

Vulnerability of global biodiversity hotspots to climate change

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Abstract

Motivation: More than half of Earth's species are contained in a mere 1.4% of its land area, but the climates of many of these biodiversity hotspots are projected to disappear as a consequence of anthropogenic climate change. There is growing recognition that spatio-temporal patterns of climate in biodiversity hotspots have shaped biological diversity over a variety of historical time-scales, yet these patterns are rarely taken into account in assessments of the vulnerability of biodiversity hotspots to future climate change. In our review, we synthesize the climatic processes that have led to the diversification of hotspots and interpret what this means in the context of anthropogenic climate change. We demonstrate the importance of mesoclimatic processes and fine-scale topographical heterogeneity, in combination with climatic variability, in driving speciation processes and maintaining high levels of diversity. We outline why these features of hotspots are crucial to understanding the impacts of anthropogenic climate change and discuss how recent advances in predictive modelling enable vulnerability to be understood better.

Location: Global.

Main conclusions: We contend that many, although not all, biodiversity hotspots have climate and landscape characteristics that create fine-scale spatial variability in climate, which potentially buffers them from climatic changes. Temporally, many hotspots have also experienced stable climates through evolutionary time, making them particularly vulnerable to future changes. Others have experienced more variable climates, which is likely to provide resilience to future changes. Thus, in order to identify risk for global biodiversity, we need to consider carefully the influence of spatio-temporal variability in climate. However, most vulnerability assessments in biodiversity hotspots are still reliant on climate data with coarse spatial and temporal resolution. Higher-resolution forecasts that account for spatio-temporal variability in climate and account better for the physiological responses of organisms to this variability are much needed to inform future conservation strategies.

KEYWORDS

biodiversity hotspots, climate change, conservation, microclimate, microrefugia, mountains, species distribution models, vulnerability

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1 | INTRODUCTION

More than half of Earth's species are contained in a mere 1.4% of its land area, and the protection of these hyperdiverse regions is a 21st century conservation priority (Myers et al., 2000). Although the need to conserve biodiversity is widely recognized, protection of many of these sites is still lacking, and anthropogenic pressures, such as land clearance, have led to significant habitat losses in these areas (Allan et al., 2019; Brooks et al., 2002). Furthermore, over the course of this century, anthropogenic climate change is projected to equal habitat loss as the greatest threat to biodiversity (Millennium Ecosystem Assessment, 2005; Thomas et al., 2004). Climate change events have occurred throughout the evolutionary history of the planet, with most extant species having persisted through some climate cycles (Nogués-Bravo et al., 2016). However, during the Pleistocene–Holocene warming (when global mean temperatures increased by *c.* 6°C), the rate of temperature change was approximately an order of magnitude less than that predicted for the future (Bush et al., 2004). As a consequence of anthropogenic climate change, there is already evidence of broad-scale changes to ecosystems, with the impact expected to continue to increase for the foreseeable future (IPCC, 2014; Parmesan, 2006). In relationship to hyperdiverse regions, the disappearance of current climates is projected for major biodiversity hotspots, including the Andes, the Philippines and Mesoamerica (Williams et al., 2007). Additionally, the appearance of novel climates and the disappearance of existing ones is projected primarily in the tropics and subtropics, where many of the biodiversity hotspots of the world are located (Garcia et al., 2014; Williams et al., 2007). Biodiversity hotspot regions host a high proportion of the world's rare climates and are thus expected to be affected disproportionately by future climate change (Ohlemüller et al., 2008). The potential loss of rare, range-restricted endemic species from hotspots has serious implications for ecosystem function, because rare species consistently hold the least redundant combination of functional traits (Mouillot et al., 2013). In consequence, accelerated extinction of rare species and major disruption to ecosystem functioning are expected.

In truth, the vulnerability of biodiversity hotspots to climate change is still highly uncertain. It is often suggested that species in biodiversity hotspots might be particularly vulnerable to climate change owing to their narrow ranges and persistence in regions of climatic stability over evolutionary time-scales. However, climate variability in space and time, and ergo the interplay between the two, is an important characteristic of biodiversity hotspots (Figure 1). Climate variability in time can occur across different scales, ranging from diurnal cycles to changes over centennial to multi-millennial time-scales, and topographical heterogeneity has a strong influence on climate variability in space. The literature currently lacks a clear synthesis of the importance of these spatio-temporal climate characteristics to the biodiversity of hotspots; here, we provide this synthesis.

We demonstrate that climate variability in space and time has helped to shape the diversity of biodiversity hotspots and contend

that fine-scale spatio-temporal modelling of biodiversity hotspots is needed to attain a better understanding of the full capacity of these systems to respond. We consider the evolutionary history of biodiversity hotspots (as defined by Myers et al., 2000) as a platform for understanding their vulnerability to anthropogenic climate change. Myers et al. (2000) famously defined “biodiversity hotspots” as geographical regions where exceptional concentrations of endemic species are undergoing exceptional habitat losses. Despite criticisms of this definition, not least that congruence between endemism and other measures of high biodiversity is low (Ceballos & Ehrlich, 2006; Orme et al., 2005), it has become the best-known analysis of its type. Biodiversity hotspots, as defined by Myers et al. (2000), are therefore the focus of this review. However, most of the issues discussed are not contingent on definitions of biodiversity hotspots and remain relevant irrespective of how hotspots are defined.

2 | THE ROLE OF CLIMATE VARIATION IN THE ACCUMULATION OF DIVERSITY

The uneven spatial pattern of biodiversity that we see today has been attributed to multiple causes. Key among these are: (a) the expected latitudinal gradients in species richness, resulting simply from the geographical range and placement of species associated with the fact that the surface area of latitudinal bands is lower at higher elevations; and (b) biological effects, such as the high productivity/energy availability at lower latitudes (Gaston, 2000). However, climate variation in space and time is also recognized as an important driver of biodiversity, especially of endemism (which, by virtue of the restricted ranges of endemic species, contributes disproportionately to global diversity).

