscany Archipelago • Mozambique Channel islands (Comoros Mayotte) • Indian Ocean islands between Madagascar and India
	Isolated massif with smaller outlier mountains:	Balearic islands
	<ul style="list-style-type: none"> • Ethiopian highlands • East African arc • Saharan massifs • Atlas Mountains • Jabal Lubnan • Drakensberg • Central European massifs • Caucasio-Iranian massifs 	<ul style="list-style-type: none"> • New Caledonia • Madagascar with surrounding islands
Linear chain of outlier islands at one end of a large island	Cordillera with outliers of mountains islands at one end of a cordillera:	Linear chain of outlier islands at one end of the mainland:
	<ul style="list-style-type: none"> • Malay peninsula • Baja California peninsula • Coastal Cordillera (South America) • Southern Andes 	<ul style="list-style-type: none"> • Aleutian and Bering Sea Islands • South Shetland Islands • Izu Islands • Solomon islands
Isolated island chains and groups	Completely isolated sky islands:	Easter Islands
	<ul style="list-style-type: none"> • Western Ghats • Pantepuis (table-top mountains) 	<ul style="list-style-type: none"> • Hawai'i • Galapagos • Seychelles • Canaries

TABLE 1 (Continued)

Type of archipelago	Mountain island examples	True island examples
High-elevation (biotic) sky islands ^a	High-altitude flora in: <ul style="list-style-type: none"> • The Northern Andes (páramos) • The Central Andes (punas) • Himalaya–Hengduan Mountains • Indonesian archipelago 	High-altitude flora on: <ul style="list-style-type: none"> • The island of New Guinea • Malaysian portion of the island of Borneo

Note: Here, we draw parallels between archipelago configurations as proposed by Warschall (1994; mountain island examples) and true islands. Further research could assess similarities and differences in patterns of endemism among and within each type of archipelago, and among and between mountain islands and true islands, also considering their isolation histories; the archipelago types proposed by Warschall represent only present-day snapshot isolation (Figures 3 and 4).

^aReferring here to high-elevation ecosystems/populations, not geological features.

(LIG, c. 129–116 ka; Felde et al., 2020; Norder et al., 2018). The consequences of sea-level changes on isolation were less drastic for remote “hotspot volcanic oceanic islands” (Glossary), such as Hawai’i, the Canary Islands, Azores and Galápagos, which mainly lost land but maintained much of their original geographical configurations. With lower sea levels, many “continental shelf islands” (Glossary) of the Sunda plain, Tasmania and the Aegean archipelago became connected to the mainland by land bridges or, as in the case of the Seychelles, to other islands, forming large micro-continental landmasses. For instance, the Cyclades islands in the Aegean Sea, currently comprising 44 islands of >1 km² and totaling 3,250 km², extended over 10,750 km² during glacial times, mainly as a single landmass (Simaiakis et al., 2017).

Numerous studies have explored the relationships between Quaternary sea-level fluctuations, speciation and endemism patterns on true islands (e.g., Ali & Aitchison, 2014; Fernández-Palacios et al., 2016; Heaney, 1985; Heaney, Walsh, & Peterson, 2005; Mayr, 1941; Norder et al., 2019; Papadopolou & Knowles, 2017; Rijdsdijk et al., 2014; Weigelt et al., 2016). Results suggest that changes in archipelago configurations related to past climatic conditions can be good predictors of present-day endemism patterns, although somewhat contradictory conclusions emphasize the need for further research. Weigelt et al. (2016) found, for instance, that the increased surface area of true islands during the Last Glacial Maximum (LGM) is important in explaining current endemism and proposed a negative relationship between past connectivity and the number and proportion of endemic species today, suggesting that past connections to neighbouring islands result in fewer single-island endemics. This, in turn, could be explained by intermixing of taxa during increased connectivity (Flantua & Hooghiemstra, 2018), although differential extinction might cause complex spatial patterns

