Global Ecology and Conservation 25 (2021) e01445

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Review Paper

Topographic diversity as an indicator for resilience of terrestrial protected areas against climate change

Alexandra Lawrence [a, *], Samuel Hoffmann [a], Carl Beierkuhnlein [a, b, c]

[a] *Department of Biogeography, University of Bayreuth, 95447, Bayreuth, Germany*
[b] *BayCEER, Bayreuth Center for Ecology and Environmental Research, 95440, Bayreuth, Germany*
[c] *GIB, Bayreuth Institute for Geography, 95440, Bayreuth, Germany*

ARTICLE INFO

Article history:
Received 26 May 2020
Received in revised form 24 December 2020
Accepted 24 December 2020

ABSTRACT

Habitat loss from unrelenting human pressure is causing an unprecedented decline in global biodiversity. Protected areas (PAs) are meant to counteract loss and fragmentation of ecosystems and today PAs form the backbone of conservation strategies worldwide. However, anthropogenic climate change can severely reduce the effectiveness of PAs. Conservation professionals are in need of concrete spatial information on climatic changes within PAs in order to put forward practicable strategies to safeguard PA effectiveness in the face of climate change. In this study, we take advantage of openly accessible data on the disappearing climate index (DCI) to examine which PA characteristics are linked to climate change resilience on a global scale. DCI provides a measure of the relative area (percent of total area) within a PA that exhibits certain climatic conditions that will either disappear entirely or move outside the boundaries of the PA by the year 2070. Our results show that topographic diversity is highly correlated with reduced climate change impacts in PAs worldwide. We analyzed three different PA characteristics representing topographic diversity: PA area, maximal elevational difference (MED) and median terrain ruggedness (TR). All three characteristics are highly correlated with a decrease in the disappearing climate index (DCI). These results hold true across localities and even PA management practices. IUCN management category IV (habitat/species management area) and V (protected landscape/seascape) exhibit on average the highest DCI values. As an indicator for PA resilience under climate change, topographic diversity can be assessed easily through publicly available data and remote sensing products. This ease-of-use leaves topographic diversity standing in marked contrast to overall environmental diversity as an actionable conservation metric. Of course, topographic diversity alone is not a sufficient criterion on which to base conservation decisions. However, neither should the potential usefulness of topographic diversity be underestimated. As an actionable and complementary metric in combination with biological information topographic diversity can be an exceptional tool for decision making by PA managers, conservation practitioners and politicians.

---

* Corresponding author. University of Bayreuth, Universitaetsstr 30, 95447, Bayreuth, Germany.

E-mail addresses: alawrence.biogeography@gmail.com, alexandra.lawrence@uni-bayreuth.de (A. Lawrence), samuel.hoffmann@uni-bayreuth.de (S. Hoffmann), carl.beierkuhnlein@uni-bayreuth.de (C. Beierkuhnlein).

https://doi.org/10.1016/j.gecco.2020.e01445

1. Introduction

Anthropogenic pressure and the associated loss and fragmentation of natural habitats are the primary cause of species extinctions and the rapid decline in biodiversity worldwide (Millennium Ecosystem Assessment, 2005; IUCN 2010; Cardinale et al., 2012; Crooks et al., 2017). To counteract these negative developments, protected areas (PAs) function as the backbone of conservation strategies (Gaüzère et al., 2016; Hoffmann et al., 2018; Pimm et al., 2014) by preserving valuable habitat for rare and threatened species (Gray et al., 2016; Langdon and Lawler, 2015; Nila et al., 2019).

However, anthropogenic climate change can severely reduce the effectiveness of PAs as nature conservation tools (Hoffmann and Beierkuhnlein, 2020; Hoffmann et al., 2019; Johnston et al., 2013). Climate change is projected to influence all ecosystems worldwide (Scheffers et al., 2016) and future persistence of suitable climatic conditions is critical for species survival (Hannah et al., 2007; Loarie et al., 2009). In many cases, climate change will lead to shifts in species distributions by compelling migration poleward and towards higher elevations as species attempt to track suitable climatic conditions (Berteaux et al., 2018; Chen et al., 2011; Root et al., 2003; Scheffers et al., 2016; Thomas and Gillingham, 2015). In contrast to species distributional ranges, PAs are static and fixed in space. While PAs may be effective in limiting threats to biodiversity caused by habitat loss and fragmentation, their inflexibility in the face of species' mobility could severely hinder their overall effectiveness in reducing extinctions tied to climate change (Araújo et al., 2011; Gaüzère et al., 2016; Hoffmann et al., 2019) Whether existing protected areas will remain effective as the climate changes is a key question that needs to be answered to develop robust long-term conservation strategies (Johnston et al., 2013; Lehikoinen et al., 2019).

A number of recent studies have dealt with the challenges PAs face under climate change and consider strategies PA managers might take to adapt their conservation efforts (Batllori et al., 2017; Hannah et al., 2007; Langdon and Lawler, 2015; Monzón et al., 2011). Unfortunately, scientific recommendations for effective PA management are often too theoretical or vaguely defined to be implementable in practice (Halpin, 1997; Monzón et al., 2011). Even well-structured recommendations are often based on little or no scientific data. As result, these recommendations can be prohibitively difficult to apply, are targeted to certain areas (Langdon and Lawler, 2015) or are based on a limited sample of case studies (Monzón et al., 2011), if any at all.

To determine which PA characteristics lead to a reduced effect of changing climatic conditions, much more information on interactions between projected climate scenarios, PA characteristics, and adaptive management strategies is needed. Information of this kind has long been unavailable on a global scale. Today, however, widely accessible future climate projections, improved climate modelling techniques, global satellite data and more open-access platforms for sharing administrative and scientific data, create the opportunity to empirically test previously stated assumptions about the relationship between PA characteristics and climate change.

It has been suggested that small PAs are more vulnerable to climatic changes than large ones, leading to greater loss of species and ecological systems as PA area decreases (Hoffmann et al., 2019; Langdon and Lawler, 2015). Therefore, it is recommended that PA area should be as large as politically feasible (Halpin, 1997; Lemieux et al., 2011).Both environmental diversity and species diversity can buffer against climate change and in particular against climatic extremes (Ackerly et al., 2010; Isbell et al., 2015; Lawler et al., 2015). Hence, environmentally heterogeneous PAs are expected to allow for adaptation or migration of species under climate change (Thomas and Gillingham 2015). While PAs located in mountainous regions are expected to experience some of the largest climatic changes (Monzón et al., 2011; Root et al., 2003), they also cover some of the most diverse environmental conditions (Carroll et al., 2017; Langdon and Lawler, 2015). Mountainous PAs that show a high topographic heterogeneity can create a high environmental diversity due to – for example - differences in solar radiation, precipitation and wind exposure (Scherrer and Körner, 2011). Heterogeneity in elevation, aspect, and slope result in a diversity of climates such that species can make smaller spatial adjustments to track suitable climatic conditions (Carroll et al., 2017; Littlefield et al., 2017). In addition, mountainous landscapes are especially prone to natural disturbance events like mud flows or avalanches. These disturbances can remove inertia from a system (e.g. non-reproductive long-lived individuals) and support accelerated establishment of new species and structures, enabling species populations to adapt more quickly to changing climatic conditions (Jentsch and Beierkuhnlein, 2003). Diversity in environmental conditions can indicate the resilience and adaptive capacity of PAs in the face of climate change (Loarie et al., 2009; Langdon and Lawler 2015; Lawler et al., 2015). High topographic heterogeneity within a PA also increases the likelihood that shifting climatic conditions still remain within the boundaries of PAs (Thomas and Gillingham 2015).

