ENVIRONMENTAL RESEARCH
LETTERS

# Efficacy of the global protected area network is threatened by disappearing climates and potential transboundary range shifts

To cite this article: Sean A Parks *et al* 2022 *Environ. Res. Lett.* **17** 054016

ENVIRONMENTAL RESEARCH
LETTERS

RECEIVED
13 December 2021

REVISED
22 March 2022

ACCEPTED FOR PUBLICATION
5 April 2022

PUBLISHED
25 April 2022

LETTER

# Efficacy of the global protected area network is threatened by disappearing climates and potential transboundary range shifts

Sean A Parks[1,*], Lisa M Holsinger[1], Caitlin E Littlefield[2], Solomon Z Dobrowski[3], Katherine A Zeller[1], John T Abatzoglou[4], Charles Besancon[5], Bryce L Nordgren[6] and Joshua J Lawler[7]

[1] Aldo Leopold Wilderness Research Institute, Rocky Mountain Research Station, US Forest Service, 790 E. Beckwith Ave., Missoula, MT 59801, United States of America
[2] Conservation Science Partners, 11050 Pioneer Trail, Suite 202, Truckee, CA 96161, United States of America
[3] Department of Forest Management, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT 59812, United States of America
[4] Management of Complex Systems, University of California, Merced, Merced, CA 95343, United States of America
[5] Global Park Solutions, Missoula, MT 59802, United States of America
[6] Fire Sciences Laboratory, Rocky Mountain Research Station, US Forest Service, Missoula, MT 59808, United States of America
[7] School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195, United States of America
[*] Author to whom any correspondence should be addressed.

**E-mail:** sean.parks@usda.gov

**Keywords:** biodiversity, climate change, disappearing climates, novel climates, protected areas, transboundary conservation

Supplementary material for this article is available online

## Abstract

Protected areas are essential to conserving biodiversity, yet changing climatic conditions challenge their efficacy. For example, novel and disappearing climates within the protected area network indicate that extant species may not have suitable climate in protected areas in the future. Further, potential transboundary range shifts, those that involve movement from one country to another, are also challenging because physical (e.g. fencing) and non-physical barriers (e.g. contrasting conservation policies) may impede climate-induced movements. Through the lens of climate analogs, we examined disappearing and novel climates within the global terrestrial protected area network and the potential for transboundary range shifts among protected areas under global warming 2 °C above preindustrial levels. We found that globally, climates in 24% of protected lands will no longer be protected within a 500 km radius of their focal location (indicating disappearing climates within the protected area network), while 36% of protected lands will gain climates not previously protected (indicating novel climates within the protected area network). Further, we found that potential transboundary range shifts are widespread but variable; for example, 23% of protected climates in Europe and >50% of protected climates in Africa under climate change are located in a different country than the focal protected areas. As the global conservation community actively deliberates conservation frameworks (e.g. 30% by 2030), our study offers insights to reduce the prevalence of novel and disappearing climates within the global protected area network via strategic conservation actions and underscores the importance of setting and accommodating targets and strategies that transcend national boundaries.

## 1. Introduction

Protected areas serve as an essential tool for conserving biodiversity (Gray *et al* 2016, Pacifici *et al* 2020). However, their efficacy in a changing climate is increasingly being questioned (Elsen *et al* 2020, Dobrowski *et al* 2021). Protected area boundaries are static and yet the organisms they protect will need to move as they shift their ranges in response to a warming climate (Hannah *et al* 2007, McGuire *et al* 2016). Because the matrix of unprotected lands can be inhospitable to some species (Newbold *et al* 2015), the most favorable destinations for many climate-driven movements, particularly for species sensitive to human land uses, are likely to be protected areas themselves. This raises the question as to whether species currently resident in protected areas will find other protected areas with similar future climate conditions to which to move. That is, to what extent will climate conditions represented in the contemporary global terrestrial protected area network have—or *not* have—analogous climates in protected areas under climate change (i.e. *disappearing climates* within the protected area network) (Hoffmann *et al* 2019)?

In cases where the climate of protected lands is not expected to disappear, climate-induced species range shifts out of some protected areas and into others can be expected, yet organisms will also need to traverse the matrix of non-protected lands where human stressors and land uses are more intense (Parks *et al* 2020, Doherty *et al* 2021). Not only will organisms face degraded and fragmented habitat as they move out of protected areas (di Marco *et al* 2018), but for some species, their movement will require crossing international borders because suitable climatic conditions lie outside of their country of origin (Titley *et al* 2021). This type of transboundary movement likely presents additional challenges for organisms shifting in response to climate change because of differences in land-use types and intensities, conservation priorities, and laws and policies among countries (Lambin *et al* 2003, Hodge *et al* 2015, Thornton *et al* 2018). Further, international borders themselves may have physical barriers (e.g. fencing) that restrict species movement (Ito *et al* 2013, Peters *et al* 2018). Consequently, transboundary range shifts pose unique challenges for conserving biodiversity and promoting landscape connectivity now and into the future (Hannah 2010).

Research at regional to continental extents has shown that species range shifts will impact the effectiveness of, and species represented in, protected areas (Hole *et al* 2009, Araújo *et al* 2011, Thomas and Gillingham 2015, Heikkinen *et al* 2020). For example, Araújo *et al* (2011) found that by 2080, 58% of plant and terrestrial vertebrate species would experience a reduction in suitable climate in European protected areas. The potential for climate-induced transboundary range shifts is a newer topic of study with limited research to date. An exception is Titley *et al* (2021), who examined the potential for transboundary range shifts for mammals and birds at the global scale; they found that by 2070, climatically suitable conditions for roughly one third of birds and mammals will primarily lie in countries in which the species are not currently found. To our knowledge, however, no studies have specifically quantified the potential for transboundary range shifts with a specific focus on the global protected area network. Given that physical and non-physical barriers along international borders can threaten biodiversity (Ito *et al* 2013, Thornton *et al* 2018), a focused analysis on the potential for transboundary range shifts among the global protected area network would quantify another metric of vulnerability that species will face as they respond to climate change.

One method for analyzing the potential for disappearing climates and climate-driven species range shifts is through the lens of climate analogs. Climate analogs are specific locations with matching climate conditions for two time periods (e.g. contemporary and future) (Wuebbles and Hayhoe 2004, Ohlemüller *et al* 2006). Climate analogs are increasingly used to quantify metrics of climate change exposure (Dobrowski and Parks 2016, Batllori *et al* 2017), to map potential movement routes for species tracking suitable conditions (Littlefield *et al* 2017, Carroll *et al* 2018, Parks *et al* 2020), to identify climatic refugia (Michalak *et al* 2018), and to model community and vegetation response to climate change (Blois *et al* 2013, Holsinger *et al* 2019). Two kinds of climate analogs can be identified (Hamann *et al* 2015): *source analogs* (also referred to as reverse or backward analogs) represent, for a focal site, the locations from which the climate is moving, and *destination analogs* (also referred to as forward analogs) represent the locations to which the climate at a focal site will move in the future. In the context of climate-induced range shifts, this can be framed as 'where organisms are moving from' (source analogs) and 'where organisms are moving to' (destination analogs) (figures 1 and 2). In this study, a *novel climate* emerges when a focal site has no protected source analogs within 500 km; a *disappearing climate* occurs when a focal site has no protected destination analogs within 500 km. We limited our search to a 500 km radius to account for dispersal constraints observed for many species shifting in response to changes in climate that are plausible by mid-21st century (Chen *et al* 2011). In conducting this study, we assume that species will shift their ranges with concomitant shifts in climate (Parmesan and Yohe 2003, Chen *et al* 2011, Alagador *et al* 2016), and consequently, we interpret spatial shifts in climate as *potential* climate-induced range shifts.

