



Global patterns of protection of elevational gradients in mountain ranges

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Protected areas (PAs) that span elevational gradients enhance protection for taxonomic and phylogenetic diversity and facilitate species range shifts under climate change. We quantified the global protection of elevational gradients by analyzing the elevational distributions of 44,155 PAs in 1,010 mountain ranges using the highest resolution digital elevation models available. We show that, on average, mountain ranges in Africa and Asia have the lowest elevational protection, ranges in Europe and South America have intermediate elevational protection, and ranges in North America and Oceania have the highest elevational protection. We use the Convention on Biological Diversity's Aichi Target 11 to assess the proportion of elevational gradients meeting the 17% suggested minimum target and examine how different protection categories contribute to elevational protection. When considering only strict PAs [International Union for Conservation of Nature (IUCN) categories I–IV, $n = 24,706$], nearly 40% of ranges do not contain any PAs, roughly half fail to meet the 17% target at any elevation, and ~75% fail to meet the target throughout $\geq 50\%$ of the elevational gradient. Observed elevational protection is well below optimal, and frequently below a null model of elevational protection. Including less stringent PAs (IUCN categories V–VI and nondesignated PAs, $n = 19,449$) significantly enhances elevational protection for most continents, but several highly biodiverse ranges require new or expanded PAs to increase elevational protection. Ensuring conservation outcomes for PAs with lower IUCN designations as well as strategically placing PAs to better represent and connect elevational gradients will enhance ecological representation and facilitate species range shifts under climate change.

Aichi Target 11 | biodiversity | climate change | conservation planning | protected areas

Mountainous regions account for less than 20% of the Earth's terrestrial land surface (1), but harbor disproportionate numbers of plant and animal species for their extent, including rare and threatened species (2). Topographic complexity in mountains increases isolation and promotes speciation, resulting in high rates of turnover along elevational gradients and high beta diversity and overall species richness (3, 4). Montane species' distributions are often structured by climatic gradients (5), and the close association between montane species' ranges and the abiotic environment has led to climate-induced elevational range shifts in both temperate and tropical mountains for a variety of taxa (6–8). Because the pace of climate change increases with elevation (9), such range shifts may accelerate in the future.

Protected areas (PAs) are critical to sustaining life on Earth, and the continued expansion of the world's terrestrial PAs has resulted in ~15% coverage of Earth's land area (10). In some cases, PAs mismatch biodiversity patterns and priorities (11, 12), but in mountain ranges, even well-placed PAs may ultimately fail to protect species, both currently and as their ranges shift in elevation over time. PAs with broad elevational coverage are more likely to facilitate species' range shifts under climate change (13), and could better represent the full array of taxonomic (2) and phylogenetic (14) diversity, as ecological turnover in mountain ranges is highly idiosyncratic over elevation (15). Enhancing protection along elevational gradients may be particularly important

in mitigating biodiversity loss as climate change is projected to simultaneously alter elevational distributions of agriculture (16), human populations (17), and natural resources (18). Despite a general understanding of the importance of protecting elevational gradients for the maintenance of ecological and evolutionary processes, we lack knowledge of where and how well elevational gradients are protected at broad geographic scales.

Here, we analyze the elevational distribution of 44,155 PAs in 1,010 mountain ranges in comparison with total land area with elevation to quantify PA coverage of elevational gradients globally. In assessments of elevational protection, we separately consider the contribution of different protection categories, including stricter [International Union for Conservation of Nature (IUCN) categories I–IV PAs, $n = 24,706$; hereafter I–IV], less stringent (IUCN categories V and VI PAs, $n = 8,668$; hereafter V–VI), and nondesignated (categorized by IUCN as “not reported,” “not assigned,” and “not applicable,” $n = 10,781$; hereafter nondesignated) PAs from the World Database on Protected Areas (WDPA) (*SI Appendix, Fig. S1* and *Methods*). While I–IV PAs place the strictest regulations on resource use, V–VI PAs constitute roughly half the total geographic coverage of PAs globally (19) and are more frequent at lower elevations (20) and in areas of higher human impact (21). Consequently, if proven effective in conserving biodiversity (21), V–VI and nondesignated PAs may prove to be an important complement to I–IV PAs in providing additional elevational protection, without requiring the establishment of entirely new PAs. Our goals are to (i) determine patterns, biases, and gaps in the protection of elevational gradients at global, continental, and regional scales; (ii) evaluate conservation targets for protecting elevational gradients and assess where targets are met; (iii) determine

Significance

Mountain ranges constitute biodiversity hotspots, and montane species are shifting their ranges in elevation in response to climate change. Protecting elevational gradients can help fully capture montane biodiversity patterns and facilitate species range shifts. We map the protection of elevational gradients for mountain ranges worldwide to reveal where elevational protection is needed and may be optimized. Most of the world's mountain ranges are narrowly protected and lack elevational distributions needed to preserve biodiversity. This could undermine the effectiveness of protected areas (PAs) under climate change. Strategic planning is required to prioritize elevational gradients in future PA establishment; otherwise, protecting roughly half of all mountainous area will be required to protect just 17% of land across nearly all elevational gradients.