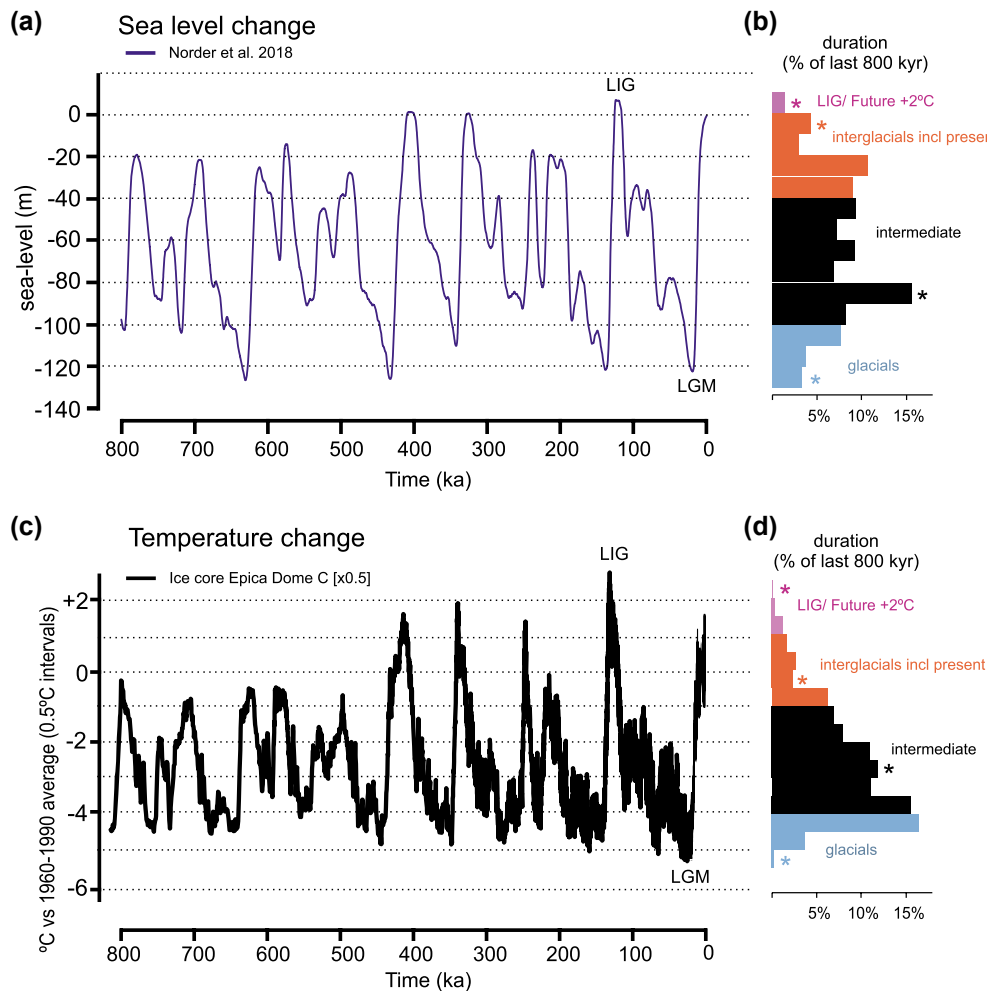


FIGURE 3 The variability of isolation for true islands and alpine islands is dictated by sea-level change and temperature change during the last c. 800 ka, respectively. (a) Changes in sea level as modelled by Norder et al. (2018) based on Bintanja, van de Wal, and Oerlemans (2005). The last interglacial (LIG, c. 129–116 ka; Felde et al., 2020) represents sea levels possibly equivalent to expectations if global temperatures rise by 1.5–2°C (2–6 m higher than present; Polyak et al., 2018). The LIG peak displayed deviates from that of Bintanja et al. (2005) because their averaged modelled values underestimated maximum sea-level rise. (b) The percentage of time over the last c. 800 kyr that sea levels were within each interval (10 m bins), recalculated from Norder et al. (2018). The intervals marked with asterisks correspond to the configurations displayed in Figure 4. (c) Temperature change (in degrees Celsius) estimates relative to the 1960–1990 average (set here at 0°C), based on EPICA Dome C Ice Core (Jouzel et al., 2007). “[x0.5]” refers to the calculated factor of polar temperature to global mean surface temperature. Adjusted from Fergus (2018). (d) The percentage of time over the last c. 800 kyr that temperatures were within each interval (0.5°C bins). The intervals marked with asterisks correspond to the configurations displayed in Figure 4

in archipelago endemism (García-Verdugo et al., 2019). Similar results were found for continental shelf islands connected via land bridges to the mainland or forming large continental shelf islands (Sondaar & Van der Geer, 2005). Norder et al. (2019) showed that on oceanic islands current endemism is better explained by long-term spatial archipelago configurations that have been more common and persistent in the Quaternary (Figure 3, “Intermediate”, cool stadials and interstadials) than those configurations characteristic of the extreme warm interglacial (Figure 3, Interglacials) or extreme cold (Figure 3, Glacials) glacial maxima conditions. This work highlights the importance of extending beyond the LGM when quantifying the role of past isolation on species richness and endemism (Porter, 1989). Clearly, past surface area and inter-island connections

(isolation history) played an important role in explaining present-day richness and genetic diversity patterns of endemics, whereas exclusively considering the current snapshot isolation state is insufficient to understand patterns of endemism.

The effects of past climatic fluctuations on processes related to endemism have likewise been substantial on mountain islands (Table 1; e.g., Adams, 1985; Simpson, 1974; Sklenář & Balslev, 2005). Considerable range shifts during the Quaternary have been recorded in mountains around the world, with alpine species lowering and raising their distribution along elevational and latitudinal gradients in response to cooling and warming temperatures, respectively (e.g., Flantua & Hooghiemstra, 2018; Flantua, O’Dea, Onstein, Giraldo, & Hooghiemstra, 2019). In contrast to true islands,