As climate changes, certain climatic conditions hitherto found within a given PA may disappear. Hoffmann, Irl, and Beierkuhnlein (2019) previously calculated the percentage of PA surface with disappearing climate conditions expressed by the so-called "disappearing climate index" (DCI). DCI closely relates to climate change velocity in that both indices assess the speed of climate change for certain areas in a way that is relevant to the ability of species to track their suitable climates. Climate change velocity measures the instantaneous local velocity (km yr^{-1}) along Earth's surface needed to maintain constant temperatures (Loarie et al., 2009). In other words, it measures the speed at which organisms would have to migrate on a 2D surface to keep up with climate change. DCI measures the percent of total area within each PA that exhibits a loss of certain climatic conditions. In that sense DCI is easier to apply and to interpret for PAs. Hence, DCI as an indicator for PA resilience against climate change can be a useful tool for conservation managers, when combined with biological information on species and habitats.

The DCI was calculated for all terrestrial PAs and is publicly available (Hoffmann et al., 2019). In our study, we hypothesize that (a) PAs which cover larger areas will show a decrease in DCI, (b) PAs with a high maximal elevational difference (MED) will show a decrease in DCI and (c) PAs with an increased terrain ruggedness (TR) will show a decrease in DCI. Further, we hypothesize that MED and TR differ in their strength affecting DCI within PAs. While TR measures a median of small-scale elevational diversity, MED simply measures the difference between the highest and the lowest elevation within a PA. Hence, especially for bigger PAs MED is measured on a larger scale compared to TR. The differing scales at which MED and TR are calculated affect their relationships with environmental diversity. We expect that MED – the large-scale measurement – correlates more strongly with DCI than TR. It is known that climatic data is correlated with elevational data at local and landscape scale. Elevational data is even built into climate data projections. Yet we believe that quantification of the relationship between climatic and elevational data across almost all of the world's PAs is useful since it has never been done with such scope and clarity.

Beyond revealing general correlations between PA characteristics and DCI we also analyzed these correlations separately for different PA management categories. The IUCN divides all global PAs into seven different management categories (Table 1) (Dudley, 2008; IUCN and UNEP 2018).

We hypothesize no strong differences in DCI among management categories since DCI is generally driven by large-scale geographic patterns and therefore it is independent of individual PA management. However, it is conceivable that some types of PA are on average more topographically diverse than others. For example, establishing PAs in mountainous landscapes is often easier and cheaper since there is less pressure to use this land for agriculture or urban expansion. In addition, especially scenic mountain landscapes often attract tourists. This may be more relevant to some IUCN management categories than others. Hence, we hypothesize higher topographic diversity among strictly protected PAs (IUCN Ia, Ib and II) linked to lower DCI values.Analysing IUCN management categories separately can demonstrate which types of PAs are more or less affected by climate change and where conservation efforts should be focussed.

2. Methods

2.1. Protected area data

This study is based on the dataset produced by Hoffmann et al. (2019). The dataset is derived from the World Database on Protected Area (WDPA) (IUCN and UNEP 2018). The original WDPA dataset was condensed to include only terrestrial PAs. Hoffmann et al. (2019) then rasterized the original PA polygons into a dataset of the same resolution (30 arcseconds, approx. 900 m at the equator) as the climate data used for identification of the areas experiencing disappearing climate conditions for each PA. Rasterization was processed via cell-center coverage. In other words, PA polygons were only included in the final dataset when the center point of a 30 arcsecond-sized raster cell falls within that polygon. Very small PAs and PAs with elongated shapes are more likely to elude the center point of any raster cell and therefore were not included in the final dataset. While this procedure was necessary in order to calculate reliable DCI values, it might distort the results since very small PAs are expected to experience high DCI values. After processing, a total of 137,432 PAs remained, comprising a total area of 20,658,583 km^2 (This is 14% of the global terrestrial surface and 99.9% of total PA-status area as of January 2018). For more details see Hoffmann et al. (2019).

2.2. Disappearing climate index

We used the open access (https://doi.org/10.6084/m9.figshare.9804350) disappearing climate index (DCI) calculated for the local scale by Hoffmann et al. (2019). This index measures the proportion of 30 arcsecond cells within a given PA that

Table 1
IUCN management categories. Adapted from Dudley (2008).

IUCN category	Name	Description
Ia	Strict nature reserve	Human visitation, use and impacts are strictly controlled and limited to ensure protection of the conservation values.
Ib	Wilderness Area	Usually large unmodified or slightly modified areas, retaining their natural character and influence, without permanent or significant human habitation.
II	National park	Large natural or near-natural areas protecting large-scale ecological processes with characteristic species and ecosystems, which also have environmentally and culturally compatible spiritual, scientific, educational, recreational and visitor opportunities
III	Natural monument or feature	Areas set aside to protect a specific natural monument, which can be a landform, sea mount, marine cavern, geological feature such as a cave, or a living feature such as an ancient grove
IV	Habitat/species management area	Areas to protect particular species or habitats, where management reflects this priority.
V	Protected landscape or seascape	Areas where the interaction of people and nature over time has produced a distinct character with significant ecological, biological, cultural and scenic value: and
VI	PAs with sustainable use of natural resources	Areas which conserve ecosystems, together with associated cultural values and traditional natural resource management systems. Generally large, mainly in a natural condition, with a proportion under sustainable natural resource management

contain climate classes which will not exist within the same PA in the future. In other words, the DCI provides a measure of the relative area (percent of total area) within each PA that exhibits certain climatic conditions that will either disappear entirely or move outside the boundaries of the PA in the future. To calculate the DCI, Hoffmann et al. (2019) used global climate data with a resolution of 30 arcseconds provided by the WorldClim project (Hijmans et al., 2005). Future climate data were downscaled from ten different general circulation models (GCMs) for the Representative Concentration Pathways RCP 4.5 covering the year 2070, i.e. the average of period 2061–2080. For further details on the calculation of DCI see Appendix A.

2.3. Protected area characteristics

To identify PA characteristics that are especially associated with climate change inside PAs, we related three distinct PA characteristics – PA area, maximal elevational difference, and terrain ruggedness - to the DCI. PA area is given by the WDPA dataset. Maximal elevational difference (MED) was calculated as the absolute difference between maximal elevation and minimum elevation for each PA. Maximal and minimum elevation data was obtained from two separate global raster datasets by Amatulli et al., (2018). These two remote sensing products (maximal elevation and minimum elevation) are based on 90 m elevation data from the Shuttle Radar Topography Mission and have a final resolution of 30 arcseconds (Jarvis et al. 2008; Reuter, Nelson and Jarvis 2007). We than calculated the highest minus the lowest point of each PA at 30 arcsecond resolution. Terrain ruggedness index (TR) of each PA is given by the original dataset of Hoffmann et al. (2019) (https://doi.org/10.6084/m9.figshare.9804350). This data was extracted from open-source digital elevation model data provided by Amatulli et al. (2018). It is based on 90 m elevation data and has a final resolution of 30 arcseconds. TR was calculated as the mean of the absolute differences in elevation between a cell within a PA and its eight adjacent cells inside the PA. It is important to note that a resolution of 30 arcsecond will show variation in grain size with latitude, which can bias or distort TR values to some degree. Hoffmann, Irl, and Beierkuhnlein (2019) assigned each PA one TR value by calculating the median of all TR values inside a single PA. For further details see Hoffmann et al. (2019).

2.4. IUCN management categories

We further analyzed the correlations between PA characteristics and DCI for separate PA management categories. The IUCN divides all global PAs into different management categories ranging from strictly protected (Ia) to PAs with sustainable use of natural resources (VI) (Table 1). This data is provided by the original WDPA dataset (IUCN and UNEP, 2018). We hypothesized no strong differences among management categories since DCI is generally driven by large-scale geographic patterns and therefore it is largely independent of individual PA management. However, our results can reveal which types of PAs are more severely affected by climate change and therefore might impact decisions about where to concentrate future conservation efforts.

