Received: 28 May 2019 | Revised: 6 January 2020 | Accepted: 14 January 2020

DOI: 10.1111/gcb.15009

PRIMARY RESEARCH ARTICLE

Global Change Biology WILEY

Human land uses reduce climate connectivity across North America

Sean A. Parks[1] | Carlos Carroll[2] | Solomon Z. Dobrowski[3] | Brady W. Allred[3]

[1]Aldo Leopold Wilderness Research Institute, Rocky Mountain Research Station, US Forest Service, Missoula, MT, USA

[2]Klamath Center for Conservation Research, Orleans, CA, USA

[3]W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, USA

Correspondence
Sean A. Parks, Aldo Leopold Wilderness Research Institute, Rocky Mountain Research Station, US Forest Service, Missoula, MT 59801, USA.
Email: sean.parks@usda.gov

Funding information
USDA National Institute of Food and Agriculture, McIntire Stennis Program, Grant/Award Number: 1012438

Abstract

Climate connectivity, the ability of a landscape to promote or hinder the movement of organisms in response to a changing climate, is contingent on multiple factors including the distance organisms need to move to track suitable climate over time (i.e. climate velocity) and the resistance they experience along such routes. An additional consideration which has received less attention is that human land uses increase resistance to movement or alter movement routes and thus influence climate connectivity. Here we evaluate the influence of human land uses on climate connectivity across North America by comparing two climate connectivity scenarios, one considering climate change in isolation and the other considering climate change and human land uses. In doing so, we introduce a novel metric of climate connectivity, 'human exposure', that quantifies the cumulative exposure to human activities that organisms may encounter as they shift their ranges in response to climate change. We also delineate potential movement routes and evaluate whether the protected area network supports movement corridors better than non-protected lands. We found that when incorporating human land uses, climate connectivity decreased; climate velocity increased on average by 0.3 km/year and cumulative climatic resistance increased for ~83% of the continent. Moreover, ~96% of movement routes in North America must contend with human land uses to some degree. In the scenario that evaluated climate change in isolation, we found that protected areas do not support climate corridors at a higher rate than non-protected lands across North America. However, variability is evident, as many ecoregions contain protected areas that exhibit both more and less representation of climate corridors compared to non-protected lands. Overall, our study indicates that previous evaluations of climate connectivity underestimate climate change exposure because they do not account for human impacts.

KEYWORDS

climate change, climate corridors, climate exposure, climate velocity, connectivity, conservation planning, protected areas

1 | INTRODUCTION

Climate connectivity—the ability of a landscape to promote or hinder species movement when responding to a changing climate—is contingent on multiple factors including the distance organisms need to move to ameliorate climate change and the resistance they experience along their movement routes (Dobrowski & Parks, 2016; Littlefield, McRae, Michalak, Lawler, & Carroll, 2017; McGuire, Lawler, McRae, Nuñez, & Theobald, 2016). Maintaining and enhancing climate connectivity is necessary to maximize the likelihood that organisms can adequately shift their geographic ranges in response to climate change and to reduce the likelihood of local extirpations or extinctions (Early & Sax, 2011; Williams et al., 2005).

Climate velocity is a climate connectivity metric that estimates the rate (e.g. km/year) at which organisms must travel to maintain similar climate conditions in future time periods (Table S1; Hamann, Roberts, Barber, Carroll, & Nielsen, 2015; Loarie et al., 2009). Climate exposure is a complementary metric that quantifies the amount of climatic dissimilarity encountered as organisms migrate in response to climate change; this was originally referred to as 'minimum cumulative exposure' (Dobrowski & Parks, 2016). Higher climate velocity and climate exposure imply decreased climate connectivity and greater risk to organisms (Carroll, Lawler, Roberts, & Hamann, 2015; Dobrowski et al., 2013). Quantifying both climate velocity and climate exposure requires identifying climate analogs, whereby specific locations with the best climatic match between one time period (e.g. contemporary) and a different time period (e.g. future) are identified (Wuebbles & Hayhoe, 2004). Assessments of climate velocity often use the closest climate analog based on geographic distance (e.g. Hamann et al., 2015). However, assessments that evaluate climate velocity based on the least accumulated cost according to landscape resistance (e.g. climate exposure) are particularly useful in identifying potential climate corridors, which are areas of high importance for facilitating range shifts under climate change (Carroll, Parks, Dobrowski, & Roberts, 2018).

Human activities have resulted in substantial changes to natural systems across the globe (Vitousek, Mooney, Lubchenco, & Melillo, 1997). Human-modified landscapes negatively impact most organisms (Newbold et al., 2015) and are considered a leading threat to global biodiversity (Di Marco, Venter, Possingham, & Watson, 2018; Foley et al., 2005). Whereas some landscapes are minimally affected by humans, others have been completely transformed (Sanderson et al., 2002), with varying implications for biodiversity (Blair, 1996; Maestas, Knight, & Gilgert, 2003). It is reasonable to assume that the ability of most organisms to shift their ranges in response to climate change decreases (i.e. increased resistance) as human land uses increase in intensity. As such, an explicit consideration of human land uses when evaluating climate connectivity will improve our ability to understand and potentially mitigate the negative impacts of climate change on biota.

There are two ways in which human land uses may influence climate connectivity. First, as organisms shift in response to climate change, they may avoid areas with intense land uses (cf. Littlefield et al., 2017; Nunez et al., 2013). Climatically, 'optimal' movement trajectories may be unavailable due to land uses that are incompatible with a given organism, and less optimal routes will be longer and have a higher exposure to dissimilar climates (climate exposure). Second, the climate analogs themselves may not be viable destinations due to incompatible human land uses (Hansen et al., 2001). Consequently, assessments of climate velocity and climate exposure that do not consider human land uses likely overestimate climate connectivity.

In this study, we assessed the potential influence of human land uses on climate connectivity by examining both climate velocity and climate exposure between a reference period (1981–2010) and late-century (2071–2100) climate across North America. We evaluated two scenarios, the first of which can be considered a baseline scenario that incorporated climatic resistance but excluded the influence of human-modified landscapes. The second scenario incorporated, in addition to climatic resistance, the influence of human land uses. Climate velocity and climate exposure were compared between scenarios. Furthermore, we introduced a novel metric of climate connectivity, 'human exposure', which measures the cumulative exposure to human land uses for organisms shifting their ranges. Given the pervasive nature of human activities on the planet, this under-explored facet of climate connectivity is likely to have major implications for our understanding of climate change vulnerability. Because our approach produced individual paths between each source and destination pixel, we also produced gridded maps that quantify the 'climate corridor score', defined as the total number of paths overlapping each pixel (cf. Carroll et al., 2018), with the assumption that pixels with higher climate corridor scores are of greater importance for facilitating range shifts under climate change. Lastly, we conducted an analysis of climate corridor scores in relation to protected areas, thereby quantifying whether the protected area network supports range shifts better than non-protected lands.

2 | MATERIALS AND METHODS

2.1 | Climate and human modification gradient gridded datasets

Gridded climate data (resolution = 1 km) for North America were obtained from AdaptWest (AdaptWest Project, 2015; Wang, Hamann, Spittlehouse, & Carroll, 2016). Reference period climate represents averages from 1981 to 2010; late-century climate represents 2071–2100 and were generated from a multi-model ensemble of 15 CMIP5 GCMs under RCP 8.5. Principal component analysis (PCA) was conducted on 11 bioclimatic variables (Table S2) representing climatic gradients such as mean annual precipitation and mean temperature of the warmest month. Following Carroll et al. (2017), climate was characterized using the first and second principal components (hereafter PC1 and PC2, respectively) under reference period climate. The PCA loadings (Table S2) from this procedure were then applied to the 11 bioclimatic variables representing late-century climate, thereby resulting in gridded PC1 and PC2 for late-century climate.

