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Potential relocation of climatic environments suggests high rates of climate displacement within the North American protection network

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Abstract

Ongoing climate change may undermine the effectiveness of protected area networks in preserving the set of biotic components and ecological processes they harbor, thereby jeopardizing their conservation capacity into the future. Metrics of climate change, particularly rates and spatial patterns of climatic alteration, can help assess potential threats. Here, we perform a continent-wide climate change vulnerability assessment whereby we compare the baseline climate of the protected area network in North America (Canada, United States, México—NAM) to the projected end-of-century climate (2071–2100). We estimated the projected pace at which climatic conditions may redistribute across NAM (i.e., climate velocity), and identified future nearest climate analogs to quantify patterns of climate relocation within, among, and outside protected areas. Also, we interpret climatic relocation patterns in terms of associated land-cover types. Our analysis suggests that the conservation capacity of the NAM protection network is likely to be severely compromised by a changing climate. The majority of protected areas (~80%) might be exposed to high rates of climate displacement that could promote important shifts in species abundance or distribution. A small fraction of protected areas (<10%) could be critical for future conservation plans, as they will host climates that represent analogs of conditions currently characterizing almost a fifth of the protected areas across NAM. However, the majority of nearest climatic analogs for protected areas are in nonprotected locations. Therefore, unprotected landscapes could pose additional threats, beyond climate forcing itself, as sensitive biota may have to migrate farther than what is prescribed by the climate velocity to reach a protected area destination. To mitigate future threats to the conservation capacity of the NAM protected area network, conservation plans will need to capitalize on opportunities provided by the existing availability of natural land-cover types outside the current network of NAM protected areas.

KEYWORDS

climate analogs, climate relocation, climate velocity, conservation, exposure assessment, global change, land-cover types, protection network

1 | INTRODUCTION

Systematic conservation planning represents the cornerstone of a strategy to protect the full range of biodiversity components and ecological processes of a region (Margules & Pressey, 2000). Reserve network design has a key role in such planning as the protection of representative sets of biodiversity critically depends on it. In most cases, the current distribution of biota has been central to the development of existing systematic conservation plans (Lawler et al., 2015). Therefore, the extent to which reserves fulfill their role largely depends on the persistence of ecological conditions that promote patterns of biodiversity. Ongoing, unprecedented rates of climate change (Diffenbaugh & Field, 2013) are altering the spatial distribution of climatically suitable areas for organisms, habitats, and biomes. As a result, shifting climatic conditions over the next century may greatly undermine the effectiveness of reserve systems in protecting their current suite of organisms and associated ecosystem properties.

In practice, the design of reserve systems has been imperfect, as the protection of lands is often carried out for ad hoc reasons resulting from political or economic realities (Margules & Pressey, 2000). Even so, protected area networks are the best and most cost-effective line of defense in the global effort to protect biodiversity (Balmford et al., 2002; Bruner, Gullison, Rice, & da Fonseca, 2001; Rodrigues et al., 2004). Ensuring the continued relevance and effectiveness of protected area networks during a period of rapid climate change is thus among the most crucial challenges for conservation planners (e.g., Groves et al., 2012; Hannah, 2010). Over the last couple of decades, spirited debate has occurred over protected area design (and re-design) and the adaptation of conservation actions to global change (e.g., Dawson, Jackson, House, Prentice, & Mace, 2011; Gillson, Dawson, Jack, & McGeoch, 2013; Groves et al., 2012; Heller & Hobbs, 2014). Open questions remain regarding the ideal proportion of protected land and protected area size that optimizes landscape conservation capacity, and about reserve connectivity and representativeness. Several other factors have been identified as key elements in evaluating landscape vulnerability to change, including the rate of change and the sensitivity and adaptation capacity of individual organisms, all of which will influence ecosystem resilience (e.g., Carpenter, Walker, Anderies, & Abel, 2001; Oliver et al., 2015).

Climate is a key driver of ecosystem structure, pattern, and functioning, and governs species distributions (e.g., Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Ordonez & Williams, 2013; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005), disturbance regimes (e.g., Dale et al., 2001; Krawchuk & Moritz, 2011), and hydrologic dynamics (e.g., Rodriguez-Iturbe, 2000). Therefore, metrics of climate change that describe its temporal and geographic patterns can be useful surrogates for assessing the exposure and sensitivity of organisms and ecological processes (Carroll, Lawler, Roberts, & Hamann, 2015; Garcia, Cabeza, Rahbek, & Araújo, 2014). The velocity of climate change (Hamann, Roberts, Barber, Carroll, & Nielsen, 2015; Loarie et al., 2009) is a simple metric that reflects the pace (e.g., in km/year) at which a given isocline of temperature or precipitation, or any set of climatic conditions, may relocate across the landscape. This concept has been largely applied to biota to indicate the rate at which organisms must migrate to retain similar climatic conditions.

Velocity computations based on climate analogs (Hamann et al., 2015) allow the assessment of both forward and backward (or reverse) velocities of change. Forward velocity relates to *outgoing* climates of a region; it considers baseline climate and identifies, for any given pixel, the nearest pixel with a similar climate (i.e., its analog) under a future time period. Reverse velocity relates to *incoming* climates of a region; it considers future climate and identifies, for any given pixel, the nearest pixel with a similar climate under the baseline time period. In other words, forward velocities can be considered a measure of exposure for organisms migrating out of any given pixel, whereas reverse velocities can be considered a measure of exposure for organisms colonizing (or migrating into) any given pixel (Carroll et al., 2015; Dobrowski & Parks, 2016). Both measures use the distance between each pixel of interest and its nearest climate analog for a given time period to calculate a velocity (Hamann et al., 2015). Forward and reverse velocity computations also allow systematic quantification of the location of outgoing and incoming climates of a region, respectively.