2.5. Statistical analyses

Statistical analyses were performed in R v. 3.6.2 (R Core Team 2019). We tested frequency distribution of our data visually by using histograms as well as qqplots. To assess the effects of PA characteristics on DCI we conducted a generalized linear model (GLM). We selected three distinct characteristics as explanatory variables, PA area, maximal elevational difference (MED), and median terrain ruggedness (TR). To account for spatial autocorrelation we assigned each PA to one of 32 climate zones based on Koeppen-Geiger climate classification (Rubel and Kottek, 2010). We initially conducted separate linear mixed models (LMMs) with disappearing climate index as response variable, PA characteristics as fixed effects and Koeppen-Geiger climate zone as random effect. In all three cases, variance explained by Koeppen-Geiger climate zone was below 0.01. This implies that our model is robust for differences in climate and the effect of spatial autocorrelation in our data is negligible. After clarifying the status of spatial autocorrelation, we conducted generalized linear model analyses (GLM) using the *glm* function in R. DCI functioned as response variable while log (PA area), MED and TR and their interactions PA area*MED, PA area*TR and MED*TR were predicting variables in our model. All predicting variables were poisson distributed and below the 0.7 threshold value for the Pearson correlation test. Stepwise, forward selection was used to select the most parsimonious model. Since most goodness-of-fit measures are not well suited for such large data sets we based our model selection on a threshold of an increase in R^2 of at least 2% for each degree of freedom used by the model. R^2 was calculated using the *rsq* package (Zhang 2020). The assumptions for linear regressions were tested via diagnostic plots and met in all cases presented in this study.

To see if different IUCN management categories have significantly different DCI values we calculated an one-way ANOVA test with IUCN category as explanatory variable and DCI as response variable. For this test we excluded PAs, which follow under one of the following IUCN categories, “Not applicable”, “Not assessed”, “Not reported”, which amounted to a total of 37784 (27.5%). The remaining 99648 PAs were analyzed. All DCI values within the seven IUCN groups followed a normal distribution. The assumptions for ANOVA were tested via diagnostic plots and met in all cases presented in this study. In addition, we performed a Tukey’s Honestly Significant Difference (Tukey’s HSD) post-hoc test for pairwise comparisons of DCI among IUCN categories using a 95% confidence interval.

To test whether PA characteristics differ significantly among IUCN management categories, we performed a Kruskal-Wallis test between IUCN category and a) PA area, b) MED and c) TR. We performed a posthoc pairwise.wilcox.test() for pairwise comparisons of PA characteristics among IUCN categories.

To test how IUCN categories interact with PA characteristics in their effects on DCI we conducted three separate GLMs with poisson distribution: DCI ~ log(PA area)*IUCN; DCI ~ MED*IUCN; and DCI ~ TR*IUCN. This analysis of IUCN management categories in relation to abiotic terrain variables should allow a description of the relative characteristics of each category. To preserve the clarity of interpretation we separated the analysis in three models, one for each abiotic terrain variable, instead of fitting all variables into a single model. We plotted our data with the *interact_plot* function from the package *interactions* (Long 2019) and included 80% confidence intervals. We chose 80% confidence intervals instead of 95% confidence intervals to improve the interpretability of the graphics.

3. Results

All terrestrial protected areas worldwide will experience a change of climatic conditions in the future. Under moderate climate change (RCP 4.5) global terrestrial PAs will lose between 1% and 85% of their relative land surface area exhibiting certain climatic conditions which will no longer be part of this PA by 2070. The best-fit model for predicting DCI within global terrestrial PAs included PA area (log-transformed) and maximal elevational difference (MED) ($R^2 = 0.63$) (Table 2).

Including TR as predicting variable in the model resulted in an R^2 increase of only 0.9% even though TR had a significant effect on DCI ($p = 0.000002$) (Appendix B, Table. B1).

The one-way ANOVA test showed significant differences in DCI for IUCN categories ($p < 0.000001$). With a 95% confidence interval, Tukey's Honestly Significant Difference (Tukey's HSD) post-hoc test for pairwise comparisons showed a significant difference in DCI between all IUCN categories except for Ib (wilderness area) and VI (PAs with sustainable use of natural resources) (Fig. 1).

When testing the differences in PA characteristics for each IUCN category (Table 3) we found area differed significantly ($p < 0.000001$) for all IUCN categories except IUCN Ia (strict nature reserve) and V (protected landscape or seascape) (Ia: $p = 0.14$). The largest median areas were found in category II (66 km^2), the smallest in category IV (1 km^2).

MED differed significantly ($p < 0.000001$) for all IUCN categories except IUCN Ia (strict nature reserve) and III (natural monument or feature) ($p = 0.51$) as well as Ib (wilderness Area) and II (national park) ($p = 0.83$). The largest median MED was found in category Ib (400m), the smallest in category V(50m) (Table 4).

TR differed significantly ($p < 0.000001$) for all IUCN categories except IUCN III (natural monument or feature) and VI (PAs with sustainable use of natural resources) ($p = 0.31$). The largest median TR was found in category Ib (10m), the smallest in category V(3m) (Table 5).

When we tested the interaction of IUCN category with PA area (DCI ~ log(PA area) * IUCN) we found that compared to the strictest protection status Ia (strict nature reserve) the other IUCN categories do not exhibit significant differences in the effects of area on DCI. Within category II (national park) we see a significant trend ($p = 0.002$) in area linked with a stronger decrease in DCI compared to IUCN Ia (Table 6). This might be due to the large sizes of PAs found in category II (Table 3). Within category IV we see a significant trend ($p = 0.005$) in area linked with a less strong decrease in DCI compared to IUCN Ia (Table 6).

The relationship between DCI and PA area for the different IUCN categories is shown in Fig. 2.

When we tested the interaction of IUCN category with MED (DCI ~ MED * IUCN) we found that compared to the strictest protection status Ia (strict nature reserve) IUCN category Ib (wilderness area) exhibits a significantly stronger decrease of DCI with MED ($p = 0.25$) (Table 7). Within category II (national park), V(protected landscape or seascape) and VI (PAs with sustainable use of natural resources) we see a weak, yet insignificant trend in MED linked with a stronger decrease in DCI compared to IUCN Ia (II: $p = 0.059$, V:$p = 0.052$, VI:$p = 0.065$). All five IUCN categories (Ia, Ib, II, V and VI) were significantly different from each other in their levels of MED except for IUCN category Ib and II (Table 4) which both resulted in a stronger decrease of DCI with MED compared to IUCN Ia (Table 7).

The relationship between DCI and MED for the different IUCN categories is shown in Fig. 3.

When we tested the interaction of IUCN category with TR (DCI ~ TR * IUCN) we found that compared to the strictest protection status Ia (strict nature reserve) IUCN category Ib (wilderness area), II (national park), V(protected landscape or seascape) and VI (PAs with sustainable use of natural resources) exhibits a significantly stronger decrease of DCI with TR (Ib:$p = 0.009$, II: $p < 0.001$, V:$p = 0.040$, VI:$p = 0.038$) (Table 8). All five IUCN categories (Ia, Ib, II, V and VI) were significantly different from each other in their levels of TR (Table 4).

Table 2
Generalized linear model results of PA characteristics as predictors of DCI. $R^2 = 0.63$

Variable	Estimate	Standard Error	z-value	P-value
DCI				
PA area (log)	−0.0398	0.003	−11.50	<0.000001 ***
MED	−0.0003	<0.001	−15.91	<0.000001 ***

Significance codes as indicated are "*" <0.05, "**" <0.01 "***" <0.001.