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where V–VI and nondesignated PAs offer opportunities to increase protection of elevational gradients, or where entirely new PAs would be needed; and (iv) understand the limitations and tradeoffs of optimizing overall versus contiguous elevational protection.

Results and Discussion

Globally, the amount of protected land area within mountain ranges declines with elevation while the proportion of total land protected increases (*SI Appendix, Fig. S2*), confirming reported biases in protection toward higher elevations referred to as the “rock and ice problem” (20). This trend in high elevation protection is most prevalent in mountain ranges in Africa, Asia, and North America due to stark regional differences in underlying topography (22). By contrast, protection in the mountain ranges of Europe and Oceania is disproportionately distributed toward low to mid elevations, and protection in South American mountain ranges is roughly proportional to available land area across most of the elevational gradient (Fig. 1).

These results indicate that species undergoing upward elevational range shifts in mountain ranges could face either increases or decreases in the amount of protection PAs will afford them, depending on the continent, and highlight priority elevational zones for future protection. For instance, conservation investments could be targeted at elevational zones with relatively low proportions of land under protection. This approach to targeting additional investment to underrepresented areas below a set threshold is exemplified under the Convention on Biological Diversity’s Aichi Target 11 goal of protecting at least 17% of terrestrial and inland water areas that are, among other things, “ecologically representative.” Meeting such conservation targets along elevational gradients would be an especially important step in meeting the mandate that protected lands should be ecologically representative because mountain ranges experience particularly high rates of endemism (4) and ecological turnover (3) that may not be sufficiently captured by broad conservation planning units, such as terrestrial ecoregions (23). Protecting elevational gradients could thus represent a fuller range of the environmental variability and ecological turnover contained within mountainous regions (24), while also facilitating climate-induced range shifts.

Our analysis reveals that only North America is currently protecting all elevations in mountain ranges at $\geq 17\%$ for I–IV PAs; all other continents are failing to protect ~ 47 – 88% of their elevational gradients at this target (Fig. 1). At the continental scale, if we were to meet the 17% target for all elevations, we would need

to increase protection of mountain ranges in low to mid elevations of Africa and Asia (below $\sim 3,000$ m), in low and high elevations of Europe (below $\sim 1,500$ m and above $3,500$ m), in mid to high elevations of Oceania (above $\sim 2,000$ m), and in nearly all elevations of South America (Fig. 1). At the continental scale, V–VI PAs significantly increase elevational protection—defined as the proportion of the elevational gradient meeting the 17% target (*Methods*)—compared with I–IV PAs for all continents except Africa (Fig. 2*A* and *SI Appendix, Table S1*), particularly at elevations above $2,500$ m in Asia, below $3,000$ m in Europe, and throughout most elevations of South America (Fig. 1).

Nondesignated PAs increase the protection of elevational gradients in mountain ranges compared with I–VI PAs for Africa and Europe (Fig. 2*A* and *SI Appendix, Table S1*). At the continental scale, nondesignated PAs significantly enhance protection of elevations below $3,500$ m in Africa, throughout most elevations of Europe, and above $4,000$ m in South America (Fig. 1). Consequently, inclusion of V–VI and nondesignated PAs would help meet the 17% target at mid elevations of Africa, from mid to high elevations of Asia, in low and high elevations of Europe, and throughout most of South America (Fig. 1). To meet the 17% target for all elevations across continents, strategic planning to establish new PAs would also be required for all continents, except North America and Europe, and would benefit from international cooperation as many ranges span two or more countries.

Mountain Ranges Within Continents. Next we examined elevational protection for individual mountain ranges to better align with the scale of many montane species’ distributions, management objectives, and land conservation decision making (25). When considering only I–IV PAs, we found $\sim 50\%$ (513 of 1,010) of all mountain ranges fail to protect 17% of terrestrial land at any elevation, and $\sim 75\%$ (738 of 1,010) of ranges have less than half of their elevational gradients protected at $\geq 17\%$ (Fig. 2*B*). These include mountain ranges in notable biodiversity hotspots, including in the Mexican and Central American highlands, large portions of the Andes, in the Drakensberg of Africa, in dozens of ranges throughout China and Southeast Asia, and across Papua New Guinea.