A high proportion of biodiversity hotspots are located in mountainous landscapes (Cadena et al., 2012; Grenyer et al., 2006; Guisan et al., 2019; Kier et al., 2009) and are commonly referred to as “cradles” or “engines” of biodiversity (Hoorn et al., 2018). Accordingly, many biodiversity hotspots have high spatial climate variability owing to the resulting elevational heterogeneity. The tropical Andes biodiversity hotspot, for example, hosts approximately half of the world's climate types in an area a fraction of the size of the Amazon (Rahbek, Borregaard, Colwell, et al., 2019). These steep climate gradients facilitate high levels of environmental niche diversity (Cadena et al., 2012; Ghalambor et al., 2006; Janzen, 1967; Pintanel et al., 2019; Rahbek, Borregaard, Colwell, et al., 2019; Stevens, 1989, 1992), permitting high concentrations of rare, range-restricted species to exist (Mouillot et al., 2013; Ohlemüller et al., 2008; Raxworthy et al., 2008). Specifically, climatic differences between mountains and valleys can be dramatic enough to act as physical or environmental barriers to dispersal, thereby promoting allopatric speciation as a result of reproductive isolation and genetic drift (Flantua & Hooghiemstra, 2018; Janzen, 1967). This, in turn, is thought to have driven diversification and promoted endemism (Kozak & Wiens, 2007; Lawson, 2010; Pintanel et al., 2019). Consequently, it is thought that many species inhabiting biodiversity hotspots and

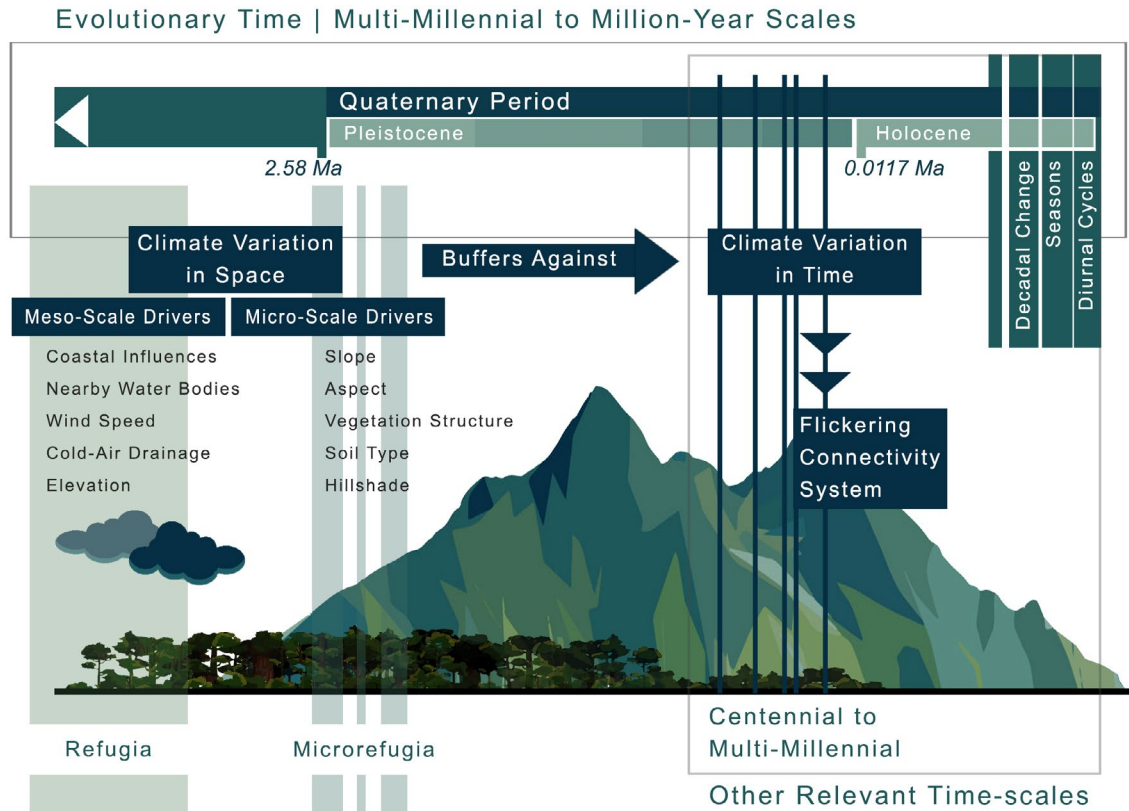


FIGURE 1 A conceptual overview of the temporal and spatial scales discussed in this review. Although many biodiversity hotspots have experienced climatic stability over evolutionary time, most hotspots will have experienced climate change to some degree at other relevant temporal scales. In particular, the historical changes that have occurred within the Quaternary period at centennial to multi-millennial time-scales will have been fundamental in shaping the capacity of species therein to respond to future changes. Additionally, during these periods of climate change, spatial variation in climate (mainly as a consequence of elevational climate gradients and topographical complexity) is thought to have facilitated speciation as a result of periodic isolation and connection of populations, termed the flickering connectivity system (Flantua & Hooghiemstra, 2018). Spatial climate variability can also help to buffer some species from climate changes. Specifically, meso- and microclimatic drivers can stabilize local climates and provide refugia and/or microrefugia, encouraging the persistence of older species lineages through environmental change. Consequently, the biodiversity hotspots most at risk from climate change are likely to have low climate variation in space and have experienced high levels of climate stability across some of these temporal scales

subject to climate zoning selection pressures have specialized and evolved narrower physiological tolerances, particularly in forested landscapes where diurnal temperature fluctuations are low. This, in itself, has acted as an effective dispersal barrier that results in fragmented, geographically near but environmentally isolated distributions of suitable habitat (Rahbek, Borregaard, Colwell, et al., 2019). In low-latitude, tropical biodiversity hotspots, the elevational climate gradient of mountain landscapes is particularly strong owing to increased elevational zonation (Janzen, 1967). In contrast to high-latitude mountains, seasonal climate fluctuations in tropical mountains are minimal, which reduces the overlap between climate zones.

Alongside elevational climate gradients, topographical complexity has been found to be a crucial driver of diversification (Bouchenak-Khelladi et al., 2015; Rangel et al., 2018; Särkinen et al., 2012). Topographical complexity can facilitate fine-scale spatial variation in meso- and microclimate (Box 1), ergo providing more opportunities for species to specialize (Jetz et al., 2004; Zuloaga et al., 2019). The physical variation in terrain generates local warm

and cold source and sink areas (Burrows et al., 2014), driven, for example, by the effects of terrain on solar radiation (Ashcroft, 2010; Dobrowski, 2011). By providing different combinations of slope and aspect, and by altering local weather patterns, topographical complexity has been found to play a crucial role in the diversification of different species clades (Rangel et al., 2018; Särkinen et al., 2012). The topographical complexity of many biodiversity hotspots means that these locations can host distinct climate zones within close proximity to one another and provide more opportunities for species to specialize (Jetz et al., 2004; Ohlemüller et al., 2008; Zuloaga et al., 2019).