Our overall goal is to examine disappearing and novel climates within the global protected area network and the potential for transboundary range shifts among protected areas under a global 2 °C warming (recognizing that all analyses are constrained to a 500 km search radius). We have four specific objectives (figures 1 and 2). The first is to quantify the potential for protected areas to gain *novel climates* that are not currently represented in the protected area network. When this is the case, the future climate conditions in protected areas have no contemporary protected source analogs within 500 km. The second objective is to quantify the potential for *disappearing climates*, in which climates currently represented by protected areas will no longer be

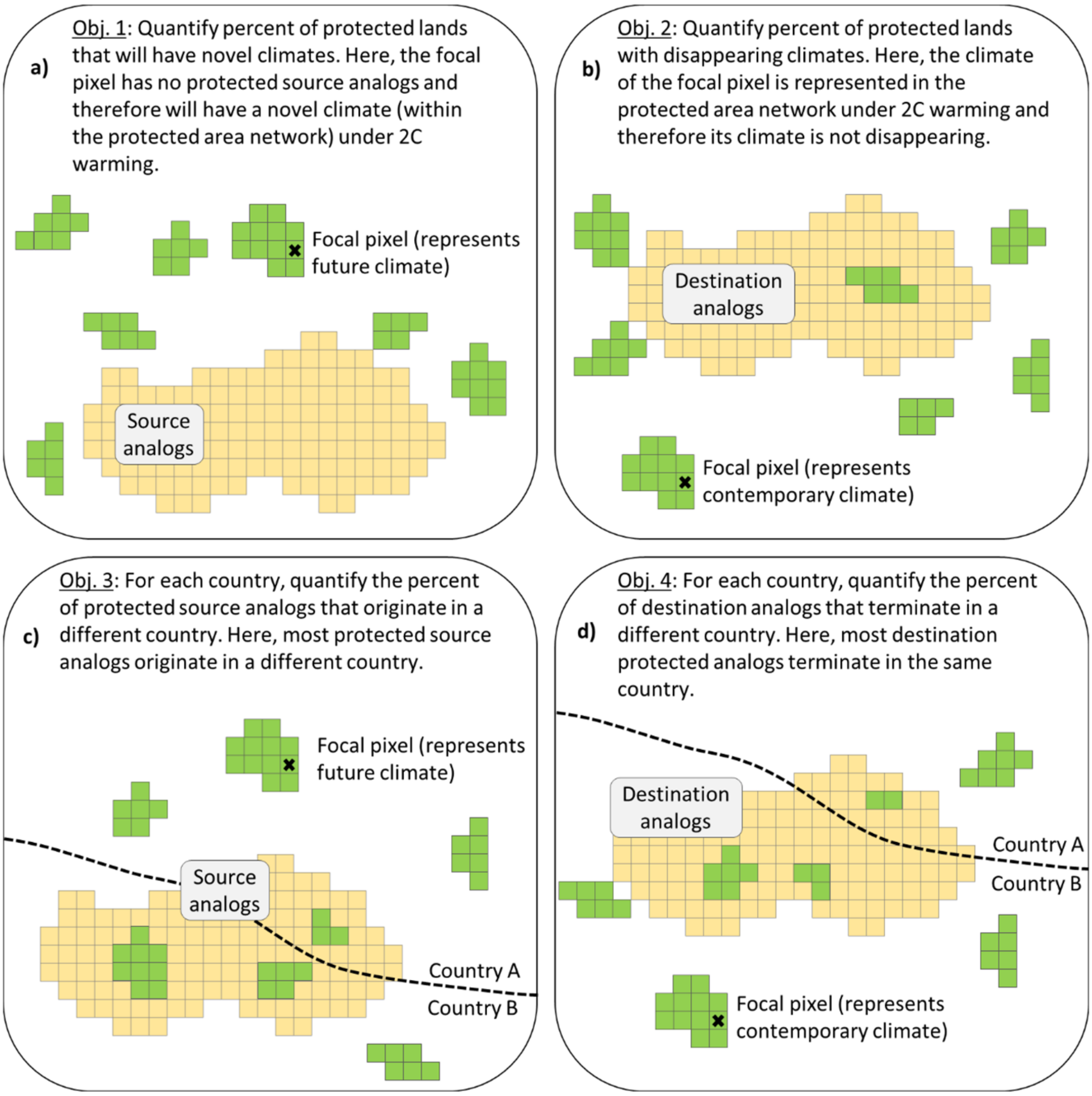

**Figure 1.** Conceptual depiction of the four objectives. For each protected 'focal pixel' across the planet, we determine whether its climate is novel or disappearing and we quantify the potential for transboundary range shifts (among protected areas) under a global 2 °C warming. Green = protected areas (or protected pixels). Yellow (panels (a) and (c)) = current locations of analogous climate to focal pixel (i.e. source analogs). Yellow (panels (b) and (d)) = future locations of analogous climate (under 2 °C warming) to focal pixel (i.e. destination analogs).

represented within the protected area network within 500 km under 2 °C warming. Third, we aim to determine the degree to which source analogs *originate in a different country*, and fourth, the degree to which destination analogs *terminate in a different country*. Our focus on climate (instead of individual species) (Schloss *et al* 2012, Titley *et al* 2021) allows us to conduct this analysis in a manner that applies to a broad range of species without making assumptions about species-specific dispersal, reproductive rate, or other factors that may inhibit or facilitate climate-induced range shifts. This coarse-filter approach (Hunter *et al* 1988, Tingley *et al* 2014) therefore provides a species-agnostic lens to characterize a subset of the many challenges the global conservation community faces in protecting biodiversity in the face of climate change.

## 2. Materials and methods

### 2.1. Data

Global gridded climate and water balance data (resolution = 4 km) including average minimum temperature of the coldest ($T_{\min}$), average maximum temperature of the warmest month ($T_{\max}$), annual actual evapotranspiration (AET), and annual climate water deficit (CWD) were obtained from TerraClimate (Abatzoglou *et al* 2018). These metrics are biologically relevant to species distributions (Stephenson 1998, Williams *et al* 2015) and have previously been used to characterize multivariate climate departures (Abatzoglou *et al* 2020). The four climate metrics were produced for each year from 1961 to 1990 and then averaged over the 1961–1990 time period to represent reference period climate normals.

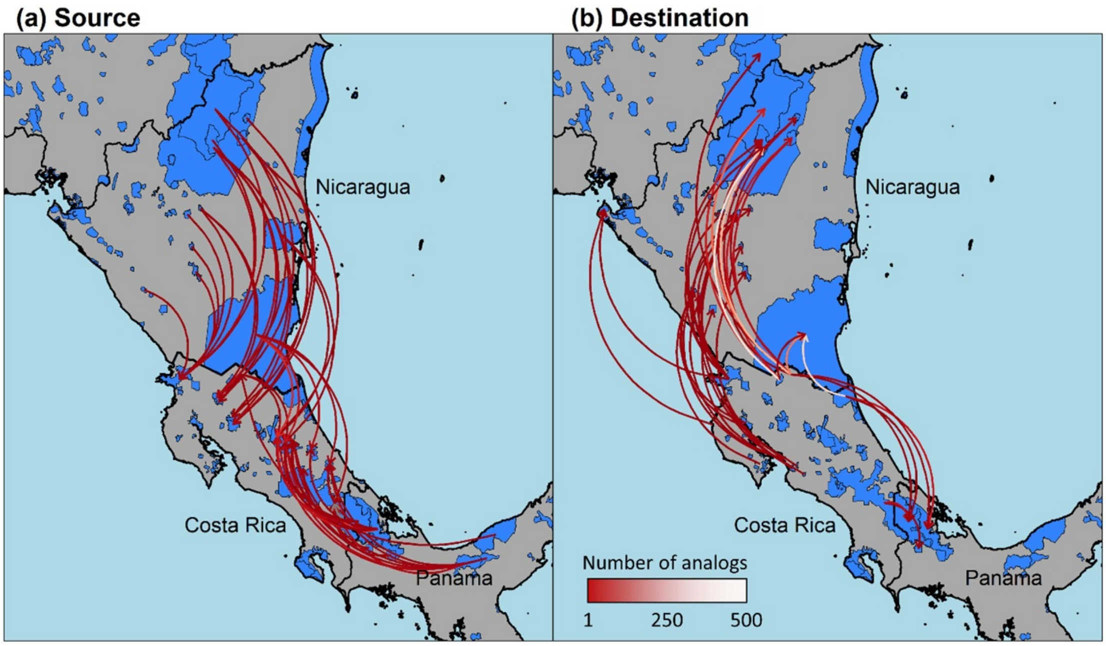

**Figure 2.** Illustration of potential transboundary movement into Costa Rican protected areas (source analogs; (a)) and out of Costa Rican protected areas (destination analogs; (b)). Note that, for simplicity, we do not show within-country analogs. Results for this illustration are summarized per protected area; for example, number of analogs moving from one Costa Rican protected area (using its centroid) to another protected area outside of Costa Rica (by centroid). Protected areas shown in blue.