In this study, we examine the climate exposure of the existing protected area network in North America (Canada, United States, México—NAM) by the end of the century (2071–2100) using projections from the 5th IPCC Assessment Report for future climate projections (IPCC, 2014). Previous research has assessed the climatic exposure of protected networks regionally in Canada (e.g., Lemieux & Scott, 2005; Scott, Malcolm, & Lemieux, 2002), the United States (e.g., Hansen et al., 2014; Monahan & Fisichelli, 2014), and México (e.g., Prieto-Torres, Navarro-Sigüenza, Santiago-Alarcon, & Rojas-Soto, 2016; Ricker et al., 2007), but existing continent-wide approaches (e.g., Carroll et al., 2015) are too coarse to reveal threats within protected areas. Here we present a fine-spatial scale approach in which we assess the vulnerability of the entire NAM protected area network to climate change. We compute forward and reverse climate velocities and, by identifying the location of the nearest climate analogs, examine the potential relocation of climates among protected and unprotected areas. To assess additional threats to the protected biota resulting from human-induced land modifications, we characterize land-cover types associated with the outgoing and incoming climates.

2 | MATERIALS AND METHODS

We assessed the vulnerability of the NAM protected area network to climate change using three approaches: (i) We calculated both forward and reverse climate velocities based on baseline (1981–2010) and end-of-century (2071–2100) climate for all pixels within protected areas, and classified each protected area through a joint forward–reverse characterization of velocities as low, moderate, or high. (ii) Using the specific locations of climate analogs (for both outgoing and incoming climates), we identified whether climate analogs are (a) located within the same protected area, (b) located in a different protected area, (c) located outside of the protected area network, or (d) correspond to a disappearing or novel climate. (iii) We identified the land-cover types associated with the locations of outgoing and incoming climates and compared them to baseline conditions.

2.1 | North America protection network and climate projections

To define the protected area network for NAM, we used the updated Terrestrial Protected Areas of North America (2010) produced by the Commission for Environmental Cooperation (CEC; www.cec.org/naatlas). This spatial data set includes protected areas that are managed by national, state, provincial, or territorial entities and represents a functional system of ecologically based protection network over México, the United States, and Canada. We retained protected areas larger than 10 km^2 within any of the categories I–VI of the International Union for the Conservation of Nature (IUCN, 1994). Linear features such as rivers, creeks, waterways, parkways, trails, and railroads were excluded. This yielded 4,512 protected areas covering 2.25 million km^2 that sustain high levels of species richness compared to unprotected locations (Fig. S1). The protected area boundaries were rasterized using the same resolution and projection as the climate data described below.

High-resolution baseline and future climate data at a 1-km resolution and in Lambert Conformal Conic projection were obtained from ADAPTWEST (Wang, Hamann, Spittlehouse, & Carroll, 2016; adaptwest.databasin.org). These data sets are based on the Coupled Model Intercomparison Project Phase 5 (CMIP5) database corresponding to the 5th IPCC Assessment Report for future projections. We selected future climate projections based on the representative concentration pathway RCP8.5, which represents continued use of fossil fuels without mitigation; emissions since the year 2000 have been closest to this concentration pathway (Peters et al., 2012). For this study, we opted to use projections of an individual general circulation model (GCM), the MPI-ESM-LR, as representative of "median" climate change projection among the eight GCMs with high validation statistics available in ADAPTWEST (Knutti, Masson, & Gettelman, 2013; Wang et al., 2016). Although uncertainties exist in all climate projections, climate specialists have demonstrated the significance of projected changes and that the strength of the signal of climate change (magnitude of projected changes) exceeds the noise (climate projections uncertainty; e.g., Cressie & Kang, 2016; Sansom, Stephenson, Ferro, Zappa, & Shaffrey, 2013). We cannot rule out that the degree of uncertainty in some of the variables used here (see Section 2.2 below) is outside the confidence interval of the current climate estimates. However, we assume that the magnitude of projected climate changes (e.g., surface temperature increases of 2.6–4.8°C by 2081–2100 under RCP8.5; IPCC, 2014) may be regarded as significant for the biota, especially given that recent historic change (e.g., 0.6°C warming since the late nineteenth century, IPCC, 1995) has already caused significant alterations in species physiology and phenology and ecosystem shifts (e.g., Chen et al., 2011; Hughes, 2000; Parmesan, 2006).

2.2 | Characterizing the climate space

We used 10 climatic variables that represent biologically relevant annual and seasonal trends in temperature, precipitation, moisture, and growing season (Fig. S2; Batllori, Miller, Parisien, Parks, & Moritz, 2014) to characterize the climatic conditions, or multivariate climate space (Metzger et al., 2013; Wiens, Seavy, & Jongsomjit, 2011), over NAM. To this end, we used principal component analysis (PCA) to collapse the initial suite of climate variables into two new orthogonal variables that incorporated the majority (75%) of the climatic variability. The PCA was performed on a random sample of 250,000 points used to extract the data for baseline (1981–2010) and six decades of future (2041–2100) climate. This representative sample of large-scale baseline and future climatic patterns across NAM was pooled together to build the PCA and obtain the loadings of each climatic variable in the first and second PCA axes (PC1 and PC2, respectively). Pooling six decades of future climate with baseline climate ensured a comprehensive characterization of the entire NAM climate space, even though the focus of our vulnerability analysis was on end-of-century conditions (2071–2100). Subsequently, we predicted PC1 and PC2 scores for each pixel across the entire NAM for baseline and end-of-century conditions. Finally, PC1 and PC2 scores were partitioned into 120 equal bins to obtain a stratification of the climate space into smaller homogeneous units (Batllori et al., 2014; Hamann et al., 2015). This approach corresponds to a relatively conservative stratification of the climate gradient and therefore of associated velocity and analog estimates (Dobrowski & Parks, 2016; Hamann et al., 2015). We used a 120-bins stratification to perform the climate exposure assessment presented here (see below), but as the precision of the climate space stratification can largely influence climate analog and velocity computations (Carroll et al., 2015; Hamann et al., 2015), we also used climate stratifications of 40 and 200 bins to evaluate the sensitivity of the results to bin size.

