Global mountain topography and the fate of montane species under climate change

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Increasing evidence indicates that species throughout the world are responding to climate change by shifting their geographic distributions[1-3]. Although shifts can be directionally heterogeneous[4,5], they often follow warming temperatures polewards and upslope[1,2,6]. Montane species are of particular concern in this regard, as they are expected to face reduced available area of occupancy and increased risk of extinction with upslope movements[6-9]. However, this expectation hinges on the assumption that surface area decreases monotonically as species move up mountainsides. We analysed the elevational availability of surface area for a global data set containing 182 of the world's mountain ranges. Sixty-eight per cent of these mountain ranges had topographies in which area did not decrease monotonically with elevation. Rather, mountain range topographies exhibited four distinct area–elevation patterns: decreasing (32% of ranges), increasing (6%), a mid-elevation peak in area (39%), and a mid-elevation trough in area (23%). These findings suggest that many species, particularly those of foothills and lower montane zones, may encounter increases in available area as a result of shifting upslope. A deeper understanding of underlying mountain topography can inform conservation priorities by revealing where shifting species stand to undergo area increases, decreases and bottlenecks as they respond to climate change.

Species are responding to climate change in a multitude of ways, including by shifting their ranges in latitude[1,2] and elevation[4,10]. Along elevational gradients, strong evidence for such shifts has been demonstrated in both temperate[4] and tropical[10] systems for a range of taxa[1,2,4,5,7,10,11]. Climate change is considered one of the largest threats to biodiversity[3] and its impact is thought to be particularly great for montane species, which show high rates of local endemism[6,12,13] and often inhabit narrow elevational ranges[8,14]. The high degree of specialization to narrow bands of temperature that montane species typically exhibit has raised concern over their fate under climate change[6,7,15]. It is widely expected that montane species will undergo further upslope shifts in the future and, in the absence of broad latitudinal shifts, that such movements will leave species with less habitable area as they approach mountain peaks[7,9] (but see ref. 16). Left with nowhere else to go, montane species are predicted to become increasingly susceptible to the stochastic extinctions typical of small or declining populations[17].

At the global scale, the surface area of the Earth decreases exponentially with elevation, with over 55 million km² of continental land below 300 m compared with less than 2 million km² above 4,500 m (ref. 18). At the scale of a single mountain peak, often depicted as a cone or pyramid, area at the top is roughly two orders of magnitude smaller than at the bottom[7]. Thus, at

both the global and local (that is, peak) scales, area declines with elevation and imposes consistent and pronounced area constraints on species shifting ranges upslope. At the landscape scale—a scale arguably more relevant to species conservation given distribution patterns of rare and threatened species[19]—steep slopes, deep ravines, and mid- and high-elevation plateaux lead to more complex topography (Fig. 1a–d). In the context of climate change and species' vulnerability, such physical geographical realities require an examination of the paradigm of declining surface area with elevation.

We obtained a global data set comprising 182 expert-delineated mountain ranges (roughly accurate to 50 m, obtained from Natural Earth), which represents the most comprehensive data set on distinct mountain ranges publicly available. We overlaid the mountain range delineations atop a global digital elevation model (DEM) at 30 arc-second resolution (SRTM30 version 2.1 (ref. 20); Fig. 2) to compute histograms of area versus elevation (a 'hypsographic curve') for each range (Supplementary Fig. 1; see examples in Fig. 1). We then classified ranges into four categories, representing the full diversity of hypsographic patterns observed, by analysing skew and modality of the elevation–area profiles for each mountain range. Categories were determined as unimodal right skew (that is, linear/exponential decline in area with elevation; 32% of ranges), unimodal left skew (that is, linear/exponential increase in area with elevation; 6%), unimodal with no skew (that is, a normal curve with peak area at mid-elevation; 39%), and a bimodal distribution, irrespective of skew (that is, a curve with peaks at low and high elevations; 23%; Supplementary Table 1). In terms of topography, we describe the four hypsographic patterns as 'pyramid', 'inverse pyramid', 'diamond' and 'hourglass' mountains, respectively (Fig. 1). Such patterns were found to be robust to grid cell size, producing patterns in similar frequencies with a finer-resolution DEM (3 arc-seconds), and to a series of more conservative delineations of mountain range boundaries (see Supplementary Information and Supplementary Table 1).

