

Climate change exposure and vulnerability of the global protected area estate from an international perspective

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Abstract

Aim: Protected areas are essential to conserve biodiversity and ecosystem benefits to society under increasing human pressures of the Anthropocene. Anthropogenic climate change, however, threatens the enduring effectiveness of protected areas in conserving biodiversity and providing ecosystem services, because it modifies and redistributes biodiversity with unknown consequences for ecosystem functioning within protected areas. Here, we assess (a) the climate change exposure of the global terrestrial protected area estate and (b) the climate change vulnerability of national protected area estates.

Location: Terrestrial protected areas worldwide.

Methods: We calculated local climate change exposure as predicted climate anomalies between the present and 2070 using ten global climate models, two emission scenarios (RCP 4.5 and 8.5) and the finest spatial resolution available for global climate projections (approx. 1 km). We estimated the climate change vulnerability of national protected area estates by analysing countrywide relationships between protected areas' climate anomalies and other protected area characteristics, that is area, elevation, terrain ruggedness, human footprint and irreplaceability for globally threatened species.

Results: We found predicted climate anomalies highest in protected areas of (sub-) tropical countries. The correlations between climate anomalies and protected area characteristics strongly differ between countries. Globally, protected areas showing large climate anomalies tend to be at high elevation and highly irreplaceable for threatened species, increasing climate change vulnerability. These protected areas are relatively large in area, of high topographic heterogeneity and less pressured by humans, decreasing climate change vulnerability.

Main conclusion: This study reveals potential hotspots of climate change impact inside the terrestrial protected area estate. It thus supports and guides climate-smart conservation policy and management, particularly national to local authorities, to ensure the future effectiveness of protected areas in preserving biodiversity and ecosystem benefits under climate change.

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KEY WORDS

biodiversity, climate change, conservation policy, environmental management, exposure, protected area, vulnerability

1 | INTRODUCTION

Protected areas (PAs) are effective in conserving biodiversity, ecosystem functioning and services under increasing human pressures of the Anthropocene. Local biodiversity is generally higher inside than outside PAs (Gray et al., 2016). PAs preserve species and populations better than other conservation measures (Geldmann et al., 2013). For global biodiversity conservation, PAs are particularly effective when they are located in biodiversity hotspots (Joppa, Visconti, Jenkins, & Pimm, 2013), actively managed and funded (Coad et al., 2019). PAs cannot stop but decelerate the global biodiversity loss (Geldmann, Manica, Burgess, Coad, & Balmford, 2019). Further, PAs safeguard ecosystem services such as climate change mitigation and adaptation (MacKinnon, Dudley, & Sandwith, 2011); natural catastrophe control and the provision of natural resources (Xu et al., 2017); tourism and recreation (Balmford et al., 2009); and poverty reduction (Andam, Ferraro, Sims, Healy, & Holland, 2010). They are consequently considered crucial tools to meet the Sustainable Development Goals (SDG) and Aichi Biodiversity Targets (Mace et al., 2018). Conservationists perceive PAs as the most important policy for biodiversity conservation in the face of climate change (Hagerman & Satterfield, 2014).

Already in the 1980s scientists have warned of climate change being an inevitable threat to PA effectiveness (Peters & Darling, 1985). PAs are exposed to various direct and indirect climate change effects, for example increasing temperatures, melting of snow and ice, more severe droughts and storms, seasonal shifts, rising sea level and increased environmental acidification (Gross, Woodley, Welling, & Watson, 2017). Climate change is predicted to cause gains (Berteaux et al., 2018) and losses of biodiversity within PAs (Velazco, Villalobos, Galvão, & De Marco Júnior, 2019). In any case, the risk of PA downgrading, downsizing and degazettement (PADDD) increases for PAs that lose the biodiversity they were meant to protect (Thomas & Gillingham, 2015). Climate change modifies and redistributes biodiversity and thus forms novel ecosystems whose functioning and contributions to human well-being are unclear (Pecl et al., 2017). Climate change additionally co-occurs with other threats to biodiversity, such as human land use, implying interactive effects (Schulze et al., 2018). Therefore, the future effectiveness of PAs in preserving biodiversity and ecosystem services under climate change is uncertain.

Predicting the future climate inside PAs is required to inform conservation management and policymakers of potential climate change impacts on PAs (Rannow et al., 2014). Conservation management and policy are mainly adopted at the national to local scale. However, global studies about climate change impact neither address national authorities nor represent the local extent of PAs (Williams et al., 2007; Beaumont et al., 2011; García-López & Allué,

2013; Bellard et al., 2014; Garcia et al., 2014; Ordonez et al., 2016; Li, Wu, et al., 2018; Li, Kou, et al., 2018); and the climate change research that focuses on PAs comprises a limited geographical extent only, for example North America (Batllori, Parisien, Parks, Moritz, & Miller, 2017) or Europe (Nila, Beierkuhnlein, Jaeschke, Hoffmann, & Hossain, 2019). A recent biogeographical investigation predicting climate shifts within PAs worldwide does not contemplate the governmental level either (Hoffmann, Irl, & Beierkuhnlein, 2019). A national view of the local climate change impact on individual PAs worldwide is missing but vital to support local to national conservation policy and management in reaching global conservation goals beyond 2020 despite climate change (Watson et al., 2016).

Here, we approach this research gap by assessing the climate change exposure of the terrestrial PAs worldwide at the highest spatial resolution for which global climate data is available, that is approximately 1 km. In a first step, we assessed the climate change exposure of PAs as the climate anomalies predicted for the year 2070 within each grid cell covered by a PA. In a second step, we summarized the climate anomalies by each PA and present the PAs' median climate anomalies by country and management category. In a third step, we calculated country-specific correlations between median climate anomalies and other PA characteristics to provide additional information about the climate change vulnerability of national PA estates. In a fourth step, we compare the median climate anomalies and other PA characteristics between national PA estates via a principal component analysis (PCA). The outcomes inform proactive management that can compensate for negative impacts of climate change on PA effectiveness (Game, Lipsett-Moore, Saxon, Peterson, & Sheppard, 2011). Our work sets out to support climate-smart policy and management of PAs, particularly at the national to local level.