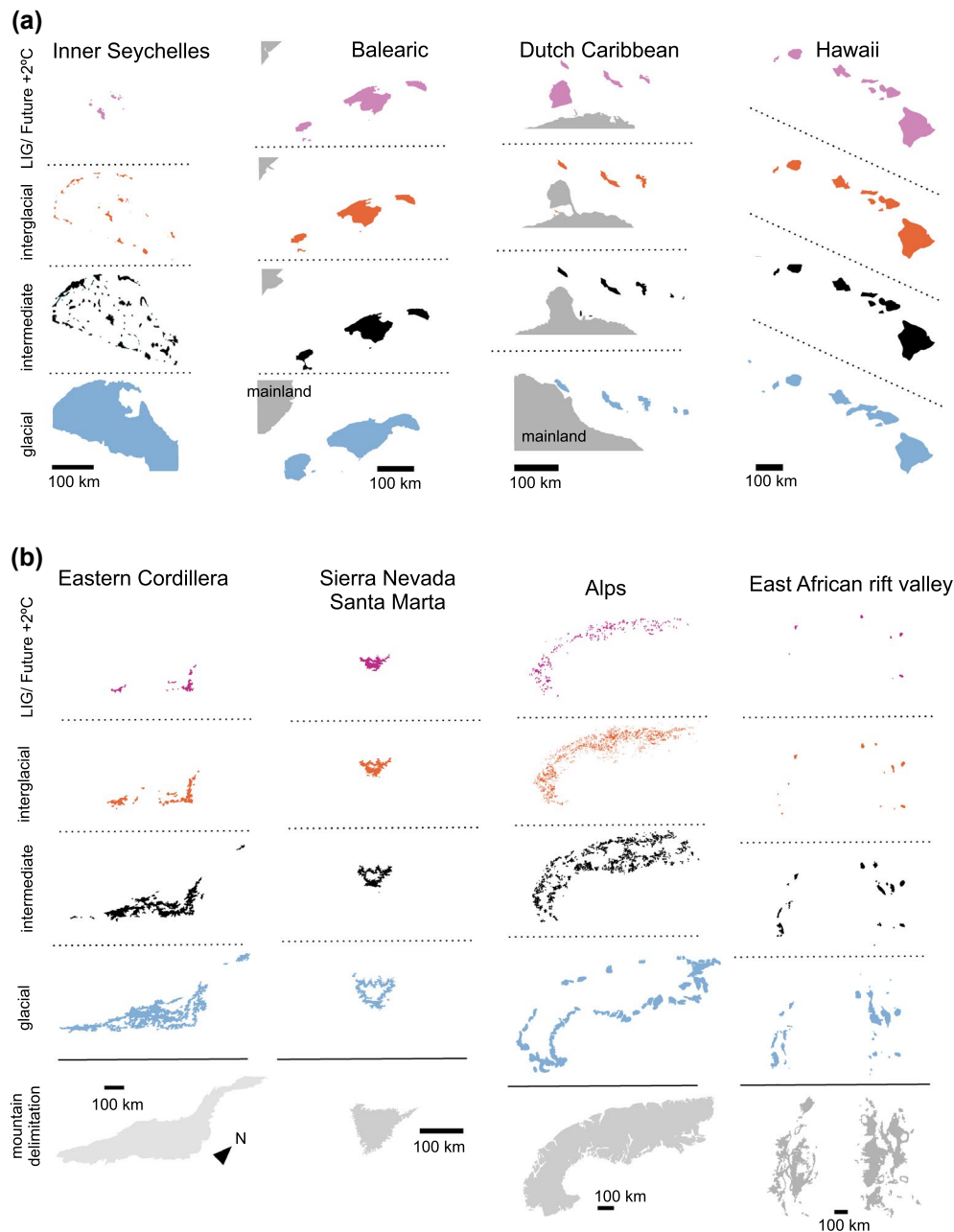


FIGURE 4 The spatial configurations of true islands and alpine islands as a result of changes in sea level and temperature, respectively (Figure 3). (a) True island reconstructions are based on those by Norder et al. (2018). (b) Alpine island reconstructions. Eastern Cordillera and Sierra Nevada de Santa Marta (Colombia): adjusted from Flantua et al. (2019). Alps, glacial: adjusted from Schönschwetter et al. (2005). Alps, intermediate: estimated distribution of alpine islands based on 90 m digital elevation model (Jarvis, Reuter, Nelson, & Guevara, 2008) and glacier extent reconstructed by Seguinot et al. (2018). Alps, interglacial: Corine Land Cover (CLC) 2018, all natural grasslands >2,000 m a.s.l. (Copernicus Land Monitoring Service, 2019); Alps, Last Interglacial (LIG)/future +2°C: CLC 2018 (adjusted by +200 m). East African rift valley: adjusted from Sklenář et al. (2014) and Chala et al. (2017). Colours correspond to Figure 3, with more frequent conditions in stronger colours. Grey shading in panel (b) shows mountain delimitation as defined by the 500 m a.s.l. isoline for the Eastern Cordillera, Sierra Nevada de Santa Marta and the Alps and the 1,500 m a.s.l. iseline for Africa

where glacial periods are associated with a greater connectivity, a long-persisting notion for alpine islands has been that glacial periods induced increased isolation because extensive glaciers reduced alpine habitat to smaller islands along the outer ridges of the mountains, the so-called “glacial refugia” (Hewitt, 2000; Schönschwetter, Stehlik, Holderegger, & Tribsch, 2005; Willis & Whittaker, 2000; Figure 4b, Alps). Based on this notion, high temporal variability of

isolation would lead to higher extinction and lower phylogenetic diversity and would have a negative influence on endemism, especially when it involves fragmentation and loss of area (Svenning, Eiserhardt, Normand, Ordóñez, & Sandel, 2015). Current endemism patterns would, therefore, result more from range contractions of formerly widespread species and less from *in situ* speciation (Tribsch & Schönschwetter, 2003). However, many high-elevation ecosystems

TABLE 2 Effect of Quaternary climate fluctuations on inter-island connectivity and present-day endemism in relationship to the type of archipelago in true islands and mountain islands

Size of archipelago and distances between islands of archipelago (Table 1)	Dynamics during glacial periods	Expected effect of Quaternary climate fluctuations on present-day endemism	Mountain island examples	True island examples
Small, very near	High degree of inter-island connectivity	Very large	Ecuadorian páramos, Northern Andes (Flantua et al., 2019; Simpson, 1974)	Scandinavian archipelagos
Small, near	Intermediate degree of inter-island connectivity	Large	Spanish Sierra Nevada	Channel Islands of California
Medium, mid-distance	Intermediate degree of inter-island connectivity	Intermediate	Colombian páramos, Northern Andes (Flantua et al., 2019; Simpson, 1974) Trans-Mexican Volcanic Belt (Mastretta-Yanes et al., 2018)	Galapagos (Ali & Aitchison, 2014)
Large, distant	Low degree of inter-island connectivity	Mainly changes in surface area	Pantepuis (Rull & Nogué, 2007); East African rift (Chala et al., 2017; Sklenář et al., 2014)	Ryukyu islands (Wepfer, Guénard, & Economo, 2016); Azores (Rijsdijk et al., 2014)

in mountains follow a similar pattern to that seen for the true islands, with an increase in surface area and connectivity during glacial periods. Examples include the Northern Andes, East African rift valley (Figure 4b), Pantepui, Papua New Guinea and the Ethiopian highlands. Spatial reconstructions from these regions show that glacial conditions facilitated expansion of the alpine mountain islands and increased inter-mountain island connections (Chala, Zimmermann, Brochmann, & Bakkestuen, 2017; Flantua & Hooghiemstra, 2018; Flantua et al., 2014, 2019; Rull, 2005; Rull & Nogué, 2007; Sklenář, Hedberg, & Cleef, 2014).

Furthermore, glacial-interglacial cycles, accompanied by high temporal variability of isolation, are shown to have triggered high pulses of *in situ* speciation in the Pyrenees, Northern Andes, Himalayas and Southern Alps of New Zealand (Wallis, Waters, Upton, & Craw, 2016). These pulses occurred as a result of glaciation-driven diversification (e.g., Weir, Haddrath, Robertson, Colbourne, & Baker, 2016), colonization associated with distributional shifts (e.g., Knowles & Massatti, 2017; Kolář, Dušková, & Sklenář, 2016; Rangel et al., 2018) and variable degrees of connectivity (e.g., Flantua et al., 2019; Nevado, Contreras-Ortiz, Hughes, & Filatov, 2018; Rull, 2005). This strengthens the support for hypotheses on Quaternary diversification that move beyond refugial speciation alone (Rull, 2020). In summary, in mountain islands high temporal variability of isolation has been suggested to be both a strong driver of extinction with a negative influence on endemism (Harrison & Noss, 2017; Sandel et al., 2011) and a driver of rapid diversification with a positive influence on endemism (Flantua & Hooghiemstra, 2018; Flantua et al., 2019). Understanding where and why these differences occur requires further research; the framework we present herein might be useful in guiding this research.

Drawing case-to-case parallels between mountain islands and true islands (Figure 4) using similar approaches can much improve our understanding of the variable effects of Quaternary climate fluctuations on connectivity dynamics and evolutionary processes in archipelagos. Additional tools that consider different dispersal probabilities among species, “asymmetric connectivity” (Martensen, Saura, & Fortin, 2017), can be especially relevant for testing hypotheses related to directional dispersal vectors, such as wind, oceanic currents and birds (Carvalho et al., 2015; Fernández-Palacios et al., 2016; Steinbauer, 2017). Likewise, simulation models that capture the effect of connectivity dynamics on evolutionary processes (e.g., Melián, Seehausen, Eguíluz, Fortuna, & Deiner, 2015) have high potential when combined with landscape reconstructions (e.g., Flantua et al., 2019; Norder et al., 2018).