We examined numerous geographic and physical properties that could potentially contribute to the distribution of hypsographic classifications we observed (Supplementary Fig. 2). All mountain classes were represented on every continent, except Europe, which contained only pyramid and diamond mountains (Fig. 2 and Supplementary Tables 2 and 3). Furthermore, mountain classes did not differ statistically in their area (analysis of variance (ANOVA), $F_{3,178} = 0.101$, $P = 0.959$) or amplitude (ANOVA, $F_{3,178} = 1.878$, $P = 0.135$), and were equally likely to be coastal or inland (ANOVA, $F_{3,178} = 0.865$, $P = 0.461$). Mountain classification was significantly related to both mean elevation (ANOVA, $F_{3,178} = 20.96$, $P < 0.001$) and latitude (ANOVA, $F_{3,178} = 2.882$, $P = 0.037$). *Post hoc*

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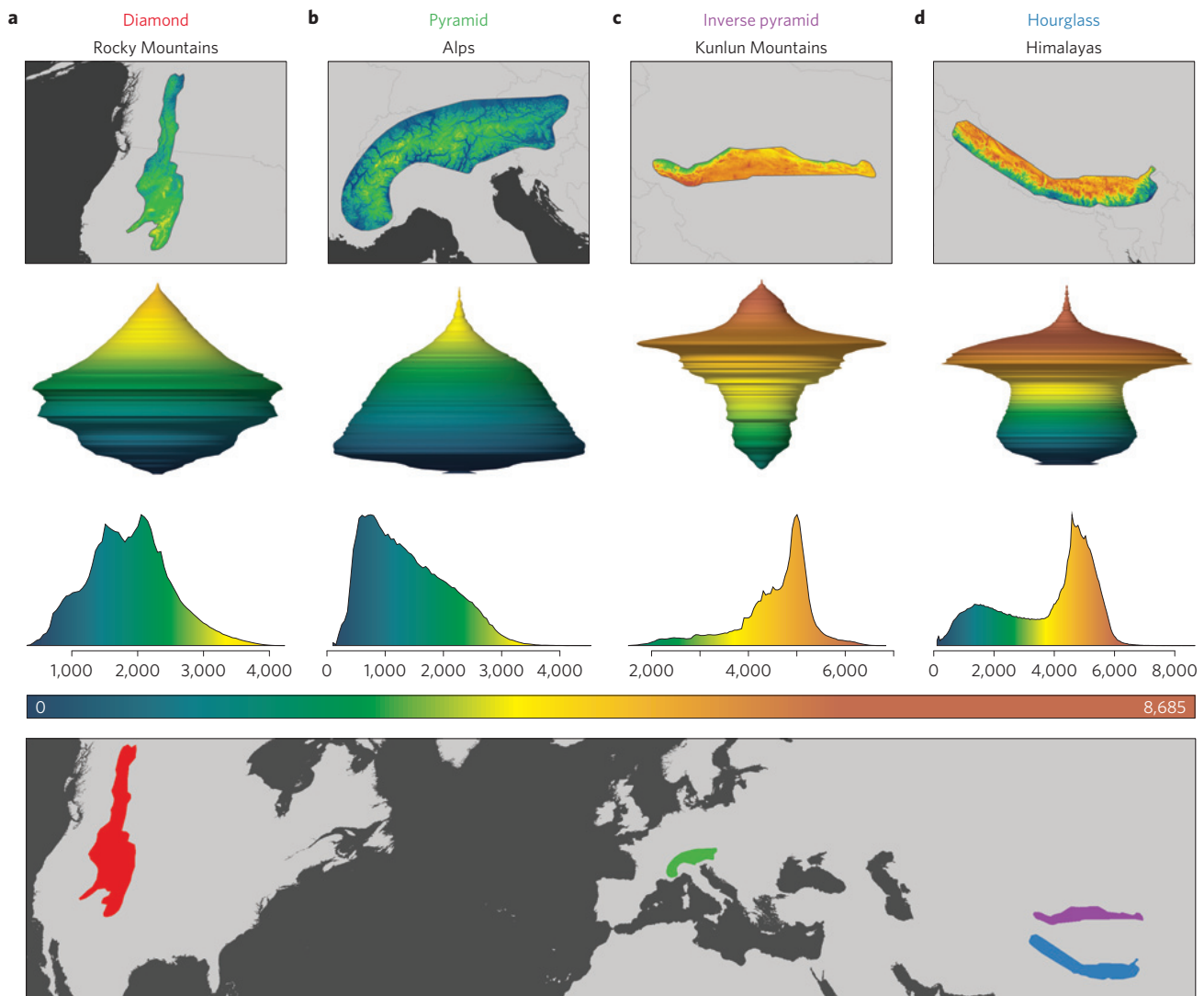
Figure 1 | Examples of each of four mountain hypsographic classifications. a–d, Top panel: SRTM topography for the Rocky Mountains (a diamond range; **a**), the Alps (a pyramid range; **b**), the Kunlun Mountains (an inverse pyramid range; **c**) and the Himalayas (an hourglass range; **d**). Middle panels: (top) three-dimensional model spindles representing the relative surface area available (xy planes) with elevation (z plane), derived from the DEM for each range and (bottom) the hypsographic curves derived from the DEM for each range (note elevation along x axis). All ranges, spindles and histograms are coloured relative to a maximum elevation of 8,685 m observed in the Himalayas. Bottom panel: the geographical extent of each of the four ranges, coloured by classification (red, diamond; green, pyramid; purple, inverse pyramid; blue, hourglass).