Although species vary widely in their response to different types of human land use (Blair & Launer, 1997), cumulative measures of land-use intensity are frequently used as a general approximation of the extent to which habitat is degraded by anthropogenic alteration (Venter et al., 2016). Consequently,

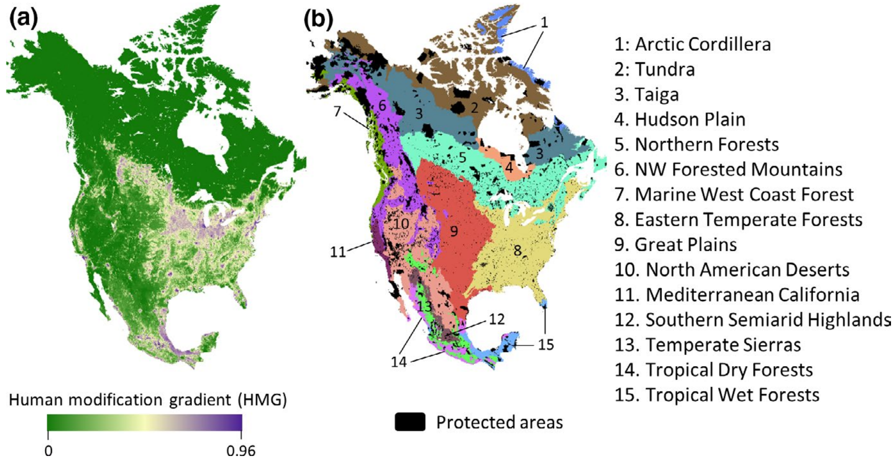

FIGURE 1 Human modification gradient (HMG; a) US EPA level I ecoregions, and protected areas (IUCN I–VI; b) for North America

we incorporated the influence of human land uses using the human modification gradient (HMG), which is a gridded dataset (resolution = 1 km) representing a cumulative measure of human modification to terrestrial lands based on 13 anthropogenic stressors and their estimated impacts (Kennedy, Oakleaf, Theobald, Baruch-Mordo, & Kiesecker, 2019). The HMG is scaled from 0 to 1 (Figure 1a) and roughly represent the year 2016. However, some of our methodology required that we rescale raw HMG values (described below), and as such, we rescaled HMG to range from 1 to 50 (HMG.rs). The climate (reference period and late-century PC1 and PC2), HMG, and HMG.rs gridded datasets were reprojected to a common coordinate system (equidistant conic) and then aggregated to a 5 km resolution using the mean values of the 1 km pixels falling within each 5 km pixel. Consequently, all analyses were conducted using a pixel resolution of 5 km. We acknowledge, however, that finer-resolution variability in human land uses and climate is evident across North America, and we were not able to capture this variability in a continental-extent analysis due to computation limitations.

2.2 | Scenarios

We developed two scenarios to evaluate the anthropogenic influence on climate connectivity: the climate scenario and the climate–HMG scenario.

2.2.1 | Climate scenario

Analogs are defined as being climatically similar to the source pixel. The individual analog (i.e. pixel) that minimized exposure to dissimilar climates was identified using a resistance surface based on climatic dissimilarity from each source pixel (Equation 1; cf. Dobrowski & Parks, 2016). This is the null model (i.e. no influence from human land uses) which we compare to the climate–HMG scenario.

2.2.2 | Climate–HMG scenario

Analogs are defined as being climatically similar to each source pixel and have HMG values that are less than or equal to each source pixel. The individual analog (i.e. pixel) that minimized exposure was identified using a resistance surface based on both climatic dissimilarity and the HMG.

2.3 | Identifying analogs

For the climate scenario, we followed previous studies (Batllori, Parisien, Parks, Moritz, & Miller, 2017; Carroll et al., 2017; Hamann et al., 2015) and identified analogs for reference period climate as any pixels under late-century climate that are within a pre-determined bin width in bivariate (PC1 and PC2) climate space (Table S3). To facilitate the objective identification of climate analogs, we rescaled the reference period PC1 and PC2 to range from 1 to 100 and used the same parameters to rescale PC1 and PC2 for the late-century time period. Bin width was assigned 1/25th of the data range (which is ±2.0 scaled PC units). To reduce boundary effects (i.e. to avoid pixels with small differences in climate treated as separate climate bins), we followed the methods of Parks, Holsinger, Miller, and Parisien (2018; illustrated in Table S3) which uses a moving climate window to identify analogs.

The climate–HMG scenario has an additional constraint in that human land uses are also used to identify analogs (Figure 1a). Specifically, the HMG value of the destination pixel (representing late-century climate) must be less than or equal to the HMG value of the source pixel (representing reference period climate). Therefore, the analogs for the climate–HMG scenario are a subset of the analogs for the climate scenario. The HMG constraint was motivated by the rationale that a pristine site (i.e. low HMG) whose nearest climate analog (under late-century climate) located in a highly modified region (e.g. urban or agriculture with high HMG value) will not necessarily be accessible to a large number of organisms present at the source pixel. Alternative analogs with similarly low human influence are likely more appropriate candidates, even though they may be further away.

2.4 | Resistance surfaces for scenarios

For the climate scenario, resistance surfaces were produced for each of 4,752 unique combinations of reference period PC1 and PC2 (after scaling from 1 to 100; rounded to integers); these unique PC1 and PC2 combinations are hereafter referred to as 'climate types'. Climatic resistance for each climate type is calculated as follows:

$$C.resistance_i = \left(\left(|t1.PC1_s - t1.PC1_i| + |t1.PC2_s - t1.PC2_i|\right) + \left(|t2.PC1_d - t2.PC1_i| + |t2.PC2_d - t2.PC2_i|\right)\right) \div 2, \quad (1)$$

where $C.resistance_i$ is the climatic resistance for pixel i, $t1.PC1_s$ and $t1.PC2_s$ are the scaled PC1 and PC2 values for the reference period climate type of the source pixel (s), $t1.PC1_i$ and $t1.PC2_i$ are the scaled PC1 and PC2 values for the reference period climate for pixel i, $t2.PC1_d$ and $t2.PC2_d$ are the scaled PC1 and PC2 values for the late-century climate of the destination pixel (d), and $t2.PC1_i$ and $t2.PC2_i$ are the scaled PC1 and PC2 values for the late-century climate for pixel i. Using climate from reference period and late-century acknowledges that both are relevant for assessing climate connectivity through time.

The resistance surfaces for the climate–HMG scenario were also unique to each climate type but incorporated the influence of the HMG. This was achieved by multiplying the climatic resistance for each climate type (Equation 1) by rescaled HMG values (HMG.rs), as follows:

$$C.HMG.resistance_i = C.resistance_i \times HMG.rs_i, \quad (2)$$

where $C.HMG.resistance_i$ is the resistance based on both climate and HMG at pixel i, $C.resistance_i$ is the climatic resistance at pixel i (Equation 1), and $HMG.rs_i$ is the rescaled HMG value at pixel i. HMG values were rescaled to 1–50 (HMG.rs) when producing these resistance surfaces, as previously described, because multiplying the climatic resistance by the native HMG range (0–1) would not achieve the desired results where HMG = 0. Consequently, pixels with the highest degree of human modification are 50 times more difficult to traverse compared to pixels without any measurable human modification. We acknowledge that our results will likely be sensitive to the manner in which we incorporated human land uses. Had we given the HMG less weight, there would be less contrast between the climate and climate–HMG scenario; the opposite is also true (Figure S1). Topographic barriers were not considered in the resistance surfaces for either scenario (cf. Theobald, Reed, Fields, & Soulé, 2012). In both scenarios, we assumed that organisms prefer to traverse terrestrial areas, and therefore assigned open water an extremely high resistance value so that individual paths avoid water where possible (cf. Dobrowski & Parks, 2016).