2.3 | Forward and reverse climate analogs

We applied the algorithms detailed in Hamann et al. (2015) to identify climate analogs and the associated forward and reverse climate velocities for each 1-km pixel in the protected area network. We used a fast k-nearest neighbor search algorithm (Crookston & Finley, 2007) to identify forward and reverse climatic analogs between baseline and end-of-century periods. That is, for each pixel in the protected area network, we found the nearest location across all NAM with *future* climate conditions that correspond to the climate conditions *currently* found in that pixel; this represents forward or outgoing climate analogs. To compute reverse or incoming climate analogs, we found the nearest location over NAM with *current* climate conditions that correspond to the *future* climate conditions projected for each pixel in the protected area network. We used the distance and location of both forward and reverse climate analogs to compute climate velocity (in km/year).

2.4 | Climate exposure assessment

We performed a vulnerability assessment based on climate velocity to examine exposure to climate change within the protected area network. This was achieved by averaging the pixel-based velocities within each protected area. We then partitioned the range of forward and backward velocity values into low, moderate, and high using three equal-area quantiles on the log-transformed velocity estimates (Carroll et al., 2015). In this and subsequent approaches (see below), most of our results are aggregated to individual protected areas to capture general trends within the network, but we also present some of the pixel-level results to illustrate the finer-scale variability within protected areas.

Next, we examined the potential climatic relocation across NAM protected areas by determining protection status of the locations of their outgoing and incoming climate analogs (Figure 1). We used forward climate analog computations to identify whether outgoing climates were relocated: (i) within the source protected area, (ii) in other protected areas, or (iii) outside the protected area network (Figure 1a). Likewise, reverse climate analogs were used to quantify whether incoming climates were currently located: (i) within the same protected area, (ii) in other protected areas, or (iii) outside the protected area network (Figure 1b). Alternatively, some areas may not have climate analogs within the future climatic space of the study region (disappearing climates) or may show future conditions that do not exist within the current climate space (novel climates). Additionally, for both outgoing and incoming climates, we set an arbitrary threshold of 1,000 km (>10 km/year) to acknowledge those areas that may be exposed to climatic changes that exceed the migrating capacities of most species (e.g., Santini et al., 2016).

Finally, we evaluated land-cover characteristics associated with the location of outgoing and incoming climates and compared them to current, or baseline, characteristics. We aimed to determine: (i) whether climates are predicted to relocate to different cover types (e.g., relocation between forested and nonforested habitats), and (ii) whether current climates that are in biologically relevant land-cover types (i.e., protected areas) may relocate to unsuitable land-cover types (e.g., urban, croplands) or whether future protected climates may come from degraded lands. Our intention was thus to assess additional constraints, imposed by land-cover and human-induced land-use modifications, that migrating biota may experience in response to climate change. We used the 2005 Land Cover of North America (2013) version 2.0 (CEC, www.cec.org/naatlas/) to extract the land-cover characteristics of all pixels in protected areas and compare it with land cover of the locations representing their forward and reverse climate analogs. For this analysis, we used eight major land-cover types computed on the basis of the original land-cover data set: forests, shrublands, grasslands, lichen/moss communities, wetlands, barren/water/snow, croplands, and urban.

3 | RESULTS

The velocity-based vulnerability assessment shows that the majority (78.8%) of protected area units over NAM, covering 1.95 million km^2, may be exposed to moderate-to-high combined forward and reverse climatic velocities (Figure 2a and Fig. S3). About one-third of protected area units are predicted to face either high forward (37.0%) or high reverse (31.6%) velocities, and 17.2% of them will face both high forward and high reverse velocities of change. A much smaller percentage (6.7%) will face low combined velocities. Important geographic differences in projected climatic alteration over the NAM protected area network are apparent at both coarse- and fine-spatial scales and within a given protected area (Figures 2c and

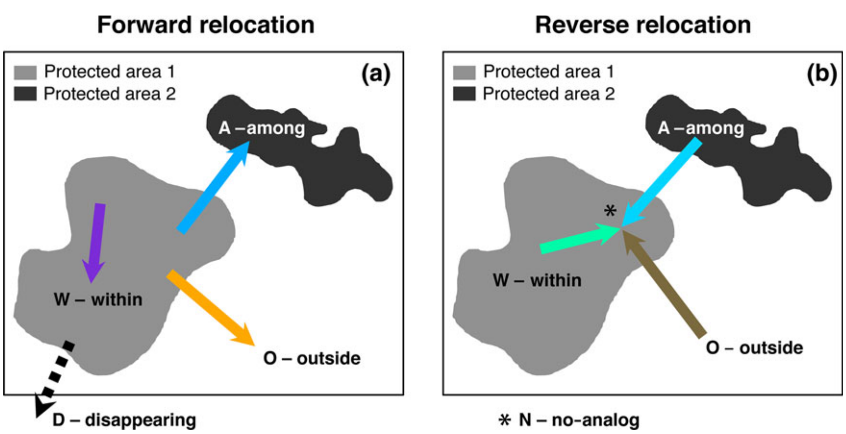

FIGURE 1 Conceptual framework to assess the potential relocation of climates within the network of protected areas of North America; baseline climate conditions correspond to 1981–2010 and future to 2071–2100. Arrows join climatic analogs of hypothetical pixels within and outside protected areas, and the framed, white background represents the climatic space as defined by future conditions. In (a), the future location (arrowhead) of the nearest climatic analogs of conditions currently found within a given protected area (protected area 1) is depicted (forward relocation or outgoing climates), whereas in (b) the arrows show where future conditions of that protected area are currently found (reverse relocation or incoming climates)

