

RESEARCH ARTICLE

Protected areas not likely to serve as steppingstones for species undergoing climate-induced range shifts

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Abstract

Species across the planet are shifting their ranges to track suitable climate conditions in response to climate change. Given that protected areas have higher quality habitat and often harbor higher levels of biodiversity compared to unprotected lands, it is often assumed that protected areas can serve as steppingstones for species undergoing climate-induced range shifts. However, there are several factors that may impede successful range shifts among protected areas, including the distance that must be traveled, unfavorable human land uses and climate conditions along potential movement routes, and lack of analogous climates. Through a species-agnostic lens, we evaluate these factors across the global terrestrial protected area network as measures of climate connectivity, which is defined as the ability of a landscape to facilitate or impede climate-induced movement. We found that over half of protected land area and two-thirds of the number of protected units across the globe are at risk of climate connectivity failure, casting doubt on whether many species can successfully undergo climate-induced range shifts among protected areas. Consequently, protected areas are unlikely to serve as steppingstones for a large number of species under a warming climate. As species disappear from protected areas without commensurate immigration of species suited to the emerging climate (due to climate connectivity failure), many protected areas may be left with a depauperate suite of species under climate change. Our findings are highly relevant given recent pledges to conserve 30% of the planet by 2030 (30×30), underscore the need for innovative land management strategies that allow for species range shifts, and suggest that assisted colonization may be necessary to promote species that are adapted to the emerging climate.

KEYWORDS

climate change, climate change vulnerability, climate connectivity, climate connectivity failure, climate-wise connectivity, protected areas, species range shifts

1 | INTRODUCTION

The global protected area network serves as a critical means for protecting Earth's biodiversity (Pacifi et al., 2020), and great efforts

have been undertaken to quantify contemporary or current connectivity of the protected area network in order to understand the potential for species movement among protected areas (Brennan et al., 2022; Santini, Saura, et al., 2016). In an era of rapid climate

change, however, the geographic distributions of flora and fauna may shift while protected area boundaries remain static (Dobrowski et al., 2021; Hannah, 2008). As species distributions shift in response to climate change (Chen et al., 2011; Parmesan & Yohe, 2003), protected areas can be expected to lose some species, and at the same time, may also gain species that were not originally present (Hole et al., 2011; Monzón et al., 2011). Given that protected areas often harbor higher levels of biodiversity compared to the unprotected matrix (Gillingham et al., 2015; Gray et al., 2016) and many species are dependent on protected areas for their continued persistence (Jackson & Gaston, 2008; Lehikoinen et al., 2019), it is important to understand whether species will be able to successfully undergo range shifts that include movement from one protected area to another. That is, will protected areas serve as steppingstones for species undergoing climate-induced range shifts (Hannah et al., 2014; Thomas & Gillingham, 2015)? A useful construct to evaluate the potential for successful range shifts among protected areas is 'climate connectivity', which can be defined as the ability of a landscape to promote species movement when responding to a changing climate (McGuire et al., 2016). A comprehensive evaluation of climate connectivity of the global protected area network would therefore complement recent assessments involving contemporary connectivity (i.e., in the absence of climate change) (e.g., Brennan et al., 2022).

It is generally assumed that species will need to track their suitable climate through space and time to undergo successful range shifts and respond to climate change (Corlett & Westcott, 2013; Devictor et al., 2008). However, climate connectivity, or lack thereof, plays an important role, as there are several factors that may facilitate or impede the ability of species to undergo successful climate-induced movement among protected areas. First, the actual distance that needs to be traveled to track suitable climate conditions may exceed the dispersal ability of many species (i.e., climate velocity may exceed biotic velocity) (Figure 1a) (Burrows et al., 2014; Carroll et al., 2015). Second, because human modified landscapes negatively impact many species (Newbold et al., 2015), it is likely that high levels of land use intensity in the unprotected matrix will limit successful climate-induced range shifts among protected areas (Figure 1b) (Parks et al., 2020; Robillard et al., 2015). Third, exposure to increasingly dissimilar climates may impede climate-induced range shifts (Carroll et al., 2018; Dobrowski & Parks, 2016). For example, consider a montane species whose future optimal climate is located on an adjacent mountain range, yet there is a hot desert between locations that acts as a barrier to movement (Figure 1c). Lastly, the lack of protected lands with suitable future climate conditions may hinder successful species movement (i.e., novel/disappearing climates) (Figure 1d) (Hoffmann et al., 2019; Parks et al., 2022). These constraints on species range shifts—dispersal limitations, human modified landscapes, exposure to dissimilar climates, and novel/disappearing climates—have been well established, yet they have not yet been integrated or simultaneously evaluated at a local, regional, or global level.

Evaluations of climate connectivity are a relatively recent line of scientific inquiry (Keeley et al., 2018; Littlefield et al., 2019; Nuñez et al., 2013) and often incorporate the concept of climate analogs (Brito-Morales et al., 2018; e.g., Littlefield et al., 2017; Senior

et al., 2019). Climate analogs are generally defined as specific locations with matching climate conditions between two time periods (e.g., contemporary vs. future climate) (Ohlemüller et al., 2006; Wuebbles & Hayhoe, 2004). Two types of climate analogs can be identified (Hamann et al., 2015): backward analogs (also referred to as reverse analogs) represent, for a focal site, the locations from which the climate is moving, and 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 among protected areas, this can be framed as "where organisms are moving from" (backward analogs) and "where organisms are moving to" (forward analogs). In this study, we quantify various measures of climate connectivity between focal locations (constrained to protected areas) and locations representing climate analogs (constrained to protected areas) using both backward and forward analogs. Although climate is not the sole driver of current and future distributions of species and ecological communities, climate analogs can capture latent, geographically structured factors that influence such distributions (e.g., edaphic conditions, disturbance regimes) (Dobrowski et al., 2021).