2.5 | Climate velocity, climate exposure, and human exposure

Each reference period pixel can have up to thousands of analogs. We generally followed the methods of Dobrowski and Parks (2016) to identify the individual analog (i.e. pixel) that minimized exposure to dissimilar climate (the climate scenario; Equation 1) or to climate and human land uses (the climate–HMG scenario; Equation 2). Specifically, we used the *gdistance* package (van Etten, 2017) in the R statistical platform (R Core Team, 2016) to identify the individual pixel with the least accumulated cost (i.e. least-cost path) from each source pixel based on resistance surfaces. Both ordinal and cardinal directions were considered in the least-cost models. The velocity for each source pixel is simply the length of the least-cost path divided by the number of elapsed years between our reference and future time periods (90 years; e.g. Hamann et al., 2015).

Calculating climate exposure, particularly for the climate–HMG scenario, is not possible without post processing because the least-cost paths were delineated using a resistance surface incorporating both climate and human land uses. Consequently, once the least-cost paths were delineated for each scenario, we re-ran the least-cost procedure but used only the climatic resistance layers (Equation 1) to calculate climate exposure and forced the algorithm to choose the pre-determined path. This was achieved by giving all pixels that were not the delineated path an extremely high resistance value. The resulting least accumulated cost therefore reflected only the climatic resistance (Equation 1) even though the actual least-cost paths were determined (for the climate–HMG scenario) using resistance to both climate and human land uses. Climate exposure (CE) was calculated as:

$$\mathrm{CE} = \sum_{s}^{d} (C.resistance_i \times L_i), \quad (3)$$

where $C.resistance_i$ is the climatic resistance of pixel i (Equation 1), which is summed from s, the source pixel to d, the destination pixel, and L_i is the length (km) of the trajectory though pixel i (this acknowledges that a diagonal trajectory through pixel i is longer than the horizontal or vertical equivalent).

Human exposure was calculated in a similar manner since the least accumulated cost for both scenarios incorporated climate and not just the HMG. Specifically, we re-ran the least-cost procedure for both scenarios using only the native HMG as the resistance surface and forced the algorithm to choose the pre-determined path by giving all pixels that were not the delineated path an extremely high resistance value. Human exposure (HE) is therefore reflective of the cumulative HMG encountered along each delineated path as follows:

$$\mathrm{HE} = \sum_{s}^{d} (HMG_i \times L_i), \quad (4)$$

where HMG_i is the native HMG value (range: 0–1) of pixel i, which is summed from s, the source pixel to d, the destination pixel, and L_i is the length (km) of the trajectory though pixel i.

2.6 | Climate corridors and protected areas

For each scenario, we produced gridded datasets characterizing the number of individual paths overlapping each pixel. This characterization is termed the 'climate corridor score' and provides a ranking of the contribution of each pixel in serving as a climate corridor; locally high climate corridor scores assumes greater importance for facilitating range shifts and greater ability to serve as a climate corridor (cf. Carroll et al., 2018). To evaluate if protected areas are providing necessary protections for potential movement routes, we overlapped the gridded climate corridor scores with protected (IUCN categories I–VI) and unprotected lands (CEC, 2017). As such, this measures the median number of individual paths overlapping each 5 km pixel within and outside of protected areas. We summarized these results by US EPA Level I ecoregion (Figure 1b).

3 | RESULTS

Our findings show that organisms will contend with a substantial degree of human land uses as they shift their ranges in response to climate change in most of North America (Figure 2a). Based on

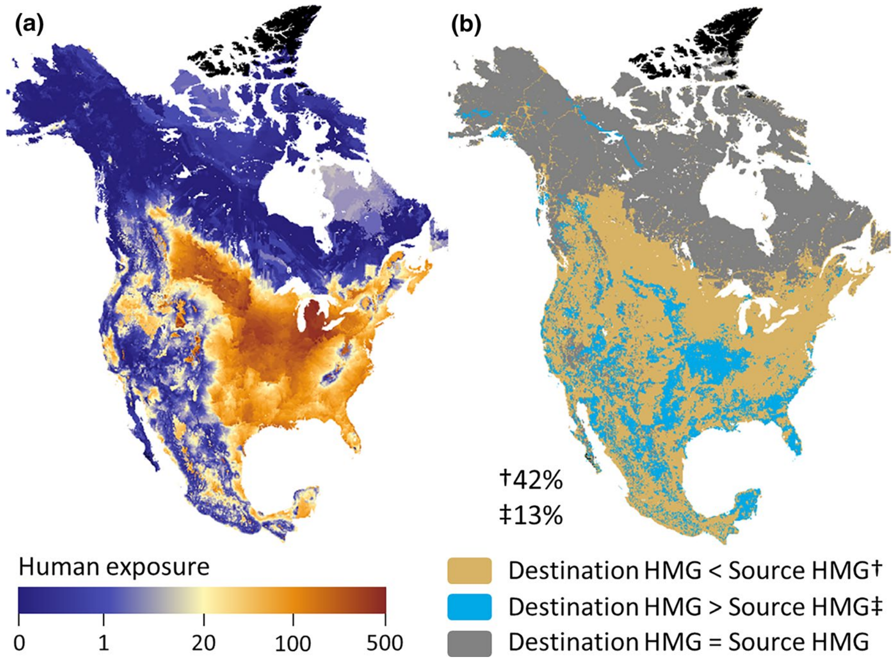

FIGURE 2 Human exposure for the climate scenario (a). Depiction of where the destination human modification gradient (HMG) values differs from the source HMG values for the climate scenario (b). Percentages in which the destination HMG values < source HMG values and the destination HMG values > source HMG values are indicated. By design, the destination HMG values are never greater than the source HMG values for the climate–HMG scenario. Black indicates disappearing climates