Future climate conditions correspond with global mean temperatures that are 2 °C above pre-industrial levels per policy targets (Rogelj *et al* 2016). While modeled projections of climate change vary across models and policy-emission pathways, many estimates suggest that global mean temperatures will reach or exceed 2 °C above pre-industrial conditions by mid-century absent massive abrupt changes in global climate policies (Friedlingstein *et al* 2014). We do not presume a specific representative concentration pathway (RCP) or climate model sensitivity, all of which involve uncertainty. Rather, we base our climate projections on the amount of global warming that may be seen following various RCP-model choices. The +2 °C scenario (available from www.climatologylab.org/terraclimate.html) superposes projected multi-model changes in climate—including changes in both the mean and interannual variability as described in detail by Qin *et al* (2020)—to the observed 1961–1990 climate record. As with the reference period climate, we produced the four +2 °C climate metrics annually and over a 30 year time period to represent future climate normals.

We obtained a geospatial dataset representing protected areas from the World Database on Protected Areas (WDPA) (IUCN and UNEP-WCMC 2020). We included all protected areas identified as IUCN (International Union of Conservation for Nature) management categories I–VI and excluded protected areas categorized as 'marine' or 'proposed'. A large number of protected areas identified by the WDPA and were not assigned an IUCN category (i.e. designated as 'not reported') but have reasonably high levels of conservation (e.g. Kruger National Park in South Africa). Therefore, we included additional protected areas where the level of human modification was similar or less than that observed within IUCN category I–VI protected areas. Human impacts were estimated using the human modification gradient (HMG), a gridded raster dataset (resolution = 1 km) representing cumulative human modification to terrestrial lands (Kennedy *et al* 2019). Following Dobrowski *et al* (2021), we calculated the mean HMG for each IUCN category I–VI protected area, identified the 80th percentile of this distribution, and included un-assigned protected areas in our study that had a mean HMG less than or equal to the identified threshold. That is, protected areas without an assigned IUCN category but having a mean HMG $\leqslant$80th percentile threshold were included in our study. This procedure increased the protected lands included in this study by 30% (compared to that of strictly using IUCN I–VI according to the WDPA). Finally, we converted the vector-based polygon dataset to raster format with a resolution of ~4 km to match gridded climate data. Following Dobrowski *et al* (2021), raster pixels were categorized as protected if $\geqslant$75% of their area were identified as protected (i.e. IUCN category I–VI or meeting the HMG threshold) ($n$ = 975 961 pixels).

### 2.2. Identifying climate analogs and characterizing potential climate-induced transboundary range shifts

We used Mahalanobis distance and its standardization based on the Chi distribution (Mahony *et al* 2017) for quantifying climatic dissimilarity between each protected pixel and all other protected pixels within a 500 km radius; this radius has been used in previous studies (Williams *et al* 2007, Bellard *et al* 2014). Based on the reference period (1961–1990) and that of the +2 °C climate projections that are likely to manifest by mid-21st century, a 500 km search radius roughly corresponds to 5 km $\text{yr}^{-1}$ and to the upper dispersal limit for many terrestrial biota (animals and plants) (Chen *et al* 2011). We chose Mahalanobis distance because it compactly characterizes multiple variables by measuring the distance in multivariate space away from a centroid through principal components analysis of standardized anomalies. Mahalanobis distance scales multivariate mean climate conditions between a focal pixel and those within the 500 km search radius by the focal pixel's covariance and magnitude of interannual climate variability (ICV; based on 30 years of climate data) across the four climate metrics ($T_{\text{min}}$, $T_{\text{max}}$, AET, and CWD). Mahalanobis distances were calculated on standardized data (i.e. normal distributions based on means and standard deviation from the reference and +2 °C time periods). For source analogs, we characterized +2 °C ICV (30 years of climate data) and reference period climate normals to calculate climatic dissimilarity; for destination analogs, we used reference period ICV (30 years of climate data) and +2 °C climatic normals to calculate climatic dissimilarity. We quantify climatic distance relative to each pixel's ICV, meaning that relatively small changes in climate in regions with low ICV will exhibit higher Mahalanobis distances compared concomitant changes in climate in regions with high ICV (see Abatzoglou *et al* 2020, Dobrowski *et al* 2021). In this way, we implicitly account for the fact that small changes in climate in some parts of the planet (e.g. tropical regions with low ICV) may experience larger physiological and ecological impacts compared to other parts of the planet (e.g. temperate regions with higher ICV) (Dillon *et al* 2010).

To account for data dimensionality (number of variables), we standardized climatic dissimilarity (i.e. Mahalanobis distance) using the Chi distribution to calculate a multivariate *z*-score ($\sigma_{\text{d}}$) (Mahony *et al* 2017). $\sigma_{\text{d}}$ is therefore defined for all protected pixels in comparison to the focal pixel, and as such, $\sigma_{\text{d}}$ expresses the similarity between each pixel and candidate source and destination analogs (i.e. all other protected terrestrial pixels within 500 km). Inferences can be made from the percentiles of the Chi distribution (i.e. $1\sigma$, $2\sigma$, and $3\sigma$ for ~68th, 95th, and 99.7th percentiles, respectively). Protected pixels with $\sigma_{\text{d}} \leqslant 0.5$ were considered climate analogs in our analyses. As such, analogs in our study fall within the 39th percentile of ICV of the focal pixel. Inversely, non-analogous pixels exceed the 61st percentile ICV of the focal pixel. This threshold ensured a strong degree of multivariate similarity between climate analogs but was not so restrictive as to disqualify candidate analogs because of a small degree of variability.

For each country, we calculated the percentage of protected lands with novel and disappearing climates under a global 2 °C warming (figure 1). We also calculated the number and percent of source and destination analogs, as defined above, that originate or terminate in a different country, thereby characterizing the potential for climate-induced transboundary range shifts among protected areas (figures 1 and 2).

Acknowledging that our findings may be contingent on the 500 km search radius we used to identify protected climate analogs, we also conducted a sensitivity analysis using different search radii. Specifically, we used 50 and 250 km search radii to recognize that dispersal abilities vary among species (see McLachlan *et al* 2005, Jenkins *et al* 2007). For this sensitivity analysis, we report the percentage of novel and disappearing climates and characterize the potential for climate-induced transboundary range shifts among protected areas globally, by continent, and by region.

## 3. Results

Globally, 24% of protected lands will have disappearing climates under a 2 °C warming scenario (figure 3 and table 1), meaning that the contemporary climate conditions in approximately one-quarter of protected lands will not be protected in the future (keeping in mind the search for analogous climates for all aspects of this study, excluding the sensitivity analysis, was limited to a 500 km radius; see section 2). Correspondingly, 36% of protected lands will have novel climates under a 2 °C warming scenario, meaning that the future climatic conditions of approximately one-third of protected lands are not currently represented in the protected area network (figure 3 and table 1). Of those protected lands that have protected source analogs (meaning those focal pixels that will not experience novel climates; figure 3(c)), 13% originate in a different country (table 1). Of those protected lands that have protected destination analogs (meaning those focal pixels that will not experience disappearing climates; figure 3(d)), 15% terminate in a different country (table 1).