Tukey honestly significant difference analysis revealed that inverse pyramid mountains have significantly higher mean elevation ranges than all other mountain shapes and that diamond mountains—although lower in elevation than inverse pyramid mountains—have significantly higher mean elevations than pyramid mountains. Notably, base and maximum elevations for pyramid, diamond and hourglass mountains were not significantly different, although inverse pyramid mountains were found to have higher minimum and maximum elevations on average compared with all other classes (ANOVA, $F_{3,178} = 10.11$, $P < 0.001$ and $F_{3,178} = 3.816$, $P = 0.011$, respectively). Furthermore, honestly significant difference analysis confirmed diamond mountains to be found at significantly higher latitudes than hourglass mountains.

Our results show that 68% of the world's mountain ranges do not conform to the dominant assumption in ecology and conservation that area decreases monotonically with elevation from a mountain range's base (Fig. 2 and Supplementary Table 1). Furthermore, our most conservative estimates derived from a series of alternative mountain boundary delineations affirm that most mountain ranges in our global analysis are not classified as pyramidal (see Supplementary Information and Supplementary Table 1). Only in a few regions—albeit those with strong histories of montane research—such as Europe, coastal North America, Southeast Asia and eastern Australia, are pyramid mountains the norm rather than the exception.

Biologists working in montane regions undoubtedly recognize the influence of plateaux and other topographic features on local to regional elevation–area relationships. Here, we show that at the scale of a mountain range, and across the globe, such complex topographies result in landscapes in which available area can actually increase with elevation throughout much (for inverse pyramid mountains) or an appreciable portion (for diamond and hourglass mountains) of the available altitudinal range (Supplementary Fig. 3). Thus, some species responding to climate change by shifting upslope may actually benefit through increases in available area (Fig. 3). For example, foothill species (<1,250 m) in the Rocky Mountains (a diamond mountain) and alpine species (3,000–4,000 m) in the Himalayas (an hourglass
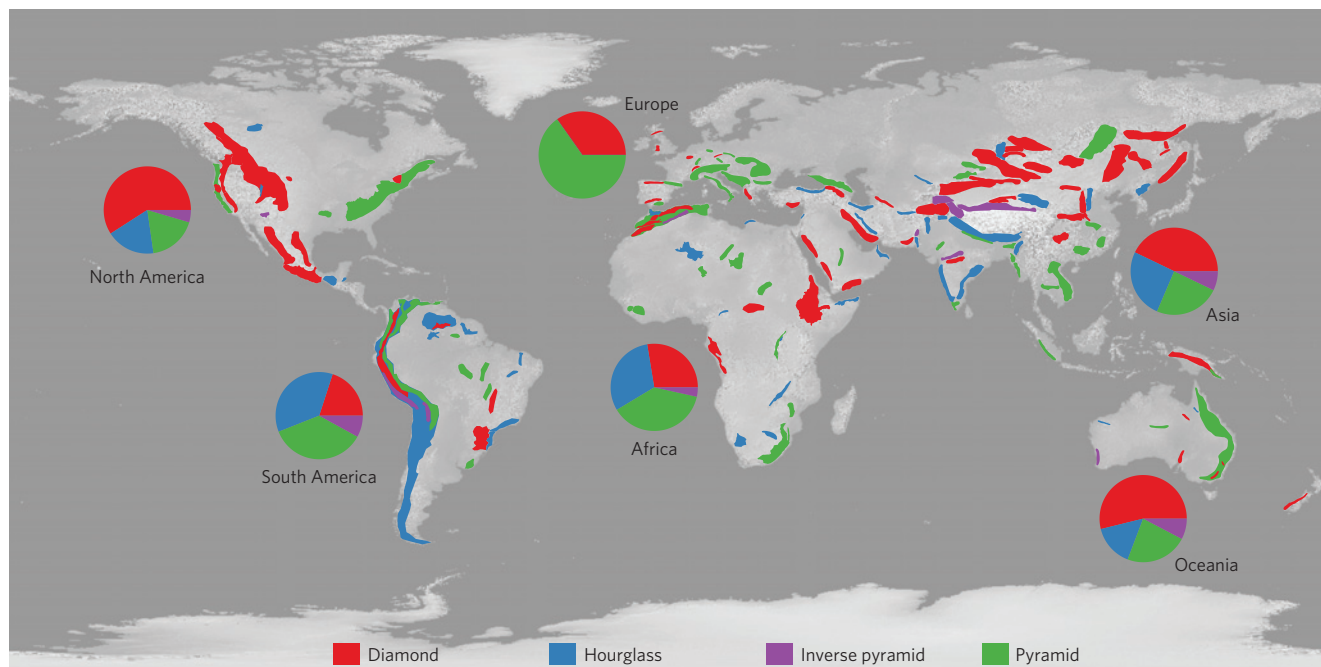
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Figure 2 | Global distribution of mountain range hypsographic classes. 182 mountain ranges were classified into four categories determined by elevation–area relationships (see Methods): diamond ($n=82$; 39% of ranges), inverse pyramid ($n=10$; 6% of ranges), pyramid ($n=64$; 32% of ranges) and hourglass ($n=49$; 23% of ranges). Pie charts depict the proportions of each classification contained in six geographic regions. Refer to text for descriptions of mountain range classes.

