ENVIRONMENTAL STUDIES

Keeping pace with climate change in global terrestrial protected areas

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Protected areas (PAs) are essential to biodiversity conservation, but their static boundaries may undermine their potential for protecting species under climate change. We assessed how the climatic conditions within global terrestrial PAs may change over time. By 2070, protection is expected to decline in cold and warm climates and increase in cool and hot climates over a wide range of precipitation. Most countries are expected to fail to protect >90% of their available climate at current levels. The evenness of climatic representation under protection—not the amount of area protected—positively influenced the retention of climatic conditions under protection. On average, protection retention would increase by ~118% if countries doubled their climatic representativeness under protection or by ~102% if countries collectively reduced emissions in accordance with global targets. Therefore, alongside adoption of mitigation policies, adaptation policies that improve the complementarity of climatic conditions within PAs will help countries safeguard biodiversity.

INTRODUCTION

Climatic conditions determine differences among biomes and habitat types (*1*), enforce species range limits (*2*), and govern global biodiversity patterns (*3*). Consequently, changes in climate have led to shifts, expansions, and contractions of species distributions (*4*) and are expected to restructure biotic communities over large areas (*5*). Concern over biodiversity conservation under climate change has motivated researchers to map climate velocity (*6*), stability (*7*), and the distribution of novel and disappearing climates (*8*), which points to changes in the availability of "climate space" for species (*9*). Country governments have responded by developing mitigation policies (*10*) and adaptation strategies that include additional protection of habitat for carbon sinks and species protection (*11*).

Protected areas (PAs) are central to climate change adaptation policies used by countries worldwide (*11*) and critical for biodiversity conservation and ecosystem functioning (*12*). While much of conservation takes place outside PAs, well-managed PAs are heralded as the most effective means of safeguarding species and the resources on which they depend (*13*). Political factors ultimately influence the creation and placement of PAs, yet despite being established toward high elevations and in remote locations (*14*), PAs are better aligned with patterns of biodiversity than with patterns of resource consumption or agricultural potential globally (*15*). PAs also provide a source of natural resources and ecosystem services while supporting human livelihoods (*12*). Expanding the PA network is thus a major goal for global strategic conservation planning of the Convention on Biological Diversity (CBD; https://www.cbd.int/sp/targets/).

In many ways, the long-term conservation potential of PAs hinges on their ability to maintain the biotic and abiotic conditions that promote biodiversity over time. With respect to climate change, a fundamental concern is that because PA locations are static, they may fail to continue to protect species as they shift their distributions beyond PA boundaries tracking changing climatic conditions (*16*–*18*). Historical biases in the locations (*14*) and associated climates of PAs (*19*, *20*) suggest that species may face reductions in the area of their climatic niches under protection over time, such that, in the absence of local adaptation, species would be forced into unprotected, potentially degraded landscapes. This process could thereby diminish the value of PAs for sustained biodiversity conservation (*17*).

Recent studies have demonstrated the positive role that PAs can play in mitigating climate change impacts on species by serving as stepping stones or otherwise accommodating species range shifts (*21*, *22*). Furthermore, capturing habitat and climatic heterogeneity within PAs is increasingly recognized as an important step in conservation planning under climate change (*23*, *24*). PAs are considered to be critically important under climate change to limit habitat loss and environmental degradation more generally (*25*). Intact habitats within PAs will likely support species that move into PAs under climate change (*26*), or may continue to provide habitat for species that persist within their boundaries within small, local climate refugia (*27*), or even under novel climates (*28*).

While we have gained an appreciation for the benefits of PAs for promoting species adaptation to climate change and have a clearer understanding of the trajectories of climatic conditions and species distributions under climate change (*29*), we lack knowledge of how these trajectories may alter the availability of climate space under protection over time. Determining the exposure of terrestrial PAs to climate change globally would reveal regions where biodiversity potentially faces greater vulnerability to climate change. Furthermore, understanding how the amount and distribution of PAs act to reduce climate exposure can provide insight into promising strategies for climate adaptation.

Here, we provide the first global assessment of climatic conditions represented within terrestrial PAs and analyze how climatic representation under protection is expected to change over time. We depict climate along two dimensions based on annual mean temperature and annual precipitation—climatic factors that typically delineate biome and ecoregion boundaries (*1*) and influence species distributions in terrestrial environments worldwide (*2*). Quantifying the expected exposure of these climatic variables within PAs thus provides a reasonable metric of their effective potential for conserving biodiversity under climate change. We use country boundaries as the unit of analysis because governmental policies largely facilitate the creation, finance, and management of PAs to meet national and international

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conservation objectives, and countries are also the standard in assessments of conservation values and performance of PAs (*12*, *15*). Our approach thus complements previous studies that have examined changes to climate space availability for select species (*16*) and biomes (*6*) in a manner that allows for global comparability and facilitates conservation action and implementation through political processes. We note that our focus is specifically on the amount and distribution of climate space under protection, without explicit consideration of its fine-scale configuration, which is beyond the scope of our investigation. This is an important consideration, however, because properties of the physical landscape, such as the degree of habitat fragmentation and barriers to movement, can facilitate or hinder connectivity for species under climate change (*30*).