The degree of variability in past climatic changes is also thought to have contributed to the accumulation of diversity in hotspots (Badgley et al., 2017; Flantua & Hooghiemstra, 2018). When compared with other regions of the planet, the relative climate stability experienced by many biodiversity hotspots over evolutionary time-scales (Fordham et al., 2019) has allowed for the long-term persistence of high levels of species diversity (Araújo et al., 2008;

BOX 1 Glossary of terms

Term	Explanation
Niche conservatism	The tendency for species to maintain their environmental preferences and specific functional traits over evolutionary time.
Species pumps	Favourable abiotic conditions that can act as a catalyst for the formation of multiple new evolutionary lineages.
Species pulse event	The turnover-pulse hypothesis, formalized by Elisabeth Vrba, proposes that historical climate-forcing changes to habitats have promoted rapid responses whereby species turnover accelerates and results in large-scale biotic change.
Refugia	Geographical regions that provide suitable habitats for the long-term persistence of populations during glacial-interglacial cycles and, potentially, during the current period of anthropogenic climate change.
Microclimate	The climate variations experienced locally that are, at some point, decoupled from the macroclimate. Microclimates are the climates directly experienced by species, occurring near the surface of the earth and within the soil, measured at fine spatial and temporal scales. Variations in topography (including steepness and aspect of slopes, height above sea level, proximity to sea or inland water, and site location) and habitat facilitate higher variation in microclimate by interacting with climatic factors including short- and long-wavelength radiation, air temperature, wind speed, humidity, and substrate temperatures and moisture levels (Kearney & Porter, 2017).
Microrefugia	Small sites or microhabitats with microclimatic conditions that harbour small populations of species outside the core of their geographical range and/or favour the persistence of species during periods of climate change, because of: (a) high microclimatic variability (Suggitt et al., 2018); or (b) slower rates of warming (Maclean et al., 2017) because their microclimate is particularly unusual (Ashcroft, 2010) or reduces exposure to climate extremes (Scheffers et al., 2014).

Harrison & Noss, 2017; Jansson, 2003; Sandel et al., 2017; Svenning et al., 2015), in addition to higher levels of endemism (Carnaval et al., 2009; Feng et al., 2020; Särkinen et al., 2012). Some level of climate stability is important to provide sufficient time for speciation to occur before disturbances wipe out incipient species (Graham et al., 2018). Consequently, biodiversity hotspots have been able to maintain older lineages of species (Fjeldså & Lovett, 1997) and have encouraged higher levels of niche conservatism (Box 1) (Antonelli, 2015; Cadena et al., 2012). Mediterranean-type biodiversity hotspots are particularly noteworthy, in that they all occur on western coastlines of the planet's major land masses (Ackerly et al., 2014). Consequently, they benefit from reliable, cold ocean currents flowing from the poles to the equator, which in turn stabilizes the climate of these hotspots (Esler et al., 2018). The Southwest Australian Floristic Region, for example, has experienced exceptionally stable climates, having been unglaciated since the Permian (Hopper & Gioia, 2004). This stability is thought to have been an influential driver of diversity for the region, where relic lineages have been able to persist, resulting in one endemic order making up > 49% of > 7,000 vascular plant species (Hopper & Gioia, 2004). Climate stability has played a major role in allowing plant diversity in mediterranean-type hotspots to accumulate outside of the highly productive tropical regions (Esler et al., 2018).

These stabilizing meso-scale climate effects are also likely to be important for other biodiversity hotspots. Many of the world's hotspots are coastal, located either in the tropics or on the southern margins of continents (Myers et al., 2000). More than 90% of the energy balance of the Earth is stored in the oceans, owing to the high

heat storage capacity of water (Cheng et al., 2017), and given that changes in the energy balance of the Earth are ultimately responsible for changes in temperature, coastal regions are significantly less prone to temperature fluctuations than the interior of continents (Brunt, 1924). A significant proportion of the coastal hotspots of the world are also located close to coastal upwelling zones (Xiu et al., 2018). The buffering effect of the ocean in these regions is likely to be particularly pronounced, as the heat storage capacity of the ocean to far greater depths becomes relevant. Coastal locations are also comparatively cloudy and become more so as temperatures increase (Bakun, 1990). Consequently, the effects of rising global temperatures in these regions might be offset, in part, by increases in cloud cover.

At a fine spatial scale, complex landscapes within mountainous regions can facilitate extremely stable environmental conditions (Malakoutikhah et al., 2018). These landscapes have therefore played a significant role in the accumulation of endemic species, by allowing relictual populations to survive unfavourable regional conditions (Fjeldså et al., 1999). For example, elevational gradients allow for high levels of spatial climate diversity in relatively small areas and have been able to buffer species against climate changes that would otherwise have led to extinctions (Esler et al., 2018). Moreover, locations with environmental conditions decoupled from regional climates owing to landscape structure, known as refugia (Box 1), are thought to have enhanced the survival of populations during the cyclical climate changes of the Quaternary (Rahbek, Borregaard, Colwell, et al., 2019) and acted as pools of genetic diversity (Wood et al., 2013). Refugia at different spatial scales, including

microrefugia (Box 1), might have minimized the need for species to relocate or disperse in response to climate cycles (Bátori et al., 2017; Carnaval et al., 2009; Dobrowski, 2011; Park, 2019) and might therefore provide disproportionate benefit to those populations most at risk from future climate changes (Ashcroft, 2010; Hannah et al., 2014). For example, on the Galapagos Islands, some upland plant species were found to have persisted during the Last Glacial Maximum and through multiple long-term droughts during the mid-Holocene when there was significant loss of upland habitat. Collins et al. (2013) suggested that localized cooling effects, as a result of the maritime influence, would have created microrefugia for certain upland plant species to persist. The persistence of climatically stable refugia at finer spatial scales over the course of the next century is likely to be instrumental in dictating whether biodiversity hotspots are vulnerable to anthropogenic climate change.

Although biodiversity hotspots have typically experienced stable climates over evolutionary time-scales (Fine, 2015), climatic changes occurring at finer temporal scales (e.g., centennial to multi-millennial scales) have also had an important influence on evolutionary and ecological processes (Graham et al., 2018). In particular, the Milankovitch climate cycles of the Quaternary (with periodicities in the order of 100,000 years) are thought to have stimulated cyclic habitat changes and influenced local diversity patterns (Flantua & Hooghiemstra, 2018; Rahbek, Borregaard, Colwell, et al., 2019). During this period, tropical regions, for example, are thought to have experienced temperature changes of $\leq 10^{\circ}\text{C}$, in addition to complex changes in precipitation patterns (Bush, 2019; Bush et al., 2004; Colwell & Rangel, 2010; Rutherford & D'Hondt, 2000; Vonhof & Kanandrop, 2010). In response to the cyclicity of the Quaternary, habitats are likely to have shifted up and down mountain slopes, and populations of a single lineage might have found themselves alternatively isolated and connected owing to the interplay of landscape and climate change (Badgley et al., 2017; Damasceno et al., 2014). Moreover, the climate cycles of the Quaternary have been found to have been interrupted by warming and cooling events occurring at an even finer temporal scale of hundreds to thousands of years (Dansgaard et al., 1993; Fordham et al., 2019), which are likely to have resulted in repeated population crashes, range shifts and gene flow in some of the most invariant tropical biodiversity hotspots. Crucially, the effect of topography and climate on speciation rates has been found to be greater at low latitudes (Steinbauer et al., 2016), where the majority of biodiversity hotspots exist.