mountain) will undergo sustained area increases as they shift upslope until their lower range limit surpasses mid- (1,500 m) or high (4,500 m) elevations, respectively (Figs 1a,d and 3a,d and Supplementary Fig. 1). This contrasts with foothill and lower montane species in the Alps (a pyramid mountain), for example, which will lose area nearly monotonically as their distributions shift upslope (Figs 1b and 3b and Supplementary Fig. 1). We calculated the mean elevation above which area declines relative to baseline to be 176 m for pyramid mountains compared with 697, 811 and 2,907 m for hourglass, diamond and inverse pyramid mountains, respectively (see Methods).

From a conservation perspective, true mountaintop species (for example, snow leopard, rosy finches (*Leucosticte* spp.) and alpine ibex) stand to face local extinction with upslope range shifts regardless of underlying topography, so these species continue to represent high conservation priority globally. Similarly, lowland species, although not explicitly considered in this study, are also expected to universally encounter area losses as they transition into foothills following upslope movements[21]. Accounting for underlying mountain topography, however, allows for targeted conservation priorities for those subsets of montane (but not truly mountaintop) species most at risk from upslope area contractions. For example, foothill species shifting upslope in hourglass mountains may undergo a bottleneck before realizing area gains at higher elevations (Fig. 3d), suggesting that habitat preservation or other conservation efforts should be targeted towards intermediate, bottleneck elevation zones. Diamond mountains show the opposite pattern, with lower-elevation species undergoing pronounced area increases before losing area again at higher elevations (Fig. 3a). Inverse pyramid mountains present opportunities for upslope shifting species throughout most of the elevational range until the very top (Fig. 3c). In pyramid mountains, all subsets of montane species would be threatened by climate change owing to expected area losses if range boundaries uniformly shift upslope (Fig. 3b). Importantly, if species richness patterns correlate with available area along elevational gradients, then across mountain classes, most

species shifting upslope will be expected to lose area monotonically as in pyramid mountains. In such cases, conservation investments are best not directed towards any particular elevational band, but should focus on the species or systems most at risk from other ongoing threats[22].