Our objectives are to (i) examine the distribution of available climate and its representation within global terrestrial PAs, (ii) quantify expected changes in the distribution of climatic representation under protection over time, and (iii) explore the degree to which four factors—subject to potential mitigation and adaptation policies—influence the retention of climate space under protection into the future. Specifically, we examine whether smaller countries and countries threatened by faster rates of climate change may be predisposed to losing more protected climate space in the future because they would likely capture smaller overall climate spaces and experience higher rates of climatic turnover. At the same time, we investigate whether countries that protect a greater proportion of land area and a greater diversity of available climates retain more protected climate

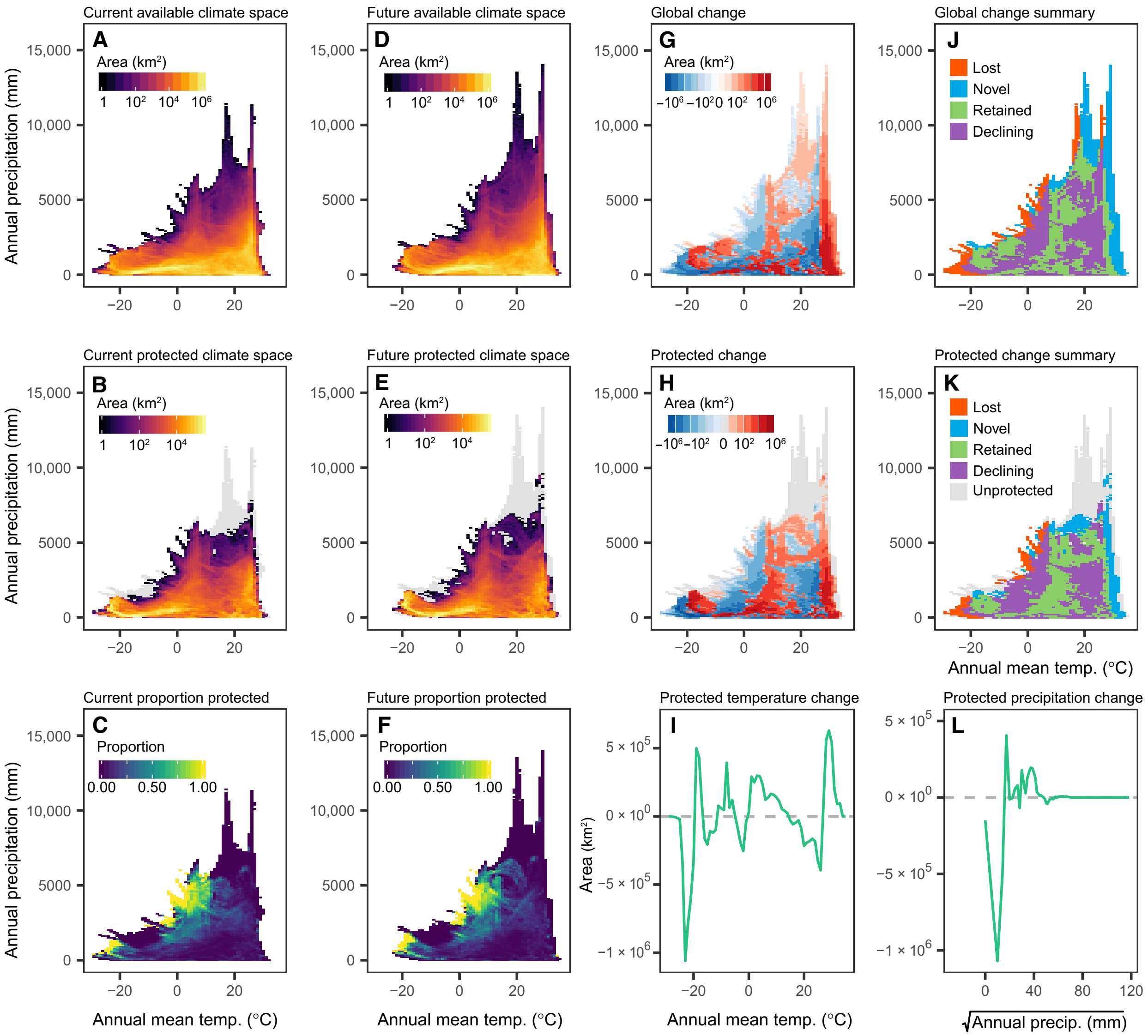

Fig. 1. Global outlook for current and future protected climate space. (**A**) Available climate is depicted as the two-dimensional frequency distribution of annual mean temperature and annual precipitation, discretized into 1°C temperature and 100-mm precipitation bins. (**B**) Protected climate space is the analogous frequency distribution within IUCN I to IV PAs. (**C**) The proportion protected of each climate bin is calculated by dividing the protected climate space distribution by the available climate space distribution protection. (**D** to **F**) As (A) to (C) for future climate. Subtracting the current from future available (**G**) and protected (**H**) climate space yields the expected temporal change. This change can then be categorized into lost, novel, retained, and declining for both available (**J**) and protected (**K**) climate space. Expected change in area protected over univariate temperature (**I**) and precipitation (**L**) gradients.

space because such protection would capture more overall climate space and potentially better capture shifting climates over time.

RESULTS

Protection of current climate space

To examine the distribution of available climate, we extracted temperature and precipitation values (*31*) for each country to map two-dimensional available climate space (Fig. 1A). We repeated this procedure for PAs [IUCN (International Union for Conservation of Nature) category I to IV and separately for I to VI; Materials and Methods] within each country to produce a distribution of protected climate space (Fig. 1B). We then divided protected by available climate space distributions to calculate the proportion of land area protected in climate space (Fig. 1C) and used this to visualize patterns and biases in the representation of available climate under protection.