Substantial variation is apparent among continents (table 1), regions (table S4 available online at stacks.iop.org/ERL/17/054016/mmedia), and individual countries (tables S7–12). In southeast Europe, for example, 17.9% of protected lands have novel climates and 4.1% have disappearing climates. For

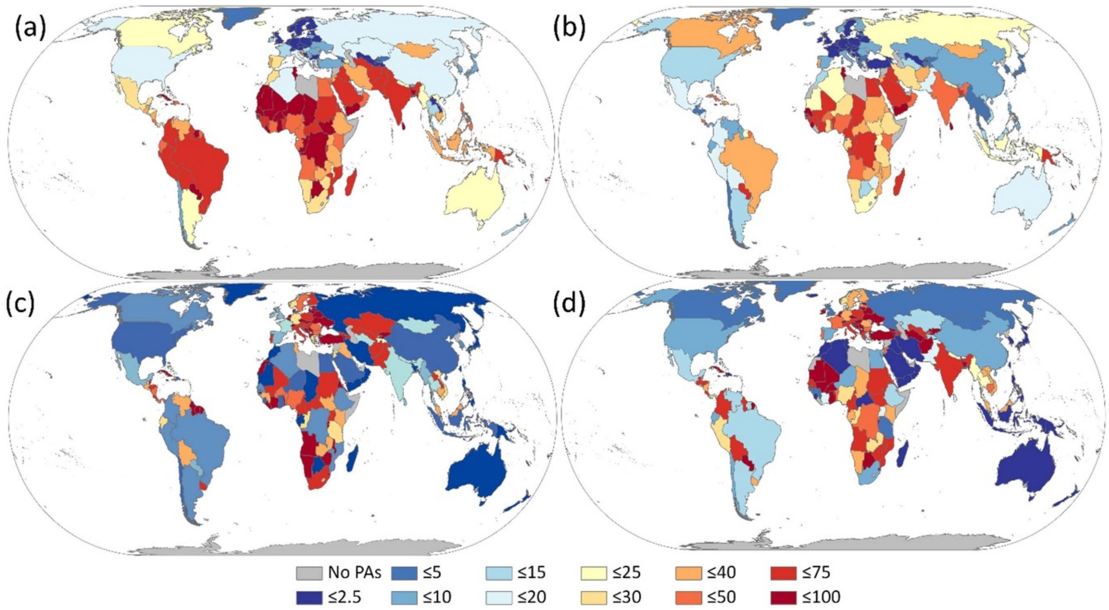

**Figure 3.** Maps depict the percent of each country's protected lands projected to have novel (a) or disappearing climates (b) (i.e. no source or destination analogs within 500 km, respectively). For the protected lands that do have analogs, maps depict the percent of protected source analogs that originate in a different country (c) and the percent of protected destination analogs that terminate a different country (d).

**Table 1.** Continental and global summaries show the percent of protected lands with novel and disappearing climates and the potential for transboundary range shifts among protected areas.

| | | | Source analogs | | Destination analogs | |
|---|---|---|---|---|---|---|
| Continent | % protected | Area protected (km$^2$) | Novel climate (% of protected lands with no protected analog) | % of all analogs originating in different country | Disappearing climate (% protected lands with no protected analog) | % of all analogs terminating in different country |
| Africa | 12.1 | 3330 272 | 51.7 | 48.2 | 35.8 | 54.7 |
| Asia | 4.9 | 1522 656 | 35.4 | 23.3 | 23.6 | 21.3 |
| Europe | 9.7 | 2219 456 | 14.5 | 22.4 | 15.2 | 23.4 |
| N. America | 13.3 | 3207 056 | 16.8 | 7.7 | 16.1 | 7.1 |
| Oceania | 17.1 | 1461 344 | 24.8 | 0.0 | 17.5 | 0.0 |
| S. America | 21.7 | 3867 568 | 54.2 | 14.1 | 28.5 | 15.7 |
| Global | 11.8 | 15 608 352 | 35.7 | 13.2 | 24.1 | 14.6 |

the protected lands in southern Europe that have protected analogs, 57.3% of source analogs originate in a different country and 71.1% of destination analogs terminate in a different country (table S4). As an example from a specific country (Romania), 7.3% and 8.2% of protected lands are expected to have novel and disappearing climates, respectively; of those protected lands with protected analogs, 49.4% originate outside of Romania (source) and 39.4% terminate outside of Romania (destination) (table S9). For each country, we also report the contributions from individual countries relating to the source and destination analogs (figures 4 and 5; S1–17; tables S13–40).

The sensitivity analysis using 50 and 250 km search radii for identifying protected climate analogs revealed predictable patterns. The percent of protected lands with novel and disappearing climates increases as the search radii becomes smaller; the prevalence of source and destination analogs that originate and terminate (respectively) in a different country decreases as the search radii becomes smaller (tables S1–6). Globally for example, novel climates are expected in 36% of protected lands when using a 500 km search radius, 44% of protected lands when using a 250 km radius, and 66% of protected lands when using a 50 km radius (tables S1–3).

## 4. Discussion

Protected areas are recognized as one of the most important tools for conserving biodiversity, yet their static borders do not explicitly recognize dynamic processes (e.g. range shifts) resulting from climate change (Hannah 2010). Our study found that roughly a quarter of protected lands will not have destination analogs in the protected area network under

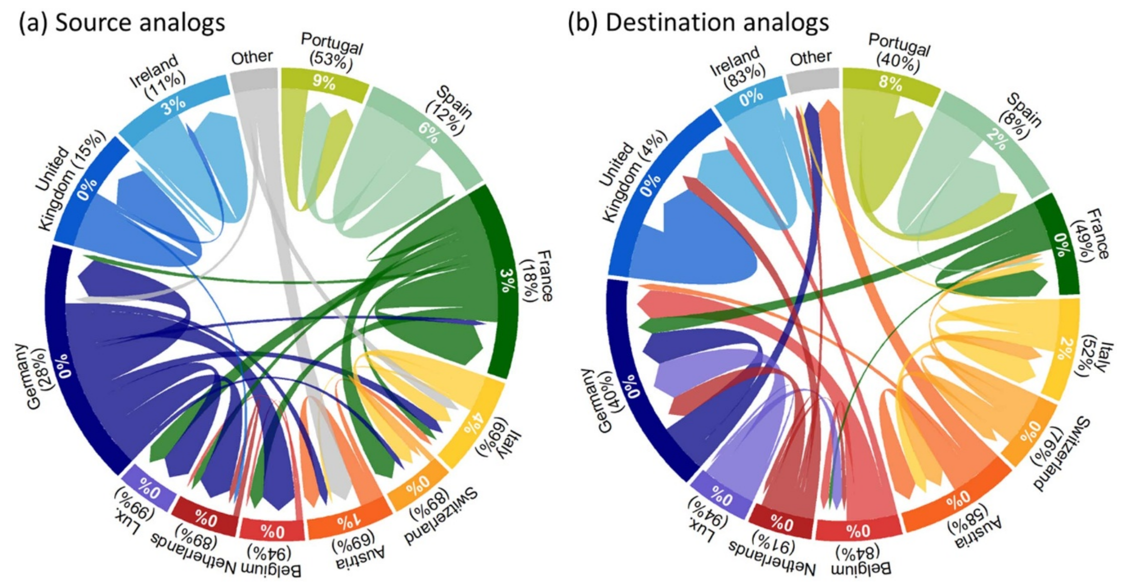

**Figure 4.** Chord diagrams depict potential source (a) and destination (b) transboundary movement among western European countries. The percent of each country's analogs that originate or terminate in a different country is indicated in **black text**. The percent of protected lands with no protected source or destination analog is indicated in **white text** (embedded within colored bar for each country). For source analogs (a), identify a country of interest and follow the incoming arrows to the country of origin; the width of the incoming arrows represents the relative contribution. In Portugal, for example, ∼40% of the source analogs originate in Spain and the remaining ∼60% originate in Portugal itself (a). For destination analogs (b), identify a country of interest and follow the outgoing arrows to the destination country; the width of the outgoing arrows represents the relative contribution. In terms of Portugal's outgoing analogs, ∼20% terminate in Spain and the remainder terminate in Portugal itself (b). For clarity, arrows between countries are only shown if ⩾5% of the total number of analogs originate or terminate in a given country. Chord diagrams for different regions can be found in the supplemental material (figures S1–17). Exact among-country values can also be found in the supplemental material (tables S13–40). The 'other' category represents countries that are not specifically shown.