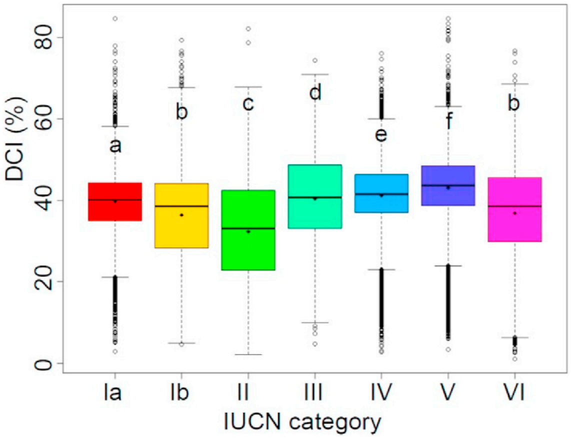

Fig. 1. DCI for IUCN management category. IUCN categories differ significantly in their DCI values. Black lines represent the median, black dots the mean, and error bars show 95% confidence intervals. Statistical significance ($p < 0.000001$) is indicated by different letters below the bars. Tukey's HSD post-hoc test showed a significant difference in DCI between all IUCN categories except for Ib (wilderness area) and VI (PAs with sustainable use of natural resources). IUCN management category IV (habitat/species management area) and V (protected landscape/seascape) exhibit on average the highest DCI values.

Table 3

The difference of PA area among PAs of different IUCN management categories. We performed a Kruskal-Wallis Test excluding PAs, which follow under one of the following IUCN categories, "Not applicable", "Not assessed", "Not reported". Comparisons are significant with $p < 0.001$ unless otherwise stated.

	Ia	Ib	II	III	IV	V	VI
Median in km^2	2	40	66	1	1	2	9
Mean in km^2	118	467	918	22	63	67	968
p-value:							
Ib		NA					
II			NA				
III				NA			
IV					NA		
V	0.140					NA	
VI							NA

Table 4

The difference of MED among PAs of different IUCN management categories. We performed a Kruskal-Wallis Test excluding PAs, which follow under one of the following IUCN categories, "Not applicable", "Not assessed", "Not reported". Comparisons are significant with $p < 0.001$ unless otherwise stated.

	Ia	Ib	II	III	IV	V	VI
Median in km^2	87	400	292	95	73	50	180
Mean in km^2	248	594	634	198	173	154	378
p-value:							
Ib		NA					
II		<0.83	NA				
III	<0.51			NA			
IV					NA		
V	0.14					NA	
VI							NA

Table 5

The difference of TR among PAs of different IUCN management categories. We performed a Kruskal-Wallis Test excluding PAs, which follow under one of the following IUCN categories, "Not applicable", "Not assessed", "Not reported". Comparisons are significant with $p < 0.001$ unless otherwise stated.

	Ia	Ib	II	III	IV	V	VI
Median in km^2	4	10	7	6	4	3	6
Mean in km^2	9	12	11	10	7	6	10
p-value:							
Ib		NA					
II			NA				
III				NA			
IV					NA		
V						NA	
VI	0.036			0.305			NA

Table 6
Generalized linear model results on the interaction of PA area and IUCN category as predictors for DCI.

Variable	Estimate	Std Error	z-value	P-value
DCI				
PA area (log):IUCN_Ib	−0.0258	0.017	- 1.55	0.121
PA area (log):IUCN_II	−0.0441	0.014	- 3.06	0.002**
PA area (log):IUCN_III	0.0106	0.012	0.85	0.392
PA area (log):IUCN_IV	0.0286	0.010	2.79	0.005**
PA area (log):IUCN_V	0.0134	0.011	1.21	0.226
PA area (log):IUCN_VI	−0.0152	0.014	- 1.11	0.269

Significance codes as indicated are “*” <0.05, “**” <0.01 “***” <0.001.

The relationship between DCI and TR for the different IUCN categories is shown in Fig. 4.

4. Discussion

All terrestrial protected areas (PAs) on earth will experience a change of climatic conditions in the near future. Certain climatic conditions within the boundaries of any given PA will disappear while others expand or change locations. This can severely reduce biodiversity conservation and other measures of PA effectiveness. Under moderate climate change (RCP 4.5) global terrestrial PAs will lose between 1% and 85% of their relative land surface area exhibiting certain climatic conditions which will no longer be part of this PA by the year 2070. The disappearing climate index (DCI) is a measure of the amount of land surface area that will lose current climatic conditions by 2070. Higher topographic diversity within PAs is strongly linked to lower DCI values. We found that all three investigated PA characteristics representing topographic diversity —PA area, maximal elevational difference (MED) and terrain ruggedness (TR)— are correlated with a significant decrease in DCI. PA area and MED alone explain 63% of the variance observed in DCI among the world’s terrestrial PAs. IUCN management category IV (habitat/species management area) and V (protected landscape/seascape) exhibit on average the highest DCI values.

In our study we analyzed the relationship between DCI and topographic diversity using the resolution of 30 arcseconds, determined by the preexisting data of DCI. To our knowledge this is the highest spatial resolution for which global climate data is available. While this allowed us to look at all terrestrial PAs worldwide, the resolution of 30 arcseconds – approximately 1 km – probably underestimates the potential for microclimates and microclimatic refugia (Suggitt et al., 2018). Therefore, a 30 arcsecond resolution might underestimate climate change indices such as DCI by overlooking fine-scale topoclimatic patterns, especially in rugged terrain and by not-detecting fine-scale sites decoupled from the regional climate (Heikkinen et al., 2020). While MED and TR values are based on elevation data of 90 m resolution, we analyzed them in a final resolution of 30 arcseconds determined by the preexisting data of DCI. This allowed us to create computationally manageable values for all terrestrial PAs worldwide. These values however are likely to underestimate the full range of topographic diversity present in any given PA.

As hypothesized, our research demonstrates that increasing PA area is significantly related to decreasing DCI. This backs up previous studies suggesting small PAs are more vulnerable to climatic changes compared to larger ones (Hoffmann et al., 2019; Langdon and Lawler, 2015; Loarie et al., 2009). Large PAs are more likely to harbor diverse climatic conditions allowing for internal climate displacement such that some portion of the PA is more likely to exhibit prior climatic conditions (Loarie et al., 2009; Thomas and Gillingham, 2015).

Our research also demonstrates that increases in both MED and TR are significantly linked to decreases in DCI. This builds on previous studies which have suggested that mountainous areas are less vulnerable to climatic changes (Lawler et al., 2015; Loarie et al., 2009). High topographic diversity leads to high climatic and thus environmental diversity (Carroll et al., 2017; Halpin, 1997; Langdon and Lawler, 2015), which increases the likelihood that species will be able to find suitable nearby habitat as climate changes (Carroll et al., 2017), for example by shifting their ranges towards higher elevations (Halpin, 1997; Scheffers et al., 2016). Further, our results show that MED is much stronger correlated with DCI and adds a higher explanatory power to DCI compared to TR.

To our knowledge, the effects of TR and MED on climate change indices have never before been analyzed separately. One reason for this lacuna could be a paucity of available data. Alternatively, TR and MED are often assumed to be too closely correlated to differ significantly in their effects on climate change indices. In our study of 137,432 terrestrial protected areas MED and TR were just below the 0.7 threshold value for the Pearson correlation test. Even if MED and TR are often correlated, they still represent two different aspects of mountainous landscapes that must be studied independent of one another. MED measures the difference between the lowest and highest elevations within a PA. TR, by contrast, is the mean of the absolute differences in elevation between a raster cell located within a PA and its eight adjacent cells inside the PA. Consequently, TR represents the roughness of a terrestrial surface independent of its altitudinal range or zonation. As such, PAs with low overall elevational difference can still have high TR. As we have hypothesized MED is linked with a much stronger decrease in DCI compared to TR. One possible explanation for this phenomenon is that MED is a more large-scale measurement compared to TR. Testing whether MED also leads to higher environmental diversity compared to TR would require additional analysis not attempted in this paper.