As a result of climate changes in biodiversity hotspots, species pulse events (Box 1) are likely to have occurred periodically (Lawson, 2010; Rahbek, Borregaard, Antonelli, et al., 2019; Toussaint et al., 2013), whereby opportunities arise for rapid speciation through forced adaptation of populations to new environments (Badgley et al., 2017; Willis et al., 2004). Recently, Flantua and Hooghiemstra (2018) proposed that this process of diversification via cyclical phases of connectivity and isolation be termed the "flickering connectivity system", which describes how the relationship between the oscillating climate cycles of the Pleistocene and landscape complexity could have helped to shape contemporary

spatial patterns of biodiversity. Rangel et al. (2018) recently found support for these predictions by simulating historical patterns of species richness in South America and modelling climate conditions for the past 800,000 years. The Andes was found historically to have acted as an episodic species pump (Box 1) for the contemporary species richness of plants, birds and mammals for the rest of the continent. Their analyses demonstrated that the cyclical climates of the Quaternary were significant drivers of diversification and extinction across the continent. Although climate variation in biodiversity hotspots during the Quaternary might not have been as extreme as in other parts of the planet, moderate levels of climate change must still have occurred and thereby avoided evolutionary stasis (Graham et al., 2018). Climate changes and the centennial to multi-millennial scale have therefore played a significant role in diversification, having driven both range shifts and extinctions in these regions.

3 | THE VULNERABILITY OF GLOBAL BIODIVERSITY HOTSPOTS TO CLIMATIC CHANGE

3.1 | Past climate change has influenced the capacity for response

The magnitude and duration of climate variability and its effects on the accumulation of species with lower tolerances to environmental changes are hotly debated. The pervading view is that climate stability over evolutionary time-scales has resulted in the evolution of species with attributes that equip them poorly to survive future climate changes (Ashcroft, 2010; Harrison & Noss, 2017; Malcolm et al., 2006). Traits that make them more vulnerable to climate change include low climatic tolerances, high habitat specialization, low dispersal ability, poor dormancy capability, low population sizes and/or low levels of genetic diversity (Harrison & Noss, 2017; Zuloaga et al., 2019), in addition to reliance on disturbance regimes or obligate mutualisms (Harrison & Noss, 2017). Additionally, the low levels of contemporary climate variation seen in many biodiversity hotspots, such as low seasonal and inter-annual climate variability, are thought to favour species with slower life histories; they have fewer offspring, lower productivity and longer life spans and potentially, therefore, respond more slowly to environmental changes (Wiersma et al., 2007). Accordingly, elevational range size generally decreases with latitude (McCain, 2009), and tropical species tend to inhabit significantly narrower temperature regimes than their temperate counterparts (Kozak & Wiens, 2010). Those biodiversity hotspots that have not experienced particularly high levels of climate variability over centennial to millennial time-scales, in addition to those experiencing contemporary stability, are likely to be particularly at risk from climate change. For example, shorter-term climate stability, in combination with homogeneous landscape structure in biodiversity hotspots such as the Maputaland-Pondoland-Albany or the Southwest Australia Floristic Region (Figure 2), imply high vulnerability to climate change. Not only will topographical invariance