While $\sim 23\%$ of mountain ranges (231 of 1,010) currently meet the Aichi Target 11 goal of 17% geographic protection from I–IV PAs, less than 3% of ranges (27 of 1,010) meet this target throughout their entire elevational range. Mountain ranges with high ($\geq 75\%$) elevational protection generally occur in more developed regions of the world: the northwestern ranges of North America, ranges in Scandinavia and Europe, in Indonesia and Japan, in Australia’s eastern ranges, and in New Zealand (Fig. 2*B*). Indeed, mountain ranges in North America and Oceania had significantly higher elevational protection than mountain ranges in Africa, Asia, or South America [analysis of variance (ANOVA), $F_{5,1004} = 49.3$, $P < 0.001$; Fig. 2*A* and *SI Appendix, Table S2*].

Despite the observed biases in the distribution of protection over elevation and the notion that PAs largely protect rock and ice (20), nearly 40% of mountain ranges (374 of 1,010) have no I–IV PAs within their geographic extents. However, many ranges show significant increases in elevational protection when also including V–VI PAs (Fig. 2*C*), including many of the highly biodiverse ranges previously reported. For example, mountain ranges in the Mexican highlands, the northern Andes, western Europe, and many ranges of South and Southeast Asia have V–VI PAs with elevational distributions that complement I–IV PAs, enhancing elevational protection within each continent (Fig. 2*C* and *SI Appendix, Fig. S3A*). Similarly, we found several ranges—such as in the central Andes, the Sierra Madre de Chiapas of Mexico, and the Great Rift Valley and Drakensberg of Africa—that have nondesignated PAs that complement designated PAs in terms of elevational protection (Fig. 2*D* and *SI Appendix, Fig. S3B*). Understanding the effectiveness of these PAs for biodiversity conservation may be warranted, because even where less stringent PAs are not as effective in reducing threats to biodiversity, there may be opportunities for upgrading investments to meet elevational protection targets without establishing new PAs.

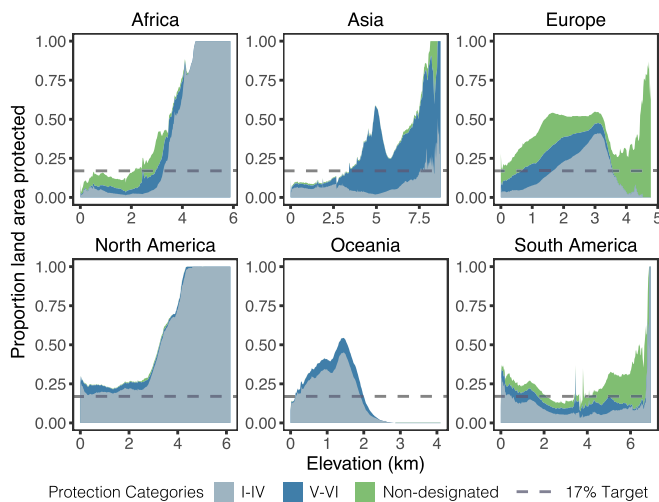


Fig. 1. Proportion of land area protected with elevation for mountain ranges in six continents, showing biases in protected area coverage along elevational gradients. Horizontal dashed lines represent a target of protecting 17% of total land area across elevation.