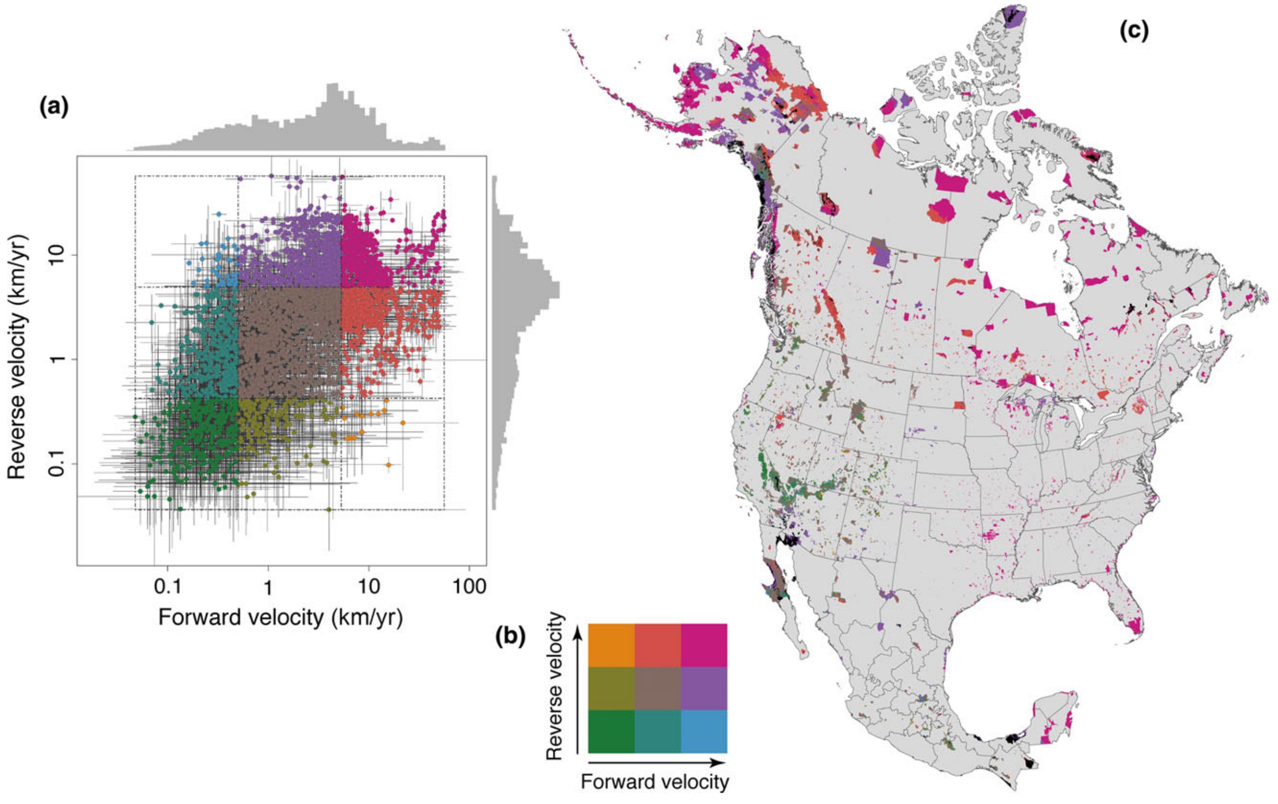

FIGURE 2 Velocity-based vulnerability assessment of each protected area within North America (a) based on nine categories (depicted in b) derived from grouping the range of values of forward and reverse velocities of climate change into three equal-area quantiles along each axis. Geographic patterns of the categories depicted in (a) are shown at the pixel level in (c). Note that in (c) disappearing and novel climates (see text for details) are depicted in black; these categories are not included in panel (a). Assessment based on baseline (1981–2010) and future (2071–2100) climate data from the MPI-ESM-LR model

S3). Protected areas in the western United States may be subject to lower velocities of climatic change, whereas the highest velocities would affect northernmost latitudes, eastern Canada, and southeastern United States. Protected areas with disappearing climates are located at northern latitudes and in southeast México, whereas novel climates appear concentrated along the NAM northern coast, in southern México, and in southern California and the Gulf of California.

Climatic relocation patterns by the end of the century at the level of protected area units (i.e., majority trends among pixels within a given protected area) reveal that the majority of protected areas have outgoing and incoming climates that may terminate or originate outside of the current protected area network (68.7% and 76.6%, respectively; Figure 3, Table 1). Additionally, for ~11% and ~12% of the protected areas, outgoing or incoming climate analogs may be located in locations >1,000 km away, respectively. Climatic relocation that mostly occurs within the protection limits of individual units (i.e., units may retain their current climates) applies to only a small percentage of protected areas (1.6%), whereas for 18.5% of protected areas outgoing climates may be found in other protected area units. The fraction of protected areas comprising the location of incoming climates from other protected areas (reverse estimates) is, however, much lower (8.6%). Only a very small fraction of protected areas (0.2%) are characterized by climates that will disappear from NAM by the end of the century, and 2.5% of them may have novel climates into the future (i.e., climate conditions that are not represented under baseline conditions; Figure 3a, Table 1). At the continental NAM scale, such protected area relocation estimates are relatively stable across climate stratifications of varying precision (Table 1, Fig. S4). Yet the proportion of climate relocation within protected areas and analogs found >1,000 km away from the current location are the ones most influenced by how climate units are defined (e.g., climate stratification on the basis of 40, 120, or 200 bins).

Climatic relocation patterns at the pixel level, however, highlight that substantial fine-spatial scale variability exists within protected areas (Table 1, Figs S5 and S6). The fraction of climatic relocation within and among protected areas, when considering all protected pixels individually, increases relative to the assessment at the level of protected units (i.e., pixels grouped by protected area), whereas relocation among protected and unprotected locations decreases. Fine-scale relocation patterns also highlight that high velocity of change (climate analogs located >1,000 km away) and disappearing or novel climates are more likely to occur locally (e.g., within a given protected area), affecting 16.3%, 2.3%, and 4.7% of all protected pixels, respectively.

