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

Suzette G. A. Flantua1,2 | Davnah Payne3 | Michael K. Borregaard4 | Carl Beierkuhnlein5,6,7 | Manuel J. Steinbauer6,8 | Stefan Dullinger9 | Franz Essl9 | Severin D. H. Irl10 | David Kienle5 | Holger Kreft11 | Bernd Lenzner9 | Sietze J. Norder2,12 | Kenneth F. Rijsdijk2 | Sabine B. Rumpf9,13 | Patrick Weigelt11 | Richard Field14

1Department of Biological Sciences, University of Bergen, Bergen, Norway
2Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Amsterdam, the Netherlands
3Global Mountain Biodiversity Assessment, Institute of Plant Sciences, University of Bern, Bern, Switzerland
4Center for Macroecology, Evolution and Climate, GLOBE Institute, University of Copenhagen, Copenhagen, Denmark
5Department of Biogeography, University of Bayreuth, Bayreuth, Germany
6Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany
7Institute of Geography (GIB), University of Bayreuth, Bayreuth, Germany
8Sport Ecology, University of Bayreuth, Bayreuth, Germany
9Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria
10Biogeography and Biodiversity Lab, Institute of Physical Geography, Johann Wolfgang Goethe-Universität Frankfurt, Frankfurt, Germany
11Biodiversity, Macroecology and Biogeography, University of Göttingen, Göttingen, Germany
12Faculdade de Ciências, Centre for Ecology, Evolution and Environmental Changes (cE3c)/Azorean Biodiversity Group, Universidade de Lisboa, Lisboa, Portugal
13Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland
14Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria

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
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, & Krefe, 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-Vilarrubia, 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 ontology, 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, as explanatory variables and if these models account for the trajectories of the history of a system.

KEYWORDS

endemic species, flickering connectivity system, geological ontology, glacial–interglacial fluctuations, island biogeography, isolation, mountain islands, palaeoclimate, past connectivity, sky islands
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 “palaoendemic” (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).
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 ("Differencesur"); and (b) the effective distance from an equivalent environment ("Distanceequiv-en"). 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 (Differencesur)

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 Differencesur, 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
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 Difference 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 (Distance_{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](image-url) **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 [Colour figure can be viewed at wileyonlinelibrary.com]
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 & Kreft, 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 [Colour figure can be viewed at wileyonlinelibrary.com]