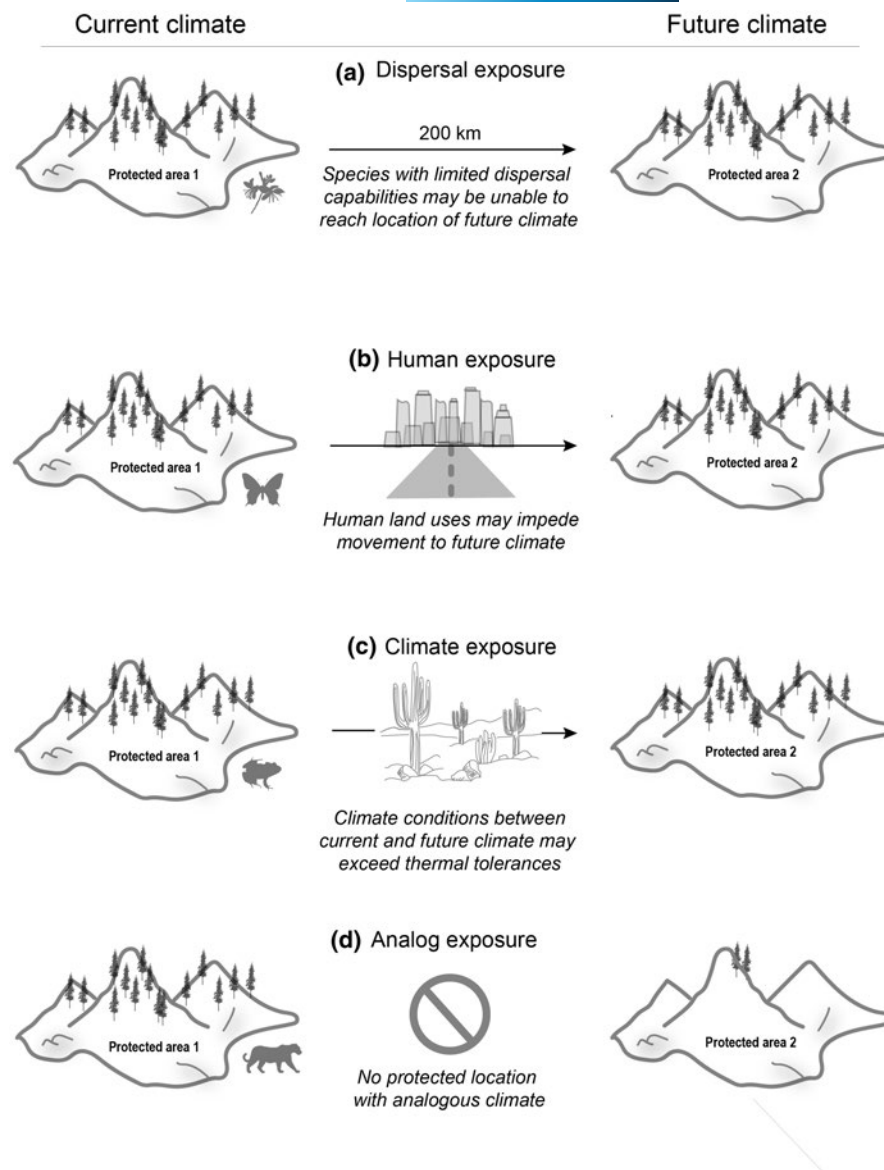
The overall goal of this study is to quantify climate connectivity among the global terrestrial protected area network. To do so, we use least-cost path modeling (Adriaensen et al., 2003) to delineate potential movement trajectories between each protected focal pixel and all of its protected climate analogs within a 500-km search radius. Our least-cost path model is parameterized with resistance to movement based on human land use intensity and climate dissimilarity (in relation to the climate of each focal pixel and pixels defined as climate analogs). We summarize four individual metrics of climate connectivity across the global protected area network, the first three of which are calculated using the potential movement paths delineated using least-cost path modeling: (1) mean distance to protected analogs (dispersal exposure), (2) mean cumulative exposure to human land uses (human exposure), (3) mean cumulative exposure to dissimilar climates (climate exposure), and (4) percent with no protected analogs (analog exposure). Using these four metrics, we then calculate the potential for climate connectivity failure, which provides insight as to whether or not protected areas can serve as steppingstones for species undergoing climate-induced range shifts. As we focus on climate and climate analogs (instead of individual species), our study applies to a broad range of species without making assumptions about the dispersal, reproductive rate, or other species-specific factors that may impede or facilitate range shifts. As such, this coarse-filter approach (Tingley et al., 2014) provides a species-agnostic lens to characterize climate connectivity failure.

2 | METHODS

2.1 | Identifying climate analogs

We followed the methods of Abatzoglou et al. (2020) and Parks et al. (2022) to characterize climate and identify backward and forward climate analogs. The specific climate variables we used were

FIGURE 1 We quantify four factors affecting climate connectivity. We calculate the mean distance from each protected pixel to all other protected climate analogs ('dispersal exposure') (a), intervening land-use intensity between each protected pixel and all protected analogs ('human exposure') (b), climatic dissimilarity between each protected pixel and all protected analogs ('climate exposure') (c), and the availability of protected analogs for each protected pixel ('analog exposure') (d).



average minimum temperature of the coldest month ($T_{\min}$), average maximum temperature of the warmest month ($T_{\max}$), annual actual evapotranspiration (AET), and annual climate water deficit (CWD). AET and CWD concurrently account for evaporative demand and availability of water (Stephenson, 1990). These four variables provide complementary information pertinent to ecological systems and collectively capture the major climatic constraints on species distributions and ecological processes across a range of taxa (Dobrowski et al., 2021; Lutz et al., 2010; Parker & Abatzoglou, 2016; Stephenson, 1998; Williams et al., 2015). Monthly data acquired from TerraClimate (Abatzoglou et al., 2018) were used to produce these annual summaries from 1961 to 1990 (resolution = ~4 km), which were then averaged over the same time period to represent reference period climate normals. The reference time period (1961–1990) is meant to represent climate conditions and climate niches prior to the bulk of recent warming. Future climate conditions were also computed from TerraClimate (available from www.climate.gov/terraclimate.html) and correspond to a 2°C increase above

pre-industrial levels that are likely to manifest by mid-21st century without immediate and massive changes in global climate policies (Friedlingstein et al., 2014). As with the reference period climate, we summarized the four +2°C climate metrics annually and over a 30-year time period to represent future climate normals. All analyses in this study were conducted in the R statistical platform (R Core Team, 2020).

We identified backward and forward analogs by estimating the climatic dissimilarity between each protected focal pixel (resolution = ~4 km to match gridded climate data) and all protected pixels within a 500-km radius using a standardized Mahalanobis distance (Mahony et al., 2017). We chose the 500-km search radius as it encompasses an upper range of dispersal for some terrestrial animals and plants (Chen et al., 2011) when assuming 2°C warming by mid-21st century; this search radius has also been used in previous studies (Bellard et al., 2014; Parks et al., 2022; Williams et al., 2007). The Mahalanobis distance metric synthesized the four climate variables (i.e., $T_{\min}$, $T_{\max}$, AET, and CWD; Figure 2a) by measuring distance in