Globally, dry-cold climates and wet-temperate climates are disproportionately represented within terrestrial PAs (Fig. 1C). Conversely, dry-temperate climates, wet-cold, and tropical climates are relatively underrepresented (Fig. 1C). We observed a global bias toward the protection of land in rare climates (Fig. 1C), which is due partly to the disproportionate protection of high elevation land globally (*14*, *20*). To evaluate trends and biases in climatic representation under protection in more detail, we calculated a metric that measures the equality of protection over ecological features (e.g., habitats, ecosystems, and elevation) and has been used to assess the representativeness of protection across countries and ecoregions in marine and terrestrial environments (*32*). Here, we use this metric to describe the representativeness of climate under protection based on the frequency distribution of the proportion of land protected in climate space per country, which we refer to as protection evenness (0 = uneven; 1 = even; Materials and Methods).

We found that protection evenness varied across continents [analysis of variance (ANOVA), $F_{4,200} = 5.647$, $P < 0.001$; Fig. 2]. Post hoc Tukey honestly significant difference (HSD) analysis revealed that countries in Europe exhibited significantly higher protection evenness than countries in Africa and Asia, but protection evenness did not significantly differ among any of the other continental pairings (Figs. 2, 3A). In general, protection evenness increases with the proportion of land protected within a country (fig. S1), but we observed some significant deviations from this pattern.

Protection of future climate space

To understand how the climate represented within terrestrial PAs is expected to change over time, we extracted our climate variables from multiple general circulation models (GCMs) (2061–2080; midpoint 2070) under representative concentration pathway (RCP) 8.5 W/m^2 (fig. S2; Materials and Methods). We calculated distributions of future available (Fig. 1D) and protected (Fig. 1E) climate space and subtracted current from future distributions to determine the distribution of overall climate change (Fig. 1G) and the expected change in area protected in climate space over time (Fig. 1H). For this analysis, we assumed no change in overall area protected.

Globally, the amount of protected land occurring in warm (~16° to 25°C) and cold (~−16° to 4°C) climates over a wide range of annual precipitation (up to ~5000 mm) is expected to substantially decline over the next 50 to 100 years (Fig. 1, H, I, K, and L). This implies a significant reduction of protective capacity for species or ecosystems adapted to these climatic conditions (*29*). For example, this would disproportionately affect tropical and subtropical moist broadleaf forests, grasslands, savannas, and shrublands; boreal forests; and tundra: These biogeographic regions are expected to have the greatest reductions in area of currently protected climate space (Materials and Methods; (Figs. 3, 4). By contrast, cool (~4° to 15°C) and hot (>25°C) climates are expected to be significantly better represented within PAs in the future, highlighting potentially favorable outcomes for species and ecosystems adapted to these portions of climate space.

We focused our subsequent analyses on whether and how the expected change in area protected in climate space over time would be zero (persistent) or positive (shown in green in Fig. 1K), which we refer to as protection retention (Materials and Methods). We found large variation in protection retention across countries (Fig. 3B) and significant variation across continents (ANOVA, $F_{4,200} = 9.191$, $P < 0.001$; (Fig. 2; Fig. 3B). Post hoc Tukey HSD analysis revealed that countries in Asia and Europe exhibited significantly higher protection retention than countries in Africa and the Americas and similar protection retention to countries in Oceania (Fig. 3B). Most (~63%) countries are expected to fail to protect >90% of their available climate at current levels. No country is expected to retain the current level of protection for even half of the range of current climatic conditions under protection (Fig. 3B). These results were largely consistent (i) when considering PAs of different protection stringencies (e.g., IUCN category I to IV PAs versus I to VI PAs), although we noted higher average protection evenness in some countries of Europe and the Americas (fig. S3); (ii) when considering a range of alternative GCMs (figs. S4 and S5); and (iii) when varying the size of the climate bins underlying calculations of protection retention (fig. S6).

Factors determining protection retention

The low rates of protection retention raise concerns about the fate of the species and ecological communities that PAs currently protect (*28*). To examine what might best explain differences in protection retention rates among countries, we used quasi-binomial regression with model selection and model averaging to evaluate how four predictors associated with potential climate change mitigation and adaptation policies—country size, the rate of climate change, the

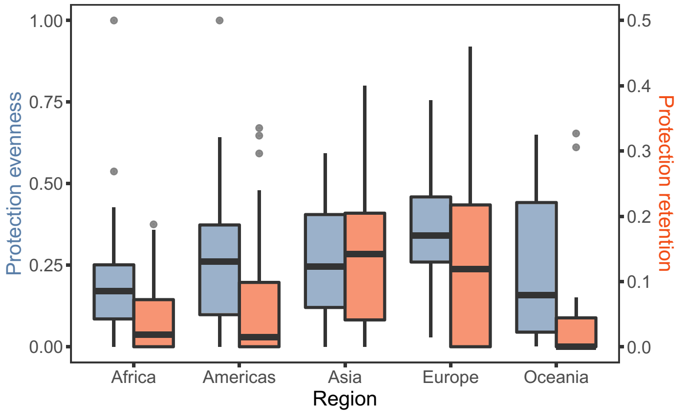

Fig. 2. Protection evenness and retention across regions. Boxplots of protection evenness and protection retention across five regions (colors of boxes match colors of axis labels; *n* = 205 countries) (see Materials and Methods and text for calculations of each metric). Protection retention calculations are based on future projections from the Community Climate System Model 4 (CCSM4) general circulation model.

proportion of protected land, and protection evenness—influence protection retention (Materials and Methods; tables S1 to S3).