(e.g., wind or water currents; biotic agents; Gillespie et al., 2012, 2020). Thus, we argue that Distanceequiv-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 Distanceequiv-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; Rijsdijk 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 submerging 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          | Stepping stone archipelago between two or more large surface areas                        | Stepping stone archipelago between a large island and the mainland or between two large islands: |
| isolated massif with outliers       | • Madrean archipelago                                                                     | • Archipelago Sea (Baltic Sea)                                                         |
|                                     | • Great Basin archipelago                                                                 | • Lesser Sunda islands                                                                |
|                                     | • Altai/Tien Shan Basin                                                                  | • Sulu archipelago                                                                    |
|                                     | • Meso-American massifs                                                                  | • Kuril Islands                                                                      |
|                                     |                                                                                          | (islands between Japan and Taiwan)                                                    |
|                                     |                                                                                          | • Lesser Antilles                                                                     |
|                                     |                                                                                          | • Tuscany Archipelago                                                                  |
|                                     |                                                                                          | • Mozambique Channel Islands (Comoros Mayotte)                                         |
|                                     |                                                                                          | • Indian Ocean islands between Madagascar and India                                    |
|                                     |                                                                                          | Balearic islands                                                                      |
| Isolated massif with                |                                                                                          |                                                                                       |
| smaller outlier mountains           |                                                                                          |                                                                                       |
|                                     | • Ethiopian highlands                                                                    | • New Caledonia                                                                       |
|                                     | • East African arc                                                                       | • Madagascar with surrounding islands                                                 |
|                                     | • Saharan massifs                                                                       |                                                                                       |
|                                     | • Atlas Mountains                                                                       |                                                                                       |
|                                     | • Jabal Lubnan                                                                         |                                                                                       |
|                                     | • Drakensberg                                                                          |                                                                                       |
|                                     | • Central European massifs                                                               |                                                                                       |
|                                     | • Caucaso-Iranian massifs                                                                |                                                                                       |
| Linear chain of outlier islands at  | Cordillera with outliers of mountains islands at one end of a cordillera:               |                                                                                       |
| one end of a large island           | • Malay peninsula                                                                        |                                                                                       |
|                                     | • Baja California peninsula                                                             |                                                                                       |
|                                     | • Coastal Cordillera (South America)                                                    |                                                                                       |
|                                     | • Southern Andes                                                                       |                                                                                       |
|                                     |                                                                                          |                                                                                       |
| Isolated island chains and groups   | Completely isolated sky islands:                                                        | Easter Islands                                                                        |
|                                     | • Western Ghats                                                                         | • Hawai’i                                                                              |
|                                     | • Pantepui (table-top mountains)                                                         | • Galapagos                                                                           |
|                                     |                                                                                          | • Seychelles                                                                          |
|                                     |                                                                                          | • Canaries                                                                            |
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 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,
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; Schönswetter, Stehlik, Holdererger, & 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, Ordonez, & Sandel, 2015). Current endemism patterns would, therefore, result more from range contractions of formerly widespread species and less from in situ speciation (Tribsch & Schönswetter, 2003). However, many high-elevation ecosystems...
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 endemism 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 distances, 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 relics of extinct mainland species, forming palaeo-endemics 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 developed 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).
| Dimension          | Measure                                      | Description                                                                 | Tools                                                                                     | Note                                                                                     | Additional reading                                                                 |
|--------------------|----------------------------------------------|------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------|
| Snapshot isolation | Integral index of connectivity (IIC); Probability of connectivity (PC) | Intra- and inter-island (patch) connectivity                                | ConforSensinode (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. Graph  
(Bothé, Cauzel, & 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 Aitlison (2014); Fernández-Palacios et al. (2016); Rijsdijk et al. (2014); Weigelt et al. (2016) |
| Temporal variability of isolation | Palaeoconfiguration of alpine islands | Calculates palaeoconnectivity change driven by temperature fluctuations | 1. ConforSensinode (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) | | | | | |
| 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 | | | | | |
| Duration of isolation (time) | Phytopalaeoaltimetry | Use of plant fossils to estimate past land surface elevation | Perrigo et al. (2020); Spicer (2018) and references therein | | 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 elevationl 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.

ACKNOWLEDGMENTS

We would like to thank Editor-in-Chief Brian McGill for supporting the submission of this paper to Global Ecology and Biogeography. The Department of Biodiversity, Macroecology & Biogeography at University of Göttingen supported a 3-day visit of S.G.A.F. to work on the manuscript with H.K. and P.W. S.G.A.F. acknowledges the support of The Netherlands Organization for Scientific Research (NWO, no. 2012/13248/ALW to H. Hooghiemstra) and European Research Council (ERC) Advanced Grant (no. 741413, Humans on Planet Earth (HOPE) to H. J. B. Birks. We thank H. Hooghiemstra for his comments on previous versions of the manuscript and we also thank the Global Mountain Biodiversity Assessment for support. M.K.B. was funded by an Individual Fellowship under the Marie Skłodowska-Curie grant agreement (no. 707968) and acknowledges the Danish National Research Foundation for support of the Center for Macroecology, Evolution and Climate (no. DNRF96). F.E. and B.L. were funded by the Austrian Science Foundation (Fonds zur Förderung der wissenschaftlichen Forschung, FWF, no. I 3757-B29). S.J.N. received funding from the Portuguese National Funds, through Fundação para a Ciência e a Tecnologia (FCT), within the project UID/BIA/00329/2013 and the research Fellowship PD/BD/114380/2016. C.B. has received funding for the ECOPOTENTIAL project from the European Union’s Horizon 2020 research and innovation programme (no. 641762).

GLOSSARY

Alpine island. The alpine zone (if present) within a mountain. Its upper limit is often delimitated 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);
habitat or region (Moore, 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 endemicity, 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). 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 atol 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, Elliot, 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
Initial ideas for this paper were developed at the Macroecology meeting in Vienna (2017) by S.G.A.F., D.P., M.K.B., M.J.S., S.D., F.E., S.D.H.I., D.K., H.K., B.L., S.B.R. and P.W., with further important contributions by R.F., C.B., S.J.N. and K.F.R. at a later stage. The conceptualization (writing and reviewing) was led by S.G.A.F., R.F. and D.P., and all authors contributed to the draft editing. Visualizations were drafted by S.G.A.F., M.J.S., R.F., K.R. and S.J.N. and commented on by all co-authors.