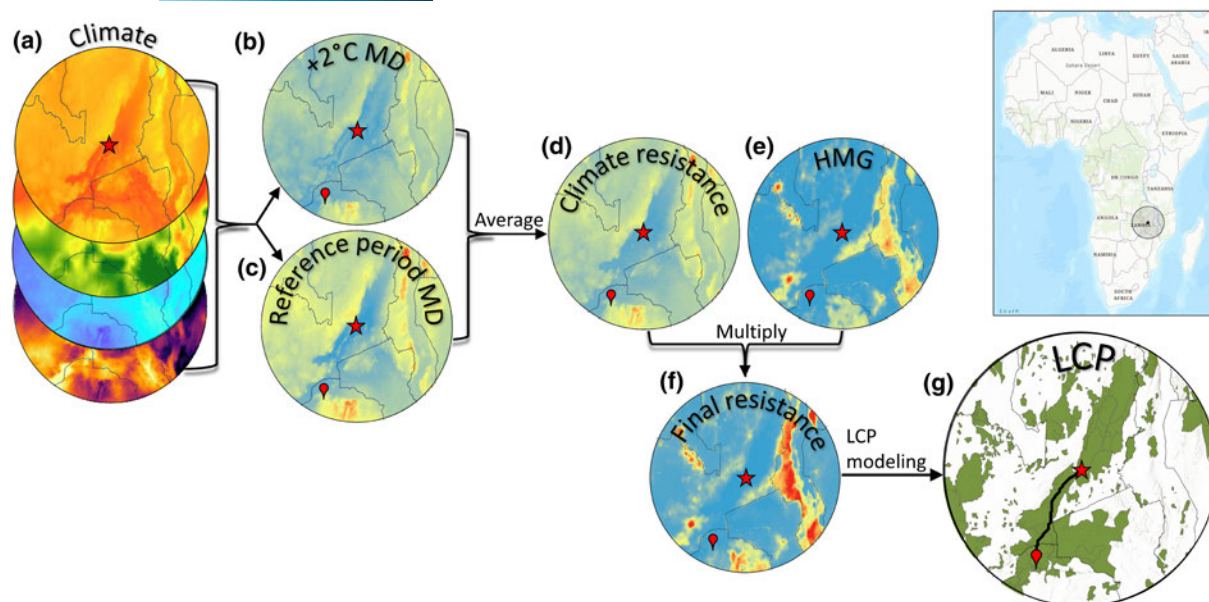


FIGURE 2 Workflow for delineating potential movement trajectories (i.e., least-cost paths) for a focal pixel (red star) in South Luangwa National Park, Zambia and its protected climate analogs (red teardrop; only one shown for illustration). Gridded Climate data ($T_{\min}$, $T_{\max}$, AET, and CWD) (a) are used to calculate two intermediate climatic dissimilarity surfaces, as measured by Mahalanobis distance (MD). The first of which, +2°C MD, represents the climatic distance among the focal pixel's future climate and surrounding pixels' future climate (b) and the second, Reference period MD, represents climatic distance among a focal pixel's future climate and surrounding pixels' reference period climate (c). Climate resistance is an average of +2°C MD and Reference MD to produce a gradient of the landscape's climatic similarity (blue) or dissimilarity (red) (d), which is then multiplied by the human modification gradient (HMG) (e). This produces the Final resistance surface for least-cost path modeling (f) which is used to delineate a least-cost path (LCP; black line), or potential movement route, from the focal pixel to its backward analog that minimizes cumulative costs in climate dissimilarity and human land uses. Map lines delineate study areas and do not necessarily depict accepted national boundaries. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16629)]

multivariate space away from a centroid using principal component analysis of standardized anomalies. Mahalanobis distance scales multivariate mean climate conditions between a pixel and those within the search radius by the focal pixel's covariance and magnitude of interannual climate variability (ICV) across the four metrics. For backward analogs, we characterized +2°C ICV and reference period climate normals to calculate climatic dissimilarity; for forward analogs, we used reference period ICV and +2°C climatic normals to calculate climatic dissimilarity. We standardized Mahalanobis distance to account for data dimensionality by calculating a multivariate z-score (σ_d) based on a Chi distribution (Mahony et al., 2017). σ_d represents the climate similarity between each focal pixel and its candidate backward and forward analogs (i.e., all other protected terrestrial pixels within 500km), and we considered any protected pixels with $\sigma_d \leq 0.5$ as climate analogs (Figure 2b) (following Parks et al., 2022). We were unable to calculate Mahalanobis distance when there was no ICV for any one of the four variables, and as a consequence, these areas are omitted from all analyses; this affects, for example, a relatively small tropical area in South America (CWD = 0 each year) and areas perennially covered by snow (CWD = 0 each year; e.g., most of Greenland).

We focused our analyses on protected areas as defined by the World Database on Protected Areas (WDPA) (IUCN & UNEP-WCMC, 2019) and included protected areas classified as IUCN (International Union of Conservation for Nature) Management Categories I–VI, except those

identified as 'proposed', 'marine', or otherwise aquatic (e.g., wetland, riverine, endorheic). A large number of protected areas, however, were not assigned an IUCN category in the WDPA (identified as "Not Reported," "Not Assigned," or "Not Applicable") but are likely to have reasonably high levels of protection (e.g., Kruger National Park in South Africa). We included these additional protected areas if the level of human modification was similar or less than that observed within IUCN category I–VI protected areas. To do so, we measured mean land-use intensity within each IUCN category I–VI protected area using the human modification gradient (HMG) raster dataset (Kennedy et al., 2019) and calculated the 80th percentile of the resulting distribution. Any unassigned protected areas with a mean HMG less than or equal to this identified threshold were included in our study (following Dobrowski et al., 2021). We then converted this vector-based polygon dataset to raster format (resolution = ~4 km to match gridded climate data; $n = 1,063,748$ pixels). It is well recognized that the WDPA contains a large number of duplicate and overlapping polygons (Palfrey et al., 2022; Vimal et al., 2021). Although this does not affect summaries across the globe or for individual countries (described below), it provides a challenge when trying to summarize by individual protected areas (due to double-counting). Consequently, we 'cleaned' the WDPA prior to summarizing the climate connectivity metrics for individual protected areas by removing polygons that exhibited $\geq 90\%$ overlap with another; this resulted in 29,752 individual protected areas (the data can be found in the Dryad repository [<https://doi.org/10.5061/dryad.1rn8pk0zf>]).

2.2 | Least-cost path modeling

Following Carroll et al. (2018) and Dobrowski and Parks (2016), we used least-cost path modeling (Adriaensen et al., 2003) to build potential climate-induced movement routes between each protected focal pixel and its backward and forward analogs. The least-cost models were parameterized with resistance surfaces based on climate dissimilarity and the human modification gradient (HMG) (Kennedy et al., 2019). For backward analog modeling, we characterized climatic dissimilarity (i.e., climatic resistance) using two intermediate surfaces, the first being the Mahalanobis distance between each focal pixel (using +2°C ICV) and all other pixels using +2°C climate normals (Figure 2b) and the second being the Mahalanobis distance (using +2°C ICV) and all other pixels using reference period climate normals (Figure 2c). These two surfaces provide a proxy for climate similarity designed to capture transient changes between the reference period and +2°C climate; these were then averaged to characterize the overall climatic resistance across time and space (Figure 2d). For forward analog modeling, the process is similar except we used reference period ICV when characterizing climatic resistance (Figure 2a–d). We then multiplied the climatic resistance (Figure 2d) by HMG (Figure 2e) to create the final resistance surface for least-cost path modeling (cf. Parks et al., 2020). Prior to this step, we rescaled HMG from its native range (0–1) to 1–25 to correspond with the range of Mahalanobis distance values and thereby grant comparable weights to climatic resistance and HMG resistance (~95% of all Mahalanobis distance values are below 25 within a 500km radius). Open water was given a resistance = 25 so that paths would avoid water when possible. Least-cost path modeling was achieved using the *gdistance* package (van Etten, 2017); paths represent the least accumulated cost across the final resistance surface (Figure 2f) between each focal pixel and analog (Figure 2g). Because paths were rarely straight lines, some were longer than the 500km that we established as a search radius. We removed these longer paths to abide by the biologically informed upper dispersal constraint.

2.3 | Calculating climate connectivity metrics and climate connectivity failure

We calculated the length (i.e., dispersal exposure), land-use modification (i.e., human exposure), and climatic resistance (i.e., climate exposure) for each path, remembering that each focal pixel may have many analogs and resultant paths. Human exposure represents cumulative HMG (Figure 2e) across all pixels in a path and climate exposure represents cumulative climate resistance (Figure 2d) along a path. Human exposure and climate exposure were calculated by multiplying the mean HMG (unscaled; Figure 2f) and mean climate resistance (Figure 2d) along each path by the length of each path, respectively. Each path's climate connectivity metric (dispersal, human, and climate exposure) was converted to a percentile (range = 0–100) to facilitate easier interpretation and comparison

among metrics; relative to other protected pixels, small percentiles represent low exposure and large percentiles represent elevated exposure. We summarized (i.e., averaged the percentiles) dispersal exposure, human exposure, and climate exposure across each protected focal pixel (again, remembering that each pixel may have multiple analogs and resultant paths). Our fourth climate connectivity metric, analog exposure, cannot be summarized on a per-path basis, because by definition, there is no least-cost path when there are no protected climate analogs. Instead, protected pixels either do or do not have protected climate analogs.