4.2 | Initial level of isolation

Geological and sedimentary processes can lead to the formation of a “new” true island (Fernández-Palacios et al., 2016). Whether a true island emerged from the sea with no terrestrial life on it (i.e., *de novo* origin, such as volcanic islands; Warren et al., 2015; “Darwinian islands” *sensu* Gillespie & Roderick, 2002) or was

previously part of another landmass from which it separated (i.e., initially not isolated, “fragment islands” *sensu* Gillespie & Roderick, 2002) is important for understanding the patterns of endemism (Sondaar & Van der Geer, 2005). When the initial level of isolation is high and persists throughout history, evolution has a limited set of lineages to work on. Here, the species composition will mostly become neoendemic through time as a result of cladogenesis (Gillespie & Roderick, 2002; Emerson & Gillespie, 2008: figure 1). Initial arrival of species is through rare dispersal (e.g., Whittaker, Bush, & Richards, 1989) of airborne or seaborne species with high dispersal capabilities. Depending on the distance to continents or pre-existing true islands, this set of species corresponds to a filtered subset of the regional species pool (Emerson & Gillespie, 2008; Fernández-Palacios et al., 2016; García-Verdugo et al., 2019; Gillespie & Roderick, 2002). This bias typically exhibits a strong relationship to geographical distance, to the dispersal capacity of species and to their ability to colonize island environments successfully (Gillespie et al., 2020; Kisel & Barraclough, 2010; Weigelt et al., 2015), also described as the attenuation of species composition across islands and archipelagos (Lomolino & Brown, 2009; Whitehead & Jones, 1969). It results in phylogenetically clustered island assemblages and “disharmonic” species assemblages (Glossary; König et al., 2019), with taxa and/or entire groups from the regional pool missing (Carlquist, 1974; Emerson & Gillespie, 2008; Gillespie & Roderick, 2002; Whittaker & Fernandez-Palacios, 2007).

In contrast, fragment islands that were initially connected to existing ecosystems before separating from them (e.g., continental island systems) start out with species sets that are more representative (i.e., more harmonic) of the regional pool (Gillespie & Roderick, 2002). This, in turn, affects how, and how fast, endemism develops if isolation is strong enough and persists long enough (see isolation history in section 5). When isolation continues, species richness “relaxes” to a new equilibrium (Diamond, 1972). Over time, speciation can lead to new species, and some of the initial island species might become relicts of extinct mainland species, forming palaeoendemics of once widely distributed taxa (Gillespie, 2009).

Initial isolation, cladogenesis and the resulting level of disharmony are important processes in driving endemism in both mountain islands and true islands, particularly with respect to the types of endemic species and their traits. For example, the true islands of Crete, Mauritius and Hawai'i, ordered increasingly distant from the nearest continent, are all characterized by a high degree of endemism, but on Crete, a continental island near the continent, terrestrial mammal endemism was prevalent, with dwarf elephants and dwarf hippos. On Mauritius, some 2,300 km away from Africa, terrestrial mammals were completely absent, and on the remote islands of Hawai'i, nearly 6,000 km away from the USA, both mammals and reptiles were absent (Burney et al., 2001; Carlquist, 1970; Cheke & Hume, 2008; Sondaar & Van der Geer, 2005; Wagner & Funk, 1995). Mauritius and Hawai'i represented much greater over-sea dispersal barriers than the Aegean islands, which have strong evidence of frequent arrivals by plants, birds and mammals from the Eurasian continent

(Kougioumoutzis et al., 2017). Equivalent examples exist for many insect groups (Gillespie & Roderick, 2002).

The level of disharmony not only affects functional diversity by causing whole groups of species and sets of traits to be present or absent, but also has knock-on effects on the speed and direction of evolution of the taxa that are present. For example, on Luzon (Philippines) only two endemic mammal clades have given rise to c. 50 species that have evolved via repeated elevation-driven isolation on different mountains within the island (Heaney et al., 2016). The overall lack of terrestrial mammals on many oceanic islands typically reduces selection for anti-predator defences (e.g., tameness; Cooper, Pyron, & Garland, 2014) and unpalatability of plants to herbivores (Cubas et al., 2019). Good colonizers repeatedly lose dispersal capacity (e.g., flightless birds) and start to occupy niches typically occupied by “missing” species groups from mainlands (e.g., tortoises or birds becoming the main grazers, lizards becoming main seed dispersers, finches using tools to get under bark on the Galápagos islands; Burns, 2019). Likewise, herbaceous lineages repeatedly develop derived (secondary) insular woodiness, possibly as a response to the ecologically new environment [e.g., adaptation to drought, release from seasonality or herbivores; for details, see Carlquist (1974), Lens, Davin, Smets, and del Arco (2013) and Nürk, Atchison, and Hughes (2019)]. Such directional evolution to exploit available opportunities is not only so common as to be predictable but may also happen rapidly (e.g., Knope, Morden, Funk, & Fukami, 2012; Linder, 2008). When this evolution involves loss of dispersal capacity, it can increase speciation rates by increasing the effective isolation of populations (Jocque, Field, Brendonck, & de Meester, 2010).

In contrast to true islands, the species composition of mountain islands is likely to be more harmonic with the regional pool than that of oceanic islands, especially Darwinian islands, because the isolation of mountain islands was initially low (because they developed on a continent) and increased gradually over geological time. Most of the regional species pool was consequently available to contribute to the build-up of mountain taxa diversity, and vice versa (mountains as “cradles” of biodiversity; see several chapters by Hoorn et al., 2018). The “birth” of alpine islands is related to the geo-ecophysiological processes that initiate the isolation of a mountain island situated on a continent. In general, mountains develop from a lower (or less topographically varied) landscape, and the initially low elevational isolation increases as uplift continues during the orogenic phase (Antonelli et al., 2018). If uplift continuously exceeds erosion rates, and elevations thereby increase, the limit of the physiological tolerances of trees can be reached, and novel alpine habitats become available (Van der Hammen, Werner, & Van Dommelen, 1973). With stronger environmental stress gradients at higher elevations, selection then acts on the fits of traits to the environment, and local adaptations along elevational gradients follow (*in situ* diversification within alpine habitats; Favre et al., 2015). During the development of isolation, the species composition on alpine islands changes gradually through evolutionary adaptation and the parallel or subsequent immigration from the lowland and other mountain regions (Favre et al., 2015; Merckx et al., 2015).