Consistent with our predictions, country size was positively related [β = 0.34; 95% confidence interval (CI), 0.20 to 0.48; Fig. 5A], and the rate of climate change was negatively related (β = −0.32; 95% CI, −0.43 to −0.22; Fig. 5B and fig. S4) to protection retention, indicating that small countries with fast rates of climate change are particularly vulnerable. However, counter to our predictions, the proportion of land protected had no significant influence on protection retention (β = −0.01; 95% CI, −0.19 to 0.10; Fig. 5C), which suggests that simply expanding the PA network under past trends will not help to retain the current climatic conditions under protection into the future. The strongest predictor of protection retention in our models was protection evenness, which exhibited a positive relationship consistent with our predictions (β = 0.71; 95% CI, 0.60 to 0.82; Fig. 5D).

DISCUSSION

Increasing complementarity of species, ecosystems, or ecological processes in conservation planning is a major pillar of an effective and efficient adaptation strategy under climate change (*11*). Here, our results extend this notion by suggesting that enhancing the complementarity of climatic conditions under protection could help safeguard biodiversity that is already represented in the PA network. On the basis of our models, establishing new PAs in portions of climate space that are currently underrepresented by PAs could yield the

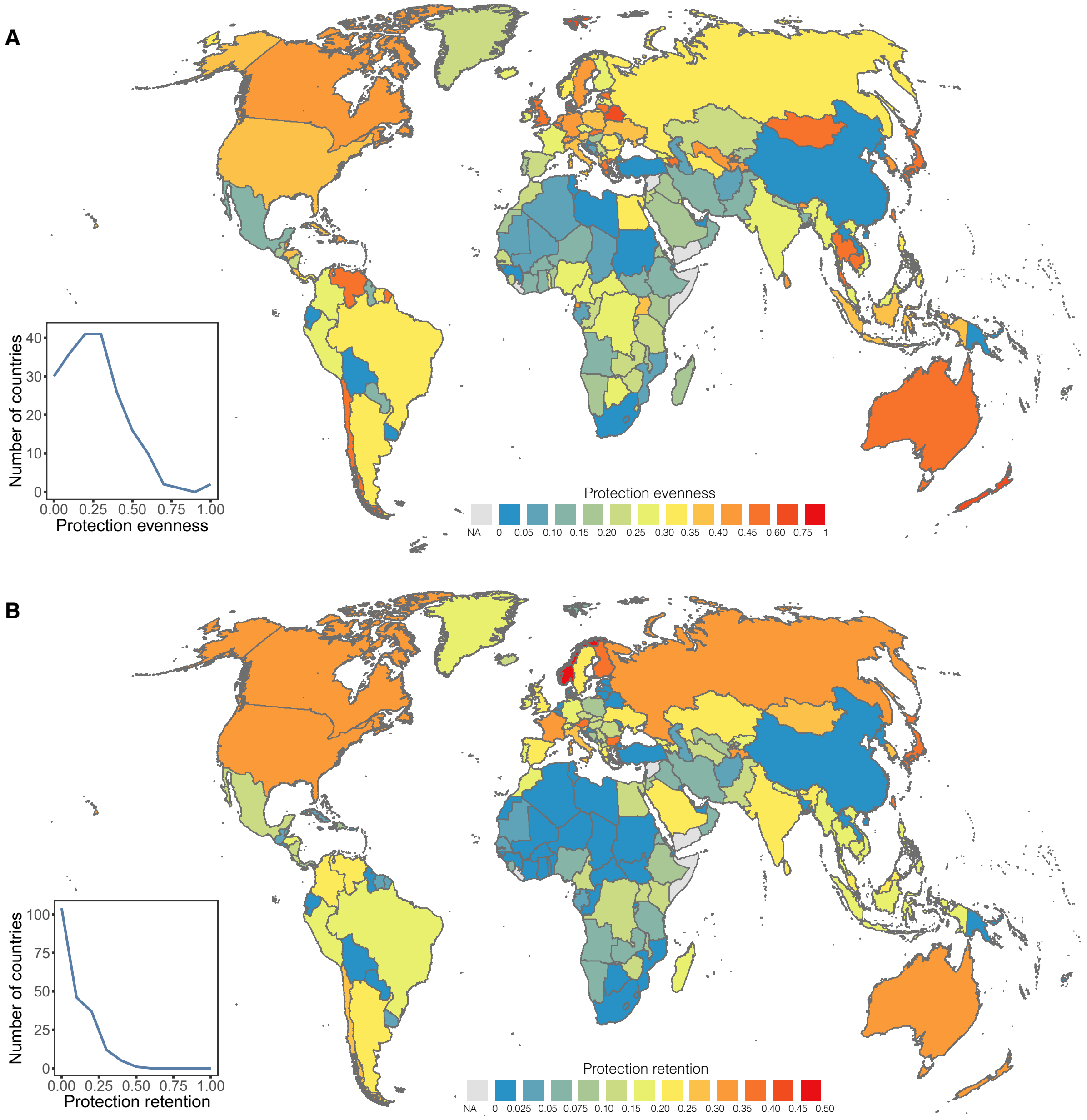

Fig. 3. Geographic distribution of protection evenness and protection retention. Maps of (**A**) protection evenness and (**B**) protection retention ($n = 205$ countries). Insets show the country frequency distribution for each metric.

greatest increases in protection retention for most countries. For example, our models show that if an average country doubled its protection evenness, it would increase its protection retention by ~118% (fig. S7). By comparison, if an average country experienced half the rate of climate change through global efforts to halt net emissions to levels roughly consistent with global emissions targets (*33*), it would increase its retention by ~102% (fig. S7). Consequently, alongside adoption of global climate mitigation policies, countries seeking to safeguard their protected biodiversity under climate change should implement climate adaptation strategies that aim to improve the complementarity of climatic conditions within PAs.