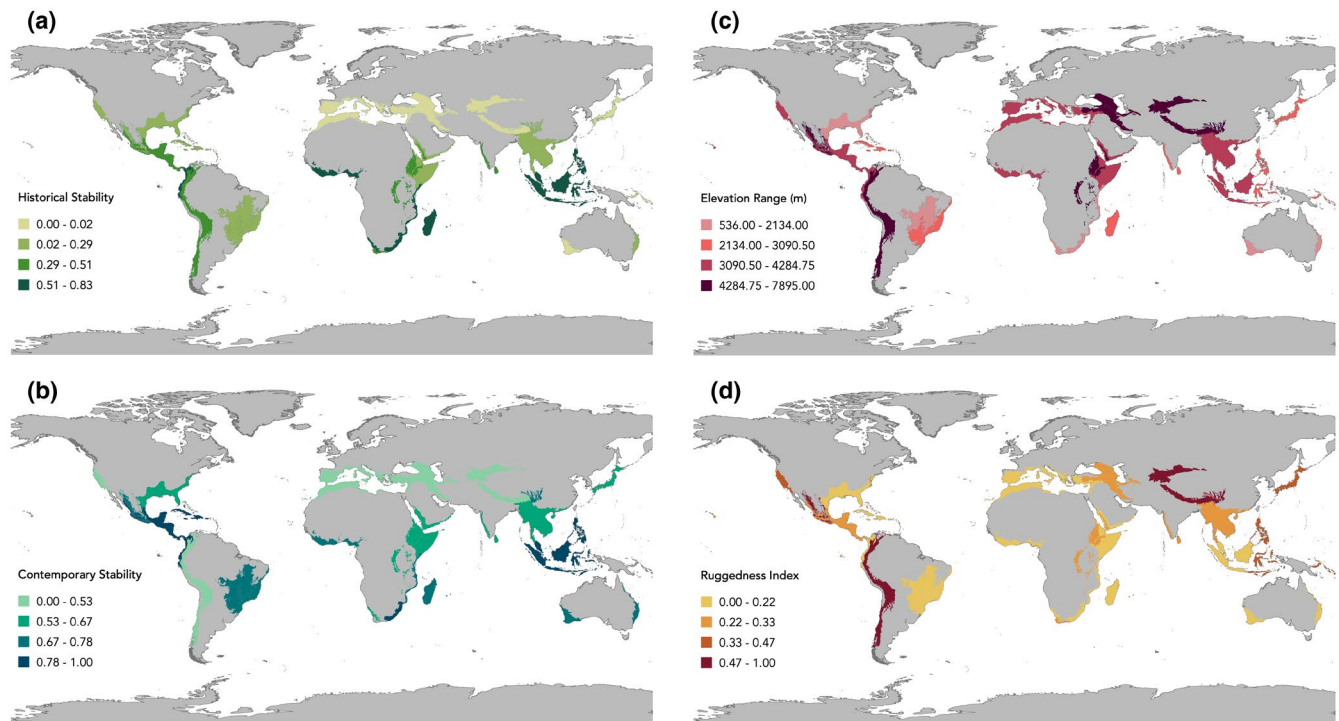


FIGURE 2 Global biodiversity hotspots defined by Conservation International (Hoffman et al., 2016) and their corresponding topography and climate characteristics. (a) Historical climate stability, defined as the proportion of time spent in an extremely stable climate between 21,000 and 100 yr BP, as quantified by Fordham et al. (2019) as those locations ($2.5 \times 2.5^\circ$ grid cells) with a linear annual mean temperature trend and variability (standard deviation about the trend) \leq 10th percentile of all grid cells globally. Using century snapshots (from 21,000 to 100 yr BP), the length of time a location spent in extremely stable climate conditions was mapped. (b) Contemporary climate stability, calculated as the standard deviation of mean annual air temperatures between 1969 and 2010 using data from the NOAA-ESRL Physical Sciences Laboratory (Kalnay et al., 1996). Biodiversity hotspots experiencing low variability across temporal scales, such as the Sundaland and Wallacea, are likely to be particularly vulnerable to anthropogenic changes in climate. (c) Elevation range, calculated as the maximum–minimum elevation of each hotspot using the elevation variable by EarthEnv (Amatulli et al., 2018). (d) Topographical ruggedness, where zero is defined as low ruggedness and one as high ruggedness, derived from the terrain ruggedness index (TRI) variable (the mean of absolute differences in elevation between a focal cell and the surrounding cells) by EarthEnv (Amatulli et al., 2018). Biodiversity hotspots with limited elevation range and low ruggedness, such as Mesoamerica and Cerrado, are likely to be particularly vulnerable to climate change. Key break values correspond to quantile ranges

fail to afford an effective buffer, but also the low temporal climate variability at the fine scale experienced by species during the course of their recent evolutionary history means that species there will be less prepared for novel climates that might emerge.

However, conclusions that the relative climatic stability of biodiversity hotspots has established concentrations of species that have poor resilience to transient changes in climate might be relying on an over-simplified narrative, for a number of reasons. First, it is likely that the same physical processes that have resulted in biodiversity hotspots experiencing climate stability relative to other locations will continue to buffer these regions against ongoing climatic changes. Therefore, those hotspots that have experienced relatively stable climates historically, especially at a fine temporal scale, are likely to continue to do so and will experience less extreme changes in climate conditions than the rest of the planet (Iwamura et al., 2010; Jansson, 2003). The magnitude of climate change varies across the surface of the Earth owing to the spatial variation in the amplitude of insolation and resulting earthbound feedbacks

(Jansson & Dynesius, 2002). A latitudinal gradient is thought to exist whereby the orbitally forced range dynamics (the change in species distributions as a result of global climate shifts) are more pronounced towards the poles (Dynesius & Jansson, 2000; Jansson & Dynesius, 2002). Thus, the highest rates of warming tend to be observed and are predicted for higher latitudes (Meehl et al., 2007; Figure 3). The buffering effects of large bodies of water are also particularly important, with the coastal areas typically experiencing far slower rates of temperature change than the interior of larger land masses (Beck et al., 2018).

Second, as highlighted previously, the Milankovitch climate cycles are such that most biodiversity hotspots have not been stable consistently (Fordham et al., 2019). The Eastern Afrotropical biodiversity hotspot, for example, has experienced climatic variation in response to these cycles, in addition to having more variable contemporary climate. This, coupled with significant variation in landscape structure, might mean that this hotspot is less vulnerable to future climate change (Figure 2). Species traits that do provide

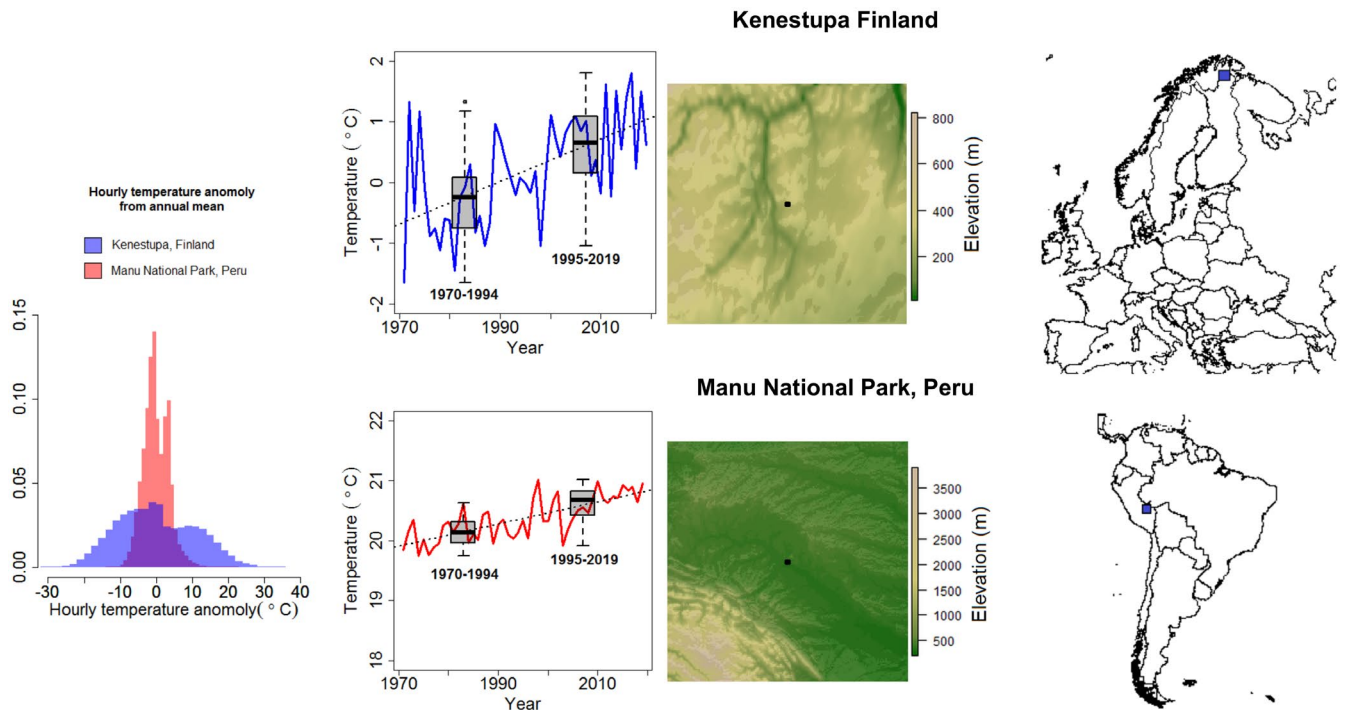


FIGURE 3 Comparison of temporal variability in temperature between an Arctic region (Kenestupa, Finland, 67.696° N, 27.185° E) and a tropical hyperdiverse region (Manu National Park, Peru, 11.793° S, 71.519° W). Here, a coupled meso- and microclimate model was used to derive hourly temperatures for the period 1970–2019 (Finland: 50 cm above ground in 25-cm-tall Arctic tundra, model from Kearney & Porter, 2020; Peru: 15 m above ground, below 20-m-tall tropical broadleaf forest, model from Maclean et al., 2019). Hourly temperatures are far less variable in Peru, ranging by $c. \pm 10^{\circ}\text{C}$ from the annual mean, in comparison to Finland, where temperatures fluctuate by $\pm 25^{\circ}\text{C}$ from the annual mean, implying that species in tropical hyperdiverse regions might be less suited to tolerating changes in temperature. Moreover, despite considerably greater warming in Finland (1.713°C) in comparison to Peru (0.864°C), inter-annual variability in the mean annual temperature is greater in Finland and, in consequence, the recent (1995–2019) temperatures in Peru are at least as novel as those in Finland