ORCID
Suzette G. A. Flantua https://orcid.org/0000-0001-6526-3037
Dovnah Payne https://orcid.org/0000-0001-9170-7834
Michael K. Borregaard https://orcid.org/0000-0002-8146-8435
Carl Beierkuhnlein https://orcid.org/0000-0002-6456-4628
Manuel J. Steinbauer https://orcid.org/0000-0002-7142-9272
Stefan Dullinger https://orcid.org/0000-0003-3919-0887
Franz Essl https://orcid.org/0000-0001-8253-2112
Severin D. H. Irl https://orcid.org/0000-0002-1734-8607
David Kienle https://orcid.org/0000-0003-4748-4236
Holger Kreft https://orcid.org/0000-0003-4471-8236
Bernd Lenzen https://orcid.org/0000-0002-2616-3479
Sietze J. Norder https://orcid.org/0000-0003-4692-4543
Kenneth F. Rijsdijk https://orcid.org/0000-0002-0943-2577
Sabine B. Rumpf https://orcid.org/0000-0001-5909-9568
Patrick Weigelt https://orcid.org/0000-0002-2485-3708
Richard Field https://orcid.org/0000-0003-2613-2688

REFERENCES
Adams, M. J. (1985). Speciation in the Pronophiline butterflies (Satyridae) of the Northern Andes. Journal of Research on Lepidoptera, 1, 33–49.
Ali, J. R. (2017). Islands as biological substrates: Classification of the biological assemblage components and the physical island types. Journal of Biogeography, 44, 984–994. https://doi.org/10.1111/jbi.12872
Ali, J. R., & Atchison, J. C. (2014). Exploring the combined role of eu- stasy and oceanic island subsidence in shaping biodiversity on the Galápagos. Journal of Biogeography, 41, 1227–1241. https://doi.org/10.1111/jbi.12313
Anderson, S. (1994). Area and endemism. The Quarterly Review of Biology, 69, 451–471. https://doi.org/10.1086/418743
Antonelli, A., Kissling, W. D., Flantua, S. G. A., Bermúdez, M. A., Mulch, A., Mueller-Riehl, A. N., ... Hoorn, C. (2018). Geologic and climatic influences on mountain biodiversity. Nature Geoscience, 11, 718–725. https://doi.org/10.1038/s41561-018-0236-z
Barthlott, W., Rafiqpoor, D., Kier, G., & Kreft, H. (2005). Global centers of vascular plant diversity. Nova Acta Leopoldina NF, 92, 61–83.
Baudry, J. (1984). Effects of landscape structure on biological communities: The case of hedgerow network landscapes. In J. Brandt, & P. Agger (Eds.), Landscape ecology research and planning, (Vol. 1, pp. 55–65). Roskilde, Denmark: Roskilde University Centre Denmark.