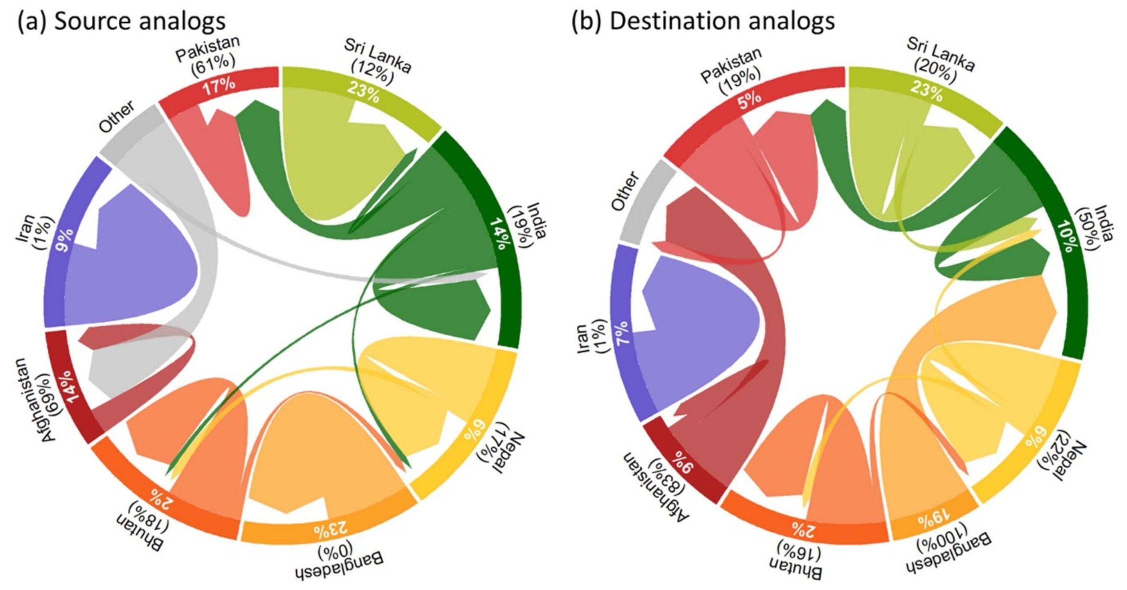

**Figure 5.** Chord diagrams depict potential source (a) and destination (b) transboundary movement among southern Asian countries. The percent of each country's analogs that originate or terminate in a different country is indicated in **black text**. The percent of protected lands with no protected source or destination analog is indicated in **white text** (embedded within colored bar for each country). For source analogs (a), identify a country of interest and follow the incoming arrows to the country of origin; the width of the incoming arrows represents the relative contribution. For destination analogs (b), identify a country of interest and follow the outgoing arrows to the destination country; the width of the outgoing arrows represents the relative contribution. For clarity, arrows between countries are only shown if ⩾5% of the total number of analogs originate or terminate in a given country. Chord diagrams for different regions can be found in the supplemental material (figures S1–17). Exact among-country values can also be found in the supplemental material (tables S13–40). The 'other' category represents countries that are not specifically shown.

a 2 °C warming (i.e. disappearing climates within 500 km). This finding indicates that biota inhabiting 3.75 million km$^2$ of the protected area network may be unable to find suitable habitat in protected areas in the future, further exacerbating the growing risk of climate-related extinctions. Additionally, roughly one-third of terrestrial protected lands across the globe have future climates that are not *currently* represented within the protected area network (i.e. novel climates within 500 km). This finding implies that 5.6 million km$^2$ of protected lands may not reach their full potential in terms of biodiversity representation because the source analog locations are not currently protected and thus may be degraded by human land uses, may support a depauperate complement of species, and may support large numbers of non-native species (Foley *et al* 2005, Didham *et al* 2007, Newbold *et al* 2015). Identifying new protected areas that encapsulate both future and current climates of protected areas (source and destination analogs, respectively) could increase the likelihood of continued biodiversity protection as the climate continues to warm (Elsen *et al* 2020). Along with explicit attention to maximizing the ability of landscapes to promote species movement when responding to a changing climate (i.e. climate connectivity) (McGuire *et al* 2016, Carroll *et al* 2018), our findings could help prioritize spatial planning efforts aimed at achieving global conservation initiatives (Convention on Biological Diversity 2020).

Although recent explorations into enhancing the terrestrial protected area network are starting to consider climate-induced movements (Carroll and Noss 2021), static boundaries such as international borders are not generally considered even though they have the potential to act as barriers to organisms undergoing range shifts. For the 64% and 76% of protected lands with protected source and destination analogs, respectively, our study indicates that species in protected areas undergoing climate-induced range shifts will often contend with international borders. In the protected areas of eastern Africa, for example, 33% of destination analogs terminate in a different country, in southeast Europe, 71% terminate in a different country, and in central America, 30% terminate in a different country (table S4). Although some international boundaries are remote and porous (Liu *et al* 2020), transboundary range shifts can challenge some organisms because international borders may act as impermeable or semi-permeable barriers. These may be physical barriers (e.g. fencing, water) or barriers imposed by different national biodiversity policies, contrasting land use practices, limited social acceptance of new species, or an overall lack of international coordination regarding conservation and species management (Hannah 2010, Hodge *et al* 2015, Peters *et al* 2018, Thornton *et al* 2018).

Even in the absence of climate-induced range shifts, it is clear that physical barriers such as border fencing negatively impacts some species (Pokorny *et al* 2016, Peters *et al* 2018). Directional movements to track suitable climatic conditions will exacerbate the deleterious effects of border fences on Earth's biota. For example, there is a 4000 km fence along the border of India and Bangladesh (Liu *et al* 2020) and a 500 km fence along the border of India and Pakistan (Ellison 2014), yet 59% of Pakistan's source analogs originate in India, 47% of India's destination analogs terminate in Pakistan, and 100% of Bangladesh's destination analogs terminate in India (tables S8, S21, S22 and figure S8). In total, there are approximately 30 000 km of border fencing in Eurasia, with border fence construction increasing in response to refugee crises and geopolitical unrest (Linnell *et al* 2016). Border barriers have also been constructed beyond Eurasia, for example, along the Botswana–Zimbabwe border, US–Mexico border, among many others. As such, our results underscore the need for increased international cooperation and investment to make borders more porous for organisms undergoing climate-induced range shifts (Mason *et al* 2020). Conservation practitioners could also strategically expand the protected area network within individual countries so that current and future climates are adequately represented, thereby reducing the necessity for transboundary range shifts. Recognizing that neither of these options are always practical or even possible, conservation practitioners could consider managed relocation (also referred to as assisted migration) when appropriate (McLachlan *et al* 2007).

Physical barriers like border fencing are more likely to inhibit climate-induced movement of large-bodied mammals compared to insects, small mammals, birds, and wind dispersed plants that can more easily circumvent such barriers. However, non-physical barriers (e.g. different biodiversity policies, contrasting land-use practices) may pose an even greater threat to many organisms. Different national policies may affect the ability of countries to coordinate management responses to species migration at a time of climate change. Examples of differing national policies include the asymmetry of species listing as endangered or threatened and dissimilar conservation priorities (Selier *et al* 2016, Thornton *et al* 2018). Also, differences between global and national priorities could have a deleterious impact on efforts to conserve biodiversity in an era of climate change. When neighboring countries have different policy frameworks for species protection, the ability of government agencies and non-government orginizations to achieve biodiversity conservation targets can be impaired (Vasilijević *et al* 2015). As such, transboundary range shifts provide an additional challenge for international conservation efforts and provide ample rationale for improving international cooperation relating to the conservation of biodiversity (Bartoń *et al* 2019, Thornton *et al* 2020, Titley *et al* 2021). When countries do not have aligned national policies, international agreements such as the Convention on Migratory Species can facilitate cooperation (Trouwborst 2012). For countries in the European Union, the Birds Directive and the Habitats Directive provide useful policy frameworks for the transboundary protection of species under the Natura 2000 network of protected sites, despite the fact that the climate change provisions of those directives are non-binding (Cliquet 2014).

The IUCN defines *Transboundary Conservation*, as 'a process of cooperation to achieve conservation goals across one or more international boundaries'. It proposes a typology of transboundary conservation that includes three types of international cooperation for protected areas across borders relevant to this discussion of climate analogs and transboundary range shifts. The first is *Transboundary Protected Areas*, defined by IUCN as 'a clearly defined geographical space that includes protected areas that are ecologically connected across one or more international boundaries and involves some form of cooperation'. The second is a *Transboundary Conservation Landscape and/or Seascape*, defined as 'an ecologically connected area that includes both protected areas and multiple resource use areas across one or more international boundaries and involves some form of cooperation'. The third is *Transboundary Migration Conservation Areas*, defined as, 'wildlife habitats in two or more countries that are necessary to sustain populations of migratory species and involve some form of cooperation'. Establishing formal and informal cooperation that encapsulate these and other concepts could provide the basis for policy coherence on transboundary species dispersal and migration in the face of climate change.