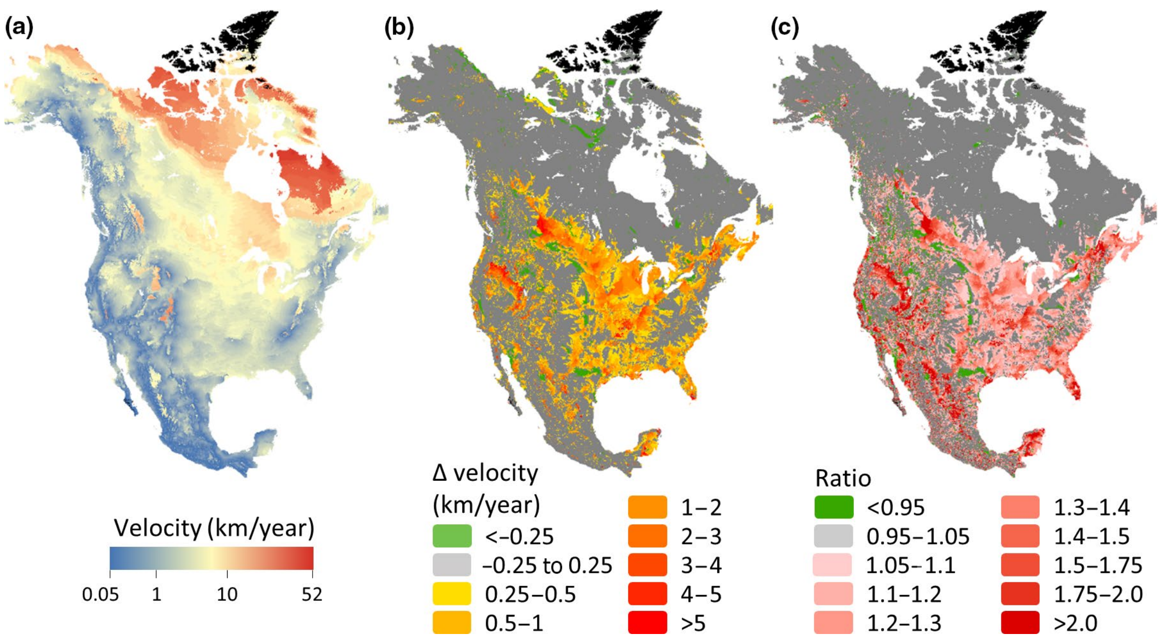

FIGURE 3 Climate velocity for North America for the climate scenario (a). The difference (km/year) between the climate velocity of the climate-HMG scenario and the climate scenario (b). The ratio of climate velocity of the climate–HMG scenario to the climate scenario (c). Black indicates disappearing climates. HMG, human modification gradient

the climate scenario, ~4% of North America exhibits zero human exposure; these areas are predominantly confined to the northern regions of the continent. Furthermore, 13% of the destination locations (i.e. analogs with the lowest climate exposure) have higher HMG values than the source pixel, highlighting the importance of including the human land uses when identifying analogs (e.g. the climate–HMG scenario). However, 42% of destination locations have a lower HMG values than the source pixel (Figure 2b), which reflects that destination locations are often north or upslope of the source pixel and have less intense land uses. For the remainder of North America (45%), the HMG values of the source and destination locations are identical.

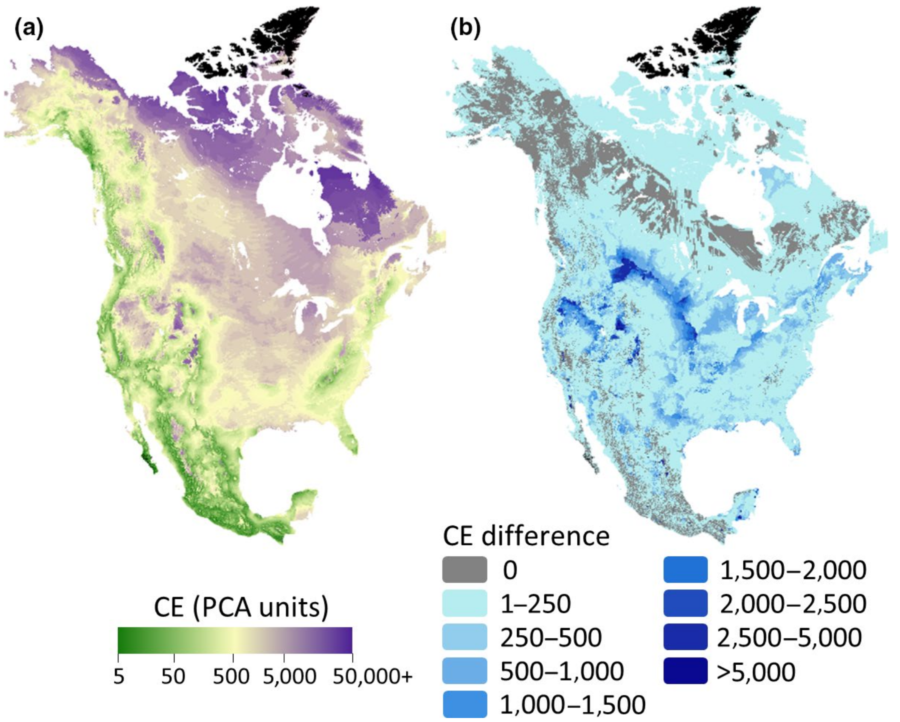

FIGURE 4 Climate exposure (CE) for North America for the climate scenario (a). The difference in climate exposure between the climate-HMG scenario and the climate scenario (b). Black indicates disappearing climates. HMG, human modification gradient; PCA, principal component analysis

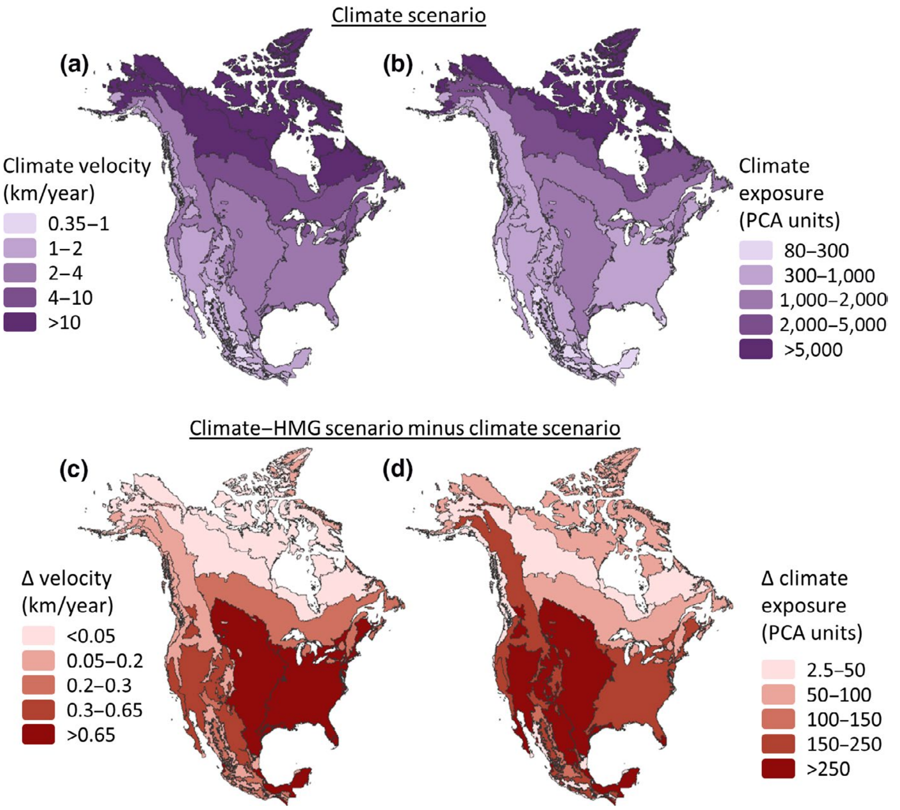

FIGURE 5 Two metrics of climate connectivity are summarized by (i.e. averaged within) US EPA Level I ecoregions: climate velocity (a) and climate exposure (b). The climate scenario was subtracted from the climate–HMG scenario to illustrate differences between scenarios (c, d). HMG, human modification gradient; PCA, principal component analysis

In terms of climate velocity, the climate–HMG scenario shows an average increase in 5% compared to the climate scenario (Figure 3); this equates to an additional 0.3 km/year across North America, on average. This said, the climate–HMG scenario exhibits much higher climate velocity compared to the climate scenario in localized areas (Figure 3). Compared to the climate scenario, ~83% of North America exhibits an increase in climate exposure under the climate–HMG scenario (Figure 4). The largest increases in climate velocity, when comparing the climate–HMG scenario to the climate scenario, are found in the Tropical Wet Forests, Great Plains, and Eastern Temperate Forests ecoregions (Figure 5c). The largest increases in climate exposure are found in the Great Plains, Tropical Wet Forests, and North American Deserts ecoregions (Figure 5d).