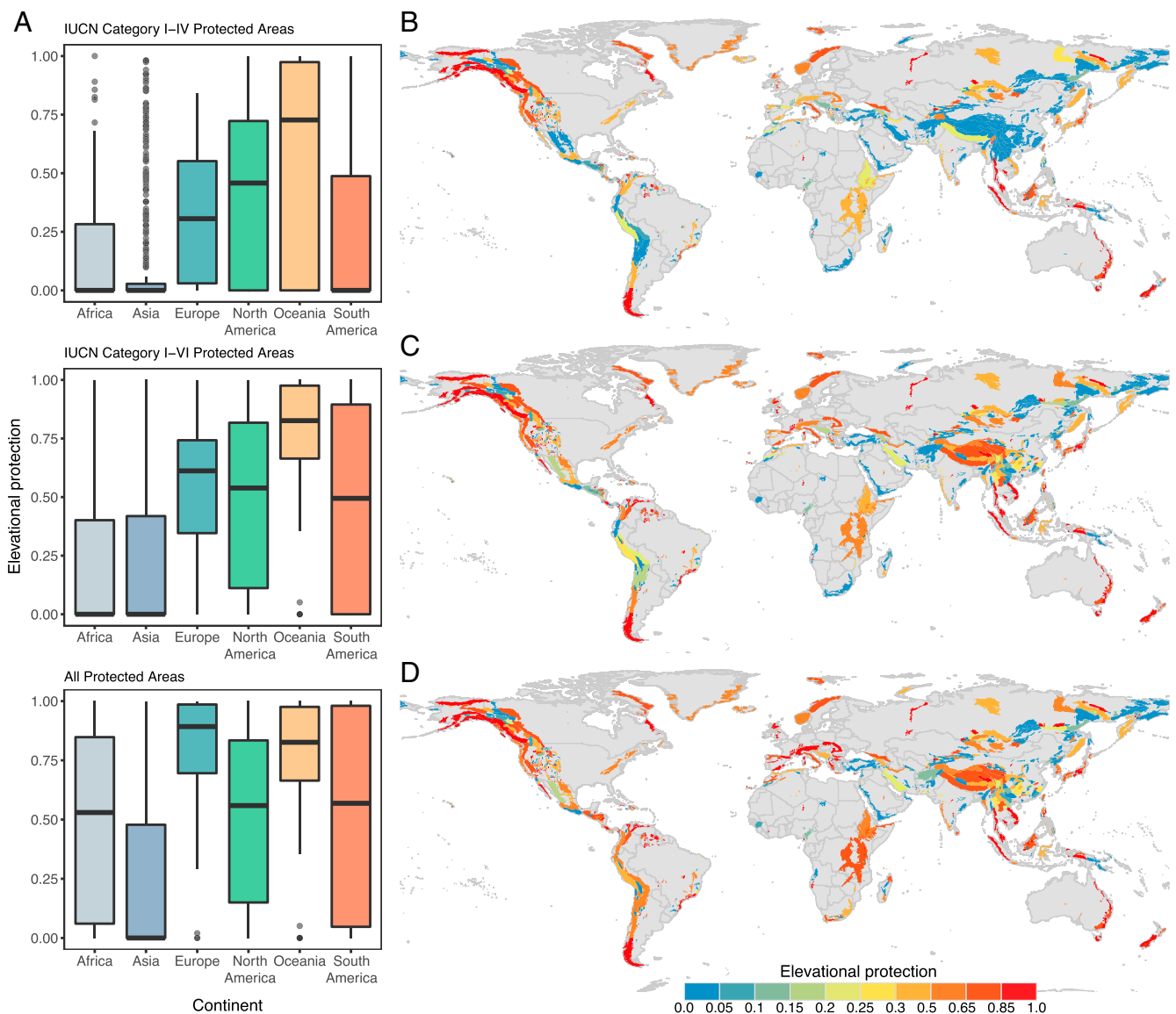


Fig. 2. (A) Boxplots of elevational protection by continent, based on the contribution of I-IV (Top), I-IV plus I-VI (Middle), and all (I-IV plus I-VI plus nondesignated; Bottom) protected areas (colored by continent). Elevational protection is defined as the proportion of each mountain range's elevational gradient protected at $\geq 17\%$ and is calculated as the number of 20-m elevational bands protected at $\geq 17\%$ divided by the total number of 20-m elevational bands per mountain range. (B-D) Geographic distribution of mountain ranges and the protection of elevational gradients worldwide, considering contributions from I-IV (B), I-IV plus I-VI (C), and all (I-IV plus I-VI plus nondesignated) (D) protected areas included in the World Database on Protected Areas ($n = 1,010$ ranges).

Still, PAs in several mountain ranges fail to cover any or even modest portions of the elevational gradient, even when considering any form of protected land within the WDPA (Fig. 2D). For example, ranges in northern Central America, the central Andes, West Africa, Madagascar, the Middle East, throughout East and Southeast Asia, eastern Russia, and across Papua New Guinea have elevational gradients that are mostly unprotected. In such cases, newly established PAs would be required to enhance elevational protection and increase opportunities for species to move elevationally in response to climate change. Protecting elevational gradients in these regions may be particularly prudent because they tend to also have low natural intactness and climate stability (26), thus increasing species vulnerability to climate change and elevational range shifts.

Null and Optimal Models of Elevational Protection. As PA extents continue to expand globally to meet Aichi Target 11, there will be inevitable progress toward enhancing elevational protection.

Aichi Target 11 specifies that PAs should be ecologically representative and, generally speaking, the current distribution of PAs is failing in this regard (12). Currently, mountain ranges with $\sim 17\%$ of protected land area are, on average, protecting $\sim 43\%$ of the elevational gradient at or above that target (Fig. 3A). To interpret this figure with respect to other possible configurations of elevational protection, we compared results to those obtained under null and optimal models of protection, while controlling for the total amount of protection in each range (Methods). Observed elevational protection is well below the optimal model where elevational protection at the 17% target is maximized (Fig. 3A). Furthermore, in most cases, it is also considerably lower than if protection under a null model was uniformly distributed across elevational gradients (Fig. 3A). On average, observed elevational protection is 21.6% lower than optimal elevational protection ($SD = 23.5\%$) and 8.1% lower than uniform elevational protection ($SD = 13.7\%$). We found no discernible geographic trends to explain variation in differences in uniform or optimal elevational