One hurdle to increasing climatic representation in PAs is to reduce bias in the geographic location of PAs. We documented a bias of protection toward rarer portions of climate space (Fig. 1C), particularly colder and wetter environments that presumably conflict less with historical human settlement patterns. Studies have documented biases in the locations of PAs toward high elevations (*20*) and away from human settlements and infrastructure (*14*). Such biases could reduce the potential for species tracking more common climates to access adequate protection (*17*) and could also leave the widespread areas of more common climates vulnerable to other ongoing threats, such as land-use change (*34*, *35*).

Our analysis of the change in area protected in climate space revealed unexpected nonlinearities leading to reductions and gains in area protected over certain ranges of temperature and precipitation (Fig. 1, H, I, and L). In particular, the sizeable global reduction

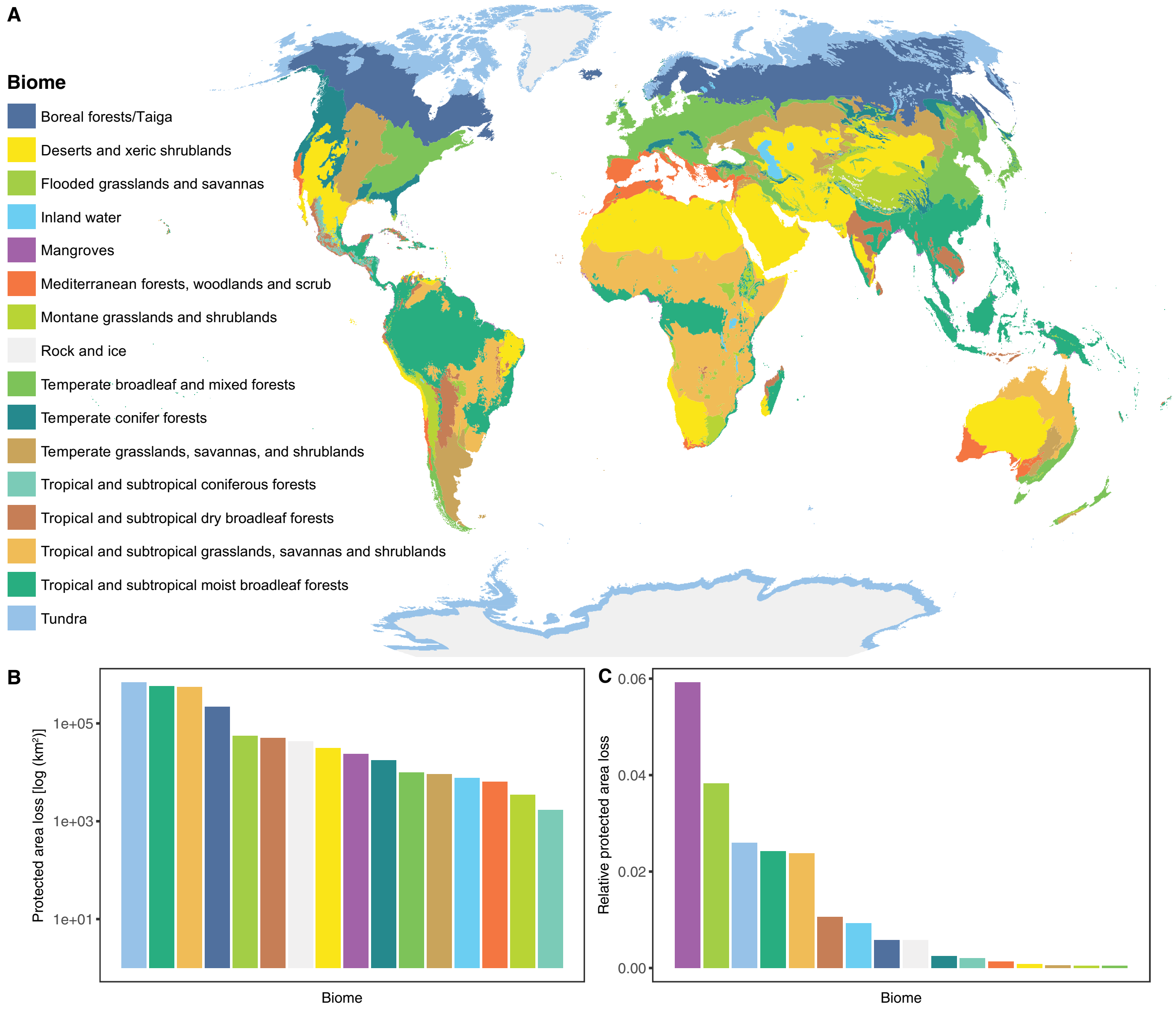

Fig. 4. PA loss across biomes. Global distribution of biomes (**A**) and expected total loss in area protected (**B**) and loss in area protected relative to biome size (**C**) based on differences in protected climate space with respect to current climate. Plots in (B) and (C) are ranked by total and relative loss, respectively (see Materials and Methods for details of loss calculations).