Focal pixels were identified as exhibiting climate connectivity failure when they exceeded the 75th percentile for dispersal or climate exposure, exceeded the 90th percentile for human exposure, or had no protected climate analog. We assumed that focal pixels exceeding these percentiles are located in landscapes that hinder successful range shifts among protected areas (i.e., climate connectivity failure) for a non-negligible proportion of extant species, considering that the biodiversity at a given site comprises mammals, birds, insects, mollusks, amphibians, reptiles, fish, crustaceans, annelids, vascular plants (e.g., trees grasses, shrubs), and non-vascular plants (e.g., fungi, mosses, lichens). The numerous and diverse species at given site have a wide range of dispersal abilities, sensitivities to human land uses, and climatic tolerances. We used a higher threshold (90th percentile) for describing climate connectivity failure due to human exposure because large, remote protected areas in the network skew human exposure toward lower values from a global perspective. These percentile thresholds are likely conservative when considering the large number and diversity of species at a given site. In terms of dispersal, for example, many species have maximum dispersal capabilities on the range of 1km/year or less (Jenkins et al., 2007; McLachlan et al., 2005; Schwartz et al., 2001). This represents dispersal of 75km under 2°C warming in the 75 years covering the midpoint of the reference period (1975) to mid-21st century. In our study, the 75th percentile path length, is ~385km, well above such these dispersal limits, supporting our assertion that the 75th percentile is conservative for estimating climate connectivity failure. Furthermore, the mean HMG value for a 100km path at the 90th percentile threshold is 0.22, which is well above the 0.1 threshold that Brennen et al. (2022) used to identify areas moderately to highly impacted by human land uses. Lastly, the mean climatic distance for a 100km path at the 75th percentile is well over two standard deviations different, on average, from the focal pixel and analog.

We report the percent of protected pixels across the globe and within each country that exhibits climate connectivity failure. We also assessed the potential for each of the 29,752 individual protected areas (e.g., Yellowstone National Park, Serengeti National Park) to undergo climate connectivity failure using a slightly different method. To do so, we calculated the mean percentile among pixels within each protected area for each of dispersal exposure, human exposure, and climate exposure (each metric was averaged across a protected area; the metrics themselves were not averaged with each other). We then calculated the percent of each protected area that

did not have a protected climate analog (analog exposure). Although a binary approach (has or does not have an analog) is appropriate when evaluating individual focal pixels, a percent-based valuation is most appropriate and informative when evaluating individual protected areas with up to thousands of pixels. Individual protected areas exhibited climate connectivity failure if the mean dispersal exposure or climate exposure exceeded the 75th percentile, mean human exposure exceeded the 90th percentile, or the analog exposure exceeded 75%.

Lastly, we provide a detailed case study showing an individual protected area (the Cloud Peak Wilderness, USA) to illustrate some of the factors that may impede climate-induced range shifts among protected areas. We show, through a series of maps, the protected area's climate analogs, potential movement trajectories (least-cost paths), and regional vegetation. We also show the distributions of four species that are not currently residing within the protected area, yet they are co-located with the protected backward analogs.

We present only backward analog results in the main text because (1) because backward analogs are more often used to predict and communicate analog-based climate change impacts (Fitzpatrick & Dunn, 2019; Parks et al., 2018; e.g., Pugh et al., 2016) (plus2c.org) and (2) from the perspective of protected area management, backward analogs give a characterization of a given protected area's potential future—more relevant for management decision-making—whereas forward analogs offer a characterization of where a given protected areas current conditions may end up. However, forward analog results are available in the supplemental material and online repository.

3 | RESULTS

Of all protected lands across the globe (17 million km² in our study), 58% exhibit climate connectivity failure under 2°C warming, indicating that a large proportion of protected land is located in landscapes that hinder climate-induced species movements. This includes 7.1% of protected lands that exceed the dispersal exposure threshold defining climate connectivity failure, 8.5% that exceed the human

exposure threshold, 13.6% that exceed the climate exposure threshold, and 37.8% that have no protected climate analog (Table 1). About a third of protected lands exhibit climate connectivity failure when considering only those lands that have climate analogs (which is a subset of all protected pixels) (Table 1). When summarized by the protected lands within each country, Kuwait, Qatar, Czechia, Hungary, and Lithuania exhibit the highest degrees of climate connectivity failure, whereas Tajikistan, Finland, Norway, Sweden, and Chile exhibit the lowest climate connectivity failure (Figure 3). As expected, individual countries vary in terms of which climate connectivity metric is most responsible for climate connectivity failure (found in the Dryad repository <https://doi.org/10.5061/dryad.1rn8pk0zf>). For example, analog exposure of protected lands in Germany is very low (<1%), whereas the mean human exposure of protected lands is very high (97th percentile). Furthermore, mean climate exposure for protected lands in Rwanda is high (88th percentile), whereas the mean dispersal exposure on the lower end (30th percentile) (found in the Dryad repository <https://doi.org/10.5061/dryad.1rn8pk0zf>).

Of all the protected area units across the globe ($n = 29,752$ in our 'cleaned' dataset), 67% exhibit climate connectivity failure (found in the Dryad repository <https://doi.org/10.5061/dryad.1rn8pk0zf>). As expected, there is substantial variability in the four climate connectivity metrics among protected areas (Figures 4 and 5; found in the Dryad repository <https://doi.org/10.5061/dryad.1rn8pk0zf>). Wood Buffalo National Park (Canada), for example, has relatively low exposure across all climate connectivity metrics and does not exhibit climate connectivity failure, whereas Serengeti National Park (Tanzania) has relatively high exposure across all metrics and exhibits climate connectivity failure. Other protected areas, such as Pyrénées National Park (France; no climate connectivity failure), show a range of exposure depending on the individual climate connectivity metric (Figure 5; found in the Dryad repository <https://doi.org/10.5061/dryad.1rn8pk0zf>).

The detailed case study showing the Cloud Peak Wilderness, USA, illustrates some of the factors that may impede successful climate-induced range shifts for some species (Figure 6). For example, mean climate exposure for Cloud Peak Wilderness is very high

Assessment type	Exceeds dispersal exposure threshold	Exceeds human exposure threshold	Exceeds climate exposure threshold	Analog exposure	Climate connectivity failure
Protected pixels with analogs ^a	11.5% ^b	13.9% ^b	21.9% ^b	NA	32.7%
All protected pixels ^a	7.1%	8.7%	13.6%	37.8%	58.2%

^aWe provide results for protected pixels that have protected analogs (62.3% of the global protected area network) and for all protected pixels.

^bBecause the path-based percentiles are averaged for each protected pixel (remembering that each protected pixel may have several analogs and least-cost paths), the percentages reported here do not conform to the percentile thresholds we used to define climate connectivity failure. For example, although 25% of the paths exceed the 75th percentile value (by definition), only 11.5% of the pixels exceed the 75th percentile after this averaging.

TABLE 1 Percent of terrestrial protected pixels across the planet exceeding dispersal, human, and climate exposure thresholds that define climate connectivity failure, percent of pixels with no climate analogs (analog exposure), and total percent of pixels exhibiting climate connectivity failure.