capacity for species to respond to future climate change are likely to have developed in response to past climate fluctuations, especially those at finer centennial to multi-millennial temporal scales. This historical climate variability is likely to have been more important than gradual changes in long-term mean climates in shaping biodiversity patterns, particularly in low-energy, low-rainfall hotspots outside of the tropics, such as those with mediterranean climates, where other conventional drivers of diversity do not offer sufficient explanation (O'Brien, 1993; O'Brien et al., 2000; Thuiller et al., 2006). Climate fluctuations are likely to have played a key role in the diversification of these regions and the capacity of the species therein to respond.

3.2 | Landscape complexity can act as a buffer against climate change

We know that fine-scale climate heterogeneity has influenced speciation rates in biodiversity hotspots through interspersed isolations and habitat partitioning (Flantua & Hooghiemstra, 2018). We also know that climate heterogeneity has buffered species against the impacts of historical climatic changes (Ohlemüller et al., 2008; Suggitt et al., 2018). It is, therefore, likely that climate heterogeneity

also has the potential to buffer against the impacts of future anthropogenic climate change. Montane slopes provide climate diversity in space by way of their steep elevational climate gradients, which can mitigate against climate-driven extinctions by reducing the local velocity of climate change for affected species (Dobrowski, 2011; McCain & Colwell, 2011; Verboom et al., 2015). Accordingly, Sandel et al. (2011) demonstrated that range-restricted animal species are concentrated where climate-change velocity is low, meaning that these species can respond to climate changes via elevational displacement, minimizing their exposure to climate changes by ensuring that favourable climates are found within short dispersal distances (Loarie et al., 2009; Raxworthy et al., 2008; Sandel et al., 2011). Elevational range shifts are currently the most commonly documented response to historical climate changes (Bush et al., 2004; Chen et al., 2011; Colwell et al., 2008; Freeman et al., 2018).

Furthermore, the fine-scale topographical complexity (i.e. terrain ruggedness) found in many hotspots (Figure 2) can also reduce the vulnerability of species to climate change (Figure 4) by creating microclimatic variation at spatial scales finer than those caused by elevation (Barber et al., 2016; Graae et al., 2018; Li et al., 2018). Topographical complexity can also influence meso-scale processes, such as cold-air drainage, ultimately increasing spatial

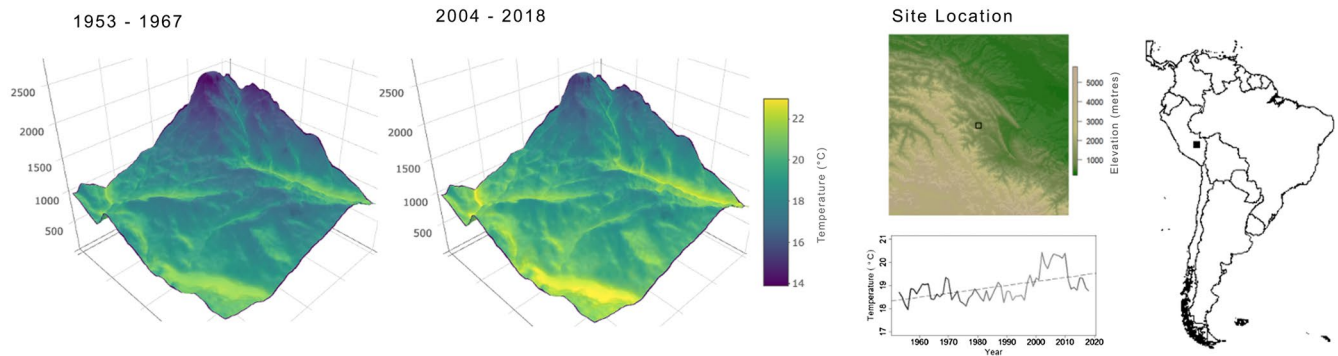


FIGURE 4 Topographical complexity and fine-scale climate heterogeneity in a mountainous hyperdiverse region. Here, the coupled meso- and microclimate model of Kearney and Porter (2020) was used to derive mean daily maximum temperatures for the period 1953–2018 at 30 m resolution over a 6 km × 6 km region of Manu National Park in Peru (12.629° S, 71.668° W). The region spans an elevational range of c. 700–2,000 m. Despite a warming of c. 1.5°C over this period, species would need to move only a short distance to find analogous climate over this period of warming

variation in climate at scales of hundreds of metres to kilometres (Maclean, 2020). Additionally, many biodiversity hotspots benefit from close proximity to large water bodies, such as lakes and oceans, which means that both climate variability and rates of warming are likely to be reduced. In temperate regions, research has shown that species are more likely to persist in the face of climate change in areas with high microclimate heterogeneity (Maclean et al., 2015; Suggitt et al., 2018), because the provision of microclimatic variation increases the probability that a viable set of environmental conditions exists for a given species within dispersal distance. Studies have demonstrated that heterogeneity in temperature resulting from fine-scale variation in vegetation and topography exceeds the magnitude of temperature changes projected under anthropogenic climate change (Bennie et al., 2008; Suggitt et al., 2011). Therefore, spatial variability over a distance of only a few metres has the potential to act as an environmental buffer against climate change (Ackerly et al., 2010; Schwantes et al., 2018).

This spatial heterogeneity in climate might facilitate the use of refugia and microrefugia by populations of species most at risk from climate change (Dobrowski, 2011). Microrefugia are increasingly seen as vitally important for maintaining biodiversity (Collins et al., 2013), and a growing body of evidence demonstrates their importance in the face of anthropogenic climate change. For example, Cheddadi et al. (2017) assessed the impact of recent climate change on Atlas cedar populations in the Rif Mountains and found that although the species range had contracted by 75%, populations were persisting in some isolated areas with cooler, wetter mesoclimates that were significantly decoupled from the North African regional climate. Micro- and meso-scale climate complexity might, therefore, allow low-density populations of range-restricted species to persist locally as regional climatic conditions become increasingly unfavourable (Ashcroft, 2010; Dobrowski, 2011).