2 | METHODS

2.1 | Protected area data

The World Database on Protected Area (version January 2018) includes boundary data for 201,464 PAs excluding marine, coastal (i.e., semi-terrestrial) and non-designated PAs (IUCN & UNEP-WCMC, 2019). Non-designated PAs are PAs without legal recognition whose effectiveness is dubious. We rasterized the PA polygons by the same resolution as the climate data (30 arc seconds, i.e., approximately 1 km at the equator) via cell center coverage. We thus produced a global raster grid containing all cells that are covered by any of the PAs we selected. Because small PAs may cover no cell centroids, 137,735 PAs remained after rasterization, which compose 26,038,594 cells and 20,658,583 km², that is 14% of the global terrestrial surface and 99.9% of the terrestrial area under protection.

The area and IUCN management category of each PA was retrieved from the WDPA. We consider PA area as a proxy for the amount of available resources for biodiversity to adapt to climate change within PAs. The IUCN management categories I to IV mean stricter protection, while categories V and VI allow for the sustainable use of natural resources, for example via silviculture and agriculture (Dudley, 2008). We applied the Terrain Ruggedness index (TR) as a measure of topographic heterogeneity. The TR index has also a resolution of 30 arc seconds (Amatulli et al., 2018). Planar area has a TR of 0m, whereas mountain areas can have a TR of up to 2,000 m in the Himalayas (Amatulli et al., 2018). The median of the TR values inside PAs was used to represent the topographic heterogeneity of each PA. The median is more robust against extreme values than the mean. The human footprint index 2009 is the most recent global indicator of human pressure and involves eight indicators of human land use (Venter et al., 2016a): population density, buildings, electric infrastructure, roads, railways, navigable waterways, cropland and pasture. We calculated the median human footprint of each PA by taking the median of the raster cell values that fall within each PA polygon. The irreplaceability index provided by Le Saout et al. (2013) reflects the conservation value of PAs in terms of the species diversity covered by PAs (Hoffmann, Beierkuhnlein, Field, Provenzale, & Chiarucci, 2018). This irreplaceability index represents the degree of overlap between each PA included in the WDPA (version October 2012) and the ranges of species on the IUCN Red List (Le Saout et al., 2013). The index involves ranges of 21,296 species: 6,240 amphibians, 9,793 birds and 5,263 mammals.

2.2 | Climate data

We used the WorldClim global climate data provided by Hijmans et al. (2005) including 19 bioclimatic variables with a resolution of 30 arc seconds. The 19 bioclimatic variables cover the full climate spectrum relevant for biodiversity, from annual trends (e.g., mean annual temperature and annual precipitation) to seasonal trends (e.g., annual range in temperature and precipitation) and extreme conditions (e.g., temperature of the coldest and warmest month, and precipitation of the wettest and driest quarters of the year). The 19 bioclimatic variables are listed in Table S.1. Each current bioclimatic variable represents the mean value across the years 1960 to 1990; each future bioclimatic variable represents the mean value across the years 2061 to 2080, that is of 2070. WorldClim's current climate data were generated by interpolating climate station data. WorldClim's future climate data were downscaled from the GCMs of the Coupled Model Intercomparison Project Phase 5 (Intergovernmental Panel on Climate Change, Fifth Assessment Report). We considered projected data for the Representative Concentration Pathways (RCP) 4.5 and 8.5 as well as 10 GCMs: BCC-CSM1-1, CCSM4, CNRM-CM5, GFDL-CM3, HadGEM2-AO, INMCM4, IPSL-CM5A-LR, MIROC5, MPI-ESM-LR and MRI-CGCM3. We selected the ten GCMs based on data availability (Hijmans et al., 2005) and dissimilarity between GCM outputs (Knutti, Masson, & Gettelman, 2013) to represent

a diversity of predictive skills for different geographical regions worldwide.

Since WorldClim does not provide a monthly time series of mean climate variables for the period 1960–1990, we used the monthly time series provided by Abatzoglou et al. (2018). These data represent locally observed interannual climate variability (ICV), that is the standard deviation of mean monthly climate data from 1960 to 1990. The ICV data have a resolution of 2.5 arc minutes, which is coarser than the resolution of WorldClim's mean climate data of current and future conditions (30 arc seconds). To assign the ICV data to the mean climate data of current and future conditions, we disaggregated the ICV data to the resolution of 30 arc seconds. Matching both datasets in this way is appropriate, because the WorldClim data were used as input data for the calculation of the ICV data by Abatzoglou et al. (2018). For the ICV data, we calculated the 19 bioclimatic parameters via the biovars function of R package dismo (Hijmans, Phillips, Leathwick, & Elith, 2017).

2.3 | Calculating climate change exposure

Climate change exposure can be measured by a variety of climate change metrics (Bellard et al., 2014; Dawson, Jackson, House, Prentice, & Mace, 2011; Li, Wu, et al., 2018). Climate change metrics are either calculated for a single locality, that is at the local level, or for a set of localities, that is at the regional level (Garcia et al., 2014). Here, we aim at analysing future climate change at the local level of PAs. Hence, we applied a local climate change metric. The most fundamental local climate change index is the climate anomaly metric, which is a measure of the magnitude of climate change at a given location indicating demographic population changes, particularly of species close to their climatic tolerance limits and with low adaptation capacity (Garcia et al., 2014). We refer to this local climate change index as climate change exposure.

We calculated the climate anomaly of each climate cell covered by a PA as the standardized Euclidean distance (SED) between independent climate variables of mean current (1960–1990) and mean future (2061–2080) climate conditions relative to the current ICV (1960–1990). The SED is a widely applied metric to estimate future climate anomaly (Bellard et al., 2014; Garcia et al., 2014; Mahony, Cannon, Wang, & Aitken, 2017; Ordonez et al., 2016; Williams et al., 2007). The standardization of climate distance by the ICV makes the SED robust against distance inflation, which occurs when interannual climate variability is high but not considered by the distance metric. The SED between the mean current and mean future climate at a given location will be lower under high ICV than under low ICV, all else being constant.

We computed the SED based on independent climate variables. By applying the SED to independent climate variables, we avoid variance inflation resulting from intercorrelated climate variables. To produce independent climate variables, we projected the mean current, mean future and ICV climate data onto the first five principal components of the ICV data. In other words, the axes of the PCA

represent the spatial variation of 1960–1990 interannual climate variability. Thus, the PCA well reflects the entire spatial and temporal variation of current climate conditions as a reference to measure future climate anomaly. We log₁₀-transformed the precipitation variables before we conducted the PCA to correct for nonlinearity. We thus reduced the 19 bioclimatic variables to five independent climate variables that were computationally practicable for us. The first five PCA axes account for 92% of the variation in the ICV data. The PC loadings are shown in Table S.1. The PC space was built on the ICV data of all climate cells covered by a PA ($n = 26,038,594$). In the PCA space with axes scaled to have unit variance, the SED equals the Mahalanobis distance (Mahony et al., 2017).