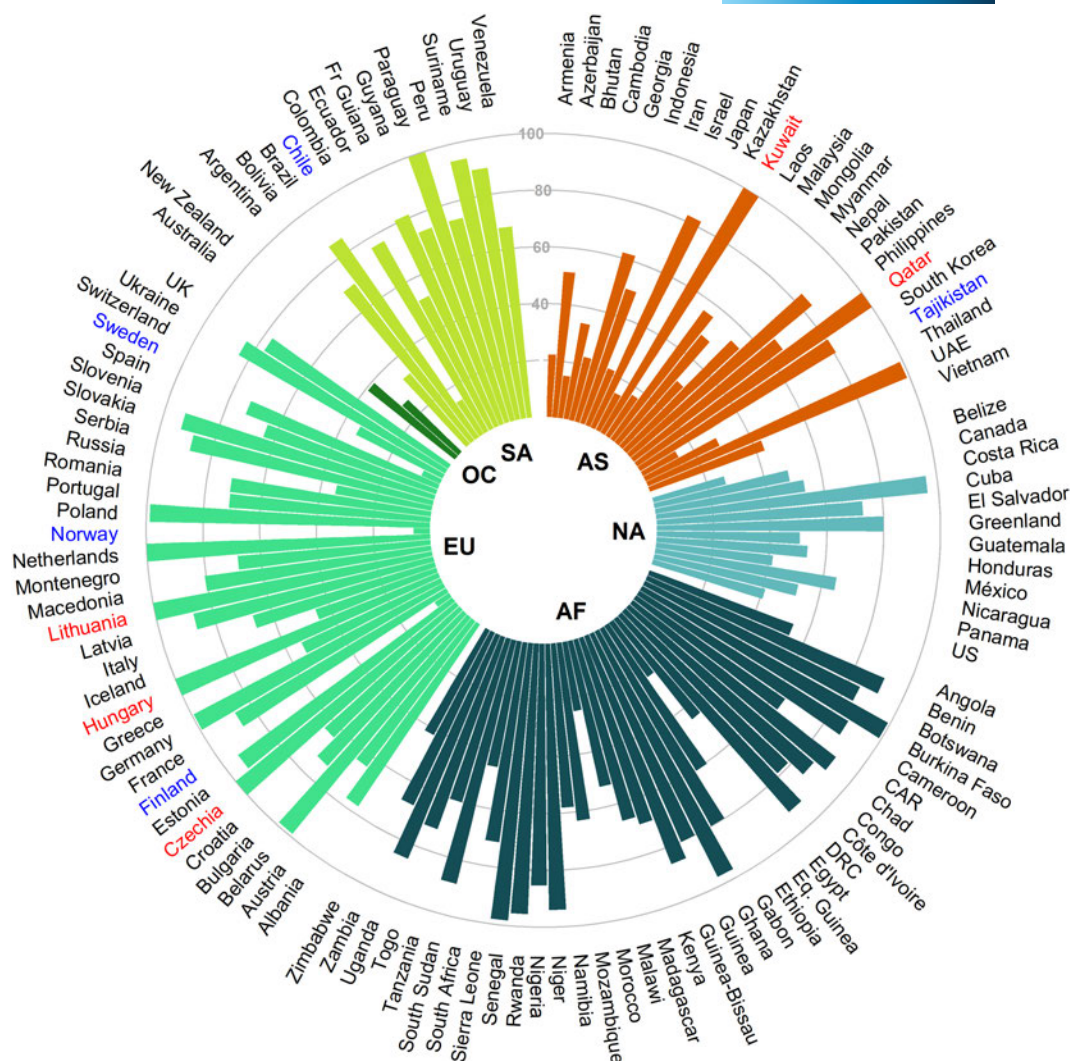


FIGURE 3 Percent of protected lands in each country exhibiting climate connectivity failure (backward analogs). The five countries with the highest and lowest values are indicated by red and blue text, respectively. For clarity, we excluded non-island countries $<8763 \text{ km}^2$ (corresponding to the 5th percentile), island countries $<86,179 \text{ km}^2$ (corresponding to the 90th percentile), and countries with less than 5% of their area in protected status, noting all countries are reported in <https://doi.org/10.5061/dryad.1rn8pk0zf>. Likewise, results for forward analogs are reported in Figure S1. AF: Africa; AS: Asia; EU: Europe; NA: North America; OC: Oceania; SA: South America. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

(94th percentile, indicating climate connectivity failure), which is illustrated and corroborated by the large extent of dry shrubland overlapping the potential movement trajectories. Furthermore, the mean length of potential movement trajectories is 339 km, and although this length does not achieve the climate connectivity failure threshold, many of these paths clearly exceed the dispersal capabilities of some species. These factors raise doubts whether the species collocated with the backward climate analogs will be able to successfully undergo climate-induced range shifts into the Cloud Peak Wilderness.

The full set of results is available in the supplemental material and online repository. This includes an indication of climate connectivity failure and summaries of the four climate connectivity metrics (dispersal exposure, human exposure, climate exposure, and analog exposure) by country and for individual protected

areas ($n = 29,752$; we also provide a binary indication of climate connectivity failure for each protected area). Results are available for both backward and forward analogs. As previously mentioned (see Section 2), most analog-based evaluations of climate change impacts use backward analogs (as we did in the main paper). However, we also supply the forward analog results for interested readers. Globally, the results between backward and forward analogs are fairly similar (Table S1), as are they when looking at individual countries (compare Figure 3 to Figure S1). And although there is considerable overlap for most individual protected areas, there are some key differences (e.g., compare Figure 5 to Figure S2). Given that the choice between backward and forward analogs depends on the specific use (backward = “where organisms are moving from”; forward = “where organisms are moving to”), we do not provide a detailed comparison of the two.