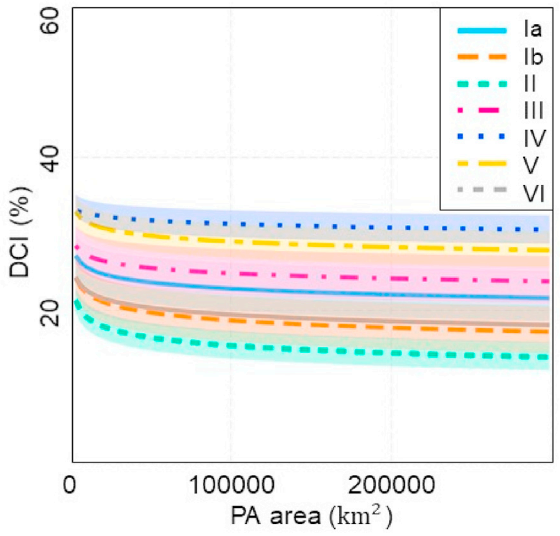

Fig. 2. Decreasing DCI with increasing PA area among all IUCN management categories. Colored sections around the trendlines represent an 80% confidence interval. Compared to the strictest protection status Ia (strict nature reserve) IUCN category II (national park) exhibits a significantly stronger decrease of DCI with PA area ($p = 0.002$), while IUCN category IV (habitat/species management area) exhibits a significantly less strong decrease of DCI with PA area ($p = 0.005$).

Table 7
Generalized linear model results on the interaction of MED and IUCN category as predictors for DCI.

Variable	Estimate	Std Error	z-value	P-value
DCI				
MED:IUCN_Ib	−0.0002	<0.001	- 2.25	0.025*
MED:IUCN_II	−0.0002	<0.001	- 1.89	0.059
MED:IUCN_III	<0.0001	<0.001	<0.01	0.999
MED:IUCN_IV	<0.0001	<0.001	0.66	0.511
MED:IUCN_V	−0.0001	<0.001	- 1.94	0.052
MED:IUCN_VI	−0.0002	<0.001	- 1.85	0.065

Significance codes as indicated are “*” <0.05, “**” <0.01 “***” <0.001.

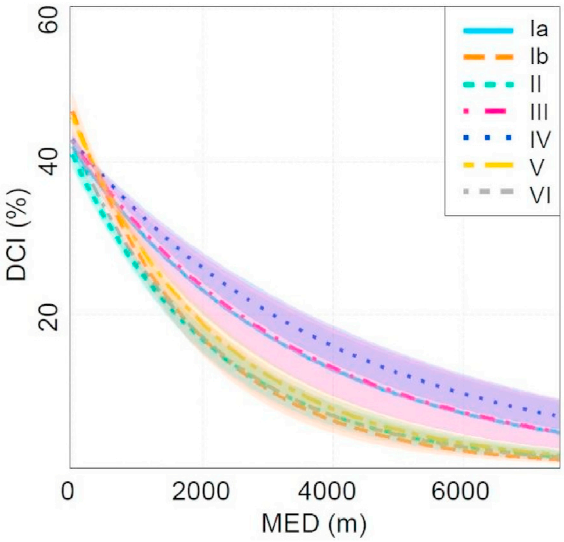

Fig. 3. Decreasing DCI with increasing MED among all IUCN management categories. Colored sections around the trendlines represent an 80% confidence interval. Compared to the strictest protection status Ia (strict nature reserve) IUCN category Ib (wilderness area) exhibits a significantly stronger decrease of DCI with MED ($p = 0.25$).

Table 8
Generalized linear model results on the interaction of TR and IUCN category as predictors for DCI.

Variable	Estimate	Std Error	z-value	P-value
DCI				
TR:IUCN_Ib	−0.0110	0.004	- 2.61	0.009**
TR:IUCN_II	−0.0198	0.004	- 5.25	<0.001***
TR:IUCN_III	−0.0011	0.003	- 0.39	0.699
TR:IUCN_IV	0.0017	0.002	0.67	0.501
TR:IUCN_V	−0.0056	0.003	- 2.05	0.040*
TR:IUCN_VI	−0.0069	0.003	- 2.07	0.038*

Significance codes as indicated are “*” <0.05, “**” <0.01 “***” <0.001.

DCI differs significantly among all IUCN categories. IUCN management category IV (habitat/species management area) shows a generally high DCI (second highest mean and median DCI after IUCN management category V). Regardless of whether or not this difference can be explained by topographic diversity, this is an important finding since PAs managed under category IV are specifically designated to protect “particular species or habitats, where management reflects this priority” (Dudley, 2008, Table 1). Yet, while management in category IV PAs might be effective for protecting particular species and habitats today, our results suggest that these management practices will not be as effective in mitigating habitat loss from climate change in the future. Therefore, we recommend incorporating climate change indices, such as DCI, into decision making for category IV PAs. The lowest mean and median DCI value was found in category II (national park). PAs within category II – however - also exhibit the largest range of DCI values. Overall IUCN category II has the highest median PA area, the second highest median MED and the second highest median TR (the order of mean values is comparable). This might be a result of political interests in preserving especially large and scenic mountain landscapes as national parks. IUCN category Ib (wilderness area) exhibits the second highest median values in PA area and the highest in MED and TR. This may be due to less pressure from land use by agriculture or urban expansion in mountainous landscapes, which creates room for larger, more strictly protected PAs. The highest DCI values are found in category V (protected landscape or seascape), which usually consists of small (median area = 2 km^2) and flat areas with the lowest median MED and TR values among all IUCN categories.

We found no strong differences in the interactions of IUCN categories and PA characteristics in its effects on DCI. However, there was one notable exception: IUCN management category II (national parks) exhibits lower DCI values compared to even the strictest protection status Ia (strict nature reserve) based on all three PA characteristics. While the interaction of IUCN II and PA area is not quite significant ($p = 0.054$) there is a weak trend in decreasing DCI by an additional 3.6% for each km^2 PA area increases compared to IUCN Ia (strict nature reserve). The interaction of IUCN II and MED shows a weak trend ($p = 0.059$) in decreasing DCI for an additionally 0.02% for each additional 1 m increase in MED compared to IUCN Ia. The interaction of IUCN II and TR shows a significant decrease in DCI ($p < 0.000001$) for an additionally 2% for each additional 1 m increase in TR. IUCN management category IV (habitat/species management area) shows a generally high DCI and tends to reduce the decrease of DCI with increasing PA area, MED and TR. However, none of these relationships tested significant (PA area*IUCN IV: $p = 0.058$, MED* IUCN IV: $p = 0.511$, TR*IUCN IV: $p = 0.501$). While our results demonstrated no significant effect of the interactions of PA area, MED and TR with IUCN category IV it nevertheless showed elevated levels of DCI. For future research it is worth examining the factors driving climate change indices especially within IUCN category IV since these PAs are specifically designated to protect “particular species or habitats, where management reflects this priority” (Dudley, 2008, Table 1). Thus, if we want to preserve specific species or habitats, we need to consider doing this during times of climatic change, so that species can still profit from PAs currently listed under IUCN management category IV. DCI as a climate index is generally driven by large-scale geographic patterns and it is therefore independent of individual PA management. However, our results show which types of PAs are more affected by climate change compared to others. Our study demonstrates which PA characteristics are most influential in determining DCI for different PA management categories. However, DCI can vary tremendously between individual PAs even if they are part of the same IUCN management category. Therefore, IUCN management category alone cannot be used to inform practitioners of individual PAs about potential future strategies in reducing DCI. The results of our study are the first to demonstrate topographic diversity as a meaningful and practicable guide for conservation managers to design effective PA’s in the face of climate change.