Although hourglass and diamond mountains may reveal optimistic futures for subsets of species shifting upslope, it is important to note that the position along the elevational gradient where species encounter bottlenecks (on hourglass mountains) or mid-peak areas (on diamond mountains) depends on the mountain range. In the case of the Himalayas and Western Ghats, two hourglass mountains of the Indian subcontinent, the bottlenecks occur at approximately 5,000 m and 500 m, respectively (Supplementary Fig. 1). The Rocky Mountains and the Cascade Range, two diamond mountains of North America, exhibit mid-peak areas at approximately 2,000 m and 1,500 m, respectively (Supplementary Fig. 1). Such variability requires context-specific evaluation of a mountain range's elevation–area relationship during conservation planning.

We recognize that available surface area does not always constitute suitable habitat for species shifting ranges[23], but argue that physical space limits species persistence at least as strongly as a lack of suitable habitat for species undergoing range shifts. For some species, new climate regimes, disruptions in species interactions resulting from non-analogue communities[24], and unfamiliar habitat types (particularly at high elevations where poor geomorphic or climatic conditions may prohibit the occurrence of many species[23,25]) following upslope range shifts will pose significant threats. For others, these same factors may present opportunities. Still, without physical space to move into, even highly adaptable or otherwise favoured species shifting upslope will be forced to disperse to neighbouring mountain ranges or face local extinction.

Although conservation of montane species is primarily concerned with upslope range shifts[7,8], our results have equally important implications for those species expected to shift
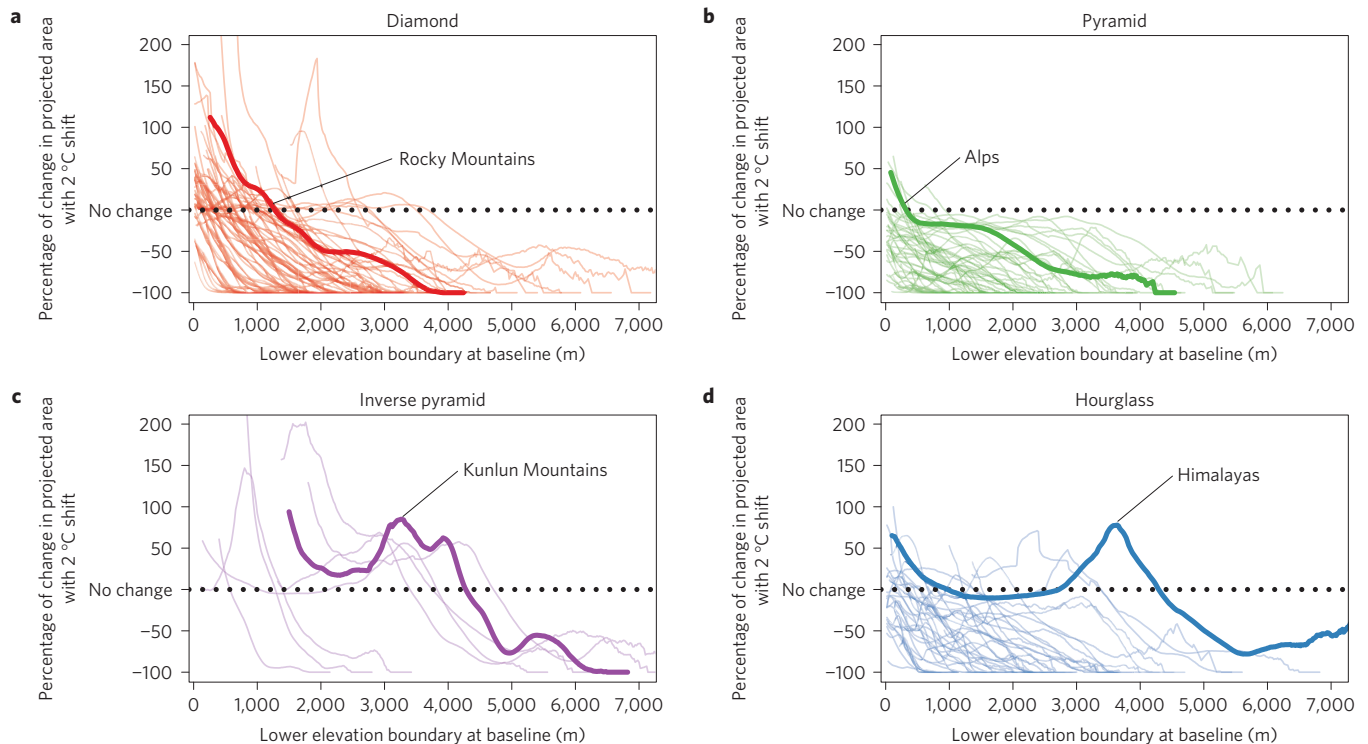
Figure 3 | Percentage of change in available area following a 2 °C upslope range shift for a hypothetical montane vertebrate species in mountain ranges around the world. a–d, For each mountain range (thin lines), plots show the percentage of change in available area resulting from upslope shifts (projected) relative to initial range area (baseline) for a hypothetical montane species inhabiting an 800 m range. At each elevation, percentage of change is calculated as $((\text{Area}_{\text{Projected}}/\text{Area}_{\text{Baseline}}) - 1) \times 100$, thus illustrating patterns of area increases (above the horizontal dotted line) and decreases (below the dotted line) as the species' baseline lower boundary varies from sea level to mountaintop. Note that lines would look qualitatively different for other species' range amplitudes (for example, a narrow-ranged species inhabiting 100 m) and for other climate change scenarios (for example, >2 °C warming), but general patterns of area increases or decreases will be similar within hypsographic classes. Bold lines in **a–d** represent the percentage of change in available area resulting from upslope range shifts for the example ranges specified in Fig. 1a–d, respectively. See Methods for further details.