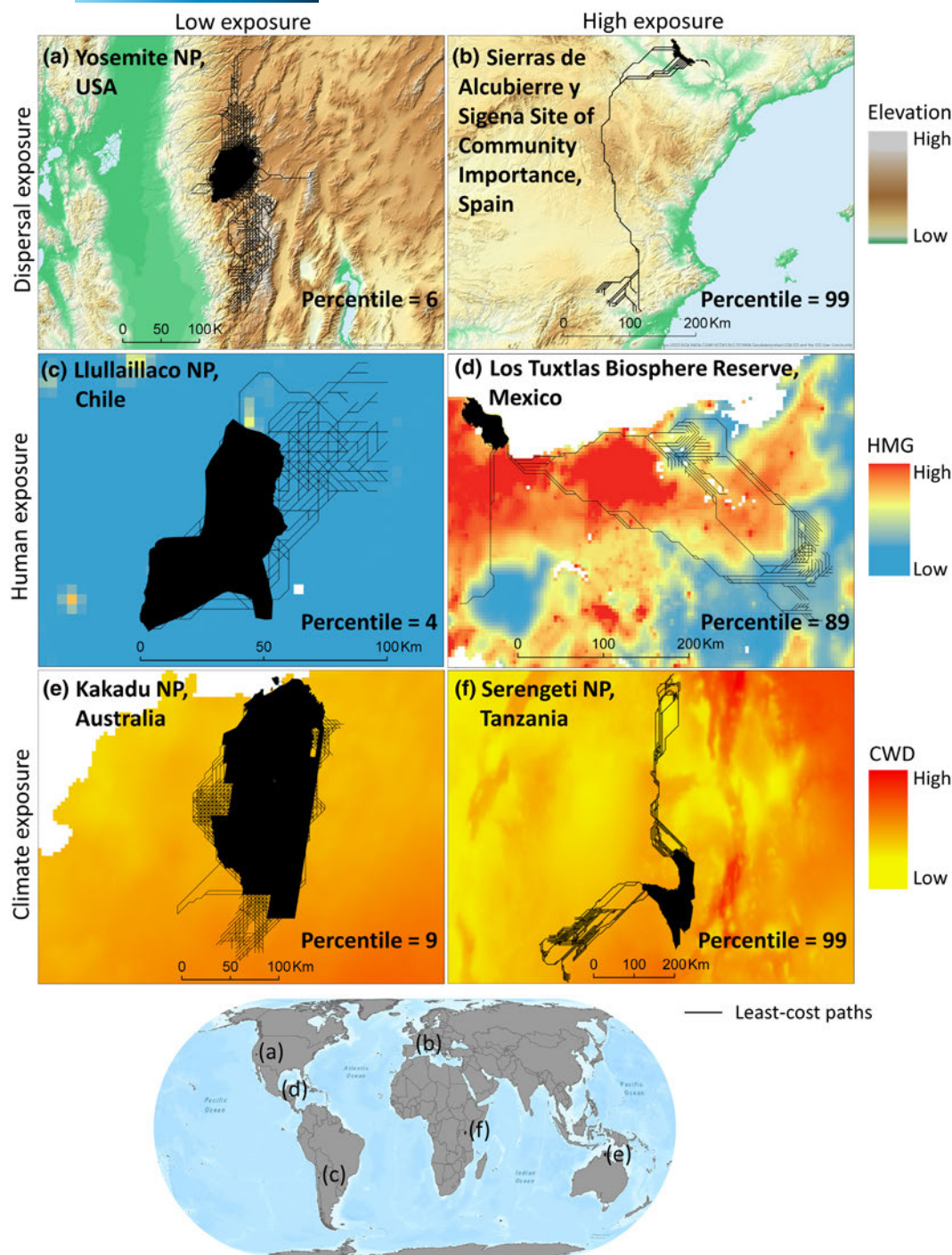


FIGURE 4 Mapped examples of individual protected areas with low and high exposure for dispersal exposure (a, b), human exposure (c, d), and climate exposure (e, f). The percentile (see Section 2) for each exposure metric is indicated. Yosemite National Park (NP) exhibits low dispersal exposure (6th percentile), meaning that the protected climate analogs, on average, are a relatively short distance from Yosemite NP (a) compared to the Sierras de Alcabierre y Sigüenza Site of Community Importance (99th percentile) (b). Lluillallaco NP exhibits low human exposure (4th percentile), meaning that there is fairly minimal cumulative land-use intensity as measured by the human modification gradient (HMG), on average, along potential movement trajectories (c) compared to Los Tuxtlas Biosphere Reserve (89th percentile) (d). Kakadu NP is shown in relation to the climatic water deficit (CWD) and exhibits fairly low climate exposure (9th percentile), meaning that the cumulative exposure to dissimilar climates along potential movement routes is much less than that of Serengeti NP (f) (99th percentile). Lines on world map delineate study areas and do not necessarily depict accepted national boundaries. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

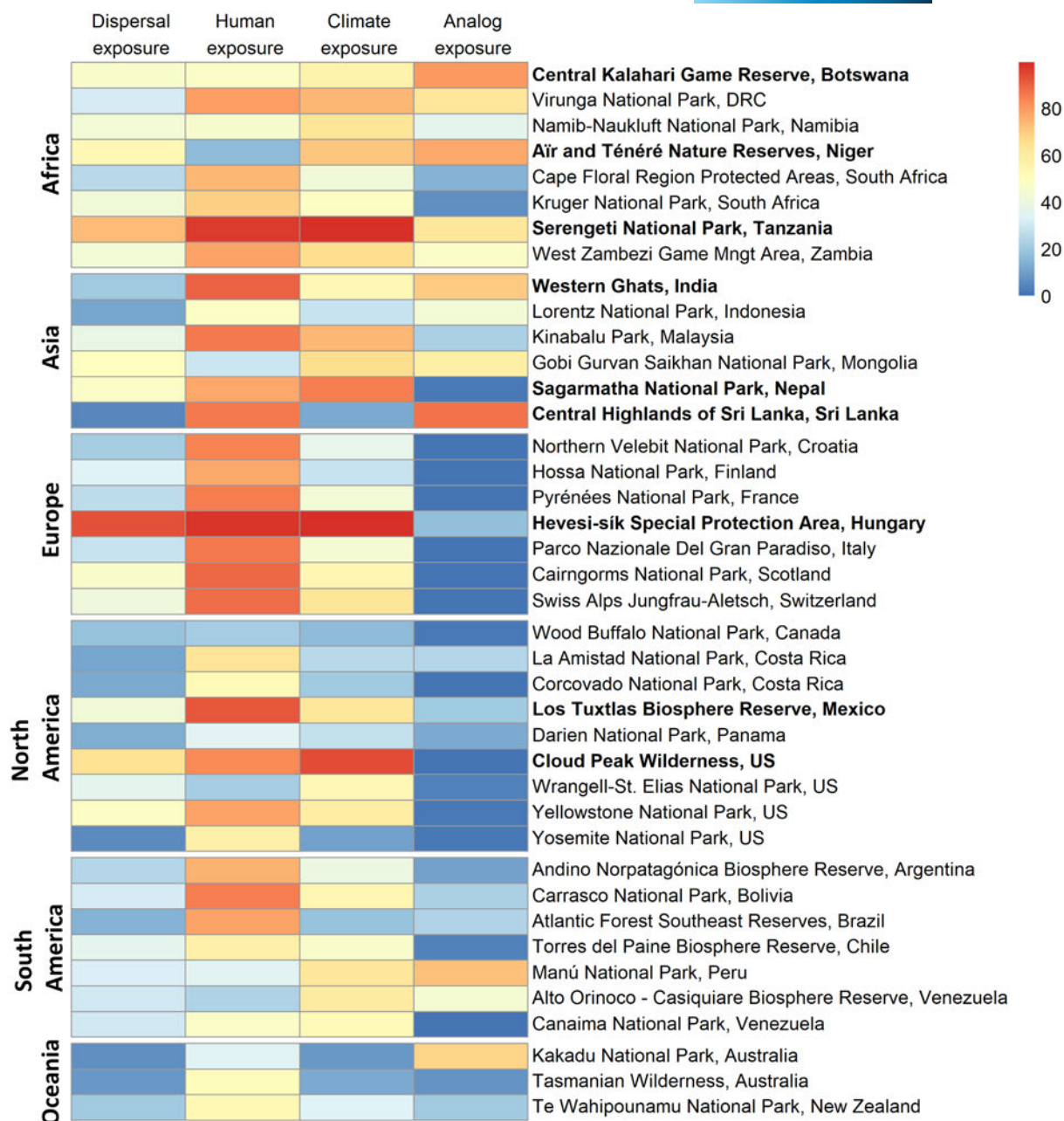


FIGURE 5 Summaries of dispersal exposure, human exposure, climate exposure, and analog exposure for a subset of protected areas (backward analogs). This subset of protected areas represents those that are large, iconic, or biodiverse, with the intent that one or more of these protected areas is at least somewhat familiar to readers on all continents. Protected areas in bold exhibit climate connectivity failure, meaning that the mean human exposure exceeds the 90th percentile, the mean dispersal or climate exposure exceeds the 75th percentile, or the analog exposure exceeds 75%. Results for each of the 29,752 protected areas are available in the Dryad repository <https://doi.org/10.5061/dryad.1rn8pk0zf>. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)] [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)

4 | DISCUSSION

Achieving adequate climate connectivity among the global terrestrial protected area network is crucial for conserving biodiversity under a warming climate (McGuire et al., 2016; Sonntag & Fourcade, 2022). However, we found that over half of the global protected area estate and two-thirds of the 29,752 protected area units across the globe is at risk of climate connectivity failure under 2°C warming, meaning that key thresholds were exceeded

in terms of the distance necessary to track suitable climate (dispersal exposure), human land use intensity along potential movement trajectories (human exposure), climate dissimilarity along potential movement trajectories (climate exposure), and novel/disappearing climates (analog exposure). Consequently, our findings indicate that the global protected area network, as is, cannot adequately serve as steppingstones for many species undergoing climate-driven range shifts (Hannah et al., 2014; Thomas & Gillingham, 2015) (Figure 6) and suggest that biodiversity within