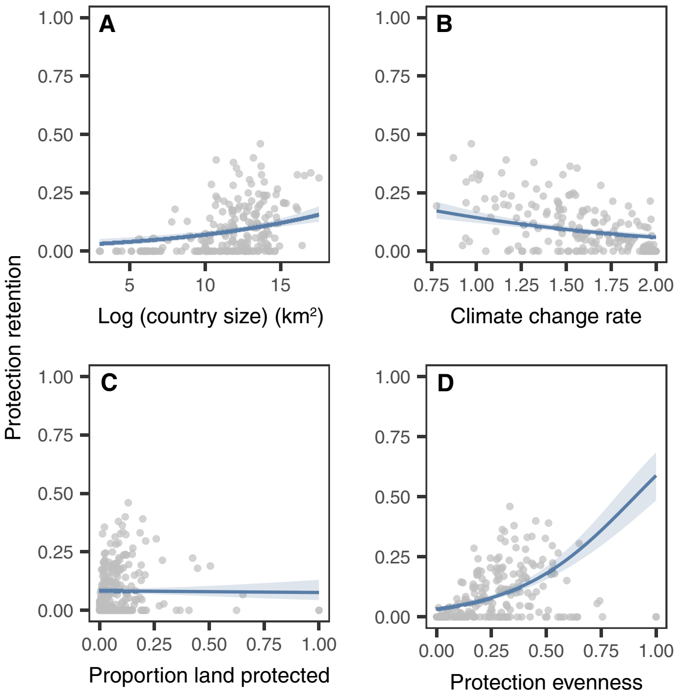

Fig. 5. Predicting protection retention. Relationships between protection retention and (**A**) country size, (**B**) the rate of climate change, (**C**) the proportion of land area protected, and (**D**) protection evenness for 205 countries (gray points). Colored lines are weighted quasi-binomial model fits with 95% CIs (shaded regions).

in the amount of area under protection in warm (16° to 25°C) and cold (−16° to 4°C) temperatures over a wide range of precipitation suggests that conservation managers might anticipate increased protection needs for species projected to occupy this climate space over the next 50 to 100 years. Not only are the biomes and broad-scale vegetation communities comprising these climate zones (such as boreal forests, montane grasslands, and tundra) likely to experience significant area reductions according to our analysis (Fig. 4), but these same ecosystems also face heightened vulnerability to climate change from other stressors, such as wildfire (*36*). Enhancing protection in the warm (16° to 25°C) portion of climate space could also help act as a stepping stone for species seeking colder refugia under warming (*21*, *37*). By contrast, our results suggest that ecosystems adapted to hotter (>25°C) climates are likely to be better represented within PAs in the future, and some of these ecosystems, such as tropical and subtropical moist broadleaf forests, may have comparatively high resilience to climate change given high thermal tolerances and relatively low water stress (*36*). This combination of factors may, to some degree, relieve pressure on species occurring in this portion of climate space in the future.

Another unexpected and important finding from our study is that the proportion of land protected across countries had no influence on protection retention (Fig. 5C). Thus, assuming a space-for-time substitution, simply adding protected land following existing trends of establishment would not be expected to bolster protection retention. Countries seeking to establish new PAs to meet conservation area targets, such as those set by CBD's Aichi Target 11, should consider how newly protected land would act to conserve biodiversity over time in addition to how it would capture current patterns of biodiversity (*24*). Doing so would also help countries meet the tenet of Target 11 that PAs should be "ecologically representative" by capturing different components of biodiversity adapted to different climatic conditions. Failing to take climate space into account during PA planning could lead to newly established PAs capturing the climatic conditions underlying species distributions only temporarily, potentially leading to future vulnerabilities.

It is important to note some limitations and caveats of our study. First, our assessment ignores the portions of "novel" future climate space and their potential conservation value because they do not contribute to protection retention. Yet, novel climates are likely to be suitable for some species and may provide new opportunities for species colonization (*5*). Thus, PAs that are expected to encompass novel climates could still retain much of their conservation value (*28*). Furthermore, the sensitivity and adaptive capacity of most species to climate change are poorly known, such that species may be able to persist in climate space that spans beyond their current climatic envelopes (*38*).

Second, our analysis focuses on conservation strictly within PAs, ignoring the potential conservation value of unprotected lands, which can harbor high levels of biodiversity that, in some cases, exceed those of intact landscapes (*39*). Nevertheless, our analysis underscores how the total availability of climate space is expected to change over time (Fig. 1G), identifying the distinct portions of climate space that are expected to shrink and expand, which closely reflect those of protected lands. Thus, species in unprotected lands will likely face similar contractions and expansions in the amount of area of suitable climatic conditions to those in protected lands.

Third, species vary in their thermoregulatory abilities (*40*), and many can use finer-scale microclimates to cope with climatic stress (*41*). Such species may therefore be able to persist within PAs that are not expected to retain the same coarse-scale climatic conditions in the future. However, given that species ranges appear more strongly structured by climate in the tropics than in the temperate regions (*42*), retaining climatic representation under protection might be particularly important in tropical regions.

Fourth, our analysis focuses strictly on broad distributions in the amount and availability of protected climate space, without explicitly assessing the fine-scale configuration of climate gradients that give rise to climate connectivity potential (*30*). Aforementioned biases in the locations of PAs may hinder their ability to protect continuous climatic gradients (*20*), which could limit connectivity and the ability for species to access suitable climatic conditions that may have shifted to other portions of a landscape or country. An important future extension of our study would be to incorporate the configuration of climate space to develop a climate protection retention statistic that accounts for variation in species dispersal abilities.

Last, in certain contexts, enhancing protection evenness may not align with other conservation objectives. PAs are often established to serve multiple objectives, including providing habitat and species protection and livelihoods and ecosystem services to human communities (*12*); these factors must be taken into account during conservation planning under climate change (*43*). Our results thus add to recent calls for increased attention to the additional role that PAs can serve in mitigating climate change impacts on species (*22*).