TABLE 3 Means to quantify snapshot isolation, isolation continuity and isolation history

Dimension	Measure	Description	Tools	Note	Additional reading
Snapshot isolation	Integral index of connectivity (IIC); Probability of connectivity (PC)	Intra- and inter-island (patch) connectivity	CONEFOR SENSINODE (Pascual-Hortal & Saura, 2006; Saura & Pascual-Hortal, 2007; Saura & Torné, 2009)	Can also calculate asymmetric connectivity and provide a measure of overall connectivity (ECA) at the level of an archipelago	Cabral et al. (2014); Martensen et al. (2017); Supporting Information Appendix S2 (this paper)
Snapshot isolation	Cost-distance function	Calculates various distance measures and routes in heterogeneous geographical spaces	1. ESRI ArcGIS: Cost distance (ESRI, 2014) 2. R package gdistance (Van Etten, 2017) 3. CIRCUITScape ArcGIS Toolbox (McRae, Shah, & Edelman, 2016) 4. GRAPHAB (Foltête, Clauzel, & Vuidel, 2012)	Considers the full matrix as a measure of connectivity	Kupfer, Malanson, and Franklin (2006); Weigelt and Kreft (2013)
Temporal variability of isolation	Palaeoconfiguration of true islands	Calculates palaeo-area change driven by sea-level fluctuations	R workflow (Norder et al., 2018)	Isolation was calculated only as the distance to the nearest other island	Ali and Aitchison (2014); Fernández-Palacios et al. (2016); Rijdsdijk et al. (2014); Weigelt et al. (2016)
Temporal variability of isolation	Palaeoconfiguration of alpine islands	Calculates palaeoconnectivity change driven by temperature fluctuations	1. CONEFOR SENSINODE (Pascual-Hortal & Saura, 2006; Saura & Pascual-Hortal, 2007; Saura & Torné, 2009) 2. CIRCUITScape (McRae et al., 2016)	Model called the "flickering connectivity system" (Flantua et al., 2019)	Flantua and Hooghiemstra (2018)
Initial isolation	Taxon-based palaeoclimate	The use of identifiable plant parts (pollen grains, macrofossils and spores) to reconstruct biome composition through time	Identifying fossils in terms of their nearest living relatives (NLRs)		Hoorn et al. (2019); Torres, Hooghiemstra, Lourens, and Tzedakis (2013); Van der Hammen and Cleef (1986); Wijninga (1996).
Duration of isolation (time)	General dynamic model of oceanic island biogeography (GDM) and ATT^2 (i.e., area + time + time ²)	The ATT^2 model considers island area (area, in square kilometres), time elapsed since island formation (time, i.e., date of emergence of each island, in millions of years ago) and a quadratic term for the time elapsed (time ² , which refers to the cycle of an island)	Borregaard et al. (2016); Steinbauer et al. (2013); Valente et al. (2014); Whittaker et al. (2008)		Lenzner, Weigelt, Kreft, Beierkuhnlein, and Steinbauer (2017); Loiseau et al. (2019)
Duration of isolation (time)	Taxon-based altimetry approach	The first appearance of cold-adapted taxa can indicate the appearance of alpine habitats		Multi-proxy studies are often needed to set the timing of events	Perrigo et al. (2020); Spicer (2018) and references therein
Duration of isolation (time)	Phytopalaeoaltimetry	Use of plant fossils to estimate past land surface elevation			Perrigo et al. (2020); Spicer (2018) and references therein; Wijninga (1996).

In the páramos of the Northern Andes, for example, the early species-poor páramo (the “proto-páramo”; Hooghiemstra, 1984; Van der Hammen & Cleef, 1986; Van der Hammen et al., 1973) was later enriched by the numerous immigrating genera from Neotropical and temperate zones (Cleef, 1979; Sklenář, Dušková, & Balslev, 2011; Wallace, 1880). Present-day páramo endemism, therefore, consists of a mix of taxa originating from páramo ancestors and more recent immigrants, both of which contributed to endemism through evolutionary radiations during the Pleistocene (Morrone, 2018; Nürk et al., 2020). Thus, the initial isolation of mountain islands is often less than for true islands, with an increase in disharmony and endemism with respect to the regional species pool through time.

5 | ISOLATION HISTORY

The length of time over which isolation has operated (duration of isolation) is the final key dimension in our framework for understanding patterns of endemism. We combine isolation continuity with the duration of isolation to discuss “isolation history” (Figure 2c). The first models of island biogeography, including the equilibrium theory of island biogeography (ETIB; MacArthur & Wilson, 1967), treated physical characteristics, such as island size and elevation, as static over time. More recently, the general dynamic model (GDM; Whittaker, Triantis, & Ladle, 2008) was developed, which accounts for the life cycle of hotspot volcanic oceanic islands and the changes in geological processes from the origination of the island to its disappearance (Table 3; Borregaard et al., 2017; Borregaard, Matthews, Whittaker, & Field, 2016). Processes such as volcanic activity, uplift and erosion influence the processes that generate and maintain endemic species on these islands through time. The duration of isolation (from island emergence to submergence) is considered to have a positive influence on the presence of endemics such as those observed in ancient continental fragments, including New Caledonia and Madagascar (Kier et al., 2009). Similar patterns are observed in ancient mountain areas, such as southwestern Cape (South Africa) and southeastern Australia (Goldblatt & Manning, 2002; Antonelli et al., 2018; Supporting Information). The total duration of isolation that species experience can be increased effectively in oceanic archipelagos through the progression rule (e.g., Shaw & Gillespie, 2016), according to which island lineages may persist for longer than the islands they inhabit because they colonize new islands in the archipelago before the original islands disappear.

For most mountain islands and true islands, accurate data on the timing of isolation based on the age of the island setting are scarce. In mountainous settings, relief formation can be estimated by various radiometric dating techniques of island substrates or using thermochronometric data that measure the time at which certain minerals crossed thermal boundaries in the upper 10 km of the crust (Antonelli et al., 2018). However, these estimates of age do not necessarily represent when a mountain reached the necessary elevation for elevation zones of ecosystems to form. Such radiometrically dated emergence ages are likewise problematic for

true islands to estimate when an island emerged fully from the sea (Borregaard et al., 2017). Palaeoaltimetric approaches are often complex and highly debated, and new ones are under development (Table 3; see overview table by Perrigo, Hoorn, & Antonelli, 2020). The influence of island ontogeny on evolutionary dynamics has been assessed for individual islands (Lim & Marshall, 2017). However, to date, a global synthesis of palaeoaltimetric data that contains both uplift rate and palaeoaltitude with a high degree of fidelity is still lacking, hindering our ability to infer the age of a mountain range and thus the time-scales over which geo-evolutionary processes have influenced endemism in isolated conditions. Multi-proxy studies that integrate different palaeoaltimetry proxies (Perrigo et al., 2020) with adequately calibrated phylogenies would be of great value (also see Pennington, Richardson, & Lavin, 2006).