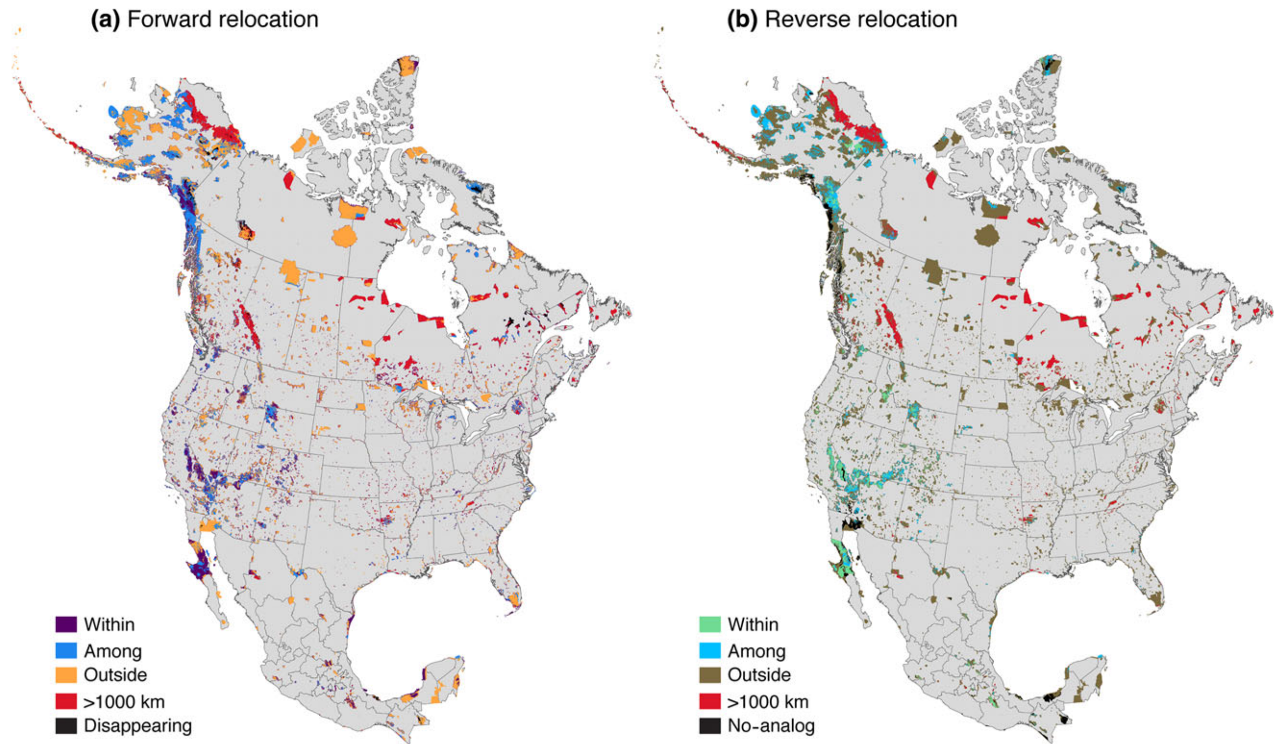

FIGURE 3 Geographic patterns of the potential relocation of climates within the network of protected areas of North America. Following the framework in Figure 1, (a) depicts the future location of the nearest climatic analogs of conditions currently found within protected areas (forward relocation or outgoing climates), whereas (b) depicts from where future conditions within protected areas may come from (reverse relocation or incoming climates). Those pixels with future climate analogs further than 1,000 km away are depicted in red, whereas disappearing climate conditions in (a) and no-analog climates in (b) are depicted in black. Baseline (1981–2010) and future (2071–2100) climate data come from the MPI-ESM-LR model

TABLE 1 Potential relocation (in percentage) of future climate analogs among protected areas or into unprotected destinations

Outgoing climate relocation					
	Within	Among	Outside	>1,000 km	Disappearing
Area-wise	1.6 [5.5–0.8]	18.5 [16.9–17.2]	68.7 [68.0–65.9]	11.0 [9.4–15.9]	0.2 [0.06–0.3]
Pixel level	8.2 [13.8–6.7]	21.5 [19.6–21.6]	51.7 [54.6–50.7]	16.3 [11.2–17.4]	2.3 [0.7–3.5]
Incoming climate relocation					
	Within	Among	Outside	>1,000 km	Novel
Area-wise	0.8 [3.2–0.5]	8.6 [7.3–8.1]	76.6 [82.3–76.4]	11.5 [6.3–12.4]	2.5 [1.0–2.6]
Pixel level	6.5 [10.8–5.5]	13.3 [16.2–13.2]	58.1 [60.5–56.8]	17.5 [10.3–19.2]	4.7 [2.2–5.3]

Area-wise proportions are based on a majority approach including the potential relocation of all pixels within a given protected area. Climatic relocation is based on estimates of both forward and reverse velocities of climate change to identify the geographic destinations and sources of outgoing and incoming climates from and to protected areas into the future (see main text for *further methodological details*). Note that for each relocation class the value corresponding to a conservative 120-bins stratification of the climatic space over North America is presented, whereas "bounded variability" values from 40- and 200-bins stratifications are presented in brackets ([left–right], respectively).

The analysis of the major land-cover types associated with the location of outgoing and incoming climatic analogs (Figure 4) reveals that substantial differences exist between the land cover within the current protected areas and the land cover in locations representing forward and reverse climatic analogs. Forward relocation patterns show that, overall, locations representing analogs of outgoing climates from protected areas comprise less forest, shrubland, grassland, lichen/moss, and wetlands, and substantially more barren/water/snow cover types. Species currently inhabiting grasslands, lichen/moss, and wetlands may the ones subject to stronger constraints imposed by changes in land-cover characteristics (Figure 4). On the other hand, reverse relocation patterns reveal that some of the areas representing incoming climates to the protection network correspond to croplands and urban areas. Although our assessment suggests this pattern may not prevail across the entire protected area network, it is relevant for some forested regions of the network (Figure 4). Reverse relocation patterns also indicate that grasslands, lichen/moss, and barren/water/snow will likely be the protected