Although we used the same set of variables ($T_{\mathrm{min}}$, $T_{\mathrm{max}}$, AET, and CWD) to identify climate analogs across the planet, we recognize that species will respond to changes in these and other climate variables to different degrees and in different ways (Alfaro-Sánchez *et al* 2017). Some species may also exhibit different sensitivities to different climate variables in different portions of their distribution (Gavin and Hu 2006, Benito Garzón *et al* 2011). Although this analysis could be tailored to specific sets of climate variables known to be critical for specific taxa, the climate variables we used are known to influence the distributions of a wide array of species, and consequently, our study provides a coarse-filter lens in which to consider the potential for climate-induced range shifts. Likewise, our coarse-filter approach did not explicitly include many of the dynamics that will shape species range shifts (e.g. specific habitat needs, dispersal dynamics, reproduction rates). Instead, we focused on climate analogs with the inherent assumption that species, both plants and animals, will shift their ranges with concomitant shifts in climate (Alagador *et al* 2016), an assumption that some studies have documented under previous and contemporary climate changes (Davis and Shaw 2001, Chen *et al* 2011). This approach is therefore a broad-brush effort to encapsulate the potential needs of a wide range of species. This said, we acknowledge that dispersal abilities will be important in determining whether individual species can undergo successful climate-induced range shifts (Jenkins *et al* 2007). Dispersal abilities vary by orders of magnitude among species, and in some cases, the rate of climate change (i.e. climate velocity) may exceed the dispersal capabilities of some species (Schloss *et al* 2012, Corlett and Westcott 2013), as has been documented after the last glacial maximum with plant species in Europe (Normand *et al* 2011). These differences in dispersal rates will lead to time lags between animal range shifts and plant range shifts. Furthermore, because there will likely be a reshuffling of plant and animal communities, some animal species may not find suitable habitat conditions or prey species—or maybe excluded by new competitors or predators—in areas of suitable climate in the future (see Svenning and Sandel 2013, Fricke *et al* 2022).

Related, we searched for climate analogs within a 500 km radius of each protected pixel. This radius has been used in previous studies (Williams *et al* 2007, Bellard *et al* 2014) and roughly corresponds to the *upper dispersal limit* for many terrestrial biota (animals and plants) (Chen *et al* 2011). However, this threshold is likely too optimistic given that some species have dispersal abilities of only 1 km $\mathrm{yr}^{-1}$ or less (Bowman *et al* 2002, McLachlan *et al* 2005, Jenkins *et al* 2007). Our sensitivity analysis acknowledges varying dispersal capabilities among species and taxonomic groups by limiting the search for protected climate analogs to 50 and 250 km radii. The results were somewhat predictable in that the percent of novel and disappearing climates increase with decreasing search radii; this is because the total pool of candidate analogs is reduced as the search radius decreases. Overall, this suggests that that species that are more dispersal limited in the protected area network are at heightened risk under climate change. Conversely, the percent of analogs originating and terminating in a different country decreases with decreasing search radii. This is simply a mathematical artifact: focal pixels greater than the search radius from the boundary of the country in which it is located, by definition, will not have analogs that originate or terminate in a different country.

We also did not consider habitat fragmentation or the intervening matrix of human land uses that may impede successful range shifts (Schwartz *et al* 2001, Garcés-Restrepo *et al* 2018). Roads, agricultural fields, cities, and other human infrastructure and activities will likely reduce species' ability to track changing climatic conditions (Nunez *et al* 2013, McGuire *et al* 2016, Parks *et al* 2020). Yet another factor that may impede successful range shifts among protected areas is that the potential routes organisms must traverse may include sites with climatic conditions that exceed the thermal tolerance for some species (see Dobrowski and Parks 2016). For example, consider a montane species whose future climate is on an adjacent mountain range, yet between the mountain ranges, there is a hot and dry desert that serves as a barrier to climate-induced movement. Given these limitations on species dispersal, our results might in fact be optimistic. Hence, understanding and quantifying connectivity among protected areas, and specifically, connectivity assessments that incorporate factors that inhibit or promote movement such as habitat needs, human land uses, and climatic tolerances, will be a critical feature of future protected area networks (Hannah 2010, Littlefield *et al* 2019, Ward *et al* 2020). Although there are several caveats to our methodology and assumptions, the climate analog approach is an effective means for predicting and communicating broad scale changes in biodiversity patterns (Blois *et al* 2013, Parks *et al* 2018, Holsinger *et al* 2019).

Our study is not intended to convey that protected areas are not a useful construct in an era of climate change. Protected areas will continue to play an important role in conserving biodiversity even though we expect some species to move out of some protected areas and into others as they shift their ranges in response to climate change (Thomas and Gillingham 2015); individual protected areas will simply protect a different set of species than are currently extant. In addition, because our analyses were conducted at a relatively coarse grain, it is possible that some species may be able to find suitable climates within the protected areas they currently occupy. Finer grained analyses would be needed to identify such finer scale refugia within protected areas. While biodiversity conservation is often a key motivation for establishing protected areas, it is also important to recognize that protected areas may have primarily been created for several other reasons, such as the protection of unique geological or cultural features (e.g. Grand Canyon and Mesa Verde National Park, USA, respectively). Regardless of why protected areas were primarily established, they serve myriad of ancillary functions and features, including soil conservation, carbon sequestration, watershed protection, aesthetics, recreation, and human well-being (e.g. Melillo *et al* 2016, Puhakka *et al* 2017, Dinerstein *et al* 2019). This is all to say that existing protected areas are critically important to the conservation of biodiversity and other features and functions even in an era of rapid climate change.

As nations grapple with changing climates and the loss of biodiversity, protected areas remain one of the best solutions to ensure the survival of species (Hannah *et al* 2007, Elsen *et al* 2020). The Global Biodiversity Framework currently being negotiated by the parties to the Convention on Biological Diversity has a 2050 shared vision of 'living in harmony with nature'. Proposals to realize this vision include a target to conserve 30% of the planet, with a focus on areas that are important to biodiversity, by 2030 (30 × 30) (Convention on Biological Diversity 2020) as well as the half-Earth conservation movement (Wilson 2016). Current estimates suggest that 15.7% of the planet's terrestrial area is protected according to the IUCN classification system (UNEP-WCMC, IUCN and NGS 2021). As nations designate new protected areas to achieve these targets, our study offers insights to reduce the prevalence of novel and disappearing climates within the global protected area network via strategic conservation actions.

Moreover, the potential for climate-induced transboundary ranges shifts suggests that international cooperation is needed to remove physical and non-physical barriers to facilitate species movement. This can be achieved, for example, by creating connectivity corridors (Hilty *et al* 2020), developing cooperation models using the IUCN framework for transboundary conservation, alignment of national policies, and through new programs, initiatives, and protocols developed within regional and international conventions and treaties. International cooperation could also include 'knowledge sharing' or 'experience sharing' workshops and developing best practice guidelines, in that countries gaining new climates and species can learn management and conservation considerations from other countries with knowledge of those climates and the associated species. As removing physical and non-physical barriers is not possible in all cases, other strategies such as managed relocation might be necessary to conserve biodiversity within the protected area network (see Hoegh-Guldberg *et al* 2008). Managed relocation might be necessary even with good international cooperation because climate-induced movement might be impeded by incompatible land uses or climate conditions that exceed the thermal tolerance for a given species. As the global conservation community deliberates a 2030 conservation framework, our study underscores the importance of setting and accommodating targets and strategies that transcend national boundaries.

## Data availability statements

Protected area boundaries were obtained from the World Database on Protected Areas (available at: www.protectedplanet.net).

The data that support the findings of this study are openly available at the following URL/DOI: www.climatologylab.org/terraclimate.html.

## Acknowledgments

We thank Vincent Sanders and Joey Jones at Mississippi State University for their inestimable assistance in computer processing on the Ceres High Performance Computing cluster, and Stan Kosecki (USDA Agricultural Research Service) and Wesley Worrell (USDA Forest Service) for facilitating this project within the USDA-ARS initiative for scientific computing SCINet system. We also thank two anonymous reviewers for providing feedback that substantially improved this manuscript. This research was supported in part by the USDA Forest Service, Rocky Mountain Research Station, Aldo Leopold Wilderness Research Institute. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or US Government determination or policy.