We defined the following parameters to calculate the SED: $[A]$ is a $(n \times K)$ matrix of n climate cells of K mean climate variables for the period 1960–1990. $[B]$ is a $(n \times K)$ matrix of n climate cells of K mean climate variables for the period 2061–2080. Each climate cell i thus represents a mean climate value a_{ik} and b_{ik} for a period of time and a climate variable k . $[C_i]$ is a $(T \times K)$ matrix of T annual mean observations (31-year time series) and K climate variables of a climate cell i . c_{itk} is the mean value of climate variable k at year t , i.e., of the ICV reference period 1960–1990. s_{ik} is the standard deviation of the ICV reference period at cell i in variable k across the 31 c_{itk} values. The SED of cell i based on independent climate variables can finally be calculated by $SED_i = \sqrt{\sum_{k=1}^K (b_{ik} - a_{ik})^2 / s_{ik}^2}$.

The fewer climate variables are considered in measuring climate distance, the lower is the risk of Type I inference error (i.e., overestimating climate distance) and the higher is the risk of Type II inference error (i.e., underestimating climate distance). Because five variables are relatively few to represent all dimensions of the climate space, our results may underestimate the climate change impact in regions of low climate anomaly (Mahony et al., 2017).

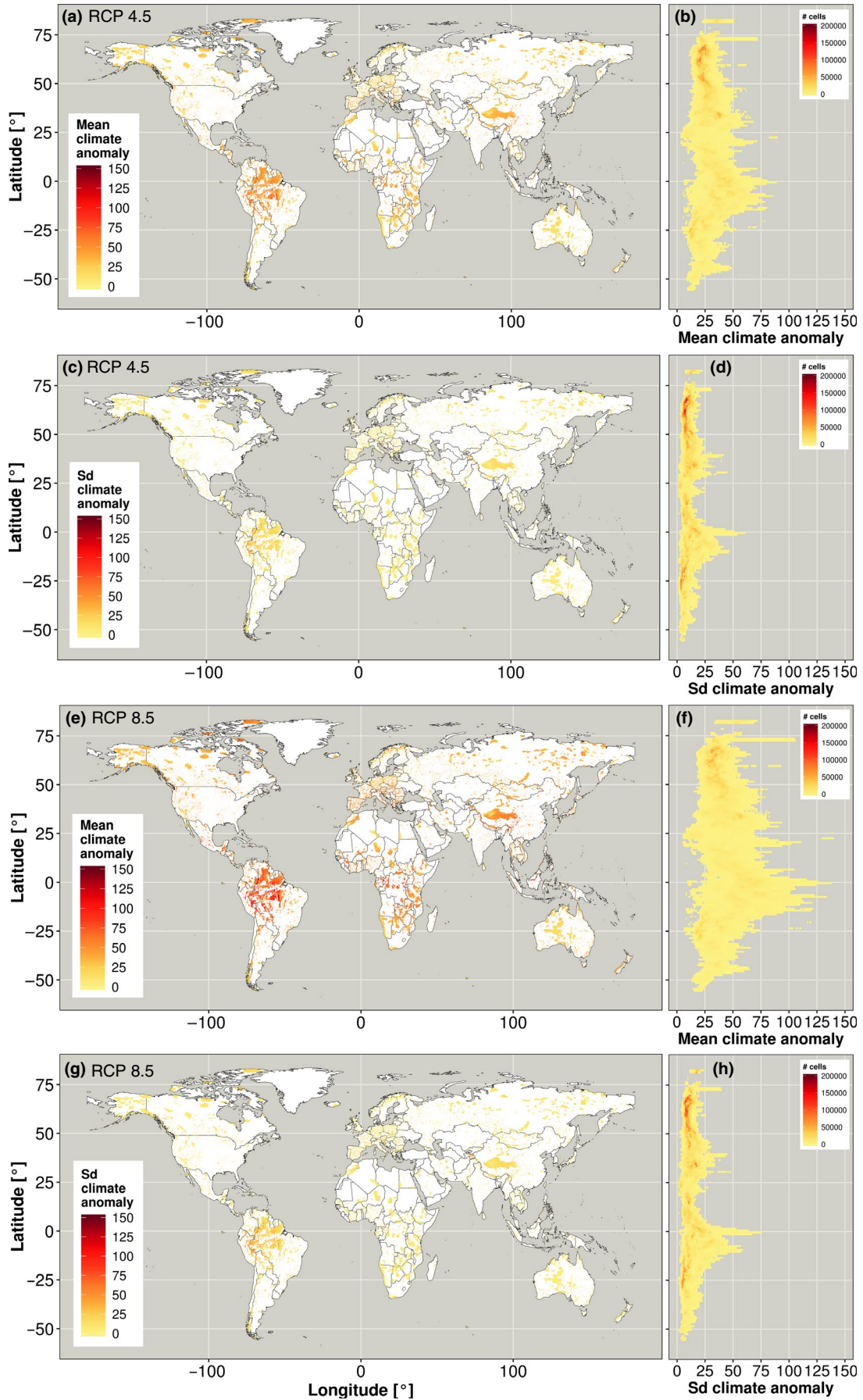
2.4 | Estimating climate change vulnerability of national PA estates

We consider the PA characteristics “area,” “elevation” and “terrain ruggedness” as indicators for the PAs’ capacity to buffer climate change impact. The larger the PA area, the more and more diverse resources are likely provided for species to adapt to climate change via migration and adaptation. High resource diversity is also found in PAs of mountain regions, that is of higher elevation and terrain ruggedness. Terrain ruggedness is a proxy for climate and habitat diversity, and thus of resource availability and the adaptation capacity

of PAs’ biodiversity to impacts of climate change (Carroll et al., 2017; Lawler et al., 2015). We further assume that an increasing human footprint decreases the adaptive and buffer capacity of PAs because high human footprints indicate landscape fragmentation and human land use, lowering habitat extent, connectivity and resource availability, and hindering species adapting and migrating to track suitable climate conditions (Di Marco, Venter, Possingham, & Watson, 2018; Venter et al., 2016b). “Irreplaceability” represents the PAs’ ecological importance for the conservation of globally threatened species (Le Saout et al., 2013).