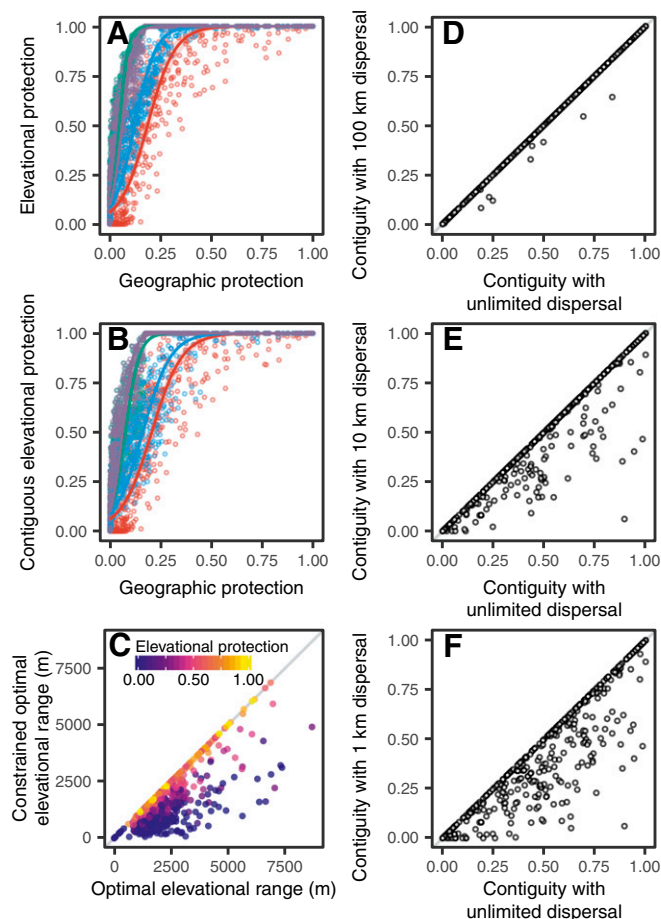


Fig. 3. Relationship between geographic protection of mountain ranges and (A) elevational protection and (B) contiguity, considering I–IV protected areas ($n = 1,010$ ranges). Contiguity is defined as the maximum number of contiguous elevational bands meeting the 17% target divided by the total number of elevational bands per mountain range. Points in A and B show observed (red), null (blue), optimal (green), and contiguous optimal (purple) model values for each mountain range (Methods). Colored lines in A and B are weighted quasibinomial model fits with 95% CI. (C) Tradeoffs in the elevational range over which some elevational bands meet the 17% target under the optimal and contiguous optimal models. Point colors show the observed elevational protection for each range. (D–F) Comparisons between contiguity calculated under unlimited dispersal and under 100-km, 10-km, and 1-km dispersal scenarios (Methods; only mountain ranges with >1 PA are plotted; $n = 514$ ranges).

protection from observed (SI Appendix, Fig. S4). Combined, these results suggest that protection in mountain ranges is generally biased toward fewer elevational bands, which could limit ecological representation and undermine PA effectiveness in promoting climate resiliency.

If future PA establishment follows the current relationship between geographic and elevational protection, it would require a significant expansion of protected land—protecting roughly half of all mountainous area—to protect just 17% of land across nearly all elevational gradients (Fig. 3A). However, strategic conservation planning could drastically reduce the extent of PAs required to obtain elevational representation. Optimally adding or expanding existing PAs going forward to meet the 17% target for all elevations would require protecting $\sim 21\%$ of global mountainous terrain. This represents an approximate doubling of the footprint of I–IV PAs located in mountain ranges, compared with the fivefold increase that would be required under the current trajectory of PA establishment. Strategic, proactive conservation planning is also likely to reduce future PA planning needs and costs compared

with reactive plans that consider current and future biodiversity patterns in a two-step process (27).

Spatial Configuration. While maximizing elevational protection would likely enhance ecological representation and facilitate range shifts, it is important to also consider the spatial configuration of protection, given variation in species' dispersal abilities to track climate change (28) and potential PA distributions that could limit connectivity and movement across elevations (29). Consequently, for each mountain range we also calculated a measure of contiguous elevational protection (hereafter “contiguity”)—defined as the maximum number of contiguous elevational bands meeting the 17% target, divided by the total number of elevational bands. High and low contiguity thus reflects protection that is highly contiguous or highly fragmented over elevation, respectively. We evaluated contiguity for PAs within a range of dispersal distances to assess how protection spans continuous elevational gradients while accounting for PA spatial configuration.