In the climate scenario, in which the human land uses were not considered, we found that locally high climate corridor scores exhibited diffuse and linear patterning (particular in areas with low topographic variability; Figure 6; Figures S2 and S3). In contrast, when we incorporated human land uses (the climate–HMG scenario), locally high climate corridor scores converged and became more circuitous. Notably, there were obvious qualitative shifts in the location of locally high climate corridor scores between scenarios (Figure 6).

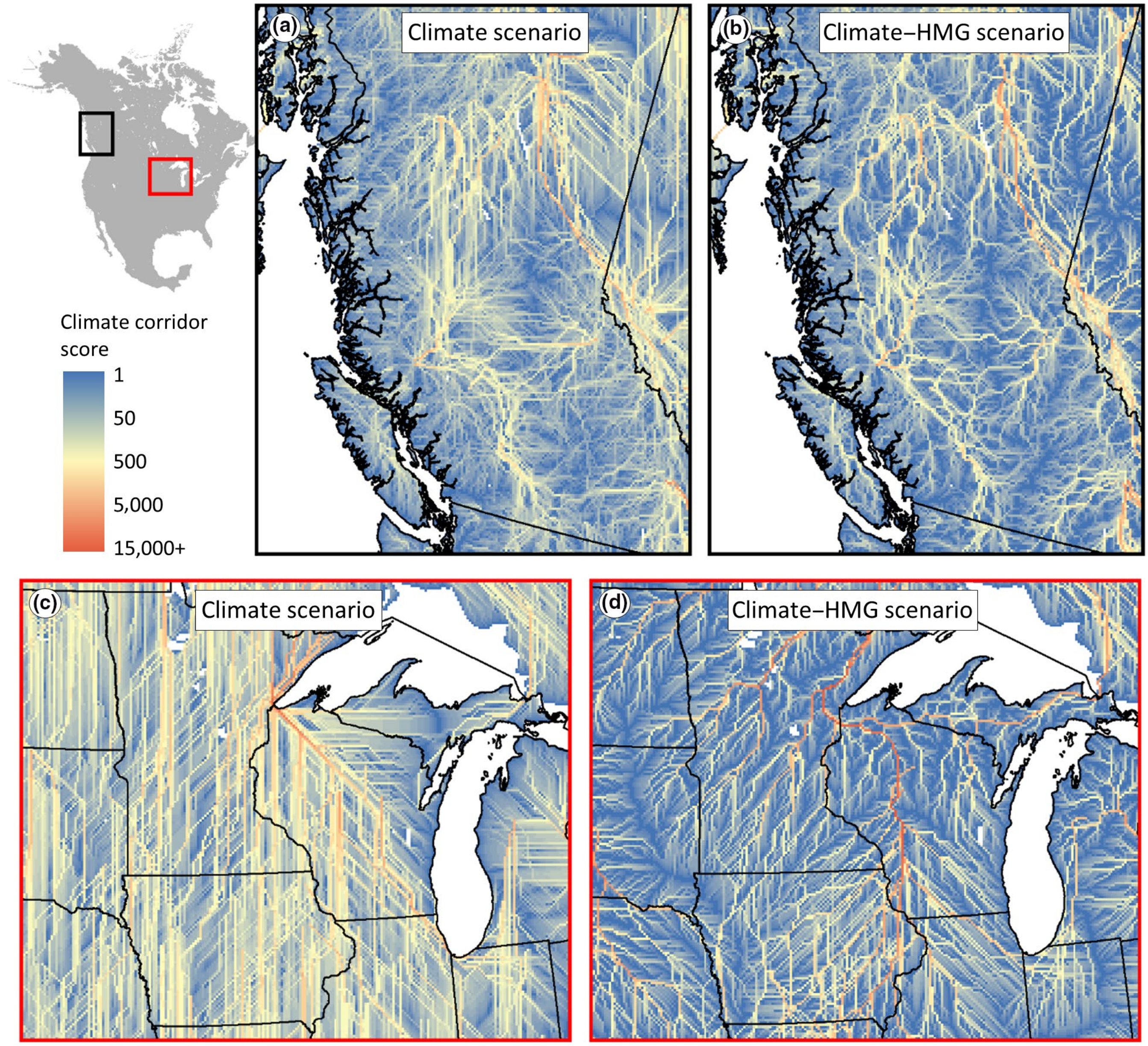

FIGURE 6 Maps depict climate corridor scores for the climate scenario (a, c) and the climate-HMG scenario (b, d). Climate corridors (qualitatively represented by locally high climate corridor scores) are more diffuse and linear in the climate scenario compared to the more convergent and circuitous corridors in climate–HMG scenario, the latter of which accounts for the HMG. Climate corridor scores are heavily right-skewed and therefore we use a logarithmic scale to display these maps. The two regions depicted contrast in both topography and human land-use intensity: panels (a) and (b) show a region of North America that is fairly topographically complex and, for the most part, has low HMG values, whereas panels (c) and (d) show a region that is relatively flat but has high HMG values. Figures S2 and S3 show climate corridor scores for the entire continent. HMG, human modification gradient

TABLE 1 Ecoregional summary of the median climate corridor score that overlaps protected (IUCN I–VI) and non-protected lands in North America. The interquartile range (IQR) is also shown. The ratio shows the proportion between the median score inside versus outside of protected areas (PAs)

		Climate scenario			Climate–HMG scenario		
Ecoregion	Percent protected	Median climate corridor score within PAs (IQR)	Median climate corridor score outside of PAs (IQR)	Ratio	Median climate corridor score within PAs (IQR)	Median climate corridor score outside of PAs (IQR)	Ratio
1. Arctic Cordillera	22.2	13 (3–55)	9 (3–38)	1.4	13 (3–61)	8 (2–37)	1.6
2. Tundra	16.9	20 (6–75)	19 (6–88)	1.1	18 (5–78)	18 (5–86)	1.0
3. Taiga	12.9	23 (8–87)	26 (8–88)	0.9	23 (7–91)	23 (7–88)	1.0
4. Hudson Plain	12.3	12 (4–63)	30 (14–97)	0.4	10 (3–72)	27 (10–99)	0.4
5. Northern Forests	9.2	24 (9–81)	23 (8–77)	1.0	17 (4–90)	8 (2–46)	2.1
6. NW Forested Mountains	20.3	16 (5–52)	13 (5–41)	1.2	19 (5–82)	8 (3–30)	2.4
7. Marine West Coast Forest	35.9	6 (3–15)	6 (2–14)	1.0	6 (2–17)	4 (2–13)	1.5
8. Eastern Temperate Forests	3.7	13 (5–42)	15 (6–42)	0.9	9 (2–66)	4 (1–14)	2.3
9. Great Plains	2.9	13 (5–38)	18 (7–55)	0.7	8 (2–40)	3 (1–14)	2.7
10. North American Deserts	14.0	7 (3–20)	8 (3–20)	0.9	9 (3–38)	5 (2–19)	1.8
11. Mediterranean California	9.3	7 (3–23)	6 (3–18)	1.2	9 (2–39)	3 (1–12)	3.0
12. Southern Semiarid Highlands	5.9	13 (5–35)	6 (3–15)	2.2	8 (3–24)	4 (2–11)	2.0
13. Temperate Sierras	13.7	7 (3–22)	6 (2–15)	1.2	9 (3–27)	6 (2–17)	1.5
14. Tropical Dry Forests	7.7	3 (1–11)	3 (1–6)	1.0	3 (2–12)	2 (1–6)	1.5
15. Tropical Wet Forests	16.9	7 (3–15)	5 (2–13)	1.4	5 (2–23)	3 (1–8)	1.7
All of North America	12.0	14 (5–48)	15 (5–50)	0.9	14 (4–60)	7 (2–34)	2.0