Similarly, enhancing protection evenness may not always constitute the most effective adaptation strategy. For example, small and geographically isolated countries likely have little opportunity to enhance protection retention even through strategic PA expansion given high climatic turnover following even modest rates of climate change; such countries may benefit more from coordinated PA planning through transboundary cooperation (*44*). Enhancing protection evenness may also be hindered by current land-use patterns and biases in the climates conducive to agriculture, human settlement, and development (*19*).

However, for most countries and in many contexts, our results suggest that protection that spans the full complement of climates will improve landscape resiliency for biodiversity and therefore represents a particularly promising climate adaptation strategy. For conservation planners, this means incorporating distributions of current and future climate variables (temperature and precipitation, at a minimum) into assessments—which can reveal gaps and biases in protection along climatic gradients—and then targeting underrepresented climatic zones for protection. To strengthen and complement this approach, conservation planners can also focus on ensuring representation of landscapes that drive climate variability, such as topographically complex environments or regions with high habitat heterogeneity that tend to promote biodiversity and allow for fine-scale adaptation to climate change (*45*), or act as climate refugia. This approach to expanding PAs is robust to future uncertainty in climate change trajectories and can readily be combined with other approaches, such as promoting climate-wise landscape connectivity (*46*, *47*) and addressing habitat suitability needs and threats from land-use change (*48*). These strategies can be implemented immediately to help countries safeguard biodiversity.

MATERIALS AND METHODS

Climate data

We obtained global gridded data at 30 arc sec (~1 km^2) for current and future annual mean temperature (hereafter "temperature") and annual precipitation (hereafter "precipitation") from WorldClim v1.4 (*31*). We used WorldClim v1.4 because our analysis relied on current and future climate layers, and future layers are not yet available for WorldClim v2.0 at 30 arc sec resolution (*49*). Temperature and precipitation data in WorldClim v1.4 originate from a global network of tens of thousands of weather stations (*31*). These data are then used to create interpolated surfaces, which are generated using the thin-plate smoothing spline algorithm, using latitude, longitude, and elevation as independent variables (*31*). Downscaled future climate layers in WorldClim v1.4 are based on projections by the IPCC (Intergovernmental Panel on Climate Change) Fifth Assessment Report using 17 different GCMs for four RCPs. Future scenarios in the IPCC Fifth Assessment Report are based on results from the Coupled Model Intercomparison Project Phase 5 (CMIP5) models (*50*). The downscaling procedure in WorldClim calculates projected change in a given weather variable as the difference (absolute difference for temperature and relative difference for precipitation) between GCM output for the current period (1971–2000) and the future time horizon considered. These differences are interpolated to the resolution of the current period (30 arc sec), and the changes are applied to the interpolated climate data for calibration (for additional details, see the documentation by the author of WorldClim at https://worldclim.org/data/downscaling.html).

We selected RCP 8.5 W/m^2 to model changes under the "business as usual" scenario for an approximately 50-year time horizon (2061–2080, referred to as 2070). We evaluated differences in temperature and precipitation projections across all GCMs available in WorldClim and selected nine to bound credible estimates of future climate change and represent a range of scenarios along warm-hot temperature and dry-wet precipitation axes of climate change (fig. S2; see also "Sensitivity analyses" section below). We present results from the Community Climate System Model 4 (CCSM4) model throughout the paper because it represents an intermediately warmer-wetter future climate scenario, and this model consistently resulted in minimal differences from the median value across all GCMs we considered (table S1).

Country boundaries and PAs

For country boundaries, we used the Global Administrative Areas boundaries layer (version 2.8; www.gadm.org; accessed November 2017). We compiled delineations of PAs from the World Database on Protected Areas (http://protectedplanet.net/; accessed November 2017). With our focus on PAs, IUCN categories Ia, Ib, II, III, and IV are important to consider because their main objectives are the conservation of wild species and their ecosystems, and thus, they have strict mandates that prohibit resource extraction and substantially limit the degree of human use. However, analyses of all formerly designated PAs (including PAs with IUCN categories V and VI, which are focused on conserving landscapes of cultural significance, in addition to those with IUCN categories I to IV) gave qualitatively similar results to those using IUCN categories I to IV, with the exception of higher average protection evenness (see definition below) in some countries of Europe and the Americas (fig. S3).

The PA dataset contained 90,496 IUCN I to IV PA polygons, some of which were overlapping. We dissolved overlapping polygons and retained larger areas for polygons with stricter protection categories. We then dissolved all polygons by protection categories to facilitate faster processing, resulting in one multifeature polygon per IUCN category. We then intersected the PA polygons with country boundaries. All preprocessing was performed in ArcMap 10.5.1 [ESRI (Environmental Systems Research Institute), Redlands, CA; 2015].

Available and protected climate space

We extracted the temperature and precipitation values from the current and future climate data for each country and, subsequently, within all PA polygons within each country. We then plotted the two-dimensional frequency distribution of available climate space (Fig. 1, A and D) and protected climate space (Fig. 1, B and E) on temperature and precipitation axes for each country, binning temperature into 1°C bins and precipitation into 100-mm bins, as well as conducted sensitivity analyses with alternative bin sizes, which yielded qualitatively similar results (fig. S6; see "Sensitivity analyses" section below).