Nevertheless, as quickly as the leading edge of a species range gains suitable microclimate, it might also lose suitable microclimate at the trailing edge. In consequence, the existence of microclimate heterogeneity does not necessarily guarantee that species will be

safeguarded. The potential for refugia to maintain diversity depends, therefore, on the extent to which local climatic changes are decoupled from regional changes and whether the degree of decoupling is sufficiently long lived (Keppel et al., 2012; Maclean, 2020). Evidence of microclimate decoupling has started to emerge in recent years (e.g., Maclean et al., 2017), but the magnitude, direction and duration of decoupling are crucial. In many places, decoupling is driven by landscape structure interacting with changes in local weather patterns, and the extent of these changes might be relatively short lived (Maclean, 2020; Maclean et al., 2017). Additionally, in places where microclimates warm at faster rates than the macroclimate, the opposite of a microrefugial effect would be expected. Here, instead, there might be localized extinction hotspots. It is also the case that although the role of microrefugia is fairly well documented in temperate regions (Petit et al., 2003; Tzedakis et al., 2013), there is less understanding of their role for tropical mountain and islands ecosystems (Condamine et al., 2017).

3.3 | Montane species are nonetheless vulnerable to climatic changes

Despite the potential for spatial heterogeneity in climate to buffer species against temporal changes, in montane terrain this might be negated by the lower physiological tolerances of low-latitude montane species to environmental changes. For instance, Enquist (2002) demonstrated that high-elevation zones were more sensitive to changes in temperature, because endemism (the prevalence of species with narrower environmental tolerances) increases with elevation. As a result, endemic species living at high elevations are thought to be particularly vulnerable to climatic changes (Colwell & Rangel, 2010; Elsen & Tingley, 2015; Ghalambor et al., 2006; McCain & Colwell, 2011; Raxworthy et al., 2008; Sorte & Jetz, 2010). For example, tropical cloud forests host disproportionately high diversity that is at particular risk of expatriation owing to projected temperature increases altering the height of the cloud base (Karmalkar

et al., 2008; Şekercioğlu et al., 2012). Specifically, if these cloud bases were to shift 600 m upslope, there would be a significant loss of this crucial hyperdiverse habitat (Bush, 2002).

The expectation that the vulnerability of species increases with elevation depends, to some extent, on the assumption that area declines monotonically with elevation; however, a study of the topographical complexity of hyperdiverse montane regions revealed that 68% of mountain ranges did not match this assumption (Elsen & Tingley, 2015). Instead, the complex topography of mountains includes features such as plateaus, which can mean that some species could benefit from the available surface area increasing with elevation. Research by Elsen and Tingley (2015) suggests that many mountain ranges within biodiversity hotspots are either diamond or hourglass shaped, whereby foothill or mid-elevation species will benefit from migration upslope.

Obstacles in geographical or environmental gradients, attributable to topographical complexity, can hinder species dispersal. For example, migration from one mountain to another of higher elevation might be impeded if there is a significant drop in elevation between the two. Complex topography encountered along downslope migrations might push species into dead ends when area declines with elevation (such as inside crevices and canyons). Moreover, the upslope migration of plants is often less rapid and effective than downslope migration (Bush, 2019). Seeds can be dispersed easily downslope using waterways, but upslope migration is heavily dependent on animals.

Dispersal limitations, whether physical or environmental, increase the likelihood of extinction for species because they prevent species from tracking climatic changes (Williams et al., 2007). For example, Sorte and Jetz (2010) modelled the extinction risk of 1,009 montane bird species based on different dispersal scenarios and found that species with no dispersal ability and small to large vertical ranges experienced 75%–100% loss of range. It is also the case that mountaintop species are likely to be most at risk, even where dispersal is possible, because there is limited capacity for this to take place (Pounds et al., 1999). For instance, Freeman et al. (2018) found that several common Peruvian bird species have been extirpated from their high-elevation habitats. In general, therefore, species inhabiting hyperdiverse mountain regions, many with narrow ranges and limited dispersal ability, are likely to be exceptionally vulnerable to climate change (Laurance et al., 2011).

Recorded observations of species shifting downslope or towards lower latitudes is a complication in assessing vulnerability and runs counter to the expected response to climate warming (Crimmins et al., 2011; Lenoir & Svenning, 2015; Tingley et al., 2012). In these cases, species are thought to be tracking local environmental conditions, such as water availability, not regional temperatures. Moreover, reduced levels of precipitation on mid-mountain slopes might be driving species downhill as precipitation patterns change. For example, bird species across the Sierra Nevada region were found to have heterogeneous range shifts within species because they were pulled simultaneously upslope by increasing temperature and downslope by increasing precipitation (Tingley et al., 2012). These observed

movements along elevational gradients are concerning, because they suggest that important environmental variables are shifting in opposite directions, and species are unable to track both.

3.4 | Non-montane hotspots are also vulnerable to climatic changes

In mediterranean-type hotspots, the interactions between landscape and meso-climatic processes are particularly important for temporal stability. Any changes in ocean circulation and/or wind patterns as a result of climate change have the potential to cause significant reduction in the intensity of upwelling along these coastlines, increasing the temperatures of the sea surface (Ackerly et al., 2014). This, in turn, could lead to more warming than predicted by global circulation models (Ackerly et al., 2014). Although research by García-Reyes and Largier (2010), for example, suggested that the upwelling off the coast of central California was strengthening and could ultimately offset the warming sea surface temperatures and buffer climate changes to the California Floristic Province, the coastal-to-inland temperature gradients found in mediterranean-type hotspots can be as steep as elevational gradients in tropical biodiversity hotspots. Instead of aiding migration, these gradients push species closer to the coast in warming climate conditions. For example, in the California Floristic Province the maximum summer temperatures 100 km inland can be reduced by $\leq 20^{\circ}\text{C}$ at the coastline, which is the equivalent of ascending 3,000 m up a mountain slope (Ackerly et al., 2014). As a result, mediterranean-type hotspots in southern latitudes, such as the Cape Floristic Region and the Southwest Australia Floristic Region, are likely to be particularly vulnerable to climate change, because movements poleward, away from hotter temperatures, are blocked by the ocean. The species in these hotspots are in similar vulnerable positions to mountaintop species. Thus, the impact of climate change on these mediterranean-type biodiversity hotspots is likely to be highly dependent on the buffering effect of topographical complexity, and ergo, the existence and effectiveness of local refugia and microrefugia. Accordingly, research has indicated that the diversity of refugia found within some mediterranean-type hotspots historically has allowed the co-occurrence of both new and ancient species and has therefore been associated strongly with low rates of extinction (Elser et al., 2018).

There are also some tropical lowland biodiversity hotspots that have neither elevational range nor topographical complexity and might therefore be particularly vulnerable to climate change (Colwell et al., 2008). The Amazon Basin, for example, might experience significant loss of area in the form of a near-future dieback of lowland forest owing to the interaction between drought induced by climate change and human burning. Owing to the absence of steep thermal gradients or nearby mountain slopes along which species could migrate, species would need to move greater distances to track their environmental niche (Laurance et al., 2011). Even for those lowland hotspots that lie close to mountains, the dispersal of specialist species to higher-elevation areas is often blocked by agricultural land

(Guo et al., 2018; Senior et al., 2019); although for species with broader habitat requirements this might not be the case.