Previous studies have projected tremendous differences in the degree of climatic change individual PAs will experience (Langdon and Lawler, 2015; Loarie et al., 2009; Wiens et al., 2011). While some studies show a projected increase in biodiversity for certain areas under climate change, either through direct or indirect means (Lim et al., 2018; Pawson et al., 2013), most research predicts negative effects of climatic changes on overall biodiversity in the long-term. Environmentally heterogeneous PAs are expected to allow for adaptation or migration of species under climate change (Scherrer and Körner, 2011; Thomas and Gillingham, 2015). Hence, environmental diversity within PAs is considered to act as a buffer in climatic change (Ackerly et al., 2010; Heller et al., 2015; Lemieux et al., 2011). Our goal was to assess if and how topographic diversity may buffer the impacts of climate change. We found three meaningful PA characteristics representing topographic diversity —PA area, maximal elevational difference (MED) and terrain ruggedness (TR)— that are strongly linked to a decrease in DCI. This robust correlation holds true for all terrestrial PAs worldwide and all IUCN management categories.

Hence, topographic diversity can be used as an indicator for the resilience and, to some extent, the effectiveness of PAs under climatic change as it is based on evidence from many climatic regimes which shows that different geophysical settings

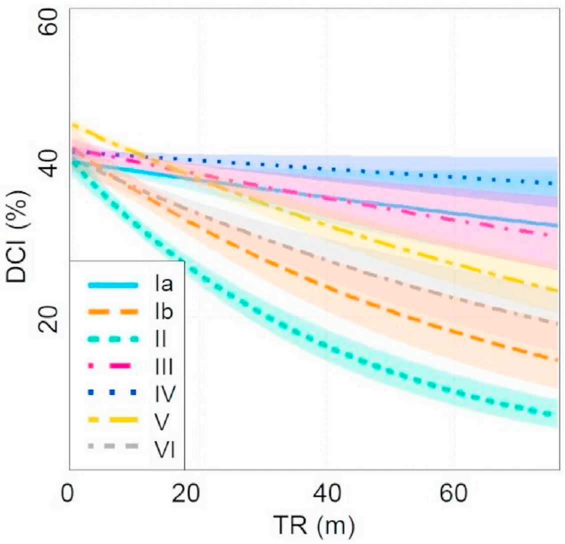

Fig. 4. Decreasing DCI with increasing TR among all IUCN management categories. Colored sections around the trendlines represent an 80% confidence interval. compared to the strictest protection status Ia (strict nature reserve) IUCN category Ib (wilderness area), II (national park), V(protected landscape or seascape) and VI (PAs with sustainable use of natural resources) exhibits a significantly stronger decrease of DCI with TR (Ib:p = 0.009, II: p < 0.001, V:p = 0.040, VI:p = 0.038). Category IV (habitat/species management area) exhibits a less strong decrease in DCI compared to IUCN category Ia, this weak trend is – however – not significant (p = 0.501).

can maintain distinct ecological communities under a wide range of climates (Jones et al., 2016). In this way our results support the theory of Conserving Nature's Stage (CNS), which advocates for conserving an abiotically diverse stage, which is considered to exhibit high climate change resilience and is easier to identify and measure than biotic diversity (Lawler et al., 2015). However, it is important to note that representing heterogeneity alone is unlikely to preserve specific species or aspects of biodiversity that are most threatened by climate change. Hence, representing heterogeneity within PAs should be complemented by specific conservation approaches which will incorporate biological information to conserve individual species or communities (Jones et al., 2016; Tingley et al., 2014). Applying topographic diversity as an indicator for PA resilience under climate change is an important first step toward climate smart conservation that will be especially useful for PA managers, conservation practitioners and politicians because topographic diversity can be assessed easily through publicly available data and remote sensing products. This ease-of-use puts topographic diversity in marked contrast to overall environmental diversity as an actionable metric. Assessing overall environmental diversity is a much more complex undertaking, usually demanding intensive and costly fieldwork for which most conservation practitioners are understaffed, underfunded, and underequipped. Thus, in most circumstances, topographic diversity is a better measure for designing and managing effective PAs.

In the age of "big data," topographic diversity offers a relatively simple and inexpensive guide for estimating climate change resilience in PAs worldwide. It can help in maintaining effectiveness of current and future PAs given projected climatic changes. Most mountainous PAs with high MED and TR are relatively well situated to cope with climatic change while PAs located in flat terrain likely experience higher DCI values. Wessely et al. (2017) suggests that habitat restoration has high potential to mitigate species loss due to climate change in the lowlands of Europe but limited potential in high mountain landscapes. The likely reason is that semi-natural habitats are restricted to remnant patches in Central European lowlands while they still represent the matrix at (sub-) alpine elevations. Pairing practical and applied conservation studies like this with our results on the spatial distribution of climate change resilient PAs based on topographic heterogeneity might help guide conservationists in distributing limited funds in preparing current PAs for remaining their effectiveness under climate change. Beyond managing current PAs our results have the potential to help in designing new PAs with an eye to climate-smart conservation strategies. Our results concur with Lawler et al. (2020), who also point out that creating new PAs in mountainous regions with the intention of providing future climatic refugia will be relatively inexpensive, making the protection of rare climate refugia a low-cost adaptation strategy. However, while managing for topographic diversity is a comparatively simple approach, conservation decisions also need to be based on other criteria such as biological diversity, quality of habitat inside the PA, or the uniqueness of its species (Heikkinen et al., 2020; Hoffmann et al., 2018).

While we investigated the correlation of topographic diversity on DCI we did not include information on species movement. DCI does inform about the disappearing climatic conditions comparable to climate velocity or climate anomaly indices, however these are based on abiotic conditions and processes. When inferring direct measures for species conservation climatic indices should be paired with biological information on species movement in order to predict future climate refugia or biodiversity hotspots. Underlying mechanisms such as dispersal limitations, demographic shifts, species interactions, and evolution, however play key roles in mediating biotic responses to climate change (Littlefield et al., 2017; Urban, 2015). In addition to mountain-top extinction or low-elevation bottlenecks, physical structures, such as insurmountable environmental barriers, can further prevent successful climate tracking (Littlefield et al., 2017; Reside et al., 2018).

Our results underscore the findings of previous studies that suggest future-oriented conservation approaches that maximize environmental diversity to buffer impacts of climate change (Ackerly et al., 2010; Heller et al., 2015; Lawler et al., 2015; Scherrer and Körner, 2011). However, maximizing environmental diversity is difficult to put into practice. One often-used proxy for environmental diversity is PA size. While it is widely acknowledged that increasing PA area leads to a reduction in climatic change impacts within PAs it is also understood that expanding PA area is often unfeasible due to limited funds, human land use pressures, depleted natural habitats, political will, and other factors (Hoffmann et al., 2019; Langdon and Lawler, 2015; Thomas and Gillingham, 2015). In such cases PA management might profit from new, more flexible approaches to PA management and design. However, it is important to note that in this study we focused on PAs only and did not analyze the surroundings of PAs. In this sense we treated PAs as islands, assuming that species will not be conserved outside PAs and that species are unable to move through non-PA areas into other PAs to track their climatic niche. There is a vast body of research which looks at the optimal shape and connectivity of PAs and their effects on species movement (Heller and Zavaleta, 2009; Hodgson et al., 2009; Ward et al., 2020; Wegmann et al., 2014). While species movement is already tremendously restricted by human activity, climate change is projected to further constrain potential movement routes while simultaneously creating a higher need for species movement (Littlefield et al., 2017). In order to put connectivity-enhancing strategies forward, future climate projections, landscape permeability due to human modification, and dispersal capabilities need to be considered simultaneously (Littlefield et al., 2017; Urban et al., 2013).