## ORCID iDs

Sean A Parks https://orcid.org/0000-0002-2982-5255
Caitlin E Littlefield https://orcid.org/0000-0003-3771-7956
Solomon Z Dobrowski https://orcid.org/0000-0003-2561-3850
Katherine A Zeller https://orcid.org/0000-0002-2913-6660
John T Abatzoglou https://orcid.org/0000-0001-7599-9750

## References

Abatzoglou J T, Dobrowski S Z and Parks S A 2020 Multivariate climate departures have outpaced univariate changes across global lands *Sci. Rep.* **10** 3891

Abatzoglou J T, Dobrowski S Z, Parks S A and Hegewisch K C 2018 TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958–2015 *Sci. Data* **5** 170191

Alagador D, Cerdeira J O and Araújo M B 2016 Climate change, species range shifts and dispersal corridors: an evaluation of spatial conservation models *Methods Ecol. Evol.* **7** 853–66

Alfaro-Sánchez R, Muller-Landau H C, Wright S J and Camarero J J 2017 Growth and reproduction respond differently to climate in three Neotropical tree species *Oecologia* **184** 531–41

Araújo M B, Alagador D, Cabeza M, Nogués-Bravo D and Thuiller W 2011 Climate change threatens European conservation areas *Ecol. Lett.* **14** 484–92

Bartoń K A, Zwijacz-Kozica T, Zięba F, Sergiel A and Selva N 2019 Bears without borders: long-distance movement in human-dominated landscapes *Glob. Ecol. Conserv.* **17** e00541

Batllori E, Parisien M-A, Parks S A, Moritz M A and Miller C 2017 Potential relocation of climatic environments suggests high rates of climate displacement within the North American protection network *Glob. Change Biol.* **23** 3219–30

Bellard C, Leclerc C, Leroy B, Bakkenes M, Veloz S, Thuiller W and Courchamp F 2014 Vulnerability of biodiversity hotspots to global change *Glob. Ecol. Biogeogr.* **23** 1376–86

Benito Garzón M, Alía R, Robson T M and Zavala M A 2011 Intra-specific variability and plasticity influence potential tree species distributions under climate change *Glob. Ecol. Biogeogr.* **20** 766–78

Blois J L, Williams J W, Fitzpatrick M C, Jackson S T and Ferrier S 2013 Space can substitute for time in predicting climate-change effects on biodiversity *Proc. Natl Acad. Sci.* **110** 9374–9

Bowman J, Jaeger J A G and Fahrig L 2002 Dispersal distance of mammals is proportional to home range size *Ecology* **83** 2049–55

Carroll C and Noss R F 2021 Rewilding in the face of climate change *Conserv. Biol.* **35** 155–67

Carroll C, Parks S A, Dobrowski S Z and Roberts D R 2018 Climatic, topographic, and anthropogenic factors determine connectivity between current and future climate analogs in North America *Glob. Change Biol.* **24** 5318–31

Chen I-C, Hill J K, Ohlemüller R, Roy D B and Thomas C D 2011 Rapid range shifts of species associated with high levels of climate warming *Science* **333** 1024–6

Cliquet A 2014 International and European law on protected areas and climate change: need for adaptation or implementation? *Environ. Manage.* **54** 720–31

Convention on Biological Diversity 2020 Update of the zero draft of the post-2020 global biodiversity framework

Corlett R T and Westcott D A 2013 Will plant movements keep up with climate change? *Trends Ecol. Evol.* **28** 482–8

Davis M B and Shaw R G 2001 Range shifts and adaptive responses to quaternary climate change *Science* **292** 673–9

di Marco M, Venter O, Possingham H P and Watson J E M 2018 Changes in human footprint drive changes in species extinction risk *Nat. Commun.* **9** 4621

Didham R K, Tylianakis J M, Gemmell N J, Rand T A and Ewers R M 2007 Interactive effects of habitat modification and species invasion on native species decline *Trends Ecol. Evol.* **22** 489–96

Dillon M E, Wang G and Huey R B 2010 Global metabolic impacts of recent climate warming *Nature* **467** 704–6

Dinerstein E *et al* 2019 A global deal for nature: guiding principles, milestones, and targets *Sci. Adv.* **5** eaaw2869

Dobrowski S Z, Littlefield C E, Lyons D S, Hollenberg C, Carroll C, Parks S A, Abatzoglou J T, Hegewisch K and Gage J 2021 Protected-area targets could be undermined by climate change-driven shifts in ecoregions and biomes *Commun. Earth Environ.* **2** 198

Dobrowski S Z and Parks S A 2016 Climate change velocity underestimates climate change exposure in mountainous regions *Nat. Commun.* **7** 12349

Doherty T S, Hays G C and Driscoll D A 2021 Human disturbance causes widespread disruption of animal movement *Nat. Ecol. Evol.* **5** 513–519

Ellison A M 2014 Political borders should not hamper wildlife *Nat. News* **508** 9

Elsen P R, Monahan W B, Dougherty E R and Merenlender A M 2020 Keeping pace with climate change in global terrestrial protected areas *Sci. Adv.* **6** eaay0814

Foley J A *et al* 2005 Global consequences of land use *Science* **309** 570–4

Fricke E C, Ordonez A, Rogers H S and Svenning J-C 2022 The effects of defaunation on plants' capacity to track climate change *Science* **375** 210–4

Friedlingstein P *et al* 2014 Persistent growth of $CO_2$ emissions and implications for reaching climate targets *Nat. Geosci.* **7** 709–15

Garcés-Restrepo M F, Pauli J N and Peery M Z 2018 Natal dispersal of tree sloths in a human-dominated landscape: implications for tropical biodiversity conservation *J. Appl. Ecol.* **55** 2253–62

Gavin D G and Hu F S 2006 Spatial variation of climatic and non-climatic controls on species distribution: the range limit of *Tsuga heterophylla J. Biogeogr.* **33** 1384–96

Gray C L, Hill S L L, Newbold T, Hudson L N, Börger L, Contu S, Hoskins A J, Ferrier S, Purvis A and Scharlemann J P W 2016 Local biodiversity is higher inside than outside terrestrial protected areas worldwide *Nat. Commun.* **7** 12306

Hamann A, Roberts D R, Barber Q E, Carroll C and Nielsen S E 2015 Velocity of climate change algorithms for guiding conservation and management *Glob. Change Biol.* **21** 997–1004

Hannah L 2010 A global conservation system for climate-change adaptation *Conserv. Biol.* **24** 70–77

Hannah L, Midgley G, Andelman S, Araújo M, Hughes G, Martinez-Meyer E, Pearson R and Williams P 2007 Protected area needs in a changing climate *Front. Ecol. Environ.* **5** 131–8

Heikkinen R K, Leikola N, Aalto J, Aapala K, Kuusela S, Luoto M and Virkkala R 2020 Fine-grained climate velocities reveal vulnerability of protected areas to climate change *Sci. Rep.* **10** 1678

Hilty J *et al* 2020 Guidelines for conserving connectivity through ecological networks and corridors *Best Practice Protected Area Guidelines Series* vol 30 (Gland: International Union for Conservation of Nature) p 122

Hodge I, Hauck J and Bonn A 2015 The alignment of agricultural and nature conservation policies in the European Union *Conserv. Biol.* **29** 996–1005

Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer D B, Parmesan C, Possingham H P and Thomas C D 2008 Assisted colonization and rapid climate change *Science* **321** 345–6

Hoffmann S, Irl S D H and Beierkuhnlein C 2019 Predicted climate shifts within terrestrial protected areas worldwide *Nat. Commun.* **10** 4787

Hole D G, Willis S G, Pain D J, Fishpool L D, Butchart S H M, Collingham Y C, Rahbek C and Huntley B 2009 Projected impacts of climate change on a continent-wide protected area network *Ecol. Lett.* **12** 420–31

Holsinger L, Parks S A, Parisien M, Miller C, Batllori E and Moritz M A 2019 Climate change likely to reshape vegetation in North America's largest protected areas *Conserv. Sci. Pract.* **1** e50

Hunter M L Jr, Jacobson G L Jr and Webb T III 1988 Paleoecology and the coarse-filter approach to maintaining biological diversity *Conserv. Biol.* **2** 375–85

Ito T Y, Lhagvasuren B, Tsunekawa A, Shinoda M, Takatsuki S, Buuveibaatar B and Chimeddorj B 2013 Fragmentation of the habitat of wild ungulates by anthropogenic barriers in Mongolia *PLoS One* **8** e56995

IUCN and UNEP-WCMC 2020 Protected planet: the World Database on Protected Areas (WDPA) (Cambridge: UNEP-WCMC and IUCN (available at: www.protectedplanet.net) (Accessed September 2019)