As with overall elevational protection, increasing geographic protection enhances contiguity, and observed contiguity was again considerably lower than contiguity calculated under either the null or optimal models (Fig. 3B). In general, observed PA distributions in mountain ranges protect less of the elevational gradient and are more fragmented than if PAs were distributed uniformly over elevation. For most ranges, optimizing elevational protection that is contiguous over elevation imposes only a modest tradeoff in overall elevational protection compared with an optimal model with no constraint on contiguity (Fig. 3A). However, contiguous optimal protection can result in substantial tradeoffs in the overall range of elevations that meet the 17% target, due to reductions in protection of lower or upper elevations in favor of more contiguous protection (Fig. 3C). We found that $\sim 39\%$ (391 of 1,010) of mountain ranges show a reduced range of elevations over which the 17% target is met under a contiguous optimal model compared with an unconstrained optimal model (Fig. 3C). Consequently, PA planning in mountain ranges often necessitates a choice between prioritizing ecological representation versus contiguity. Increasing overall elevational protection would be an important step to minimize this tradeoff (Fig. 3C).

Finally, we found that, in general, contiguity is not strongly influenced by the spatial configuration of PAs within mountain ranges. Under 100-km, 10-km, and 1-km dispersal scenarios, compared with an unlimited dispersal scenario, differences in contiguity were $<5\%$ in 99%, 87%, and 73% of ranges with >1 PA, respectively (Fig. 3D–F and Methods). However, in some cases such differences were considerable, such that while large contiguous elevational gradients are protected, the distances between PAs could undermine species' abilities to access those protected lands. This was particularly evident in some ranges (e.g., Coast Mountains of North America, the Greater Caucasus of Asia) where contiguity declined by $>50\%$ under dispersal distances of <1 km (Fig. 3F). In such circumstances, potential barriers to range shifts, the spatial distribution of the naturalness and permeability of the landscape, and the dispersal abilities of the species of concern, would all be important considerations in finer-scale planning for species movement under climate change.

Implications. We recognize that meeting a 17% target across elevations may not guarantee sustainable biodiversity outcomes and that more stringent targets may be needed to maintain viable populations for some species. This may be a particularly important consideration in regions of montane landscapes where surface area declines with elevation (22). In such contexts, protecting 17% of all elevations would result in overall reductions of protected land area with elevation. Greater proportions of protected land area in “bottleneck” or mountaintop elevation zones could attenuate reductions in the total amount of land protected with elevation and help minimize potential population declines for range-shifting species. Furthermore, conservation priorities (such as protecting threatened or endemic species) are likely not uniformly distributed over elevation. For instance, global rates of endemism in plants (4)

and levels of extinction risk in birds (30) increase with elevation, suggesting that higher elevations might represent greater priorities for biodiversity conservation.

At the same time, not all species will respond to climate change by shifting their distributions (31). Species vary widely in their thermoregulatory capacities (32), exhibit behavioral adaptations to cope with climatic stress (31, 33), and can utilize local microclimatic refugia (34). Furthermore, species that do shift their ranges in response to climate change may do so across latitude rather than elevation, as has been observed for several taxa in temperate regions (35). In such cases, enhancing elevational protection may be less important than protecting large areas of high-quality habitat (36), maximizing habitat or climatic heterogeneity within PA networks (13), and ensuring PAs are well connected geographically through habitat corridors (27, 36), although applying these principles more generally would strengthen PA networks along elevational gradients, too. However, in the tropics, where 339 (34%) of Earth's mountain ranges are partly distributed, such latitudinal shifts seem unlikely, given drastically attenuated climatic gradients across latitudes (37). Protecting low elevations in tropical montane areas to facilitate range shifts from lowlands may therefore be particularly prudent.

Furthermore, we note that human population densities worldwide are also typically highest at low elevations (38). Extensive human modification of land cover may limit our ability to establish intact PAs. In such regions, we must recognize that strict PAs alone may be insufficient for conservation (39, 40) and look to opportunities for restoration to build ecological resilience, bolster biodiversity, and promote human well-being (41). At the same time, PAs in human-dominated landscapes can positively contribute to local livelihoods and economies (42), and careful, integrated planning can better ensure that PAs are established to optimize benefits to ecosystems, biodiversity, and human populations (19). Conservation strategies have too often focused on static patterns of biodiversity and human populations. In reality, both global biodiversity patterns and the footprint of human populations have changed rapidly in recent years (40), and will continue to change (17, 35). Protecting elevational gradients will likely be an increasingly important, practical, and achievable strategy for effectively meeting human needs while mitigating biodiversity loss under climate change.