6 | CONCLUSIONS

Present-day conditions provide only a snapshot within the life span of mountains and islands, and the past is bound to have left a strong legacy on modern patterns of endemism (Rull, 2020; Wallace, 1880; Whittaker, Willis, & Field, 2001). How much the present is representative of the past depends on “isolation continuity” and “isolation history”, which are driven by geological and environmental changes through time. Islands and archipelagos (*sensu lato*) have taken numerous spatial configurations, with changes in surface area, connectivity and environmental conditions. As discussed throughout this contribution, fluctuations in sea levels and climates, and mountain building and island/archipelago ontogeny (and fragmentation attributable to human impact), are all possible causes of changes in isolation (also see Gillespie et al., 2020). A major challenge in island and mountain biogeography is to understand what legacies the past trajectory and spatial configurations have had on contemporary endemism and what will happen in the future. Until now, only a few studies have addressed island trajectories through a range of different configurations (rather than only change from the LGM to the present-day), such as the palaeoconfigurations of oceanic islands by Norder et al. (2019) and the flickering connectivity system of high Andean islands by Flantua et al. (2019). Considering the effects of longer-term environmental changes on contemporary endemism (e.g., not only the last glacial and the Holocene for present-day endemism) is a key area for future research in biogeography and macroecology.

Isolation is key to understanding patterns of endemism, but it is a complex phenomenon that varies greatly between taxa and among and within islands, and even more so for mountain systems, depending on their surrounding landscape matrix. Arguably, the strongest commonality between true islands and mountain islands is their high variability of isolation in space and time. Although we acknowledge that the “sky island” and “mountain/alpine islands” analogy is useful to some extent, we argue that a more nuanced spatio-temporal approach will improve our understanding of endemism in both mountains and true islands, in addition to other biogeographical patterns. Such an approach is equally applicable to any type of island-like

system (Whittaker & Fernandez-Palacios, 2007). We argue that it is essential to embrace the manifold dimensions of isolation that may affect endemism (and other biogeographical and ecological patterns) in different ways, and we provide a framework to do so. Similar levels of endemism in island and mountain systems may result from different pathways in response to changing environmental conditions (Figure 2), emphasizing the need for better representation of historical processes in models of contemporary biodiversity. We suggest that research on endemism needs to move beyond the focus on processes that promote allopatry and to explore other drivers of diversification, such as isolation history and shifting degrees of archipelago connectivity, while acknowledging differences between species.

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GLOSSARY

Alpine island, The alpine zone (if present) within a mountain. Its upper limit is often delimited by the snowline of glaciers and the lower limit by the uppermost contour of closed forest (upper forest line). Typically, the alpine zone is split up into separated alpine habitats dispersed across a large number of mountain tops within a mountain (chain). Only for volcanic terrestrial isolates is it likely that there is a single "alpine island". Examples are the páramos and punas in Northern and Central Andes. Sometimes also called "mountain top islands" or (confusingly) "sky islands"; **Archipelago**, A cluster of islands in the form of an island group or island chain. The concept was later on echoed in mountains to describe the collections of alpine islands that show biogeographical similarities to oceanic archipelagos (e.g., Flantua & Hooghiemstra, 2018; Kirkpatrick, 2002; Van der Hammen, 1974; Warschall, 1994);

Connectedness, The degree of physical connection between patches/islands. Related to "structural connectivity" that corresponds to spatial relationships (continuity and adjacency) between patches or islands. It is a structural attribute of a landscape and can be mapped [Farina (2000) citing Baudry, 1984].; **Connectivity**, (a) The degree to which the landscape facilitates or impedes movement among resource patches (Taylor, Fahrig, Henein, & Merriam, 1993). This definition emphasizes how the types, amounts and arrangement of habitat or land use on the landscape influence movement and, ultimately, population dynamics and community structure (Taylor et al., 2006). (b) The process by which subpopulations are interconnected in demographic functional units (Farina, 2000). (c) The functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure (With, Gardner, & Turner, 1997); **Connectivity, functional**, The degree of reachability of suitable habitat based on the dispersal abilities of a species. For example, valleys and sea constrain functional connectivity more for amphibians than for birds (also see Supporting Information Appendix S1).; **Connectivity, structural**, Corresponds to spatial relationships (continuity and adjacency) between the structural elements of a system. A decrease of structural connectivity, for example, owing to a change in sea level, implicates fragmentation of previously connected islands (increase of number of islands), loss of surface area (habitat loss) and increase of inter-island distance (isolation). This concept is independent of the ecological characteristics of the species (see "functional connectivity"; also see Supporting Information Appendix S1).; **Continental shelf islands**, Islands situated on the (relatively shallow) continental shelf. The continental shelf is formed by wave base erosion in response to sea-level fluctuations, resulting in a relatively smooth surface surrounding the islands. These islands are regularly connected to the continent during low-sea-level glacials via land bridges and isolated again during interglacials. Often large. Examples include the Bass Strait islands, British Isles, Florida Keys, Newfoundland and Sicily.; **Continental (tectonic) fragments**, Islands tectonically separated from the continental mass, but not considered large enough to be a separate continent. Examples include Crete, Madagascar, New Caledonia and New Zealand.; **Disharmony**, (a) Taxonomic "imbalance" of island biotas (Carlquist, 1965, 1974). (b) Biased representation of higher taxa (e.g., families) in island biotas compared with their mainland source regions (Whittaker & Fernandez-Palacios, 2007) as the result of selective assembly (see review by König et al., 2019). Disharmony represents a case of phylogenetic clustering that arises from non-random distribution of traits that foster island colonization among the evolutionary lineages in the source species pool.; **Dispersification**, Increased rates of diversification associated with biogeographical movements into newly formed environments (Moore & Donoghue, 2007).; **Endemism**, (a) A species (or other taxon) is defined as endemic if its natural range is restricted to a confined area (Anderson, 1994). (b) Species that have a relatively narrow geographical range, such as on/in a particular island,