We summarized the cell-based climate anomalies by individual PAs using the median, grouped the resulting median climate anomalies of each PA by country and correlated the median anomalies of PAs to other PA characteristics (see Section 2.1). We tested for correlations by using Pearson's correlation coefficient r and a modified t-test accounting for spatial autocorrelation (Dutilleul, Clifford, Richardson, & Hemon, 1993). The countrywide correlations between PAs’ climate anomalies and other characteristics add information about the climate change vulnerability of entire national PA estates. Climate change vulnerability of PAs increases with climate anomalies (i.e., climate change exposure), the human footprint and irreplaceability scores and decreases with PA area, elevation and terrain ruggedness. The magnitude of Pearson's correlation coefficient r and the p -value indicate the goodness of the fit of the country-specific relationships between climate anomalies and PA characteristics. Please note that the r and p -values cannot be compared between countries and do not represent the degree of climate change vulnerability of nationwide PA estates. However, the presence or absence of a significant correlation adds information about the climate change vulnerability of national PA estates. For example, a negative correlation between climate change exposure and PA area means that smaller PAs are more exposed to climate anomalies in the country, which is a valuable information for national conservation policy. To compare the median climate anomalies and other PA characteristics of national PA estates, we additionally performed a PCA. We used the PAs’ median climate anomaly, latitude, area, elevation, terrain ruggedness, the human footprint and irreplaceability as input data for the PCA ($n = 84,032$). We then calculated group centroids of the PAs’ seven PC scores using countries as grouping factors and show these centroids along the first two PCA axes. The first two PCA axes account for 48% of the variation in the PA data for RCP 4.5 and 8.5. The data on PAs’ median climate anomalies and characteristics are supplied under <https://doi.org/10.5061/dryad.f4qrfj6tf> and linked to the WDPA via the WDPA ID.

FIGURE 1 Predicted climate anomalies within the terrestrial PA estate for the year 2070 under the moderate emission scenario RCP 4.5 and the high emission scenario RCP 8.5. The climate anomaly represents the magnitude of future climate change at a given location. Climate anomalies were calculated for each grid cell of approximately 1km resolution, using the standardized Euclidean distance between the current and future climate conditions. Here, we show the mean and standard deviation (SD) of climate anomalies resulting from future climate projections of ten global climate models. The SD is a measure of the variation among future climate predictions. (a) Mean climate anomalies under RCP 4.5. (b) Density distribution of mean climate anomalies by degree latitude under RCP 4.5. (c) SD climate anomalies under RCP 4.5. (d) Density distribution of SD climate anomalies by degree latitude under RCP 4.5. (e) Mean climate anomalies under RCP 8.5. (f) Density distribution of mean climate anomalies by degree latitude under RCP 8.5. (g) SD climate anomalies under RCP 8.5. (h) Density distribution of SD climate anomalies by degree latitude under RCP 8.5



3 | RESULTS

The predicted mean climate anomaly under RCP 4.5 (Figure 1a,b) and 8.5 (Figure 1e,f) is highest inside tropical and subtropical PAs between -25° and 25° latitude, but also remarkably high in polar PAs at high northern latitudes. The geographical pattern of the standard deviation (Figure 1c,d,g,h) largely conforms to the pattern of the mean (Figure 1a,b,e,f): the larger the predicted climate anomaly is, the higher is the variation of the predictions.

From a national perspective, Albania, Bhutan, Bolivia, Bosnia and Herzegovina, Burundi, Cameroon, Central African Republic, Colombia, Congo, Equatorial Guinea, French Guiana, Guatemala, Guinea, Guyana, Macedonia, Malawi, Malaysia, Mexico, Montenegro, Nepal, Nicaragua, Palestine, Peru, Rwanda, Sierra Leone and Uganda are among the top ten countries containing PAs of any IUCN management category with on average highest median climate anomalies under RCP 4.5 (Figure 2); see Figure S.1 in Appendix S1 for RCP 8.5. Considering the global pool of PAs (see "Global" in Figure 2), the median climate anomalies of PAs marginally differ between management categories.

At the global scale, the median climate anomalies of PAs under RCP 4.5 correlate positively with PA area ($r = .05$, $p < .001$), elevation ($r = .40$, $p < .001$), terrain ruggedness ($r = .32$, $p < .001$) and irreplaceability ($r = .06$, $p < .001$) (see "Global" in Figure 3). There is no significant global correlation between climate anomaly and the human footprint under RCP 4.5; see Figure S.2 in Appendix S1 for results of RCP 8.5. Those worldwide correlations were weak. The country-scale relationships are on average stronger than the global relationships and even change direction. They differ considerably between countries.

The vectors of the PA characteristics in the two-dimensional PCA space (Figure 4) also show a clear correlation between elevation, terrain ruggedness and median climate anomaly; between latitude and the human footprint; and between area and irreplaceability; see Figure S.3 in Appendix S1 for results of RCP 8.5. The PC loadings reveal the contributions of PA characteristics to the PCs (in decreasing order of importance for PC1): elevation (PC1: -0.57 , PC2: -0.17), terrain ruggedness (PC1: -0.54 , PC2: -0.24), median climate anomaly (PC1: -0.45 , PC2: -0.15), human footprint (PC1: 0.30 , PC2: -0.18), latitude (PC1: 0.24 , PC2: -0.24), irreplaceability (PC1: -0.15 , PC2: 0.61) and area (PC1: -0.13 , PC2: 0.66). The first PCA axis is mostly spanned by elevation, terrain ruggedness, median climate anomaly, the human footprint and latitude, while the second PCA axis correlates mostly with area and irreplaceability. PC1 and PC2 can explain 30.2% and 17.6% of the variance in the PA