Methods

Mountain Ranges. We obtained a global data set of 1,003 delineated mountain ranges (1), the most exhaustive dataset of mountain ranges currently available to our knowledge. To this we added seven ranges included as supplemental data that were not already largely covered by the initial dataset. Mountain ranges were originally delineated from several references, including maps, atlases, and inventories. Mountain range boundaries were further informed by elevational ruggedness, a metric of elevational change between focal and neighboring cells of a digital elevation model (DEM), and were optimized to maximize inclusion of rugged terrain while minimizing inclusion of nonrugged terrain. Collectively, the mountain ranges analyzed here account for ~26 million square kilometers of terrestrial land, ~17.5% of Earth's terrestrial surface area, and ~83.7% of Earth's mountainous terrain (1).

Elevation Data. We compiled and combined the two highest-resolution global DEMs currently available for the delineated mountain ranges. As our primary dataset, we used a void-filled version of the NASA Shuttle Radar Topography Mission global DEM at 1 arc-second (30 m) resolution (SRTMGL1 V003). Thirty mountain ranges extended beyond the extent of SRTMGL1, so for latitudes above 60° N, we used the ASTER version 2.0 DEM at 1 arc second (ASTGTM V002), which contains some cells where elevation data are unavailable. Thirty mountain ranges in Europe and Asia included such nonvoid-filled cells, so for those we used a coarser (30 arc second, 1 km), void-filled DEM (SRTMGL30 V021). In total, we analyzed 950 ranges strictly using SRTMGL1, 15 ranges with extents entirely above 60° N using ASTER, 15 ranges with extents spanning 60° N using a combination SRTMGL1 and ASTER, and 30 ranges using SRTMGL30 (*SI Appendix, Fig. S5*). All elevation data are available at <https://lpdaac.usgs.gov>.

Protected Areas. We compiled PAs from the World Database on Protected Areas (<https://protectedplanet.net/>; accessed December 2016). We included all designated and nondesignated PAs represented by polygons in the

database. Following a recent global PA study (14), we grouped designated PAs with more stringent (IUCN categories Ia, Ib, II, III, and IV) and less stringent (IUCN categories V and VI) protection categories, and also included a third group of delineated but nondesignated PAs (IUCN categories termed not reported, not applicable, and not assigned) for all analyses (*SI Appendix, Fig. S1*). We excluded PAs represented as points in the database because the analyses required spatially explicit information on PA size and extent.

A total of 44,155 PA polygons intersected the mountain range delineations, which we clipped to the extents of our mountain range boundaries. Some PAs in the dataset had overlapping polygons, so we dissolved polygons to remove such overlaps, retaining larger areas for those PAs with stricter protection. To facilitate faster processing time, we then dissolved all individual PAs by IUCN category within each mountain range, resulting in at most one multifeature polygon per IUCN category per mountain range. All preprocessing was performed in ArcMap 10.4.1 (Environmental Systems Research Institute, 2015).

Elevational Protection. We extracted elevations (raster cell values) from the DEMs of each delineated mountain range and within all PA polygons within each mountain range (*SI Appendix*). While some mountain ranges abut each other or overlap geographically, we considered each mountain range to be distinct in the analysis because they are uniquely identified by name (1) and are often ecologically and/or geomorphologically distinguishable from other proximate ranges, with potentially range-restricted or specialized species assemblages. We then divided the amplitude of each range into 20-m elevational bands. We chose 20-m bands as the unit of analysis to best represent true area-elevation distributions while accommodating the degree of vertical error in the DEMs and to align with the spatial scale of empirically documented elevational range shifts on decadal-to-century time scales (7, 8). While we considered this spatial scale most relevant to conservation planning decisions, we recognize that 20-m elevational bands are finer than average montane species elevational range sizes (3) and typical rates of ecological turnover in mountain ranges, so we also performed analyses using 100-m, 500-m, and unlimited width bands that, collectively, more adequately align with montane species elevational range sizes (see *Sensitivity Analyses* below). For each range, we calculated the total number of pixels per band in the entire mountain range and in I–IV, V–VI, and nondesignated PAs. We followed the CBD's Aichi Target 11 goal to protect 17% of terrestrial land area to set a conservation target for each elevational band.

To calculate elevational protection—the proportion of the elevational gradient protected at or above the 17% target—we summed the number of elevational bands meeting the target and divided by the total number of elevational bands in each range (Fig. 2). We explored potential continental differences in protection of elevational gradients using one-way ANOVAs and, when finding significant differences between continents at $P < 0.05$, we performed post hoc Tukey honestly significant difference tests between all pairwise comparisons (*SI Appendix, Tables S1 and S2*).