The climate scenario revealed that protected lands do not represent climate corridors at a higher rate than non-protected lands across North America; the median climate corridor score in protected areas was 14 and in non-protected areas was 15 (Table 1). However, ecoregional variation was evident; protected lands have lower climate corridor scores than non-protected lands in several ecoregions, with the Hudson Plain and Great Plains showing the largest disparity (Table 1). Conversely, protected lands exhibit higher climate corridor scores than non-protected lands in other ecoregions, notably in the Southern Semiarid Highlands, Arctic Cordillera, and Tropical Wet Forests ecoregions. Note, however, that the findings from the climate-HMG scenario show a different pattern (Table 1).

4 | DISCUSSION

Recent assessments of climate connectivity have not incorporated human land uses into their evaluations (Burrows et al., 2014; Carroll et al., 2018; Dobrowski & Parks, 2016; Hamann et al., 2015; but see Littlefield et al., 2017; McGuire et al., 2016). It is clear, however, that altered landscapes often have a negative effect on organisms and their ability to disperse (Di Marco et al., 2018; Dyer, O'Neill, Wasel, & Boutin, 2002), suggesting that human land uses should be explicitly incorporated into evaluations of climate connectivity (Robillard, Coristine, Soares, & Kerr, 2015). We show that organisms will cumulatively contend with high degrees of human land uses across broad swaths of North America as they shift their ranges in response to climate change (see Figure 2a). The increases in climate velocity and climate exposure suggest that recent assessments of climate connectivity underestimate 21st-century climate change exposure. Overall, our findings show that human land uses pose an additional threat to organisms as they shift their ranges in response to climate change (Hansen et al., 2001).

Previous research has noted that human land uses impact climate connectivity (e.g. McGuire et al., 2016; Senior, Hill, & Edwards, 2019). Nonetheless, our study makes several important contributions. For example, although previous studies included human land uses in their analyses of climate connectivity (Littlefield et al., 2017; Nunez et al., 2013), no previous studies, to our knowledge, have quantified the potential impact of human land use since they did not provide parallel evaluations without human land uses. In contrast, we evaluated climate connectivity under two scenarios, thereby allowing us to quantitatively compare climate velocity, climate exposure, and climate corridor scores with and without human land uses. Additionally, we introduce a new metric, human exposure, which quantifies an unexplored and important facet of climate change vulnerability (e.g. Figure 2a). This metric serves as an additional measure of climate change exposure that complements metrics such as climate velocity and climate exposure, as it characterizes a unique dimension of climate change exposure not yet addressed. Our results also provide a solid foundation for explicitly considering human land uses when identifying climate analogs, as some pixels identified as climate analogs, but heavily impacted by humans, are not necessarily available to all organisms of the source pixel. Lastly, unlike previous studies, our results encompass all of North America, providing a wall-to-wall assessment of climate connectivity while considering human land uses.

Climate velocity is a climate connectivity metric that estimates the rate at which organisms must shift to maintain similar climate conditions under a changing climate (Loarie et al., 2009). Due to factors such as dispersal distance, competition, and disturbance, many have expressed concern that climate velocity may exceed the rate that organisms can shift their ranges (Liang, Duveneck, Gustafson, Serra-Diaz, & Thompson, 2018). Our analysis suggests that current estimates of climate velocity may be underestimated, thereby amplifying such concerns, particularly for poorly dispersing organisms or organisms that are sensitive to human land uses (Newbold et al., 2015; Schloss, Nuñez, & Lawler, 2012).

Climate exposure is an additional climate connectivity metric that measures the accumulated climatic dissimilarity between each pixel and its 'nearest' climate analog (Dobrowski & Parks, 2016). When human land uses were incorporated into resistance surfaces, climate exposure increased for most (83%) of the continent, thereby adding an additional stressor on organisms as they shift in response to climate change. And although our study did not explicitly address this stressor, human land uses themselves alter local climate (warmer and drier) and potentially decrease the climate suitability for some organisms (Williams & Newbold, 2020). Consequently, human land uses could effectively preclude some organisms from tracking their optimal climates, thereby increasing risk of local extirpations or even extinction (Krosby, Tewksbury, Haddad, & Hoekstra, 2010).

Climate corridors (qualitatively represented by pixels with locally high climate corridor scores) for the climate–HMG scenario are more concentrated and circuitous compared to the baseline scenario that only considered climate (see Figure 6; Figures S1 and S2). This has two important implications for effective climate corridor planning. First, our understanding of climate corridors may be more constrained in comparison to corridors based solely on climate (e.g. Carroll et al., 2018) or human land uses (Belote et al., 2016), thereby decreasing the land base that serves as effective climate corridors. Second, our findings provide a template for prioritizing conservation efforts in areas that are currently identified as climate corridors (i.e. locally high climate corridor scores) given that human land uses are generally expected to increase in intensity in the coming decades (Lawler et al., 2014). Indeed, we may lose opportunities to restore and maintain climate connectivity as land-use intensity increases in regions such as the boreal forest and western US (Copeland, Pocewicz, & Kiesecker, 2011).

The results from the climate scenario show that destination HMG values are greater than source HMG values for 13% of North America. This highlights that these destination pixels may not be able to serve in the same capacity in maintaining species richness and biodiversity compared to their source pixels and provides another indication that climate change and human land uses threaten biodiversity (Jetz, Wilcove, & Dobson, 2007; Sala et al., 2000). Conversely, destination HMG values are less than source HMG values for 42% for North America, largely a result of poleward migration toward regions that currently have less intense human land uses. This suggests that organisms migrating into these regions may have less anthropogenic stress in future decades, which could be considered positive. However, because the suite of organisms at the source pixel may be currently reduced by human activities, this may increase the likelihood that the destination pixel will support a depauperate complement of species. Basically, some source pixels are potentially 'diluted' in terms of biological resources since human land uses are more intense than the destination pixels. Our estimates, however, do not account for increased human activities that are expected in some regions of the continent (e.g. increased energy development in northern and western North America; Copeland et al., 2011; Northrup & Wittemyer, 2013).

Several previous studies have evaluated connectivity among protected areas and how protected areas facilitate movement under a stationary climate (e.g. Belote et al., 2016; Opermanis, MacSharry, Aunins, & Sipkova, 2012). However, interest is gaining in terms of quantifying connectivity among protected areas under a changing climate (Littlefield et al., 2017; McGuire et al., 2016). As such, our analysis of climate corridor scores within and outside of protected areas (under the climate scenario) revealed that some ecoregions exhibit poor representation of climate corridors (e.g. Great Plains). Because some of these ecoregions (i.e. Hudson Plain and Taiga) are located in the far north and are largely unmodified in terms of human land use (Kennedy et al., 2019), this finding might not necessarily be considered a conservation concern. However, because of projected expansion of more intensive land uses in these regions (Northrup & Wittemyer, 2013), and concern for negative impacts on biodiversity (Hebblewhite, 2017), our findings suggest that the protected area network can be strategically expanded to better represent climate corridors. Conversely, protected areas in other ecoregions exhibit higher representation of climate corridors compared to non-protected lands (e.g. Southern Semiarid Highlands and Tropical Wet Forests). Though we are not able to determine an 'optimal' ratio of climate corridor scores between protected and unprotected lands, it is clear that higher climate corridor scores in protected landscapes will better facilitate range shifts under climate change.