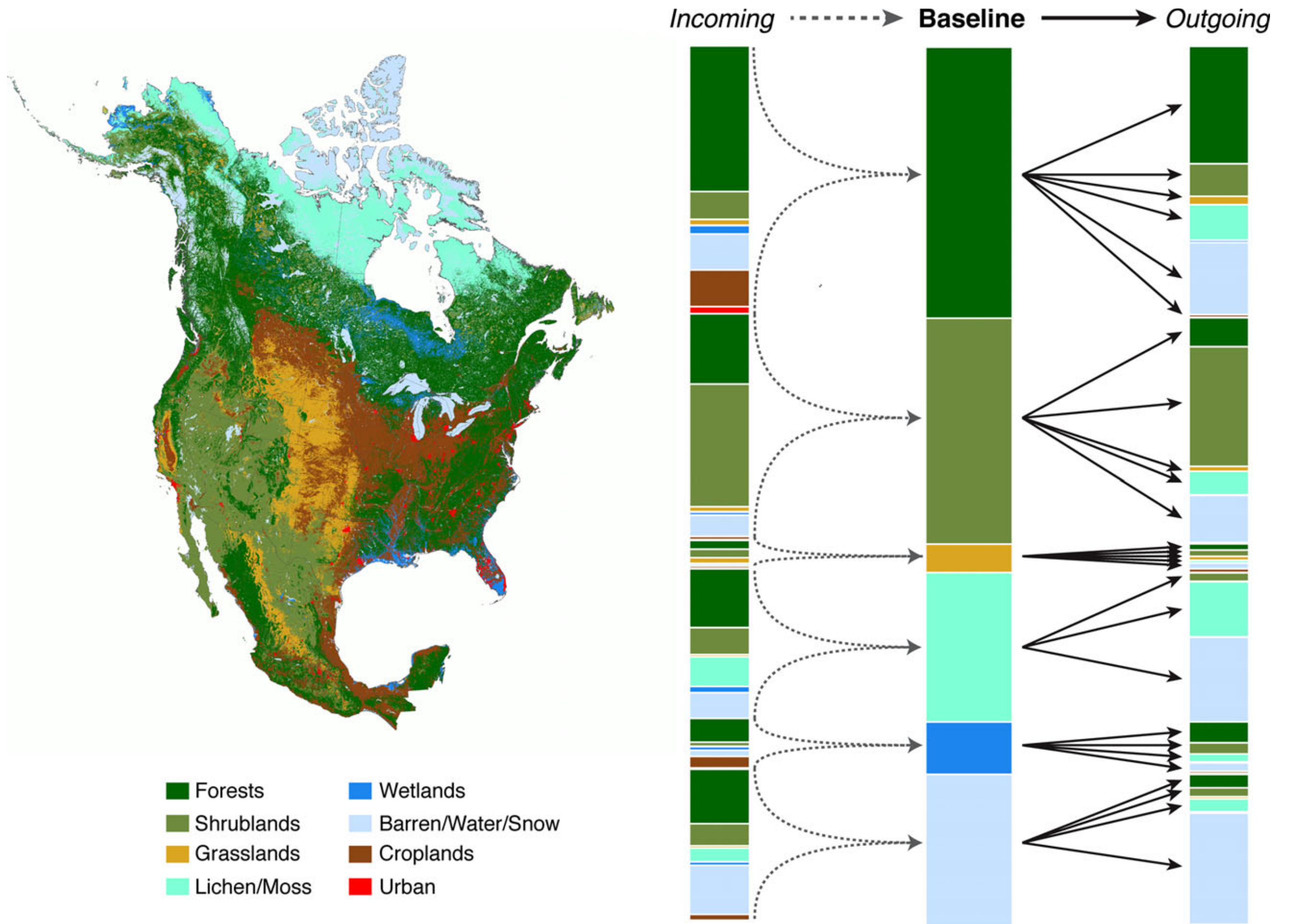

FIGURE 4 Assessment of the land-cover characteristics in relation to the climate relocation analysis. The map shows the current land-cover coverage across North America (modified from the Land Cover of North America version 2.0; www.cec.org/naatlas/) and the middle barplot ("baseline") depicts the fraction of the different land-cover types within the existing protection network. Contingent on each cover type in "baseline", the barplot in the left ("incoming") shows the fraction of land-cover types in locations representing the source of incoming climates to the protection network, and the barplot to the right ("outgoing") shows the fraction of land-cover types associated with locations where outgoing climates from protected areas may be found into the future. Baseline (1981–2010) and future (2071–2100) climate data come from the MPI-ESM-LR model

land-cover types mostly receiving a pool of species from different cover types than the ones they currently have, especially from forests and shrublands.

4 | DISCUSSION

Political and economic realities have resulted in an ad hoc design of the network of protected areas over North America that does not fully capture its ecological range of climates, cover types, and species (e.g., Batllori et al., 2014; Scott et al., 2001, 2002). Our analysis suggests that climate change will further compromise the ability of the NAM protection network to effectively preserve currently protected species and ecosystems. The estimates of the velocity of climate change presented here highlight that the majority of protected areas may be exposed to high rates of climate displacement. Such forcing may promote important shifts in species distribution (e.g., Burrows et al., 2014; McGill, 2010), with potentially dramatic alterations to ecological communities, biodiversity, and ecological processes within the network. Additionally, only a relatively small portion of protected areas may have future climates that represent analogs of conditions currently characterizing other protected areas. Overall, the potential for climatic relocation of outgoing climates from protected to non-protected areas is high, as is the proportion of incoming climates from unprotected areas into the network. Encouragingly, our examination highlights opportunities to complement or redefine the current protected area network and promote its connectivity given the prevalence of natural land-cover types in locations representing outgoing and incoming climate analogs of currently protected areas.