downslope with climate change. Downslope shifts have been documented under warming conditions due to species tracking changes in abiotic factors other than temperature (for example, precipitation[5] or water balance[11]). Although one might consider downslope-shifting species to be of lower conservation concern given expected uniform area increases with declining elevation, montane species in inverse pyramid, diamond or hourglass mountains may undergo pronounced area declines with downslope shifts.

Conservation priorities for montane species have largely focused on identifying areas where mountains are isolated (increasing dispersal limitation)[6], where species richness[24] and endemism[13] are high, or where globally rare species exhibit narrow elevational ranges[6,7,13]. Beyond these recommendations, we urge scientists assessing species' vulnerability as well as on-the-ground conservation practitioners to account for underlying topography when making conservation decisions. The global analysis presented here provides simple metrics for setting montane conservation priorities using easily obtainable elevation data that, like other coarse-filter approaches, can be a powerful predictor of species distributions and regional patterns of diversity in the absence of finer-scale, species-specific bioclimatic models[22,26].

Much of the attention up to now has been in the context of mountaintop extinctions[9,15], with the threat of species literally being pushed off of mountaintops. In reality, multiple 'pinch points' exist for montane species well before their distributions reach mountain peaks, and for some species living in certain mountain ranges, climate change could actually be a boon. Goals of minimizing species loss in montane regions may

better be achieved by prioritizing conservation in areas where the expected reduction in available area is greatest following range shifts.

Methods

Methods and any associated references are available in the online version of the paper.

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Author contributions

Both authors contributed equally to all aspects of the research, including project conception, data analysis and manuscript preparation.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to P.R.E. or M.W.T.

Competing financial interests

The authors declare no competing financial interests.

Methods

We obtained a global data set of mountain ranges from Natural Earth's physical vectors (version 3.0.0; available at http://naturalearthdata.com) comprising 222 ranges distributed across seven continents. To our knowledge, this is the most comprehensive data set on distinct mountain ranges publicly available. Mountain ranges were delineated by a team of international volunteers and are roughly accurate to 50 m. We overlaid mountain range polygons atop a high-resolution near-global DEM (SRTM30; ref. 20, version 2.1) at 30 arc-second resolution. With a vertical accuracy of roughly 6 m, the SRTM DEM have higher elevational accuracy than a suite of alternative DEMs (ref. 27), owing to the incorporation of gap-filled, validated data from alternative elevation models. Validations of the interpolation algorithms used in the SRTM DEM data were found to be highly accurate (error of roughly 5 m) compared to a fine-scale TOPO DEM with no missing data[27].