Our study has limitations that should be considered when interpreting our results. For example, the least-cost methodology we employed results in a single-pixel wide, globally optimal path between each source and destination pixel, thereby failing to recognize that there may be alternate routes or wider paths that exhibit identical costs according to the resistance surfaces. As such, our gridded maps representing climate corridor scores may appear more constrained compared to approaches that can account for alternate routes. Also, the directional assumptions (pixel-to-pixel movement can be one of eight directions) of the least-cost methodology sometimes result in linear corridors (see Figure 6c). Other approaches to identifying climate corridors, such as circuit theory (McRae & Beier, 2007), do not have these artifacts. However, calculation of climate change vulnerability metrics such as climate exposure and human exposure is computationally challenging, and its feasibility is contingent on the use of least-cost methodology. Lastly, we acknowledge that our results are likely sensitive to the way in which we incorporated human land uses into the resistance surfaces for the climate–HMG scenario. For example, pixels with the highest degree of human modification are 50 times more difficult to traverse compared to pixels without any measurable human modification. Had we given HMG less weight in the resistance surfaces, there would be less contrast between the climate and climate–HMG scenario; the opposite is also true (see Figure S1).

Although our study was conducted in North America, the overall framework and findings are relevant to other continents, particularly given that much of the planet is modified by human land uses to some degree (Kennedy et al., 2019). In fact, because some regions of the planet have more intense land uses than North America as a whole (e.g. Europe, Southeast Asia), we expect that the influence of human land uses on climate connectivity in these regions will be greater than that reported in our study. Consequently, we suggest that human land uses should be incorporated into assessments of climate connectivity and climate change vulnerability assessments (Parry et al., 2007).

Climate change is a serious threat facing biodiversity in the coming decades and centuries (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012). Human land uses are also a major threat due to direct habitat degradation and loss (Newbold et al., 2015). Combined, climate change and human land uses will challenge the ability of many species to persist in the future. Consequently, vulnerability assessments that address both are necessary to understand and mitigate impacts to biodiversity. We show that climatic connectivity decreases when we incorporate human land uses, highlighting that evaluations that do not account for human modifications of the landscape may underestimate climate change vulnerability. Moreover, 96% of North America is expected to experience some level of human exposure. The protected area network as a whole does not represent climate corridors better than non-protected lands across North America when human land uses are not considered. Variability is evident, however, as protected areas represent climate corridors better than non-protected lands in some ecoregions. Our results demonstrate the need for proactive measures to improve the ability of protected areas to harbor biodiversity and facilitate species movement (Hannah, 2008; Thomas & Gillingham, 2015), including efforts to better protect climate corridors.

ACKNOWLEDGEMENTS

We thank three anonymous reviewers and D. Theobald for thoughtful comments that substantially improved this manuscript. SZD acknowledges support from the USDA National Institute of Food and Agriculture, McIntire Stennis Program, project 1012438.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from AdaptWest at https://adaptwest.databasin.org/pages/adaptwest-climatena (AdaptWest Project, 2015) and figshare at https://figshare.com/articles/Global_Human_Modification/7283087 (Kennedy et al., 2019).

ORCID

Sean A. Parks https://orcid.org/0000-0002-2982-5255

Carlos Carroll https://orcid.org/0000-0002-7697-8721

REFERENCES

AdaptWest Project. (2015). Gridded current and projected climate data for North America at 1 km resolution, interpolated using the ClimateNA v5.10 software. Retrieved from adaptwest.databasin.org

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

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Belote, R. T., Dietz, M. S., McRae, B. H., Theobald, D. M., McClure, M. L., Irwin, G. H., … Aplet, G. H. (2016). Identifying corridors among large protected areas in the United States. *PLoS ONE*, *11*(4), 1–16. https://doi.org/10.1371/journal.pone.0154223

Blair, R. B. (1996). Land use and avian species diversity along an urban gradient. *Ecological Applications*, *6*(2), 506–519. https://doi.org/10.2307/2269387

Blair, R. B., & Launer, A. E. (1997). Butterfly diversity and human land use: Species assemblages along an urban grandient. *Biological Conservation*, *80*(1), 113–125. https://doi.org/10.1016/S0006-3207(96)00056-0

Burrows, M. T., Schoeman, D. S., Richardson, A. J., Molinos, J. G., Hoffmann, A., Buckley, L. B., … Poloczanska, E. S. (2014). Geographical limits to species-range shifts are suggested by climate velocity. *Nature*, *507*, 492. https://doi.org/10.1038/nature12976

Carroll, C., Lawler, J. J., Roberts, D. R., & Hamann, A. (2015). Biotic and climatic velocity identify contrasting areas of vulnerability to climate change. *PLoS ONE*, *10*(10), e0140486. https://doi.org/10.1371/journal.pone.0140486

Carroll, C., Parks, S. A., Dobrowski, S. Z., & Roberts, D. R. (2018). Climatic, topographic, and anthropogenic factors determine connectivity between current and future climate analogs in North America. *Global Change Biology*, *24*(11), 5318–5331. https://doi.org/10.1111/gcb.14373

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

CEC. (2017). Protected Areas of North America, 2017. Commission for Environmental Cooperation. Retrieved from http://www.cec.org/tools-and-resources/map-files/north-american-protected-areas-2017

Copeland, H. E., Pocewicz, A., & Kiesecker, J. M. (2011). Geography of energy development in western North America: Potential impacts on terrestrial ecosystems. In D. E. Naugle (Ed.), *Energy development and wildlife conservation in western North America*. Washington, DC: Island Press.

Di Marco, M., Venter, O., Possingham, H. P., & Watson, J. E. M. (2018). Changes in human footprint drive changes in species extinction risk. *Nature Communications*, *9*(1), 4621. https://doi.org/10.1038/s41467-018-07049-5

Dobrowski, S. Z., Abatzoglou, J., Swanson, A. K., Greenberg, J. A., Mynsberge, A. R., Holden, Z. A., & Schwartz, M. K. (2013). The climate velocity of the contiguous United States during the 20th century. *Global Change Biology*, *19*(1), 241–251. https://doi.org/10.1111/gcb.12026

Dobrowski, S. Z., & Parks, S. A. (2016). Climate change velocity underestimates climate change exposure in mountainous regions. *Nature Communications*, *7*. https://doi.org/10.1038/ncomms12349

Dyer, S. J., O'Neill, J. P., Wasel, S. M., & Boutin, S. (2002). Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Canadian Journal of Zoology*, *80*(5), 839–845. https://doi.org/10.1139/z02-060

Early, R., & Sax, D. F. (2011). Analysis of climate paths reveals potential limitations on species range shifts. *Ecology Letters*, *14*(11), 1125–1133. https://doi.org/10.1111/j.1461-0248.2011.01681.x

Foley, J. A., Defries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., … Snyder, P. K. (2005). Global consequences of land use. *Science*, *309*(5734), 570–574. https://doi.org/10.1126/science.1111772