We then divided the protected climate space frequency distribution by the available climate space frequency distribution for current and future periods for each country to calculate the proportion protected for each climate bin in each period (Fig. 1, C and F). To calculate the temporal change in available and protected climate space, we subtracted the current from future climate frequency distributions (Fig. 1, G and H). This allowed us to determine where available and protected climate space would be lost (present currently, but not present in the future; red in Fig. 1, J and K), novel (present in the future, but not present currently; blue in Fig. 1, J and K), retained (present in both periods with equal or greater area in the future; green in Fig. 1, J and K), or declining (present in both periods with less area in the future; purple in Fig. 1, J and K).

While our primary focus was determining expected changes in the distribution of climatic representation under protection over time for countries, we repeated the above analyses using biomes (*51*) as the unit of analysis to additionally place our findings in a biogeographic context (Fig. 4). We calculated temporal change in protected climate space following the above approach for countries and calculated the expected change in area protected per biome by summing the differences in protection in current climate space to calculate absolute change in area protected (Fig. 4B). We also divided the absolute change by biome size to calculate change in area protected relative to biome size (Fig. 4C).

Protection evenness

We determined the evenness of climatic representation under protection—which we refer to as protection evenness—for each country by calculating the proportional Protection Equality metric described in (*23*). The proportional protection equality metric has been used to assess the representativeness of species, habitats, and ecoregions across countries and continents (*32*). We calculated the metric across the frequency distribution of the proportion of land protected in climate space to provide an indicator of the representativeness of countrywide PA networks with respect to available climate using the ProtectEqual package in R (*32*). Protection evenness scales from 0 to 1, with 0 representing completely uneven distributions of protection over climate space and 1 representing perfectly even distributions. Compared to other metrics of protection representation, this metric benefits from providing a bounded interval and correcting for small sample sizes (i.e., countries with small climate spaces), enabling unbiased comparisons of representation across countries (*32*).

Protection retention

We calculated the proportion of current protected climate space where future area protected equals or exceeds current area protected—which we refer to as protection retention—for each country as the number of climate bins that had equal or greater numbers of protected pixels in the future compared to the current, divided by the total number of climate bins in the current. Protection retention also scales from 0 to 1 (maximum observed value, 0.46), where a value of 0 indicates that in no portion of climate space is protection in the future expected to equal or exceed current levels of protection and a value of 1 indicates that future protection equals or exceeds the current level of protection in every climate bin in the two-dimensional climate space.

Statistical analyses: Evaluating factors influencing protection retention

We evaluated how four factors with direct links to climate mitigation and adaptation policy influenced protection retention. We considered two factors that could hinder retention (country size and the rate of climate change) and two factors that could facilitate retention (the proportion of land protected and protection evenness). We calculated country size and the proportion of land protected directly from the WorldClim data within the administrative and area protected boundaries, respectively. For each country, we calculated an index of the rate of climate change as the sum of all climate bin-wise absolute differences in area from the current and future periods, divided by the country size. We used our previously calculated proportional protection equality metric for each country as the metric of protection evenness (see table S1 for predictor values for each country).

Data were overdispersed, so we used quasi-binomial regression (weighting each country by its number of climate bins) to evaluate the relationship between all possible additive combinations of predictors (plus a model with a null intercept), with protection retention as the response variable (table S3). We ranked models using Akaike's information criterion, $\mathrm{QAIC_c}$, and centered and standardized all predictors to enable unbiased comparisons and performed model averaging across all models to obtain 95% CIs for each predictor (table S2). We considered the model-averaged coefficients significant when the 95% CIs did not overlap zero.

Sensitivity analyses

Alternative GCMs

To account for uncertainty in future climate projections, we performed analyses of protection retention using nine separate GCMs that represent alternative intermediate climate change scenarios and serve to bound expectations of future climate conditions at the extremes (fig. S2). These included three hot-wet futures (MI, MR, and GF), one warm-wet future (MG), one warm-dry future (IN), one hot-dry future (HD), and three intermediate scenarios (CC, CN, and BC; see table S1 for GCMs associated with codes). We evaluated the sensitivity of our results by plotting correlations between country-specific protection retention rates using each pairwise GCM combination (fig. S5). We found strong correlations between all pairwise combinations of the nine GCMs we considered (Spearman rank correlation coefficients all $r > 0.81$, $P < 0.001$), and residual errors were approximately normally distributed when comparing scenarios, suggesting that our results are generally robust to the choice of GCM. Last, we calculated pairwise differences in protection retention between all GCMs for each country (fig. S5), calculated the SD across GCMs, and mapped this variable to investigate geographic patterns in sensitivity to the choice of GCM (table S1 and fig. S4B). SDs were relatively similar across all regions, except portions of Europe, suggesting that our results for some European countries might be more sensitive to the choice of GCM.

Resolution of climate bins

Our coarse-filter global analysis along two climatic dimensions required partitioning continuous climate into bins. Our choice of bins in 1°C by 100-mm increments reflected our desire to capture reasonably fine-grained patterning of climatic gradients while being easily interpretable and on scales consistent with climate change forecasts. However, we further altered the size of climate bins to coarser (2°C by 200 mm) and finer (0.5°C by 50 mm) resolutions and repeated calculations of protection evenness and protection retention to ensure that results were not largely driven by our choice of bin size (fig. S6). We used the CCSM4 GCM for the purposes of this sensitivity analysis. All pairwise combinations had Spearman rank correlation coefficients of $r > 0.89$, and we only detected more substantial deviations for countries with small available climates at the coarsest resolution bin size (fig. S6). We conclude that our results are largely robust to the choice of bin size, with greatest confidence for smaller countries when using finer bin sizes.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/6/25/eaay0814/DC1

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