Broadly, PAs exist to preserve global biodiversity. But at the local and regional level, PAs are geared toward the preservation of characteristic species, populations, and ecosystems within static boundaries. Unfortunately, these principles appear increasingly anachronistic in the face of global climate change. The mosaic of PAs worldwide comprises a vast array of biota and habitats that need flexible principles of design to adapt to large-scale environmental changes (Abrahms et al., 2017; Thomas, 2011; Timberlake and Schultz, 2017). By focusing — as a first step - on topographic diversity as an indicator for PA resilience in the face of climate change, practitioners will have an easier, more reliably implementable guide in designing, formulating and establishing effective PAs.

Funding

This publication was funded by the University of Bayreuth in the funding programme Open-Acess Publishing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

We are grateful to Asja Bernd and Sean Lawrence for their help in proof-reading and language editing.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01445.

References

Abrahms, B., DiPietro, D., Graffis, A., Hollander, A., 2017. Managing biodiversity under climate change: challenges, frameworks, and tools for adaptation. Biodivers. Conserv. 26 (10), 2277—2293. https://doi.org/10.1007/s10531-017-1362-4.

Ackerly, D.D., Loarie, S.R., Cornwell, W.K., Weiss, S.B., Hamilton, H., Branciforte, R., Kraft, N.J.B., 2010. The geography of climate change: implications for conservation biogeography. Divers. Distrib. 16 (3), 476—487. https://doi.org/10.1111/j.1472-4642.2010.00654.x.

Amatulli, G., Domisch, S., Tuanmu, M.N., Parmentier, B., Ranipeta, A., Malczyk, J., Jetz, W., 2018. Data Descriptor: a suite of global, cross-scale topographic variables for environmental and biodiversity modeling. Sci. Data 5, 1—15. https://doi.org/10.1038/sdata.2018.40, 180040.

Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D., Thuiller, W., 2011. Climate change threatens European conservation areas. Ecol. Lett. 14 (5), 484—492. https://doi.org/10.1111/j.1461-0248.2011.01610.x.

Batllori, E., Parisien, M.A., Parks, S.A., Moritz, M.A., Miller, C., 2017. Potential relocation of climatic environments suggests high rates of climate displacement within the North American protection network. Global Change Biol. 23 (8), 3219—3230. https://doi.org/10.1111/gcb.13663.

Berteaux, D., Ricard, M., St-Laurent, M.H., Casajus, N., Périé, C., Beauregard, F., De Blois, S., 2018. Northern protected areas will become important refuges for biodiversity tracking suitable climates. Sci. Rep. 8 (1), 1—9. https://doi.org/10.1038/s41598-018-23050-w.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., MacE, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486 (7401), 59—67. https://doi.org/10.1038/nature11148.

Carroll, C., Roberts, D.R., Michalak, J.L., Lawler, J.J., Nielsen, S.E., Stralberg, D., Hamann, A., Mcrae, B.H., Wang, T., 2017. Scale-dependent complementarity of climatic velocity and environmental diversity for identifying priority areas for conservation under climate change. Global Change Biol. 23 (11), 4508—4520. https://doi.org/10.1111/gcb.13679.

Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333 (6045), 1024–1026. https://doi.org/10.1126/science.1206432.

Crooks, K.R., Burdett, C.L., Theobald, D.M., King, S.R.B., Di Marco, M., Rondinini, C., Boitani, L., 2017. Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. Proc. Natl. Acad. Sci. Unit. States Am. 114 (29), 7635–7640. https://doi.org/10.1073/pnas.1705769114.

Dudley, N. (Ed.), 2008. Guidelines for Applying Protected Area Management Categories. IUCN, Gland, Switzerland, 86pp.

Gaüzère, P., Jiguet, F., Devictor, V., 2016. Can protected areas mitigate the impacts of climate change on bird's species and communities? Divers. Distrib. 22 (6), 625–637. https://doi.org/10.1111/ddi.12426.

Gray, C.L., Hill, S.L.L., Newbold, T., Hudson, L.N., Boïrger, L., Contu, S., Hoskins, A.J., Ferrier, S., Purvis, A., Scharlemann, J.P.W., 2016. Local biodiversity is higher inside than outside terrestrial protected areas worldwide. Nat. Commun. 7 (12306) https://doi.org/10.1038/ncomms12306.

Halpin, P.N., 1997. Global climate change and natural-area protection: management responses and research directions. Ecol. Appl. 7 (3), 828–843. https://doi.org/10.1890/1051-0761(1997)007[0828:GCCANA]2.0.CO;2.

Hannah, L., Midgley, G., Andelman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R., Williams, P., 2007. Protected area needs in a changing climate. Front. Ecol. Environ. 5 (3), 131–138. https://doi.org/10.1890/1540-9295(2007)5[131:PANIAC]2.0.CO;2.

Heikkinen, R.K., Leikola, N., Aalto, J., Aapala, K., Kuusela, S., Luoto, M., Virkkala, R., 2020. Fine-grained climate velocities reveal vulnerability of protected areas to climate change. Sci. Rep. 10 (1) https://doi.org/10.1038/s41598-020-58638-8.

Heller, N.E., Kreitler, J., Ackerly, D.D., Weiss, S.B., Recinos, A., Branciforte, R., Flint, L.E., Flint, A.L., Micheli, E., 2015. Targeting climate diversity in conservation planning to build resilience to climate change. Ecosphere 6 (4). https://doi.org/10.1890/ES14-00313.1 art65.

Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biol. Conserv. 142 (1), 14–32. https://doi.org/10.1016/j.biocon.2008.10.006.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978. https://doi.org/10.1002/joc.1276.

Hodgson, J.A., Thomas, C.D., Wintle, B.A., Moilanen, A., 2009. Climate change, connectivity and conservation decision making: back to basics. J. Appl. Ecol. 46 (5), 964–969. https://doi.org/10.1111/j.1365-2664.2009.01695.x.

Hoffmann, S., Beierkuhnlein, C., 2020. Climate change exposure and vulnerability of the global protected area estate from an international perspective. Divers. Distrib. https://doi.org/10.1111/ddi.13136.

Hoffmann, S., Beierkuhnlein, C., Field, R., Provenzale, A., Chiarucci, A., 2018. Uniqueness of protected areas for conservation strategies in the European Union. Sci. Rep. 8 (1), 1–14. https://doi.org/10.1038/s41598-018-24390-3.

Hoffmann, S., Irl, S.D.H., Beierkuhnlein, C., 2019. Predicted climate shifts within terrestrial protected areas worldwide. Nat. Commun. 10 (1), 1–10. https://doi.org/10.1038/s41467-019-12603-w.

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T.M., Bonin, C., Bruelheide, H., De Luca, E., Ebeling, A., Griffin, J.N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., et al., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526 (7574), 574–577. https://doi.org/10.1038/nature15374.

IUCN, 2010. IUCN Red List of Threatened Species. IUCN, Gland, Switzerland.

IUCN and UNEP, 2018. The world Database on protected areas (WDPA) (united nations environment programme world conservation monitoring centre. Cambridge, UK. http://www.protectedplanet.net (Jan/2018).

Jarvis, A., Reuter, H.I., Nelson, A., Guevara, E., 2008. Hole-filled seamless SRTM data V4, international centre for tropical agriculture (CIAT). http://srtm.csi.cgiar.org.

Jentsch, A., Beierkuhnlein, C., 2003. Global climate change and local disturbance regimes as interacting drivers for shifting altitudinal vegetation patterns. Erdkunde 57 (3), 216–231. https://doi.org/10.3112/erdkunde.2003.03.04.

Johnston, A., Ausden, M., Dodd, A.M., Bradbury, R.B., Chamberlain, D.E., Jiguet, F., Thomas, C.D., Cook, A.S.C.P., Newson, S.E., Ockendon, N., Rehfisch, M.M., Roos, S., Thaxter, C.B., Brown, A., Crick, H.Q.P., Douse, A., McCall, R.A., Pontier, H., Stroud, D.A., et al., 2013. Observed and predicted effects of climate change on species abundance in protected areas. Nat. Clim. Change 3 (12), 1055–1061. https://doi.org/10.1038/nclimate2035.