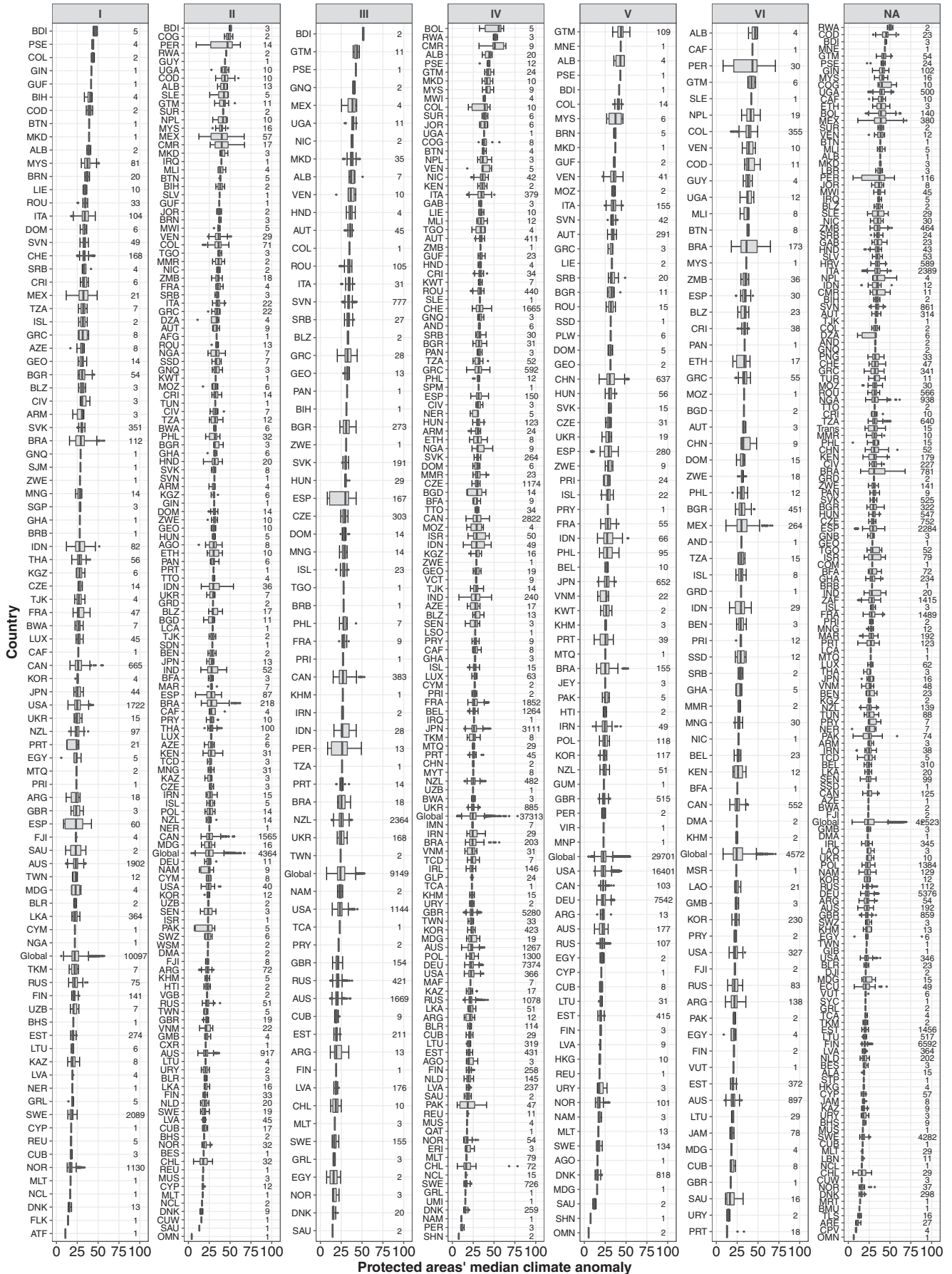
data, respectively. The national PA estates that are most associated with high elevation, terrain ruggedness and median climate anomaly are Bhutan, Rwanda, Nepal, Afghanistan and Kyrgyzstan. High irreplaceability and large area of PAs are especially found in Algeria, Niger, Venezuela, Mauritius and Botswana. Many tropical countries such as Ecuador, Bolivia, Peru and Colombia contain PAs of high elevation, terrain ruggedness, median climate anomaly, irreplaceability and large area. PA estates of most European countries are only strongly related to large human footprints.

4 | DISCUSSION

We found hotspots of predicted climate anomaly in tropical, subtropical and polar PAs. Our climate anomaly metric integrates future changes of multiple thermal and hydraulic variables. Previous investigations have disentangled the roles of temperature and precipitation in forming these climate change hotspots: temperature change is projected largest in tropical regions, while precipitation change might be greatest in polar regions (García-López & Allué, 2013; Garcia et al., 2014; Li, Kou, et al., 2018). We predicted high-resolution patterns of climate anomaly inside PAs worldwide, which geographically agree with other global climate predictions based on different methods and coarser spatial resolution (Williams et al., 2007; Beaumont et al., 2011; García-López & Allué, 2013; Garcia et al., 2014; Ordonez et al., 2016; Li, Wu, et al., 2018; Li, Kou, et al., 2018).

Our study adds to previous research in climate change of the global PA estate by applying a fundamental climate change metric to the finest spatial resolution for which global climate data are available. The SED is sensitive to interannual climate variability, and, when applied to independent climate variables, it also avoids variance inflation resulting from intercorrelated climate variables (Mahony et al., 2017). Our findings particularly complement another global analysis of climate change within PAs using a similar set of PAs as well as climatic and environmental data (Hoffmann et al., 2019). Here, we predict local climate anomalies to be highest in tropical, subtropical and polar PAs, while Hoffmann et al. (2019) predict temperate PAs to experience highest areal changes of climate zones, because temperate PAs are relatively small and contain low topographic heterogeneity. This is also in line with Loarie et al. (2009), who forecast that climate change velocities will probably make small PAs in the Mediterranean biome and in temperate coniferous forests lose largest proportions of their current climate conditions. In contrast to the pure numbers of changes of climate conditions in

FIGURE 2 Predicted climate anomalies (2070, RCP 4.5) of PAs grouped by country and IUCN management category; see Figure S.1 for results of RCP 8.5. We summarized the mean climate anomalies (Figure 1) for each PA using the median. The IUCN management categories from I to VI cover a gradient of human integration, from strict human enclosure to sustainable human land use, respectively. The black numbers represent the number of PAs within the countries and IUCN management categories. "NA" means no management category was available. The boxplots were ordered by decreasing median. The limits of the grey box show the lower and upper quartiles, that is the interquartile range. The whiskers extend to the lowest and highest values within 1.5 times the interquartile range. The black dots indicate outliers beyond the whiskers. The alpha-3 country codes are given (i.e., ISO 3166). "Global" composes all PAs, while "Trans" refers to transboundary PAs