4.1 | Protection network exposure to climate change

Our quantitative, systematic assessment of climate velocities reveals spatially varying exposure and sensitivities of the network of protected areas to climate change. Moderate-to-high velocities of climate change within the NAM protected areas (Figure 2) could have a profound impact on the distribution and abundance of a large number of species (e.g., Burrows et al., 2014; Thuiller et al., 2011). Such forecasted effects may depend upon assumptions about the width of climatic niches (e.g., narrow or truncated niches) and the adaptive capacity (e.g., niche evolution) of species. This is supported by the observed, recent climate-driven changes in species distribution (e.g., Chen et al., 2011; Ordonez & Williams, 2013; Pinsky et al., 2013; but see Currie & Venne, 2017) and by the fact that rates of species' niche change or genetic shifts are generally slower than changes in climate (e.g., Jezkova & Wiens, 2016; Parmesan, 2006), thereby limiting the capacity of species to persist. In such cases, protected species with poor dispersal capacity (e.g., Santini et al., 2016; Schloss, Nuñez, & Lawler, 2012) or those depending on late-successional habitats (e.g., Stralberg et al., 2015) may be most affected by high velocities of climate change, especially at the leading or trailing edge of species distribution. Additionally, even low velocities of climate change combined with topographical impediments may inhibit species migration (Dobrowski & Parks, 2016).

Patterns of exposure to changing climates given by coarse filter approaches such as velocity of climate change can be qualitatively similar to finer-scale species bioclimatic model projections (e.g., Garcia, Cabeza, Altwegg, & Araújo, 2016). However, in many cases climate velocities are likely to represent an upper bound of migration requirements (Carroll et al., 2015) as a species' fundamental niche may be broader than its observed realized niche. Ecosystem or vegetation inertia contingent on long-lived species may also promote lags in response to changing climates without immediate effects on populations (e.g., Ash, Givnish, & Waller, 2017; Corlett & Westcott, 2013). Furthermore, in spite of overall moderate-to-high velocities of climate change, species may not shift into new areas under changing climates but may just contract into patches of suitable habitat within their current range (suitable microrefugia; Ashcroft, Gollan, Warton, & Ramp, 2012; Tingley, Darling, & Wilcove, 2014). Our approach points to substantial spatial variability in velocity estimates within the NAM protection network (Figs S3 and S5). Finer resolutions would be required, though, to detect relevant microrefugia for many species, as the 1-km grid resolution used here is likely to average out much of the existing microclimatic climate variation (e.g., Lenoir et al., 2013; Randin et al., 2009). Local model calibration would be required to assess microclimatic diversity (e.g., 25- to 30-m resolution) for conservation and climate change planning at the level of protected area units.

From a conservation perspective, identifying and protecting climate refugia is emerging as a critical proactive conservation strategy (e.g., Keppel et al., 2012) to allow the persistence of some populations in spite of the changing climate. Also, the protection of a diverse array of abiotic conditions where connectivity allows for species movement among areas has been advocated to preserve biodiversity into the future (Lawler et al., 2015). However, the response of keystone species or the progressive decoupling of species interactions (e.g., plants and pollinators) owing to climate-driven mismatches in phenology may exacerbate the effects of climate change on ecosystems at local scales, irrespective of the abiotic setting or species' niche width and traits (e.g., Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013; Hughes, 2000). Furthermore, fast changes in some key climatic components may promote substantial alterations in paramount ecosystem processes such as disturbances (e.g., fire—Moritz et al., 2012; drought—Allen, Breshears, & McDowell, 2015). Changes in the frequency, magnitude, or intensity of disturbances could also act as a catalyst of ecosystem change in cases where ecosystem inertia or persistence is expected (e.g., Millar & Stephenson, 2015).

Although our findings suggest that disappearing climates within the NAM protection network will not be widespread over the upcoming century, biodiversity could be threatened if these climates correspond to unique conditions associated with centers of distribution of rare species (Ohlemüller et al., 2008). Conversely, our results suggest that novel climate conditions may be more prevalent, appearing in ~5% of the NAM protected pixels. Novel climatic conditions have appeared repeatedly over millennia, and changes in species distribution and abundance, together with extinction and speciation processes, resulted in the formation of new assemblages or communities (Blois et al., 2013; Stralberg et al., 2009; Williams & Jackson, 2007). Because both disappearing and novel climates could constitute "dead ends" for the conservation of specific organisms or ecological processes, they represent an important focus and challenge for conservation and management strategies, given our incomplete understanding of diversity and ecological patterns and processes (Hobbs et al., 2006).

4.2 | Potential climatic relocation across the protection network

Our examination suggests that a relatively small fraction of protected areas (8.6%; but see Table 1, Fig. S4) may be critical for future NAM conservation efforts. These represent protected areas with future climates that correspond to the closest analogs of current (but outgoing) climates of almost a fifth (17.3%) of the protected area units within the network. Nevertheless, our findings highlight that the relocation of outgoing climates from protected areas into unprotected areas may affect the majority of protected climates over NAM (Figure 3, Table 1). These calculations are intentionally based on the "lowest velocity" (i.e., the closest climate analog) on the assumption that closer is better for potential migration of species, especially for species with limited migration capabilities. Such an approach may thus underestimate the proportion of protected climates that could relocate to protected areas, as more distant protected climatic analogs (than the nearest) could exist.

To provide a wider perspective on potential climatic relocation patterns, we assessed whether protected pixels having the closest analog outside of the network of protected areas may alternatively have climatic analogs within the protection network, either: (i) among the 10 closest climate analogs for each pixel or (ii) anywhere in the current protected area network (excluding protected areas >1,000 km away). These computations indicate that the nearest analogs for 51.7% of the protected pixels are outside of the protection network (Table 1), but for a substantial proportion of them (17.4%, i.e., 9% of the total protected pixels) a protected status can be found among its 10 closest climatic analogs (Fig. S7, Table S1). Additionally, for the 16.3% of the total protected pixels whose 10 closest climate analogs are not in a protected area, at least one climate analog exists in a protected area less than 100 km away, and the remaining 14.9% of the protected pixels have a protected climate within a distance of 1,000 km (Fig. S8, Table S2). Even under this wider perspective on climate analogs, the implication remains that biota in 11.5% of the protected pixels over NAM may depend upon nonprotected areas for analog climatic conditions in the future. Additionally, although analogs may exist in protected locations, the distance at which they are found can increase dramatically relative to the closest climatic analog of each pixel (Fig. S9). This may exert additional threats other than the climate forcing itself (e.g., velocity of change) to protected species' relocation within the protection network.