Jones, K.R., Watson, J.E.M., Possingham, H.P., Klein, C.J., 2016. Incorporating climate change into spatial conservation prioritisation: a review. Biol. Conserv. 194 (November 2017), 121–130. https://doi.org/10.1016/j.biocon.2015.12.008.

Langdon, J.G.R., Lawler, J.J., 2015. Assessing the impacts of projected climate change on biodiversity in the protected areas of western North America. Ecosphere 6 (5). https://doi.org/10.1890/es14-00400.1.

Lawler, J.J., Ackerly, D.D., Albano, C.M., Anderson, M.G., Dobrowski, S.Z., Gill, J.L., Heller, N.E., Pressey, R.L., Sanderson, E.W., Weiss, S.B., 2015. The theory behind, and the challenges of, conserving nature's stage in a time of rapid change. Conserv. Biol. 29 (3), 618–629. https://doi.org/10.1111/cobi.12505.

Lehikoinen, P., Santangeli, A., Jaatinen, K., Rajasärkkä, A., Lehikoinen, A., 2019. Protected areas act as a buffer against detrimental effects of climate change—evidence from large-scale, long-term abundance data. Global Change Biol. 25 (1), 304–313. https://doi.org/10.1111/gcb.14461.

Lemieux, C.J., Beechey, T.J., Gray, P.A., 2011. Prospects for Canada's protected areas in an era of rapid climate change. Land Use Pol. 28 (4), 928–941. https://doi.org/10.1016/j.landusepol.2011.03.008.

Lim, C.H., Yoo, S., Choi, Y., Jeon, S.W., Son, Y., Lee, W.K., 2018. Assessing climate change impact on forest habitat suitability and diversity in the Korean Peninsula. Forests 9 (5), 1–16. https://doi.org/10.3390/f9050259.

Littlefield, C.E., McRae, B.H., Michalak, J.L., Lawler, J.J., Carroll, C., 2017. Connecting today's climates to future climate analogs to facilitate movement of species under climate change. Conserv. Biol. 31 (6), 1397–1408. https://doi.org/10.1111/cobi.12938.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., Ackerly, D.D., 2009. The velocity of climate change. Nature 462 (7276), 1052–1055. https://doi.org/10.1038/nature08649.

Long, J.A., 2019. Interactions: comprehensive, user-friendly toolkit for probing interactions. R package version 1.1.3.

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-Being: Biodiversity Synthesis. World resources institute, Washington, DC, USA.

Monzón, J., Moyer-Horner, L., Palamar, M.B., 2011. Climate change and species range dynamics in protected areas. Bioscience 61 (10), 752–761. https://doi.org/10.1525/bio.2011.61.10.5.

Nila, M.U.S., Beierkuhnlein, C., Jaeschke, A., Hoffmann, S., Hossain, M.L., 2019. Predicting the effectiveness of protected areas of Natura 2000 under climate change. Ecol. Process. 8 (13) https://doi.org/10.1186/s13717-019-0168-6.

Pawson, S.M., Brin, A., Brockerhoff, E.G., Lamb, D., Payn, T.W., Paquette, A., Parrotta, J.A., 2013. Plantation forests, climate change and biodiversity. Biodivers. Conserv. 22 (5), 1203–1227. https://doi.org/10.1007/s10531-013-0458-8.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344 (6187). https://doi.org/10.1126/science.1246752.

R Development Core Team, 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org/(Nov/2019.

Reside, A.E., Butt, N., Adams, V.M., 2018. Adapting systematic conservation planning for climate change. Biodivers. Conserv. 27 (1) https://doi.org/10.1007/s10531-017-1442-5.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. Nature 421 (6918), 57–60. https://doi.org/10.1038/nature01333.

Rubel, F., Kottek, M., 2010. Observed and projected climate shifts 1901-2100 depicted by world maps of the Köppen-Geiger climate classification. Meteorol. Z. 19 (2), 135–141. https://doi.org/10.1127/0941-2948/2010/0430.

Scheffers, B.R., De Meester, L., Bridge, T.C.L., Hoffmann, A.A., Pandolfi, J.M., Corlett, R.T., Butchart, S.H.M., Pearce-Kelly, P., Kovacs, K.M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W.B., Martin, T.G., Mora, C., Bickford, D., Watson, J.E.M., 2016. The broad footprint of climate change from genes to biomes to people. Science 354 (6313). https://doi.org/10.1126/science.aaf7671.

Scherrer, D., Körner, C., 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. J. Biogeogr. 38 (2), 406–416. https://doi.org/10.1111/j.1365-2699.2010.02407.x.

Suggitt, A.J., Wilson, A.J., Isaac, I.J.B., Beale, C.M., Auffret, A.G., August, T., Bennie, J.J., Crick, H.Q.P., Duffield, S., Fox, R., Hopkins, J.J., Macgregor, N.A., Morecroft, M.D., Walker, K.J., Maclean, I.M.D., 2018. Extinction risk from climate change is reduced by microclimatic buffering. Nat. Clim. Change 8, 713–717.

Thomas, C.D., 2011. Translocation of species, climate change, and the end of trying to recreate past ecological communities. Trends Ecol. Evol. 26 (5), 216–221. https://doi.org/10.1016/j.tree.2011.02.006.

Thomas, C.D., Gillingham, P.K., 2015. The performance of protected areas for biodiversity under climate change. Biol. J. Linn. Soc. 115 (3), 718–730. https://doi.org/10.1111/bij.12510.

Timberlake, T.J., Schultz, C.A., 2017. Policy, practice, and partnerships for climate change adaptation on US national forests. Climatic Change 144 (2), 257–269. https://doi.org/10.1007/s10584-017-2031-z.

Tingley, M.W., Darling, E.S., Wilcove, D.S., 2014. Fine- and coarse-filter conservation strategies in a time of climate change. Ann. N. Y. Acad. Sci. 1322 (1), 92–109. https://doi.org/10.1111/nyas.12484.

Urban, M.C., 2015. Accelerating extinction risk from climate change. Science 348 (6234), 571–573. https://doi.org/10.1111/1467-8322.12302.

Urban, M.C., Zarnetske, P.L., Skelly, D.K., 2013. Moving forward: dispersal and species interactions determine biotic responses to climate change. Ann. N. Y. Acad. Sci. 1297 https://doi.org/10.1111/nyas.12184.

Ward, M., Saura, S., Williams, B., Ramírez-Delgado, J.P., Arafeh-Dalmau, N., Allan, J.R., Venter, O., Dubois, G., Watson, J.E.M., 2020. Just ten percent of the global terrestrial protected area network is structurally connected via intact land. Nat. Commun. 11 (1), 1–10. https://doi.org/10.1038/s41467-020-18457-x.

Wegmann, M., Santini, L., Leutner, B., Safi, K., Rocchini, D., Bevanda, M., Latifi, H., Dech, S., Rondinini, C., 2014. Role of African protected areas in maintaining connectivity for large mammals. Phil. Trans. Biol. Sci. 369 (1643) https://doi.org/10.1098/rstb.2013.0193.

Wessely, J., Hülber, K., Gattringer, A., Kuttner, M., Moser, D., Rabitsch, W., Schindler, S., Dullinger, S., Essl, F., 2017. Habitat-based conservation strategies cannot compensate for climate-change-induced range loss. Nat. Clim. Change 7 (11), 823–827. https://doi.org/10.1038/nclimate3414.

Wiens, J.A., Seavy, N.E., Jongsomjit, D., 2011. Protected areas in climate space: what will the future bring? Biol. Conserv. 144 (8), 2119–2125. https://doi.org/10.1016/j.biocon.2011.05.002.