Protected areas' median climate anomaly

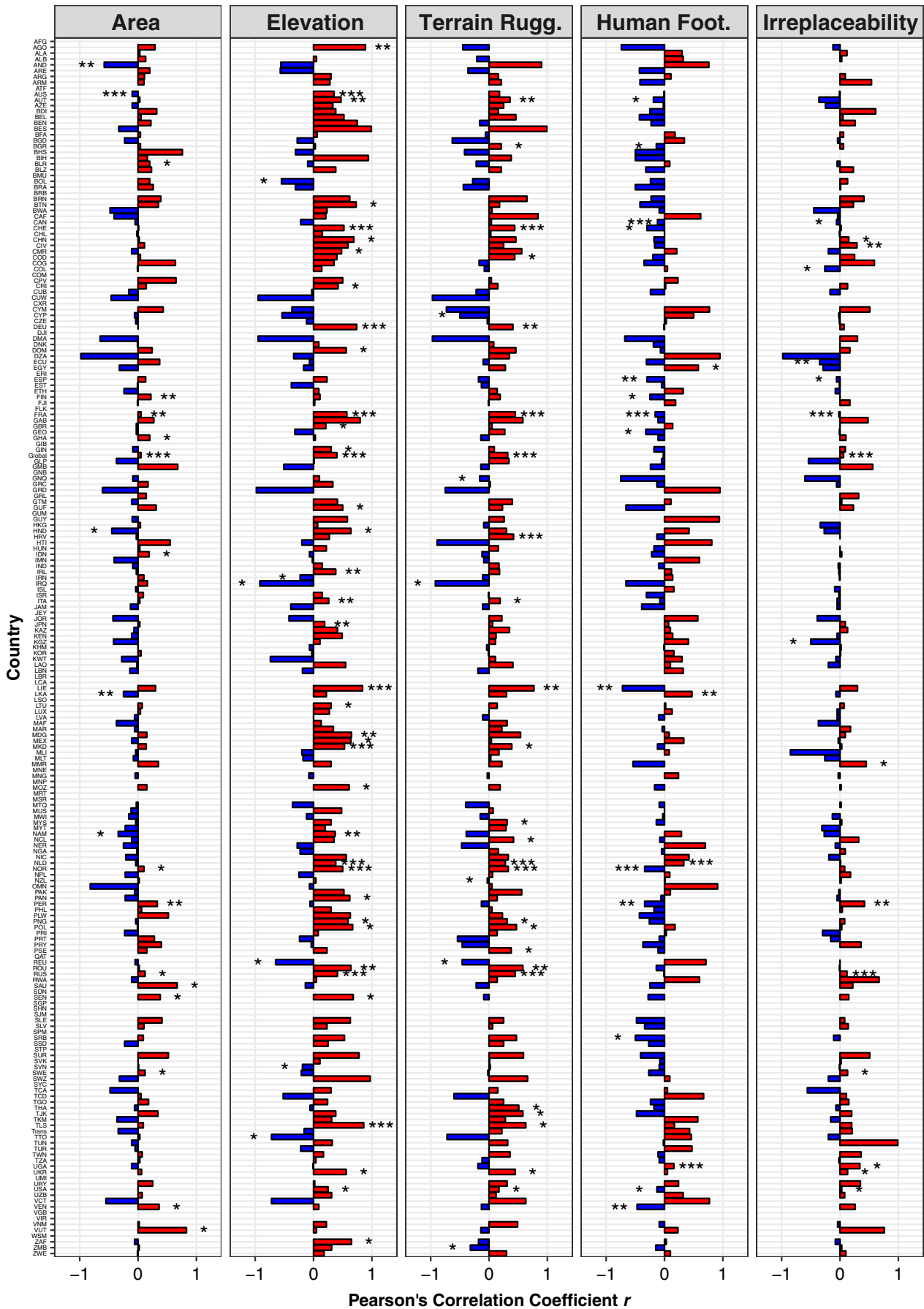


FIGURE 3 Global and country-specific correlations of the PAs' median climate anomalies (2070, RCP 4.5) with PA characteristics; see Figure S.2 for results of RCP 8.5. The PA characteristics “area,” “elevation” and “terrain ruggedness” indicate the PAs' capacity to buffer the climate change impact; “irreplaceability” represents the PAs' importance for the conservation of globally threatened species. By relating the predicted climate anomalies to the PA characteristics at the country level, we provide additional information about the climate change vulnerability of national PA estates. PAs are assumed to be particularly vulnerable to climate change when the predicted climate anomalies, the human footprint and irreplaceability are high, while the area, elevation and terrain ruggedness are low. Bars reflect Pearson's correlation coefficients r ; red for positive and blue for negative coefficients. Asterisks represent the significance level considering spatial autocorrelation ($*p \leq .05$, $**p \leq .01$, $***p \leq .001$), while no asterisk means non-significant correlation ($p > .05$). The alpha-3 country codes are shown (i.e., ISO 3166). “Global” composes all PAs, while “Trans” refers to transboundary PAs