Despite our assessment's suggestion that outgoing climatic relocation into highly altered or otherwise degraded land-cover types (croplands, urban; Figure 4) may not be extensive, unprotected landscapes could still represent migratory "dead ends" for sensitive biota. Conversely, climates that relocate from unprotected and potentially degraded lands into the protection network could adversely influence the pool of colonizing species and the suite of species that can occupy protected areas into the future. However, we only accounted for the location of the closest climatic analogs into the future (but see Fig. S10 for land-cover types associated with the 10 closest analogs), and analogs may exist in natural land-cover types that are more distant (McGuire, Lawler, McRae, Nuñez, & Theobald, 2016). Regardless, our assessment highlights that unsuitable land-cover types in the closest climatic analogs for protected areas could pose additional threats and constraints to species within protected areas in human-modified parts of the continent.

Our results show that many of the climatic environments of North American protected areas may terminate or originate in areas that have a natural land cover (Figure 4), irrespective of protection status. This may provide opportunities for reorganization of currently protected species and ecosystems under changing climates. Although vegetation lags could exert additional constraints for climate-driven species migration to and from places characterized by habitats different from the ones they currently inhabit, in the mid- to long term, these natural landscapes represent important opportunities to adjust strategies and ensure the continued relevance of conservation efforts into the future. For instance, even if, as our assessment suggests, relocation into currently nonvegetated cover types (barren, water, or snow) is likely to occur in a substantial portion of the protected areas across NAM, these areas may still represent conservation opportunities with the potential to revegetate under new climatic conditions (Roland, Stehn, Schmidt, & Houseman, 2016). However, broad-scale effective conservation across North America and elsewhere will likely require joint public- and private-land collaboration across administrative and political boundaries (Fig. S11; Batllori et al., 2014; Hannah, 2010). These challenging aspects are being tackled in ongoing initiatives and partnerships worldwide (e.g., Beever et al., 2014; https://y2y.net/).

4.3 | Framework considerations and limitations

The results of this study are contingent on data quality and decisions regarding the methodological approach. For instance, we analyzed a median scenario of climate change (the MPI-ESM-LR climate model; Wang et al., 2016), but what constitutes a worst- or best-case climatic scenario differs by climate model, region, and the climate variable of interest (Fig. S12; Maloney et al., 2014). Also, for a given partitioning precision of the climate space (e.g., 120 bins), the integration of slightly offset climate space stratifications (i.e., slightly different definitions of unique, homogeneous climatic combinations) has been proposed to reduce the effects of arbitrary boundaries between climate bins in multivariate analog-based velocity computations (Carroll et al., 2015). However, offset stratifications yielded very similar results in overall relocation patterns of climate among protected and unprotected areas at the continental scale of this study (Fig. S13). Climate stratification approaches are also sensitive to the resolution of the partitioning of the climate space (Batllori et al., 2014; Hamann et al., 2015). Here, we accounted for the variability on the potential relocation of climates contingent on different partitioning resolutions (Table 1, Figs S4 and S6), but we opted to focus on a single offset realization based on a conservative partitioning (i.e., limited number of climate combinations defined within the climate space). This approach balances the precision of climate matches to effectively capture spatial variability but avoids the prevalence of no-analog climates that can appear under more fine-grain partitioning (Dobrowski & Parks, 2016; Hamann et al., 2015). Overall, the analysis presented here must be taken as illustrative of potential implications of climate change exposure and associated relocation patterns within, among, and outside protected areas at the regional scale of North America.

The approach we used reveals important conservation challenges but is best suited for continental to regional extents, as climate is the primary factor influencing the distribution of species at broad spatial scales (McGill, 2010). At landscape to local extents, however, patterns of biodiversity and associated ecological processes are not solely a function of abiotic conditions, but they are also the result of biotic interactions that may buffer or exacerbate the climate-driven changes (Blois et al., 2013). Additionally, the extent of the climate units in analog-based approaches may be in some cases narrower than the width of climate niches of some species (Carroll et al., 2015), in which case relocation forecasts could be less relevant. Finally, the use of regional-scale multivariate metrics of climate smooths out the variability of individual variables (Ordonez & Williams, 2013), limiting our ability to characterize potential implications of changing climates at a fine-spatial scale.

4.4 | Applicability and future directions

The climate exposure assessment presented here evaluates how the ability of the North American protection network to preserve natural climatic environments may change over the century. The potential for climatic relocation illustrated here emphasizes the need to view protection networks as dynamic systems in which the distribution and abundance of species (currently protected and nonprotected) can change over time as climate conditions shift. As such, efforts to preserve biodiversity that aim for a static version of the protected biota will fail, as will efforts that ignore the spatial matrix surrounding the protection network. Both current and future biota within the network will continue to benefit from large and diverse protected areas with minimal fragmentation and sufficient connectivity to allow for species movement among them (Lawler et al., 2015). We believe that the computational efficiency, flexibility, and transparency, and the multi-scale character of our framework make it an effective conservation tool (Sarkar et al., 2006) that may aid in reserve design and large-scale conservation efforts under changing climates. Using ensemble GCM and climate scenarios to bracket the range of uncertainty (Littell, McKenzie, Kerns, Cushman, & Shaw, 2011), systematic evaluation of potential climatic relocation at regional and local scales can be imminently useful to inform current conservation initiatives and climate change vulnerability and adaptation analyses. For instance, this method could serve to (a) define nuclei of protected areas that represent potential key climatic locations for the migrating biota (outgoing–incoming species), (b) redesign conservation goals in areas that are projected to experience substantial climatic changes, (c) identify unprotected areas that may have a paramount role for the long-term persistence of biodiversity, or (d) design habitat corridors to facilitate the movement of species between conservation areas that take into account future climatic conditions. Our assessment highlights that effective integration of climate projections and robust metrics of temporal and geographic patterns of change can make a strong contribution toward ensuring the effectiveness of conservation plans as climate changes.

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SUPPORTING INFORMATION

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