Jenkins D G *et al* 2007 Does size matter for dispersal distance? *Glob. Ecol. Biogeogr.* **16** 415–25

Kennedy C M, Oakleaf J R, Theobald D M, Baruch-Mordo S and Kiesecker J 2019 Managing the middle: a shift in conservation priorities based on the global human modification gradient *Glob. Change Biol.* **25** 811–26

Lambin E F, Geist H J and Lepers E 2003 Dynamics of land-use and land-cover change in tropical regions *Annu. Rev. Environ. Resour.* **28** 205–41

Linnell J D C *et al* 2016 Border security fencing and wildlife: the end of the transboundary paradigm in Eurasia? *PLoS Biol.* **14** e1002483

Littlefield C E, Krosby M, Michalak J L and Lawler J J 2019 Connectivity for species on the move: supporting climate-driven range shifts *Front. Ecol. Environ.* **17** 270–8

Littlefield C E, McRae B H, Michalak J L, Lawler J J and Carroll C 2017 Connecting today's climates to future climate analogs to facilitate movement of species under climate change *Conserv. Biol.* **31** 1397–408

Liu J, Yong D L, Choi C-Y and Gibson L 2020 Transboundary frontiers: an emerging priority for biodiversity conservation *Trends Ecol. Evol.* **35** 679–90

Mahony C R, Cannon A J, Wang T and Aitken S N 2017 A closer look at novel climates: new methods and insights at continental to landscape scales *Glob. Change Biol.* **23** 3934–55

Mason N, Ward M, Watson J E M, Venter O and Runting R K 2020 Global opportunities and challenges for transboundary conservation *Nat. Ecol. Evol.* **4** 694–701

McGuire J L, Lawler J J, McRae B H, Nuñez T A and Theobald D M 2016 Achieving climate connectivity in a fragmented landscape *Proc. Natl Acad. Sci. USA* **113** 7195–200

McLachlan J S, Clark J S and Manos P S 2005 Molecular indicators of tree migration capacity under rapid climate change *Ecology* **86** 2088–98

McLachlan J S, Hellmann J J and Schwartz M W 2007 A framework for debate of assisted migration in an era of climate change *Conserv. Biol.* **21** 297–302

Melillo J M, Lu X, Kicklighter D W, Reilly J M, Cai Y and Sokolov A P 2016 Protected areas' role in climate-change mitigation *Ambio* **45** 133–45

Michalak J L, Lawler J J, Roberts D R and Carroll C 2018 Distribution and protection of climatic refugia in North America *Conserv. Biol.* **32** 1414–25

Newbold T *et al* 2015 Global effects of land use on local terrestrial biodiversity *Nature* **520** 45

Normand S, Ricklefs R E, Skov F, Bladt J, Tackenberg O and Svenning J-C 2011 Postglacial migration supplements climate in determining plant species ranges in Europe *Proc. R. Soc.* B **278** 3644–53

Nunez T A, Lawler J J, McRae B H, Pierce D J, Krosby M B, Kavanagh D M, Singleton P H and Tewksbury J J 2013 Connectivity planning to address climate change *Conserv. Biol.* **27** 407–16

Ohlemüller R, Gritti E S, Sykes M T and Thomas C D 2006 Towards European climate risk surfaces: the extent and distribution of analogous and non-analogous climates 1931–2100 *Glob. Ecol. Biogeogr.* **15** 395–405

Pacifici M, di Marco M and Watson J E M 2020 Protected areas are now the last strongholds for many imperiled mammal species *Conserv. Lett.* **13** e12748

Parks S A, Carroll C, Dobrowski S Z and Allred B W 2020 Human land uses reduce climate connectivity across North America *Glob. Change Biol.* **26** 2944–55

Parks S A, Holsinger L M, Miller C and Parisien M-A 2018 Analog-based fire regime and vegetation shifts in mountainous regions of the western US *Ecography* **41** 910–21

Parmesan C and Yohe G 2003 A globally coherent fingerprint of climate change impacts across natural systems *Nature* **421** 37–42

Peters R *et al* 2556 scientist signatories from 43 countries (Including 1472 from the United States and 616 from Mexico) MEXICO) 2018 Nature divided, scientists United: US–Mexico border wall threatens biodiversity and binational conservation *BioScience* **68** 740–3

Pokorny B, Flajšman K, Centore L, Krope F S and Šprem N 2016 Border fence: a new ecological obstacle for wildlife in Southeast Europe *Eur. J. Wildl. Res.* **63** 1

Puhakka R, Pitkänen K and Siikamäki P 2017 The health and well-being impacts of protected areas in Finland *J. Sustain. Tour.* **25** 1830–47

Qin Y, Abatzoglou J T, Siebert S, Huning L S, AghaKouchak A, Mankin J S, Hong C, Tong D, Davis S J and Mueller N D 2020 Agricultural risks from changing snowmelt *Nat. Clim. Change* **10** 459–65

Rogelj J, den Elzen M, Höhne N, Fransen T, Fekete H, Winkler H, Schaeffer R, Sha F, Riahi K and Meinshausen M 2016 Paris Agreement climate proposals need a boost to keep warming well below 2 °C *Nature* **534** 631–9

Schloss C A, Nuñez T A and Lawler J J 2012 Dispersal will limit ability of mammals to track climate change in the Western Hemisphere *Proc. Natl Acad. Sci.* **109** 8606–11

Schwartz M W, Iverson L R and Prasad A M 2001 Predicting the potential future distribution of four tree species in Ohio using current habitat availability and climatic forcing *Ecosystems* **4** 568–81

Selier S A J, Slotow R, Blackmore A and Trouwborst A 2016 The legal challenges of transboundary wildlife management at the population level: the case of a trilateral elephant population in Southern Africa *J. Int. Wildl. Law Policy* **19** 101–35

Stephenson N 1998 Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales *J. Biogeogr.* **25** 855–70

Svenning J-C and Sandel B 2013 Disequilibrium vegetation dynamics under future climate change *Am. J. Bot.* **100** 1266–86

Thomas C D and Gillingham P K 2015 The performance of protected areas for biodiversity under climate change *Biol. J. Linn. Soc.* **115** 718–30

Thornton D H *et al* 2018 Asymmetric cross-border protection of peripheral transboundary species *Conserv. Lett.* **11** e12430

Thornton D, Branch L and Murray D 2020 Distribution and connectivity of protected areas in the Americas facilitates transboundary conservation *Ecol. Appl.* **30** e02027

Tingley M W, Darling E S and Wilcove D S 2014 Fine- and coarse-filter conservation strategies in a time of climate change *Ann. New York Acad. Sci.* **1322** 92–109

Titley M A, Butchart S H M, Jones V R, Whittingham M J and Willis S G 2021 Global inequities and political borders challenge nature conservation under climate change *Proc. Natl Acad. Sci.* **118**

Trouwborst A 2012 Transboundary wildlife conservation in a changing climate: adaptation of the Bonn Convention on Migratory Species and its daughter instruments to climate change *Diversity* **4** 258–300

UNEP-WCMC, IUCN and NGS 2021 *Protected Planet Live Report* (Cambridge: UNEP-WCMC and IUCN) ch 2 (https://livereport.protectedplanet.net/)

Vasilijević M, Zunckel K, McKinney M, Erg B, Schoon M, Michel T R, Groves C and Philips A 2015 Transboundary conservation: a systematic and integrated approach *Page Best Practice Protected Area Guidelines Series* (https://doi.org/10.1016/j.jenvman.2014.10.013)

Ward M, Saura S, Williams B, Ramírez-Delgado J P, Arafeh-Dalmau N, Allan J R, Venter O, Dubois G and Watson J E M 2020 Just ten percent of the global terrestrial protected area network is structurally connected via intact land *Nat. Commun.* **11** 4563

Williams C M, Henry H A L and Sinclair B J 2015 Cold truths: how winter drives responses of terrestrial organisms to climate change *Biol. Rev.* **90** 214–35

Williams J W, Jackson S T and Kutzbach J E 2007 Projected distributions of novel and disappearing climates by 2100 AD *Proc. Natl Acad. Sci.* **104** 5738–42

Wilson E O 2016 *Half-earth: Our Planet's Fight for Life* (WW Norton & Company)

Wuebbles D J and Hayhoe K 2004 Climate change projections for the United States Midwest *Mitigation Adapt. Strateg. Glob. Change* **9** 335–63