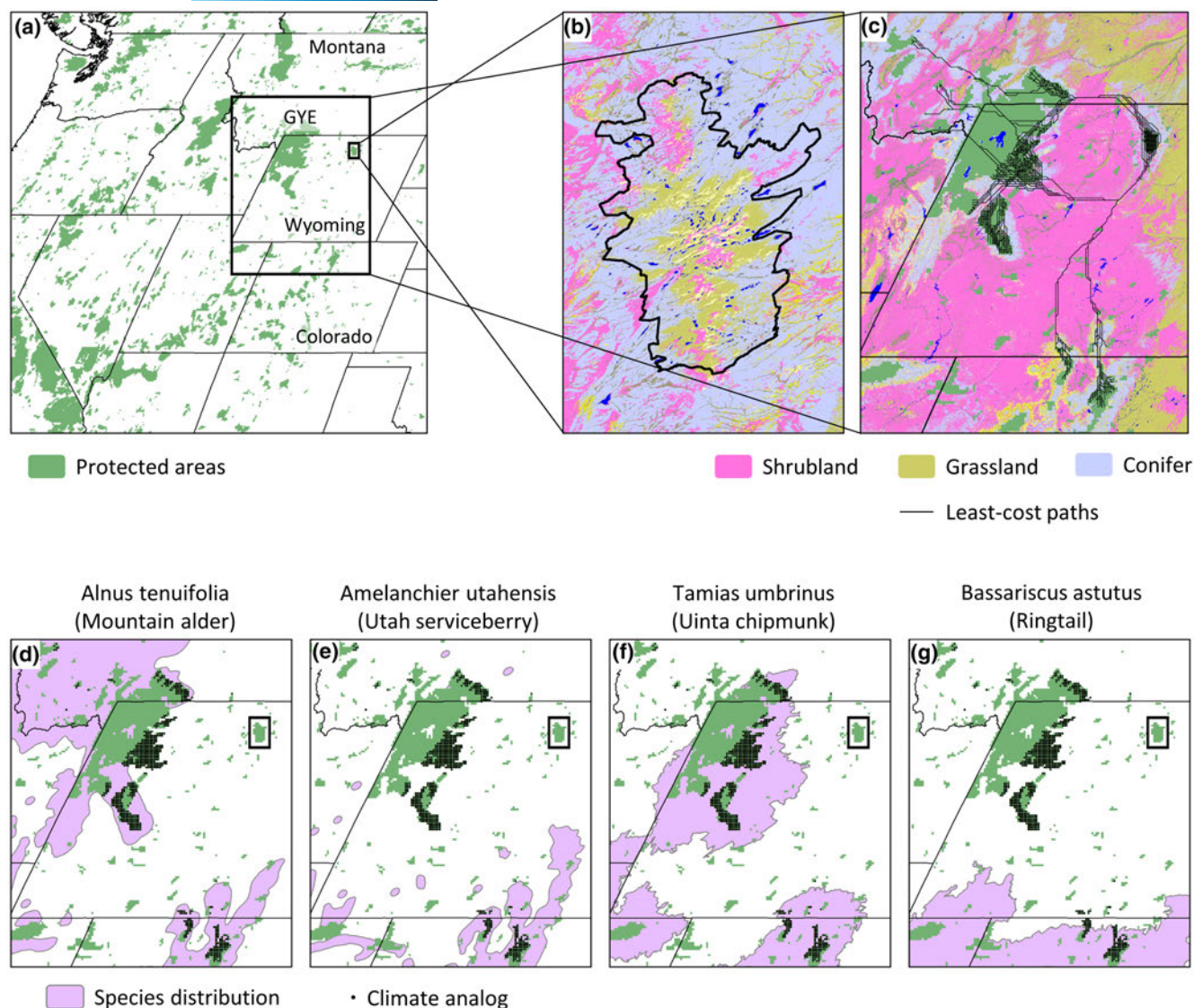


FIGURE 6 The Cloud Peak Wilderness is located in north-central Wyoming, USA, in a fairly isolated mountain range east of the Greater Yellowstone Ecosystem (GYE) (a). Extant land-cover is primarily conifer forest and alpine shrubland and grassland (b). The least-cost paths between the Cloud Peak Wilderness and its backward analogs (c) show that the climate analogs are primarily located in conifer-dominated regions of the Greater Yellowstone Ecosystem (GYE) and northern Colorado (d–g). The paths are long (339 km average) and suggest that dispersal limitations (dispersal exposure) may impede the ability of some species to undergo climate-induced range shifts into the Cloud Peak Wilderness. Furthermore, many of the paths traverse dry shrubland, indicating that exposure to dissimilar climates (mean climate exposure = 94th percentile, indicating climate connectivity failure) may also impede climate-induced species range shifts. Examples of two plant species (d, e) and two mammal species (f, g) that are not currently in the Cloud Peak Wilderness, yet are currently co-located with protected backward analogs, indicate that the emerging climate in the Cloud Peak Wilderness is suitable for these species. Will these species shift their ranges to the Cloud Peak Wilderness under 2°C warming? [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

the global protected area network is highly vulnerable to climate change.

An increasing number of studies similarly support the assertion that species may not be successful in undergoing climate-induced range shifts (indicating climate connectivity failure). Menéndez et al. (2006) and Corlett and Westcott (2013), for example, showed that the rate of climate change (i.e., climate velocity) exceeds the rate at which many species can successfully shift their ranges (dispersal exposure). Furthermore, many species are sensitive to human land uses (Newbold et al., 2015; Parks & Harcourt, 2002) or have

narrow climatic tolerances (Deutsch et al., 2008), thereby impeding their ability to successfully undergo climate-induced movements (Robillard et al., 2015). Nevertheless, as species disappear from protected areas (i.e., local extirpation or extinction) and are not “replaced” by species suited to the emerging climate of the protected area (due to climate connectivity failure), many protected areas may support a depauperate suite of species under climate change.

Improving climate connectivity to facilitate successful range shifts among protected areas is vital for the conservation of biodiversity as our climate continues to warm. Although improving

climate connectivity among the global protected area network will be challenging, there are policy options and management approaches that can be implemented. Importantly, the Conference of the Parties to the Convention of Biological Diversity (COP15) recently reached an agreement (in December 2022), as described in the Kunming-Montreal Global Biodiversity Framework (GBF), in which 190+ countries have pledged to conserve 30% of the planet by 2030, often referred to as 30×30 (Convention on Biological Diversity, 2022). Noting that approximately 17% of Earth's terrestrial lands are currently protected, increasing the protected area estate could improve climate connectivity in several ways, such as reducing the prevalence of novel/disappearing climates in the protected area network (analog exposure) and reducing the distance (dispersal exposure) between protected areas, the latter of which also has a secondary effect of reducing human exposure and climate exposure. Increasing the protected area estate would also protect species that are not currently protected (Guo et al., 2022).