In lowland hyperdiverse systems, microclimate is likely to dictate their response to climate change. Recent research has highlighted the potential for forest canopies to cool the understorey and buffer species against climate warming (De Frenne et al., 2019; Senior et al., 2018). However, tropical forest species are thought to have particularly narrow thermal niches and have been shown to retain ancestral thermal traits (Khaliq et al., 2015). Tropical lowland species are also thought already to be at their thermal limits, and therefore, not pre-adapted to warmer conditions (Watson et al., 2019). Thus, their physiological potential to overcome climatic warming might be lower. Methods for downscaling climate to scales relevant to organisms and for predicting the biotic response of organisms that align more closely to physiological tolerances are therefore much needed to assess the vulnerability of these hotspots to climate change.

4 | RECENT ADVANCES IN MICROCLIMATE MODELLING

Over the last decade, there has been renewed ecological interest and significant methodological development in the field of microclimate research (Lembrechts & Lenoir, 2020), for example, in the development of global geospatial databases of near-surface temperature measurements (Lembrechts et al., 2020). These *in situ* measurements of microclimatic conditions using miniature data loggers, coupled with a burgeoning range of thermal remote-sensing techniques, provide both temporal and spatial detail: hourly measurements of near-ground conditions in the case of *in situ* measurements, and over wide extents in the case of remotely sensed data (Bramer et al., 2018). A range of techniques for modelling microclimate are also emerging. Techniques range from interpolation of *in situ* measurements and statistical downscaling (e.g., Aalto et al., 2017; Greiser et al., 2018) through to mechanistic models of physical processes underpinning local climatic variation (e.g., Bennie et al., 2013; Maclean, 2020; Maclean et al., 2017). Mechanistic approaches seek to capture the physical processes driving variation, typically by determining the effects of terrain and vegetation on energy and water fluxes, and are likely to be particularly effective in predicting climate in novel circumstances at high temporal resolution (Maclean, 2020). They also afford the additional advantage of being able to determine the body temperatures of organisms experiencing heat and/or cold stresses, and therefore, lend themselves well to ensuring that predictions of responses to climate change are grounded physiologically (e.g., Kearney & Porter, 2009). Although at global scales and over long time periods running such models remains computationally unfeasible, they potentially facilitate identification of the conditions in which coarse-resolution models break down and the spatial scales at which this breakdown occurs. Such breakdowns are likely when mean climate conditions are not correlated closely with exposure to conditions that affect the performance and survival of organisms, as might occur, for example, when microclimate heterogeneity is high

(Suggitt et al., 2018) or when organisms exhibit thermoregulatory behaviour (Kearney et al., 2009). These methods therefore strengthen the ability to provide general recommendations for the appropriate spatial and temporal scales at which they are best to predict the vulnerability of biodiversity hotspots to climate change, complementing recommendations from existing vulnerability assessments.

Recent developments in high-resolution remote sensing also offer unprecedented opportunities to capture the environmental data needed to drive these models. Technologies such as LiDAR (airborne light detection and ranging) and high-resolution multi- and hyperspectral image capture are increasingly capable of mapping the structural complexity of vegetation and terrain at the ground-atmosphere boundary at scales relevant to elucidating organismal responses to climate change (Zellweger et al., 2019). Although the availability of existing LiDAR data is limited for biodiversity hotspots, the Global Ecosystem Dynamics Investigation (GEDI), a full-waveform spaceborne LiDAR system mounted on the International Space Station, observes nearly all tropical and temperate forests (Dubayah et al., 2020; Fabian et al., 2020). The potential to integrate these data with high-resolution climate models (see Duffy et al., 2021) affords new and exciting opportunities to understand future threats to biodiversity hotspots from climate change.

5 | CONCLUSIONS

At present, the scientific literature suggests that the spatio-temporal variation in climate experienced by many biodiversity hotspots has helped to drive the aggregation of high concentrations of specialized, rare and range-restricted species. These individual species are unlikely to be able to shift their distributions easily or respond quickly to the unprecedented speed of environmental changes caused by anthropogenic climate change. Nevertheless, evidence suggests that the landscape heterogeneity in space of many biodiversity hotspots, including steep elevation gradients and high levels of topographical complexity, might serve to buffer species against the adverse effects of climate change by providing fine-scale climate variation in space. In mountain hotspots, this spatial heterogeneity will be likely to play a dominant role in determining whether species persist or go extinct as a result of climate change, although barriers to dispersal could fragment populations and result in the disappearance of some mountaintop or coastal species. Lowland biodiversity hotspots are also likely to be particularly at risk from climatic changes, because the homogeneous nature of these landscapes allows little scope for meso-scale climate buffering. Historical and contemporary climate variability across various temporal scales is also an important influence on the vulnerability of hotspots to future climate change. Some hotspots have experienced relatively stable climates over evolutionary time and might therefore play host to species that are particularly vulnerable to changes. However, although historical and contemporary climate variation is lower relative to other areas of the planet, there are hotspots that have faced significant historical climate variation across and between the Pleistocene

glacial–interglacial cycles. These cycles have been fundamental to shaping the capacity of species therein to respond to anthropogenic climate change. Incorporating spatio-temporal climate variability, at relevant scales, into vulnerability assessments is, therefore, crucial for understanding their vulnerability to ongoing and future climatic changes. Crucially, projections of biological responses to climate change in biodiversity hotspots are much needed. The conservation science community needs to move away from low-resolution, correlative modelling towards mechanistic modelling at spatio-temporal scales relevant to most of the world's biodiversity.

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DATA AVAILABILITY STATEMENT

All data sets used are third-party data sets available freely in public repositories. The data supporting the global hotspot figure (Figure 2) were derived from the following resources available in the public domain: Polygons of global biodiversity hotspots by Conservation International (<https://doi.org/10.5281/zenodo.3261806>); historical climate stability data by Fordham et al. (2019) (<https://doi.org/10.1016/j.cub.2019.04.001>); contemporary climate stability data sourced from NCEP Reanalysis 2 by the NOAA/OAR/ESRL PSL, Boulder, CO, USA (<https://psl.noaa.gov/>); and topographical variables by Amatulli et al. (2018) (<http://www.earthenv.org/topography>). The climate data to support figures for Kenestupa, Finland (Figure 3) and Manu National Park, Peru (Figure 4) are publicly available through the *microclima* for R package (<https://doi.org/10.1111/2041-210X.13093>). Digital elevation data were provided by the Amazon Web server. All figures created for this study are also available on Figshare (https://figshare.com/projects/Vulnerability_of_Global_Biodiversity_Hotspots_to_Climate_Change/97574).

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BIOSKETCHES

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