habitat or region (Moorcroft, 2009: p. 445). (c) Species with small geographical ranges (Hughes, 2009: p. 482). The more range restricted a species is, that is, the smaller its range size or the smaller the reference area in which a species occurs (e.g., mountain range versus single mountain top or archipelago versus single island), the higher its endemism, that is, the more "endemic" it is (Guerin & Lowe, 2015; Noroozi et al., 2018; Steinbauer et al., 2016; also see **Box 1 and overview of definitions of endemic areas by Parenti & Ebach, 2009**).; **Endemic (species) richness**, The number of species that are endemic in a given region (also see Box 1).; **Fragmentation**, (a) The breaking up of a habitat, ecosystem or type of land use into smaller parcels (Curtis, 1956; Forman, 1995; Moore, 1962; see reviews by Fahrig, 2003, 2019). The definition of habitat fragmentation implies four effects of the process of fragmentation on habitat pattern: (i) reduction in habitat amount, (ii) increase in number of habitat patches, (iii) decrease in sizes of habitat patches, and (iv) increase in isolation of patches (Fahrig, 2003). (b) The state of habitat fragmentation as discontinuity, resulting from a given set of mechanisms in the spatial distribution of resources and conditions present in an area at a given scale that affects occupancy, reproduction or survival in a particular species (Franklin, Noon, & George, 2002). (c) The process of habitat fragmentation as the set of mechanisms leading to that state of discontinuity (Franklin et al., 2002). For a full list of definitions of fragmentation, see Bogaert et al. (2011).; **Habitat islands in mountains**, Isolated patches of a certain habitat type within a mountain. Often found in island-like distributions with highly variable distances, for example, seasonally dry forests in the Andes (Särkinen et al., 2012). Including but not restricted to alpine islands.; **Hotspot volcanic oceanic islands**, Islands initially formed on the ocean floor by hotspot activity and may follow a geo-ontogeny characterized by an emergent state which consists of: (a) a juvenile volcanic active growing state, (b) a mature volcanically inactive erosive state, and (c) a senile subsiding atoll to sea mount state. We can distinguish between volcanic oceanic islands that became connected during sea-level reductions or remained isolated. These islands are among the most isolated true islands on the planet and include Easter island, the Galapagos and Hawai'i.; **Islands**, (a) Areas of land surrounded by water (*sensu stricto*; i.e., true islands). (b) Landmass isolated in geographical and environmental space (*sensu lato*). Different types of true islands (Figure 2) are as follows: (a) oceanic islands, such as the Hawaiian Islands, the Canary Islands, Sulawesi, Luzon and Mindanao; (b) **continental fragments**, such as Madagascar and New Zealand; and (c) **continental shelf islands**, such as the British Isles and the Bass Strait islands in Australia, and atolls, such as the Florida Keys.; **Isolation of an island**, A continuum of processes whose strengths vary in space and time, modulated by species traits and environmental and geological conditions that influence the (spatial) characteristics of the island and, as a result, change the degree of gene flow.; **Isolation continuity**, Considers the historical dynamics of isolation of an island/archipelago in terms of: (a) the temporal variability of "snapshot isolation", and (b) the initial level of isolation when the island is formed.;

Isolation history, Considers the historical dynamics of isolation of an island/archipelago in terms of: (a) "isolation continuity", and (b) the overall duration of isolation.; **Mountain islands**, Mountains or biomes within mountains (or mountain ranges) in which the geological features, species composition, habitat and ecosystem are distinct from the surrounding landscape, often characterized by sharp gradients that accentuate the "island" boundaries. Used in this paper as a general term to describe "alpine islands", "habitat islands in mountains" and "sky islands".; **Mountain island archipelagos**, Biogeographical coherence of an assemblage of mountain islands resembling limited species dispersion and *in situ* evolutionary processes seen in true island archipelagos.; **Oceanic islands/archipelagos**, (Clusters of) islands located on oceanic crust, either at plate boundaries near subduction zones (arc islands) or those which were formed by hotspot volcanism (see hotspot volcanic oceanic islands). The geodynamics of islands are highly complex, and more detailed geological classifications are provided by Ali (2017) and Nunn, Kumar, Eliot, and McLean (2016).; **Patch**, (a) A relatively homogeneous area within a landscape that differs markedly from its surroundings (Fischer, Lindenmayer, & Hobbs, 2009: p. 431). (b) A discrete, bounded area of any spatial scale that differs from its surroundings in its biotic and abiotic structure and composition (Peters, Gosz, & Collins, 2009: p. 458).; **Percentage endemism**, The proportion of species that are endemic. At large scales, percentage endemism can reflect speciation (Steinbauer et al., 2016), whereas at smaller scales (e.g., on the plot scale) percentage endemism describes compositional uniqueness (e.g., Gillespie, Claridge, & Roderick, 2008; Irl et al., 2015; see **Box 2**).; **Sky islands**, (a) Mountain islands in a "desert sea" with limited genetic exchange between them (Dodge, 1943). (b) Continental landforms characterized by a substantially different climate, vegetation and species composition that are as different from their surroundings as if they rose from some remote sea (Heald, 1951, 1967). (c) Geological features with a species composition or ecosystem distinct from the surrounding landscape, often with steep gradients that accentuate the "island" boundaries, for example, table-top mountains in Venezuela and Colombia (Rull, 2010) and the Madrean archipelago (see Table 1). More recently, the term has been expanded also to describe mountain top islands, such as the high-elevation páramos of the Northern Andes (e.g., Diazgranados & Barber, 2017) and the Hengduan sky islands (e.g., He & Jiang, 2014). As such, true islands can also include sky islands with numerous endemics, for example, Sulawesi and Luzon.; **Snapshot isolation**, The degree of isolation of mountain islands and true islands at a point in time. The degree of isolation of mountain islands and true islands at a point in time.; **Taxon cycle**, (a) Temporal sequence of geographical distribution of species from (i) colonizing through (ii) differentiating and (iii) fragmenting to (iv) specializing (Gillespie, 2009: p. 144). (b) Taxon cycles are sequential phases of expansion and contraction of the ranges of species, usually associated with shifts in ecological distribution and adaptations to changing ecological relationships through the cycle (Ricklefs & Bermingham, 2002, citing Wilson, 1959, 1961).; **Vicariant**

speciation, A mode of allopatric speciation that involves a physical barrier, such as an ocean channel or mountain range, that subdivides a range and prevents gene flow between the two resulting populations (Phillimore, 2013)..

AUTHOR CONTRIBUTIONS

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BIOSKETCH

Suzette G. A. Flantua has a background in palaeoecology, biogeography, landscape ecology and spatial analyses and enjoys integrating them all to gain new insights into the drivers of mountain biodiversity.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX 1

Quantifying snapshot isolation using metrics from landscape ecology

The size of an island indirectly influences its degree of isolation. Larger islands can support larger populations and offer a larger variety of available niches, which results in a positive relationship between area and endemic species richness (Kisel & Barraclough, 2010; Losos & Schluter, 2000). Furthermore, larger islands are more likely to receive more propagules and have a higher gene flow (target effect; Gilpin & Diamond, 1976) than smaller islands. Ideally, area should not be treated independently from isolation (Fahrig, 2013) and explanatory models of endemism should integrate isolation, area and species traits to better represent the environmental heterogeneity and complex island configurations.