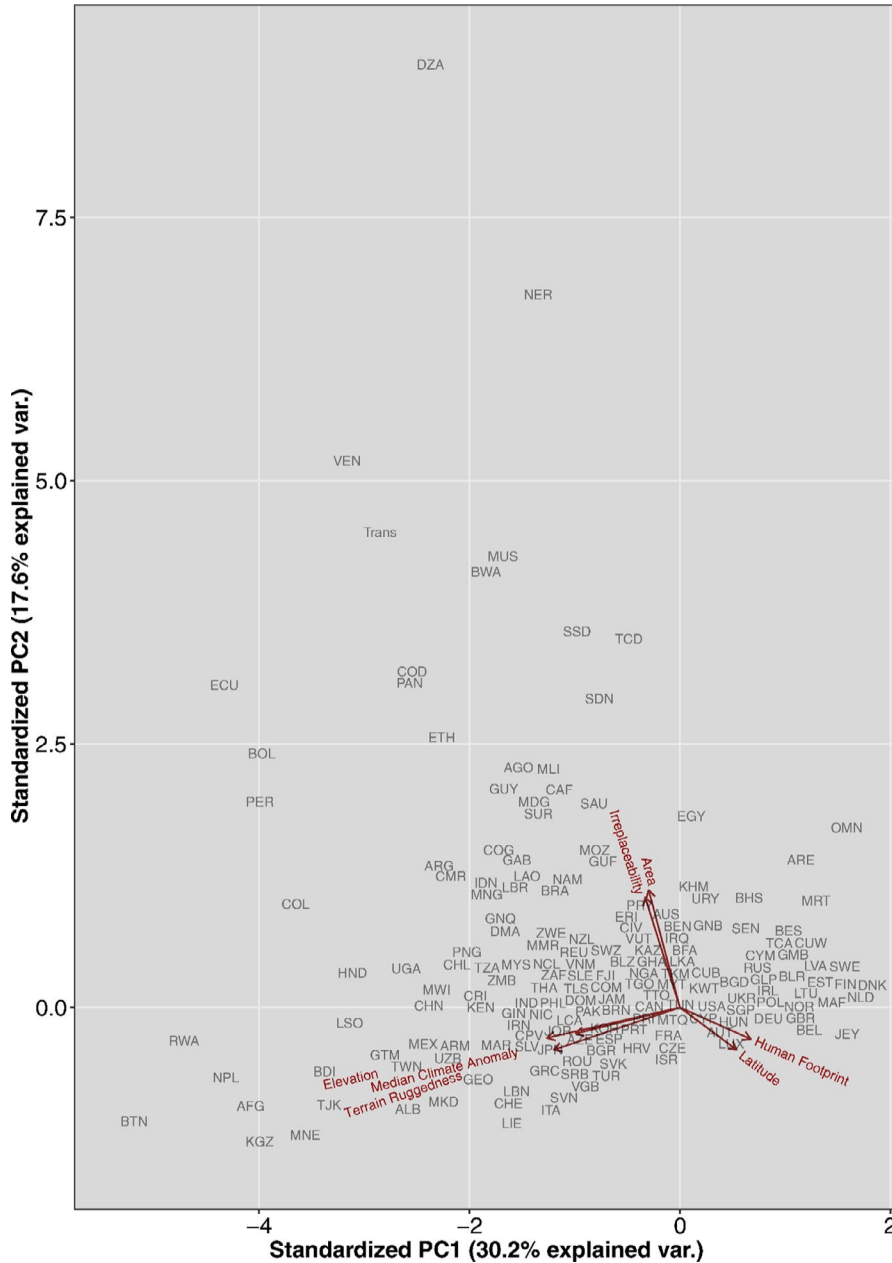


FIGURE 4 Principal components analysis of the PAs' median climate anomalies (2070, RCP 4.5) and other PA characteristics grouped by countries; see Figure S.3 for results of RCP 8.5. The PA characteristics “area,” “elevation” and “terrain ruggedness” indicate the PAs' capacity to buffer the climate change impact; “irreplaceability” represents the PAs' importance for the conservation of globally threatened species. By relating the predicted climate anomalies to the PA characteristics at the country level, we provide additional information about the climate change vulnerability of national PA estates. PAs are assumed to be particularly vulnerable to climate change when the predicted climate anomalies, the human footprint and irreplaceability are high, while the area, elevation and terrain ruggedness are low. The alpha-3 country codes are shown (i.e., ISO 3166). “Trans” refers to transboundary PAs

PAs (Hoffmann et al., 2019; Loarie et al., 2009), the high-resolution map of local climate anomalies in the present study shows climate anomaly hotspots within PAs and can consequently guide spatial conservation management even inside individual PAs. Since conservation policy is mainly adopted at the national and smaller level, it is also reasonable to highlight national responsibilities (applied here) in

addition to biogeographical regions (Hoffmann et al., 2019; Loarie et al., 2009) for climate-smart conservation recommendations. PAs are the cornerstones of conservation effort, but extending our high-resolution approach to the entire terrestrial surface would be extremely useful for environmental management worldwide. We highly recommend to follow this future perspective, although the

computational burdens are enormous and the computational capacities required are hardly available.

Climate anomalies imply various consequences for biodiversity and ecosystems. Given that all other factors are constant, high climate anomalies are more likely to modify biodiversity and ecosystems than low anomalies. The impact of climate anomalies depends on the magnitude of anomaly and on the ecological systems themselves. In general, low climate anomalies suggest locations in which present biodiversity and ecosystem functioning is likely to persist under ongoing climate change. Novel species assemblages and interactions are expected to emerge under high climate anomalies (Ordóñez et al., 2016). High local climate anomalies can lead to physiological, morphological and behavioural changes of individuals and demographic changes of populations (Peñuelas et al., 2013). Species living close to their climatic tolerance limits and having low adaptation capacity are most affected by climate anomalies (García et al., 2014), potentially leading to population declines (Foden et al., 2007) and local extinctions (Sinervo et al., 2010). Local climate anomalies can also positively affect biodiversity. Rising temperatures cause increasing plant diversity in high latitudes (Hill & Henry, 2011) and elevations (Steinbauer et al., 2018). The fitness of mountain lizards can increase due to warming (Chamaille-Jammes, Massot, Aragon, & Clobert, 2006). High-latitude PAs are projected to gain biodiversity under global warming (Berteaux et al., 2018). In Kruger National Park, climate change is expected to increase plant productivity and thus elephant populations (Scheiter & Higgins, 2012).

Climate anomalies cause new, non-analogue communities, that is communities without current analogues, because species differ in their ability to respond to climate change via dispersal, range dynamics and biotic interactions (Williams & Jackson, 2007). The functioning of such novel communities remains largely unknown (Hobbs et al., 2006). Impacts of recent climate change onto ecosystem functioning and services are manifold (Scheffers et al., 2016). Mascaro et al. (2012) show that non-native species led to increased productivity, carbon storage and nutrient cycling in lowland Hawaiian rain forests. In contrast, forest carbon storage is decreasing with increasing frequency and intensity of droughts, fires, windthrow and insect outbreaks (Holmgren, Hirota, van Nes, & Scheffer, 2013; Seidl, Schelhaas, & Lexer, 2011).