Hamann, A., Roberts, D. R., Barber, Q. E., Carroll, C., & Nielsen, S. E. (2015). Velocity of climate change algorithms for guiding conservation and management. *Global Change Biology*, *21*(2), 997–1004. https://doi.org/10.1111/gcb.12736

Hannah, L. (2008). Protected areas and climate change. *Annals of the New York Academy of Sciences*, *1134*(1), 201–212. https://doi.org/10.1196/annals.1439.009

Hansen, A. J., Neilson, R. P., Dale, V. H., Flather, C. H., Iverson, L. R., Currie, D. J., … Bartlein, P. J. (2001). Global change in forests: Responses of species, communities, and biomes: Interactions between climate change and land use are projected to cause large shifts in biodiversity. *BioScience*, *51*(9), 765–779. https://doi.org/10.1641/0006-3568(2001)051[0765:GCIFRO]2.0.CO;2

Hebblewhite, M. (2017). Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. *Biological Conservation*, *206*, 102–111. https://doi.org/10.1016/j.biocon.2016.12.014

Jetz, W., Wilcove, D. S., & Dobson, A. P. (2007). Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, *5*(6), e157. https://doi.org/10.1371/journal.pbio.0050157

Kennedy, C. M., Oakleaf, J. R., Theobald, D. M., Baruch-Mordo, S., & Kiesecker, J. (2019). Managing the middle: A shift in conservation priorities based on the global human modification gradient. *Global Change Biology*, *25*(3), 811–826. https://doi.org/10.1111/gcb.14549

Krosby, M., Tewksbury, J., Haddad, N. M., & Hoekstra, J. (2010). Ecological connectivity for a changing climate. *Conservation Biology*, *24*(6), 1686–1689. https://doi.org/10.1111/j.1523-1739.2010.01585.x

Lawler, J. J., Lewis, D. J., Nelson, E., Plantinga, A. J., Polasky, S., Withey, J. C., … Radeloff, V. C. (2014). Projected land-use change impacts on ecosystem services in the United States. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(20), 7492–7497. https://doi.org/10.1073/pnas.1405557111

Liang, Y., Duveneck, M. J., Gustafson, E. J., Serra-Diaz, J. M., & Thompson, J. R. (2018). How disturbance, competition, and dispersal interact to prevent tree range boundaries from keeping pace with climate change. *Global Change Biology*, *24*(1), e335–e351. https://doi.org/10.1111/gcb.13847

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

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

Maestas, J. D., Knight, R. L., & Gilgert, W. C. (2003). Biodiversity across a rural land-use gradient. *Conservation Biology*, *17*(5), 1425–1434. https://doi.org/10.1046/j.1523-1739.2003.02371.x

McGuire, J. L., Lawler, J. J., McRae, B. H., Nuñez, T. A., & Theobald, D. M. (2016). Achieving climate connectivity in a fragmented landscape. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(26), 7195–7200. https://doi.org/10.1073/pnas.1602817113

McRae, B. H., & Beier, P. (2007). Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(50), 19885–19890. https://doi.org/10.1073/pnas.0706568104

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*(7545), 45–50. https://doi.org/10.1038/nature14324

Northrup, J. M., & Wittemyer, G. (2013). Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. *Ecology Letters*, *16*(1), 112–125. https://doi.org/10.1111/ele.12009

Nuñez, T. A., Lawler, J. J., McRae, B. H., Pierce, D. J., Krosby, M. B., Kavanagh, D. M., … Tewksbury, J. J. (2013). Connectivity planning to address climate change. *Conservation Biology*, *27*(2), 407–416. https://doi.org/10.1111/cobi.12014

Opermanis, O., MacSharry, B., Aunins, A., & Sipkova, Z. (2012). Connectedness and connectivity of the Natura 2000 network of protected areas across country borders in the European Union. *Biological Conservation*, *153*, 227–238. https://doi.org/10.1016/j.biocon.2012.04.031

Parks, S. A., Holsinger, L. M., Miller, C., & Parisien, M.-A. (2018). Analog-based fire regime and vegetation shifts in mountainous regions of the western US. *Ecography*, *41*(6), 910–921. https://doi.org/10.1111/ecog.03378

Parry, M., Parry, M. L., Canziani, O., Palutikof, J., der Linden, P., & Hanson, C. (2007). *Climate change 2007-impacts, adaptation and vulnerability: Working group II contribution to the fourth assessment report of the IPCC* (Vol. 4). Cambridge, UK: Cambridge University Press.

R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/

Robillard, C. M., Coristine, L. E., Soares, R. N., & Kerr, J. T. (2015). Facilitating climate-change-induced range shifts across continental land-use barriers. *Conservation Biology*, *29*(6), 1586–1595. https://doi.org/10.1111/cobi.12556

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., … Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*(5459), 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., & Woolmer, G. (2002). The human footprint and the last of the wild: The human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. *BioScience*, *52*(10), 891–904. https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2

Schloss, C. A., Nuñez, T. A., & Lawler, J. J. (2012). Dispersal will limit ability of mammals to track climate change in the Western Hemisphere.

Proceedings of the National Academy of Sciences of the United States of America, *109*(22), 8606–8611. https://doi.org/10.1073/pnas.1116791109

Senior, R. A., Hill, J. K., & Edwards, D. P. (2019). Global loss of climate connectivity in tropical forests. *Nature Climate Change*, *9*(8), 623–626. https://doi.org/10.1038/s41558-019-0529-2

Theobald, D. M., Reed, S. E., Fields, K., & Soulé, M. (2012). Connecting natural landscapes using a landscape permeability model to prioritize conservation activities in the United States. *Conservation Letters*, *5*(2), 123–133. https://doi.org/10.1111/j.1755-263X.2011.00218.x

Thomas, C. D., & Gillingham, P. K. (2015). The performance of protected areas for biodiversity under climate change. *Biological Journal of the Linnean Society*, *115*(3), 718–730. https://doi.org/10.1111/bij.12510

van Etten, J. (2017). R package gdistance: Distances and routes on geographical grids. *Journal of Statistical Software*, *76*(13), 1–21. https://doi.org/10.18637/jss.v076.i13

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., … Watson, J. E. M. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, *7*, 12558. https://doi.org/10.1038/ncomms12558

Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science*, *277*(5325), 494–499. https://doi.org/10.1126/science.277.5325.494

Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE*, *11*(6), e0156720. https://doi.org/10.1371/journal.pone.0156720

Williams, J. J., & Newbold, T. (2020). Local climatic changes affect biodiversity responses to land use: A review. *Diversity and Distributions*, *26*(1), 76–92. https://doi.org/10.1111/ddi.12999

Williams, P., Hannah, L., Andelman, S., Midgley, G., Araújo, M., Hughes, G., … Pearson, R. (2005). Planning for climate change: Identifying minimum-dispersal corridors for the cape proteaceae. *Conservation Biology*, *19*(4), 1063–1074. https://doi.org/10.1111/j.1523-1739.2005.00080.x

Wuebbles, D. J., & Hayhoe, K. (2004). Climate change projections for the United States Midwest. *Mitigation and Adaptation Strategies for Global Change*, *9*(4), 335–363. https://doi.org/10.1023/B:MITI.0000038843.73424.de

SUPPORTING INFORMATION

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

How to cite this article: Parks SA, Carroll C, Dobrowski SZ, Allred BW. Human land uses reduce climate connectivity across North America. *Glob Change Biol*. 2020;00:1–12. https://doi.org/10.1111/gcb.15009