Approaches developed in landscape ecology address this complexity by integrating for instance the surface area of a patch/island with the degree of isolation ('habitat amount hypothesis'; Fahrig, 2013; Merckx *et al.*, 2019). Pascual-Hortal & Saura (2006) and Saura & Pascual-Hortal (2007) in particular developed two landscape connectivity metrics that define habitat availability ('reachability') at the landscape scale based on species dispersal capacity: the 'Integral Index of Connectivity' (IIC) and the 'Probability of Connectivity' (PC). Both metrics are partitioned into three 'fractions' that define different ways in which a patch (**Glossary**, or an island) contributes to the connectivity or 'habitat reachability' within a spatial configuration of patches. The concept of habitat reachability integrates in a single metric the connectivity that already exists within a habitat patch ('intrapatch connectivity'; where the area of the patch itself matters for connectivity) with the area of other habitat patches that are reachable ('interpatch connectivity'; Saura, 2008). Here, we replace 'patch' with 'island' and discuss the usefulness of this approach as a potential universal method that can be used in both mountain islands and true islands.

IIC or PC are partitioned into fractions as follows:

$$\text{IIC or PC} = \text{intra} + \text{flux} + \text{connector}$$

These three fractions are measured in the same units, can be directly compared, and result in an estimate for each island individually.

Intra-island connectivity: *intra*

The intra-island connectivity measures the contribution of an island to the system's connectivity in terms of surface area and habitat suitability. This first fraction of IIC or PC is completely independent of how much area is reachable for a given species on other islands, does not depend on species dispersal, and is the same even if the island is completely isolated (out of reach of the focal species). In *intra*, habitat quality and

suitability of the area available on a specific island can be taken into account. This enriches the concept of isolation often used for true islands, where the use of distance to the nearest landmass as the only proxy for isolation rests on the assumption that true islands are homogeneous entities for mainland organisms, despite the existence of considerable variation in environmental conditions within true islands (see above). Thus, an island's suitability for species can be a useful variable to include in the *intra* fraction, alongside the total surface availability.

Inter-island connectivity: *flux* and *connector*

Here we distinguish between the *flux* and *connector*; the *flux* fraction estimates how well an island (or equivalent environments or habitats) is reachable from other islands based on inter-island distances. It considers both the geographical position of the island in relation to other islands, and its area, meaning that a larger island is expected to have a higher dispersal probability (more dispersal events) to other islands, i.e. higher propagule pressure (number of individuals dispersal to other islands). With the IIC metric, this is based on a simplistic binary model where islands are either reachable by species or not. With the PC metric, this is calculated using a probabilistic model of dispersal, if the necessary estimates are available for the focal species, or simulations with different distances are used to test dispersal hypotheses. The other fraction of inter-island connectivity, called *connector*, quantifies the importance of the island to the overall connectivity. *Connector* scores are typically high when an island has high irreplaceability with respect to maintaining connectivity, e.g. within an archipelago, or because it serves a valuable stepping stone between several islands.

Together and through IIC and PC, *intra*, *flux* and *connector* are a means to calculate snapshot isolation, combining the influences of the surface area of an island or equivalent environments relevant to the focal species, habitat suitability, species traits, and the spatial configurations of islands or patches (**Table 3 main text**). Distances between islands in either the binary (IIC) or probabilistic (PC) model are by default based on Euclidean distances, but they can also be based on least-cost distance calculations. Cost-distance approaches are particularly relevant under our assumption that snapshot isolation increases with both environmental difference and geographic distance, and especially in mountainous topographies. Additionally, the software to calculate IIC and PC (CONEFOR SENSINODE, Saura & Torné, 2009) now also provides tools to analyse asymmetric connectivity (e.g. Martensen *et al.*, 2017).

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APPENDIX 2

Different types of mountains

How to define a mountain has been a long-lasting controversy. Mountains as landforms (Molnar, 2015) have recently been described in considerable detail by Karagulle, Sayre and colleagues (Karagulle *et al.*, 2017; Sayre *et al.*, 2018), who used slope, relative relief (the absolute value of the difference between the maximum and minimum elevations in a neighbourhood analysis window) and profile (a measure of the amount of gently sloping lands in upland areas) to identify High, Scattered High, Low and Scattered Low mountains. For macroecology and biogeography, the two most commonly applied definitions of mountains (Price *et al.*, 2019) are the one by Kapos *et al.* (2000) and the one developed by the Global Mountain Biodiversity Assessment (GMBA, Körner *et al.*, 2011). The former defines six classes of land area that belong to mountain terrain by combining elevation and so-called ruggedness (maximal elevational difference among neighbouring grid points and as such comparable to relative relief). Based on the argument that mountains can be defined neither by elevation nor by climate alone, the GMBA approach applies ruggedness only (as a proxy of steepness), to provide a map of global mountains for comparative biodiversity science. According to these three mainstream definitions (Sayre *et al.*, 2018), mountains cover between 12.3% and 30.5% of the global land surface area.

Mountains vary greatly in their formation, appearance and geological history. They are essentially shaped by two processes: thickening of the crust and volcanic activity due to increasing temperature of the uppermost mantle (Molnar, 2018). Thickening is the more common process and occurs where tectonic plate collision folds edges and adjacent regions upwards into mountain ranges and high plateaux (**fold mountains**; Gordon, 2018; e.g. around the Mediterranean region and the Rocky Mountains). This folding can result from one plate of the lithosphere being thrust atop the crust of the other, sometimes scraping off the upper layers while the rest moves into a subduction zone (e.g. Himalaya and Andes). **Fault-block mountains** form along faults as large blocks of rock that are uplifted and pushed downwards on opposite sides of the fault (e.g. Rhine Valley between Vosges mountains and Black Forest; Sierra Nevada, California). Surface manifestations of magma result in **volcanic mountains**, where the terrain is created by active lava flows and/or elevated by hot rising material at the Earth's surface but also by the cooling and solidification of the magma before reaching the surface ('igneous intrusions'). Examples are Mt. Kilimanjaro and Mt. Fujiyama, and the 'Avenue of the Volcanoes' in Ecuador. In some cases, however, the magma does not reach the surface and conglomerates into a dome-shaped hard rock (**dome mountain**) after cooling, because of its proximity to the Earth's surface. These circular structures tend to stand alone in flat landscapes and are, for example, found along the border of the Rocky Mountains and in the Black Hills of South Dakota (e.g. Bear Butte, South Dakota; Rauher Kulm, Northern Bavaria). **Plateau mountains** are flat-topped mountains where the surroundings are

eroded away by rivers, floods or glacial activity. Prominent examples are the table-top mountains in Venezuela, Deorasai Plains in Pakistan and the Tibetan Plateau. For more on mountain origins and plate tectonics, see Gordon (2018).

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