Bintanja, R., van de Wal, R. S. W., & Oerlemans, J. (2005). Modelled atmospheric temperatures and global sea levels over the past million years. Nature, 437, 125–128. https://doi.org/10.1038/nature03975
Bogaert, J., Barima, Y. S. S., Monge, L. I. W., Bamba, I., Mama, A., Toyi, M., & Laforteza, R. (2011). Forest fragmentation: Causes, ecological impacts and implications for landscape management. In C. Li, R. Laforteza, & J. Chen (Eds.), Landscape ecology in forest management and conservation: Challenges and solutions for global change (pp. 273–296). Berlin, Heidelberg: Springer.
Borregaard, M. K., Amorim, I. R., Borges, P. A. V., Cabral, J. S., Fernández-Palacios, J. M., Field, R., ... Whittaker, R. J. (2017). Oceanic island biogeography through the lens of the general dynamic model: Assessment and prospect. Biological Reviews, 92, 830–853. https://doi.org/10.1111/bbrv.12256
Borregaard, M. K., Matthews, T. J., Whittaker, R. J., & Field, R. (2016). The general dynamic model: Towards a unified theory of island biogeography? Global Ecology and Biogeography, 25, 805–816. https://doi.org/10.1111/geb.12348
Brown, R. M., Siler, C. D., Oliveros, C. H., Esselstyn, J. A., Diesmos, A. C., Hosner, P. A., ... Alcala, A. C. (2013). Evolutionary processes of diversification in a model island archipelago. Annual Review of Ecology, Evolution, and Systematics, 44, 411–435. https://doi.org/10.1146/annurev-ecolsys-110411-160323
Burney, D. A., James, H. F., Burney, L. P., Olson, S. L., Kikuchi, W., Wagner, W. L., ... Nishek, R. (2001). Fossil evidence for a diverse biota from Kau‘a‘i and its transformation since human arrival. Ecological Monographs, 71, 615–641.
Burns, K. C. (2019). Evolution in isolation. Cambridge, UK: Cambridge University Press.
Cabral, J. S., Weigelt, P., Kissling, W. D., & Kreft, H. (2014). Biogeographic, climatic and spatial drivers differentially affect α-, β- and γ-diversities on oceanic archipelagos. Proceedings of the Royal Society B: Biological Sciences, 281, 20133246.
Carliquist, S. (1965). Island life: A natural history of islands of the world (1st ed.). New York, NY: The Natural History Press.
Carliquist, S. (1970). Hawaii—A natural history. New York, NY: The Natural History Press.
Carliquist, S. (1974). Island biology. New York, NY: Columbia University Press.
Carvalho, J. C., Cardoso, P., Rigal, F., Triantis, K. A., & Borges, P. A. V. (2015). Modeling directional spatio-temporal processes in island biogeography. Ecology and Evolution, 5, 4671–4682. https://doi.org/10.1002/ece3.1632
Chala, D., Zimmermann, N. E., Brochmann, C., & Bakkestuen, V. (2017). Migration corridors for alpine plants among the “sky islands” of eastern Africa: Do they, or did they exist? Alpine Botany, 127, 133–144. https://doi.org/10.1007/s00035-017-0184-z
Cheke, A., & Hume, J. (2008). Lost land of the dodo: An ecological history of Mauritius, Réunion and Rodrigues. London, UK: T & AD Poyser.
Cleeef, A. M. (1979). The phytogeographical position of the Neotropical vascular páramo flora with special reference to the Colombian Cordillera Oriental. In K. Larsen & L. B. Holm-Nielsen (Eds.), Alpines in isolation—A natural history of the Rocky Mountains, 615–641. https://doi.org/10.1146/annurev-eolsys-110411-160323
Copernicus Land Monitoring Service. (2019). CORINE Land Cover. Retrieved from https://land.copernicus.eu/paan-europ-e/corine-land-cover
Crisp, M. D., Laffan, S., Linder, H. P., & Monro, A. (2001). Endemism in the Australian flora. Journal of Biogeography, 28, 183–198. https://doi.org/10.1046/j.1365-2699.2001.00524.x
Cubas, J., Irl, S. D. H., Villafuerte, R., Bello-Rodríguez, V., Rodríguez-Luengo, J. L., del Arco, M., ... González-Mancebo, J. M. (2019).
Guerin, G. R., Ruokolainen, L., & Lowe, A. J. (2015). A georeferenced implementation of weighted endemism. *Methods in Ecology and Evolution*, 6, 845–852. https://doi.org/10.1111/2041-210X.12361

Harrison, S., & Noss, R. (2017). Endemism hotspots are linked to stable climatic refugia. *Annals of Botany*, 119, 207–214. https://doi.org/10.1093/aob/mcw248

He, K., & Jiang, X. (2014). Sky islands of southwest China: I: An overview of phyleogeographic patterns. *Chinese Science Bulletin*, 59, 585–597. https://doi.org/10.1007/s11434-013-0089-1

Heald, W. F. (1951). Sky islands of Arizona. *Natural History*, 60, 56–63.

Heald, W. F. (1967). Sky island. Princeton, NJ: Van Nostrand.

Heaney, L. R. (2000). Dynamic disequilibrium: A long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecology and Biogeography*, 9, 59–74. https://doi.org/10.1046/j.1365-2699.2000.00163.x

Heaney, L. R., Balete, D. S., Duya, M. R. M., Duya, M. V., Jansa, S. A., Steppan, S. J., & Rickart, E. A. (2016). Dynamic disequilibrium: A cautionary tale of previously unsuspected mammalian diversity on a tropical oceanic island. *Frontiers of Biogeography*, 8.2, e29667.

Heaney, L. R., Walsh, J. S., & Peterson, A. T. (2005). The roles of geological history and colonization abilities in genetic differentiation between mammalian populations in the Philippine archipelago. *Journal of Biogeography*, 32, 229–247. https://doi.org/10.1111/j.1365-2699.2004.01120.x

Hewitt, G. (2000). The genetic legacy of the Quaternary ice ages. *Nature*, 405, 907–913. https://doi.org/10.1038/35016000

Hooghmiestra, H. (1984). *Vegetational and climatic history of the high plain of Bogotá, Colombia*. Dissertationes Botanicae 79. Vaduz: Lubrecht & Cramer Ltd.