Contiguity. For each range, we also estimated contiguity, calculated as the maximum number of contiguous elevational bands meeting the 17% target divided by the total number of elevational bands. Contiguity accounts for variability in the distribution of PAs along elevational gradients and penalizes ranges with protection gaps between adjacent elevational bands. Consequently, when protection is completely contiguous over elevation, contiguity is equal to elevational protection. When elevational protection is highly fragmented over elevation, contiguity approaches zero.

The spatial configuration of PAs could influence a species' ability to access protected lands across the elevational gradient. To understand and account for this potential influence, we considered three dispersal distances (100 km, 10 km, and 1 km) in our calculations of contiguity that encompass the dispersal abilities of most terrestrial vertebrates and have commonly been used in global PA planning and connectivity studies (43), in addition to an unlimited dispersal scenario. For each mountain range, we first identified clusters of PAs that were within each dispersal distance. We then calculated the contiguity metric (as described above) for each PA cluster within a mountain range and assigned the maximum contiguity score across all PA clusters for each mountain range (representing the best-case scenario for contiguity) as the final contiguity score for that dispersal scenario. We repeated this process for all four dispersal scenarios.

Null and Optimal Models of Elevational Protection. We compared the observed elevational protection to null and optimal models of elevational protection to evaluate potential elevational biases in the observed distribution of PAs. For the null model, for each range we allocated the total number of observed protected pixels evenly between all elevational bands, capping the maximum number allocated to the total number of pixels available in each band, and evenly redistributing any remaining protected pixels. By contrast, the optimal

model aims to maximize elevational protection for a given amount of geographic protection. For each range, we sorted all elevational bands by increasing total size and allocated the minimum number of protected pixels required to meet the 17% target in each band, starting with the band with the least total area, until the total number of allocated protected pixels equaled the total number of observed protected pixels. Allocating pixels in this way maximizes the number of elevational bands that meet the 17% target, without constraining contiguity of elevational bands.

To evaluate the effects of prioritizing elevational contiguity over representation, we developed a second optimal model (contiguous optimal) in which all elevational bands were sorted by decreasing elevation. We then allocated the minimum number of protected pixels required to meet the 17% target in each band, starting with the highest, until the total allocated protected pixels equaled the total number of observed protected pixels. Allocating pixels in this way enforces contiguity of protected elevational bands. The contiguous optimal model assumes mountains have decreasing area with elevation, which approximates the maximum number of contiguous elevational bands that meet the 17% target, and may underestimate elevational protection for the minority of ranges with negatively skewed area-elevation distributions (22). Consequently, it conservatively approximates elevational protection, constrained by contiguity.

Elevational Protection vs. Geographic Protection. We explored the relationship between geographic protection within mountain ranges and the two forms of elevational protection described above to elucidate general patterns and assess potential elevational biases in PA distributions (Fig. 3). Because data were overdispersed (owing to many ranges with no protection), we used quasibinomial regressions to evaluate the relationship between geographic protection and each metric. We fit models for the observed distribution of PAs, as well as for the null and optimal models, weighting each mountain range by the number of elevational bands.

Sensitivity Analyses. Because our quantification of elevational protection relies on pixel counts within elevational bands, where the number of bands is

determined by the amplitude of elevation, the calculation could be influenced by outlying elevation values. Consequently, given this issue and the potential for elevation anomalies to have arisen during the void-filling interpolation process, we performed quality checks on all extracted elevation values. We compared the elevational distribution of each range derived from its primary DEM source (SI Appendix, Fig. S5) with two alternate DEMs to evaluate the presence of outlying elevation values. Through this procedure, we identified 74 ranges (7.3% of all ranges) with potential outliers, and removed the outliers by identifying upper and lower elevation thresholds based on the elevational distributions of the alternate DEMs (SI Appendix, Fig. S6 and Table S3). We repeated all analyses with and without outliers. Overall, there was a high correlation between elevational protection calculated with and without outliers (Spearman rank correlation >0.99), and results were qualitatively similar for all but four mountain ranges (SI Appendix, Fig. S7A). For all ranges with potential outliers ($n = 74$), we present the results with the outliers excluded, which after comparison with the alternate DEMs appeared to represent more accurate elevational distributions.

To ensure that our calculations of elevational protection were not influenced by our choice of DEM, we reanalyzed all ranges below 60° N latitude ($n = 950$ ranges) using a coarser (3 arc-second resolution) DEM after removing outliers as above (SI Appendix). Finally, to ensure that our calculations were not influenced by our choice of elevational band size, we reanalyzed ranges using 100-m, 500-m, and unlimited width (i.e., no elevational binning) elevational bands as the unit of analysis (SI Appendix). We found strong correlations between our original results and results derived from the alternate DEM (SI Appendix, Fig. S7B) and alternate elevational band sizes (SI Appendix, Fig. S7 C–E).

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