The latitudinal extent of SRTM30 ranges from roughly 56° S to 60° N, so we limited our final analyses to 182 mountain ranges that were completely bound by this extent (Fig. 2) and extracted the raster cell values of the DEM within each of the delineated mountain ranges (see Supplementary Information). We treated overlapping subranges ($n = 32$; for example, Cordillera Occidental within the Andes) as distinct in the analysis because they are identified as ecologically and/or geomorphologically distinguishable from larger ranges and thus represent ranges where many species may be restricted (for example, birds endemic to the west slope of the Colombian Andes).

We classified mountain shapes by analysing the form and moment terms of the elevation–area distributions derived above, calculating skew and bimodality. Bimodality was assessed using the dip test of unimodality[28]. We assigned all distributions with a dip value > 0.01 and with significant ($p < 0.05$) deviations from unimodality to the hourglass classification. For distributions with a dip value ≤ 0.01, we assigned those with a Type-I skewness[29] ≥ 0.5 to pyramid, those with skewness ≤ -0.5 to inverse pyramid, and the remainder to diamond, representing those with approximately normal distributions. We chose skew cutoffs of 0.5 and -0.5 to capture right- and left-skewed distributions, respectively, and to bound distributions approximating symmetry. To ensure that our calculated distributions accurately reflect true topographic patterns, we conducted a series of sensitivity analyses and robustness checks using an alternative global DEM with 3 arc-second resolution and several alternative mountain delineations (see Supplementary Information).

To understand how topography can influence the available surface area for montane species following upslope shifts, we modelled upwards range shifts for a hypothetical, 'average' species on each of our mountain ranges (Fig. 3). We followed the conservative typology of mountain ranges developed by the United Nations Environment Programme World Conservation Monitoring Centre[18], which restricts mountains to elevations greater than 300 m. We chose our montane species' amplitude to be 800 m, roughly equivalent to the average amplitude of all montane vertebrates[14] and to more narrowly restricted montane bird species[6]. We

assumed a fixed adiabatic lapse rate of $-6.2\,°C\,km^{-1}$ for all ranges, which reflects the global average[6]. Finally, we used a 2 °C warming scenario, which denotes the temperature increase 'likely' to be exceeded by the RCP6.0 and RCP8.5 scenarios, and 'more likely than not' to be exceeded by the RCP4.5 scenario, as defined by the Intergovernmental Panel on Climate Change[30]. At all elevations (binned in 20-m intervals) for each range, we calculated the percentage of change in available area for a hypothetical species as it shifts upward with a 2 °C increase as:

$$\text{Percentage of change in area} = ((\text{Area}_{\text{Projected}}/\text{Area}_{\text{Baseline}}) - 1) \times 100$$

where $\text{Area}_{\text{Projected}}$ equals the amount of available surface area after an upward shift and $\text{Area}_{\text{Baseline}}$ equals the amount of available surface area preceding the shift. For each mountain range, we calculated the maximum elevation where the percentage of change in area equals 0, indicating bottleneck points above which available area will always decrease. We then took the mean bottleneck elevation across ranges per mountain class.

We explored potential geographic patterns of mountain topography classes by conducting a series of comparisons of hypsographic patterns versus a set of basic topographic and geographic range features: range area, mean range elevation, minimum range elevation, mean range latitude, range amplitude, and distance to coastline. We calculated range area, minimum and mean range elevations, and range amplitude by summarizing the DEM for each mountain and calculating the minimum, maximum and mean cell values. We calculated mean range latitude by calculating the latitude of the bounded centroid of each mountain range polygon. We calculated range amplitude by computing the difference between the maximum and minimum cell value for each range. Finally, we computed the minimum distance of the range boundary to coastline using the worldwide coastal vector data set from Natural Earth using Near in the Analysis toolbox of ArcMap 10.2.2 (ESRI). To test for relationships between mountain classifications and these features, we used one-way ANOVAs. When relationships were found to be significant at $p < 0.05$, we conducted *post hoc* Tukey honestly significant difference between all pairwise comparisons.

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