PAs are assumed to be particularly vulnerable to climate change when the predicted climate anomalies, the human footprint and irreplaceability are high, while the area, elevation and terrain ruggedness are low (Hoffmann et al., 2019). We revealed that increasing climate anomalies are, at the global scale, related to increasing elevation, terrain ruggedness, PA area and irreplaceability. We do not want to overestimate these weak global relationships. Some of the country-specific relationships were, however, strong, providing valuable information about the climate change vulnerability of national PA estates. When management resources are limited, national authorities should prioritize and pro-actively improve the characteristics of their national PA estates that are strongly associated with high climate change exposure and indicate climate change vulnerability. Generally, large PA area, high terrain ruggedness and high

irreplaceability are beneficial for conservation under climate change exposure, while large human footprints are detrimental. For example, if climate change exposure negatively correlates with PA area, elevation and terrain ruggedness, but positively with irreplaceability and the human footprint, climate-smart conservation management should prioritize the smaller PAs at lower elevation to become less climate-vulnerable, for example by expanding and connecting PA area, reducing human land use and restoring habitat of threatened biota (i.e., increasing irreplaceability). However, some characteristics of established PAs cannot simply be improved by conservation management to decrease climate change vulnerability. While reducing human footprints, restoring habitat of endangered species and expanding PA area might be feasible, terrain ruggedness can hardly be modified at larger scales. Moreover, not each particular conservation objective of individual PAs might be supported by large area, high terrain ruggedness, high irreplaceability and small human footprints. This is why a single vulnerability index for each PA that is a composite of these multiple PA characteristics would not be very useful for individual PA management.

Nevertheless, conservation planning and management are certainly more challenging in areas where climate anomaly is higher, all else being equal. We still warn of naively applying common management responses to climate change. They involve contextual drawbacks since they are biased towards specific species, ecosystems and regions (Felton et al., 2009). Management responses must be developed in the context of individual PAs because the climate predictions, their uncertainties (Belote et al., 2018), ecosystem intactness (Watson, Iwamura, & Butt, 2013), conservation targets (Belote et al., 2017), the conservation capacity of land (Gillson, Dawson, Jack, & McGeoch, 2013), the management resources available (Wintle et al., 2011) and the risks of management actions (Ando et al., 2018) differ between PAs. Climate-smart management guidelines generally aim at the persistence and resistance of present biodiversity despite climate change, or at the adaptation of biodiversity to climate change (Gross et al., 2017). Reasonable management interventions can vary from low intensity, for example monitoring, to high intensity, for example assisted migration and restoration (Dawson et al., 2011; Gillson et al., 2013). Appropriate management practice may be conservative, innovative, flexible, reversible or experimental (Belote et al., 2018). Alternatively, "no-regret" strategies could be applied, which intend to achieve conservation benefits irrespective of climate change (Hallegatte, 2009). In any case, adaptive PA management is a promising tool to ensure the enduring effectiveness and efficiency of PAs in the light of uncertain future developments (Rannow et al., 2014).

Our methodological approach implies assumptions that limit the implications of our findings. The climate anomaly index is the most fundamental indicator of climate change exposure at the local level, but cannot reveal the entire complexity of biodiversity and ecosystem responses to climate change at the local and regional level (García et al., 2014). This local indicator does, for instance, not reflect shifts in seasonal climate nor changes in climate extremes, which are both extremely relevant for biodiversity, ecosystem functioning and

services (Pecl et al., 2017; Scheffers et al., 2016). However, seasonal climate shifts and changing climate extremes are hardly predictable for the local level but global extent. Ideally, future studies would incorporate multiple climate change metrics of the local and regional level (Garcia et al., 2014) to understand the full potential of climate change impact.

Further, the predictive skills of GCMs differ between geographical regions (Bring et al., 2019). For our global assessment including national perspectives, we selected ten GCMs based on dissimilarity between GCM outputs (Knutti et al., 2013) to represent a diversity, and thus complementarity, of predictive skills. We then estimated the variation among future climate projections, but an uncertainty of the predictions remains that is inherent in the climate models and practically incalculable. Especially in mountain regions with a low density of climate stations (Hijmans et al., 2005), the quality of the WorldClim data is poor (Bobrowski & Schickhoff, 2017). Accordingly, our results must be carefully interpreted for those regions. Moreover, the climate data resolution of approximately 1 km do not consider microclimate, which can buffer climate change impact (Suggitt et al., 2018). Interacting effects between climate change and other threats to biodiversity and ecosystem functioning (e.g., invasive species) are neglected as well. Also, the human footprint index from 2009 and the irreplaceability index from 2012 are out of date and newer version are not available. Nevertheless, given that human land cover (Venter et al., 2016b) and species loss (Johnson et al., 2017) are increasing globally, our application of the human footprint and irreplaceability index may even underestimate the climate change exposure of PAs.

In addition, the climate change vulnerability of biodiversity, ecosystem functioning and services depend not only on climate change exposure, adaptive capacity and ecological importance, but also on resistance (or sensitivity, i.e., ability to remain in the original state despite change) and resilience (i.e., ability to return to the original state after change) (Dawson et al., 2011; Li, Wu, et al., 2018). We did not incorporate resistance and resilience measures since there are no appropriate datasets available yet for the local level but global extent. A new, very comprehensive, global and high-resolution (ca. 1 km) bioclimatic resilience index is in progress though (Ferrier, Harwood, Ware, & Hoskins, 2019).

Eventually, we delivered a simplistic assessment of the climate change exposure and vulnerability of the international PA estate that is intuitive and can thus be easily understood by stakeholders and policymakers. This study is to inform national and local authorities of the potential climate change impact on PAs. This work does, however, not reveal the complex responses of conservation objectives to climate change and other factors within global PAs, which is important to derive well-grounded management recommendations for individual PAs under rapid environmental changes worldwide. Such a comprehensive analysis could be the foundation of a globally coordinated and adaptive PA planning and management system in the future. We perceive the development and application of a global adaptive PA management system as a major future task to reach global conservation and sustainability targets, and safeguard human well-being of generations to come.

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CONFLICT OF INTEREST

The authors declare no conflicts of interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data used in this study are open. Data references are given in the main text. The data we produced are available online at <https://doi.org/10.5061/dryad.f4qrfj6tf>.

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BIOSKETCHES

Samuel Hoffmann is fascinated by macroecological patterns and dedicated to conservation biogeography. In his PhD, Samuel investigated the effectiveness of protected areas in conserving biodiversity under anthropogenic threats.

Carl Beierkuhnlein focuses, among other topics, on the role of biodiversity for ecosystem functioning, on the explanation of spatial patterns of biodiversity and on biogeography in the face of global change.

Author contributions: S.H. conceived the ideas, conducted the analyses and led the writing; C.B. acquired the funding, supervised the project and contributed to the writing.

SUPPORTING INFORMATION

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

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