Hoorn, C., van der Ham, R., de la Parra, F., Salamanca, S., ter Steege, H., Banks, H., … Lagomarsino, L. P. (2019). Going north and south: multiple spatial scales, with an example from the Australian vascular flora. *Journal of Biogeography*, 46, 511–520. https://doi.org/10.1111/jbi.12920

Kirkpatrick, J. B. (2002). Factors influencing the spatial restriction of vascular plant species in the archipelagos of Australia. In C. Körner & E. M. Spehn (Eds.), *Mountain biodiversity: A global assessment* (pp. 155–164). London, UK: Parthenon.

Kisel, Y., & Barraclough, T. G. (2010). Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist*, 175, 316–334. https://doi.org/10.1086/650369

Knope, M. L., Morden, C. W., Funk, V. A., & Fukami, T. (2012). Area and the rapid radiation of Hawaiian *Bidens* (Asteraceae). *Journal of Biogeography*, 39, 1206–1216. https://doi.org/10.1111/j.1365-2699.2012.02687.x

Knowles, L. L., & Massatti, R. (2017). Distributional shifts – not geographic isolation – as a probable driver of montane species divergence. *Ecography*, 40, 1475–1485. https://doi.org/10.1111/ecog.02893

Kolář, F., Dušková, E., & Sklenář, P. (2016). Niche shifts and range expansions along cordilleras drove diversification in a high-elevation endemic plant genus in the tropical Andes. *Molecular Ecology*, 25, 4593–4610. https://doi.org/10.1111/mec.13788

Körner, C. (2004). Mountain biodiversity, its causes and function. AMBIO: *A Journal of the Human Environment*, 33, 11–17.

König, C., Weigelt, P., Taylor, A., Stein, A., Dawson, W., Essl, F., … Kreft, H. (2019). Disappearance of the World’s Island Floras. *BioRxiv*, 523464.

Kougioumoutzis, K., Valli, A. T., Georgopoulou, E., Simaiakis, S. M., Triantis, K. A., & Trigas, P. (2017). Network biogeography of a complex island system: The Aegean Archipelago revisited. *Journal of Biogeography*, 44, 651–660. https://doi.org/10.1111/jbi.12920

Kupper, J. A., Malanson, G. P., & Franklin, S. B. (2006). Not seeing the ocean forest fragmentation effects. *Global Ecology and Biogeography*, 15, 8–20. https://doi.org/10.1111/j.1466-822X.2006.00204.x

Laffan, S. W., & Crisp, M. D. (2003). Assessing endemism at multiple spatial scales, with an example from the Australian vascular flora. *Journal of Biogeography*, 30, 511–520. https://doi.org/10.1046/j.1365-2699.2003.00875.x

Lambeck, K., Rouby, H., Purcell, A., Sun, Y., & Sambridge, M. (2014). Sea level and global ice volumes from the Last Glacial Maximum to the Holocene. *Proceedings of the National Academy of Sciences USA*, 111, 15296–15303. https://doi.org/10.1073/pnas.1411762111

Lens, F., Davin, N., Smets, E., & del Arco, M. (2013). Insular woodiness on the Canary Islands: A remarkable case of convergent evolution. *International Journal of Plant Sciences*, 174, 992–1013. https://doi.org/10.1086/670259

Lenzer, B., Weigelt, P., Kreft, H., Beierkuhnlein, C., & Steinbauer, M. J. (2017). The general dynamic model of island biogeography revisited...
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.

Davnah Payne is an evolutionary biologist with a wide interest in mountain conservation and biodiversity. She serves as executive director of the Global Mountain Biodiversity Assessment.

Richard Field's main interests are macroecology, biogeography, islands, geodiversity and plant ecology, with particular focus on biodiversity and the forces that structure ecological communities.

SUPPORTING INFORMATION

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

How to cite this article: Flantua SGA, Payne D, Borregaard MK, et al. Snapshot isolation and isolation history challenge the analogy between mountains and islands used to understand endemism. Global Ecol Biogeogr. 2020;29:1651–1673. https://doi.org/10.1111/geb.13155