Target 3 of the GBF specifies that the protected area network should be “ecologically representative” (Convention on Biological Diversity, 2022), and prioritization strategies have been proposed to achieve this goal (Belote et al., 2021; Carroll & Ray, 2021; Dinerstein et al., 2020). Target 3 of the GBF also states that the protected area network should be “well-connected,” presumably so plants and animals can move among protected areas and maintain healthy populations. This goal (i.e., well-connected), however, does not implicitly or explicitly acknowledge that climate connectivity is necessary to facilitate range shifts. As such, we suggest that in addition to aiming for a protected area network that is “ecologically representative” and “well-connected” as specified by the GBF, prioritization efforts to achieve 30×30 could also aim to “improve climate connectivity” to facilitate range shifts. Developing protected area prioritization strategies that maximize climate connectivity is an emerging research need (Keeley et al., 2018) that is complicated by the potential for transboundary range shifts (i.e., those that involve movement from one country to another) and the need for international cooperation (Parks et al., 2022; Titley et al., 2021).

Theoretically, climate connectivity can also be improved by reducing the human footprint. For example, Brennan et al. (2022) showed that a 50% reduction in the human footprint would decrease protected area isolation by 28%. Admittedly, reducing the human footprint is probably not practical or possible for much of the planet, yet proposals for land sharing/sparing (i.e., promoting landscapes that benefit people and biodiversity) could decrease resistance along potential movement trajectories and overall increase habitat quality and quantity in the unprotected matrix (Grass et al., 2019; Kremen & Merenlender, 2018).

As efforts to improve climate connectivity may not be possible in some regions of the planet, how to best manage for biodiversity and climate-induced range shifts in the face of climate connectivity failure will increasingly challenge land-management agencies, protected area managers, non-governmental organizations, and others. When movement to new protected areas is unlikely due to the dispersal

limitations (dispersal exposure), incompatible land uses (human exposure), and incompatible climate (climate exposure) (Figures 1, 4, and 6) (i.e., climate connectivity failure), species will likely disappear from protected areas without immigration of species that are adapted to the emerging climate. The likely result is an overall reduction in biodiversity within protected areas with reduced ecosystem functionality and increased prevalence of invasive species (Grimm et al., 2013; Hellmann et al., 2008). To address this, land management agencies and protected area managers could use assisted colonization to promote species that are adapted to the emerging climate (Butt et al., 2021; Hoegh-Guldberg et al., 2008). However, relocating species poses many potential risks and challenges such as species becoming highly invasive, introducing disease and parasites, novel species interactions, and other unintended consequences (Ricciardi & Simberloff, 2009). As climate change itself is human caused, as are other factors that are unfavorable to biodiversity (e.g., pesticides, heavily modified land uses), deciding whether or not we have the knowledge and moral and ethical authority to purposely move species (i.e., assisted colonization) to address climate connectivity failure is an urgent need that should be quickly addressed (Ahteensuu & Lehtävirta, 2014; Albrecht et al., 2013; Minter & Collins, 2010).

Our study uses climate analogs as a proxy for understanding potential climate-induced range shifts and implements consistent thresholds in factors that may impede successful climate-induced movement (e.g., human exposure). As such, our study provides a species-agnostic lens to characterize climate connectivity failure. This coarse-filter approach (Hunter Jr. et al., 1988; Tingley et al., 2014) 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. However, we recognize that there is variability among species in terms of sensitivities to the factors that may impede climate-induced range shifts. For example, most bird and bat species are fairly mobile and are not likely limited by dispersal exposure, yet some are sensitive to increasingly intense human land uses (Farneda et al., 2020; Newbold et al., 2013). Also, several plant species have broad climatic tolerances, meaning that they are less likely to be limited by climate exposure, but some of these species have limited dispersal abilities, thereby impeding climate-induced range shifts (Aitken et al., 2008; McKenney et al., 2007). Some species may be sensitive to more than one factor; for example, some ectotherms have narrow climatic envelopes and low dispersal abilities (Aragón et al., 2010; Deutsch et al., 2008). As such, future efforts could use different thresholds for identifying climate connectivity failure for individual species or use a trait-based approach for groups of species with similar sensitivities (Santini, Cornulier, et al., 2016; Schleuning et al., 2020). It is also important to note that our scale of analysis (4 km pixels) does not account for microclimatic variation that may buffer the effect of climate change (Maclean et al., 2015) or even facilitate range shifts (Hannah et al., 2014). As such, microclimatic buffering may increase climate connectivity, although it has been pointed out that increases in the frequency and severity of disturbance may substantially alter microclimate conditions (Davis et al., 2019).

In interpreting our results, it is also important to recognize that factors besides climate may influence current and future distributions of species, including biogeographic history, edaphic constraints, competition, and biotic interactions (Corlett & Tomlinson, 2020; Franklin, 2010). For example, consider an animal species that is dependent on the presence of a plant species (for food or habitat). If this plant species is unable to undergo a climate-induced range shift, the dependent animal species will also not be able to shift its range (Hodgson et al., 2022). Furthermore, we do not evaluate unprotected lands; our study is constrained to protected areas. Consequently, we do not recognize that the unprotected matrix may serve as source or destination locations for species undergoing climate-induced range shifts in and out of protected areas, respectively. Although this could be an important consideration in regions with fairly low land use intensities (e.g., Balogun et al., 2022), this is not always the case when protected areas are concentrated in particular landforms (e.g., mountains; Figure 6). Ultimately, future studies could better incorporate the unprotected matrix by, for example, including lands with low land-use intensities (cf. Brennan et al., 2022; Dobrowski et al., 2021). Lastly, our study did not include Chinese protected areas since they were not included in the World Database on Protected Areas (WDPA).

5 | CONCLUSIONS

Connectivity among protected areas is crucial for conserving biodiversity across the planet. However, recent studies have highlighted shortcomings of the global terrestrial protected area network, in that many protected areas do not have adequate connectivity necessary to maintain healthy gene flows and populations of plants and animals under contemporary climate and landscape conditions (Brennan et al., 2022; Saura et al., 2018; Ward et al., 2020). These important studies, however, did not consider how a changing climate will influence future connectivity. In contrast, we evaluated climate connectivity (McGuire et al., 2016)—the ability of a landscape to promote or hinder climate-induced species range shifts—among the global protected area network. In doing so, we found that climate connectivity among the global protected area network is compromised, raising the question as to whether or not species will be able to successfully undergo climate-induced movement among protected areas without human intervention (McLachlan et al., 2007).

In an era of rapid climate change, explicit attention to climate connectivity will improve our ability to manage for climate-induced species movement among protected areas (Mingarro & Lobo, 2021). In this study, we underscore that dispersal limitations, human land uses, exposure to unsuitable climate, and novel/disappearing climates will likely impede climate-induced species movement (e.g., Figure 6), leading to climate connectivity failure. As such, protected areas are not likely to serve as steppingstones for a large number of species undergoing climate-induced range shifts, increasing the potential for shrinking species ranges and local extinction (Kerr, 2020). Humanity faces the reality of accepting species loss in protected

areas (with an overall reduction in biodiversity) or directing changes in species composition (with a shift in biodiversity) through actions such as carefully considered assisted colonization (Butt et al., 2021; Hoegh-Guldberg et al., 2008). Of course, climate connectivity failure can be reduced with immediate and severe reductions in greenhouse gas emissions; the opposite is also true if the global community fails to limit warming to 2°C.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available as Electronic Supplemental Material in Dryad at <https://doi.org/10.5061/dryad.1rn8pk0zf>. These data were derived the following resources available in the public domain: <https://www.climatologylab.org/terraclimate.html>, <https://sedac.ciesin.columbia.edu/data/set/lulc-human-modification-terrestrial-systems>, <https://www.protectedplanet.net/en/thematic-areas/wdpa>.

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SUPPORTING INFORMATION

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