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Protected areas as potential refugia for biodiversity under climatic change

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ABSTRACT

Climate change is among the greatest challenges to biodiversity conservation globally. In response to climatic changes, species around the world have already started to shift their ranges along altitudinal and latitudinal gradients. However, it remains unclear whether the areas currently managed for biodiversity protection are optimized for these shifting ranges. Climate velocities represent a method to quantify the rate at which organisms must alter their range to maintain their current climate envelope. Here we use a case study of the Southern Rockies region in the western United States to show how forward and backward climate velocities can be used to quantify potential impacts of climatic changes and delineate abiotic climate refugia. We further illustrate how climate velocities can integrate into a process that simultaneously identifies climate refugia for suites of species while accounting for additional landscape factors contributing to protected area success. These results demonstrate how potential climatic changes may be used to prioritize the efficient selection of climate refugia, potentially aiding multi-target climate adaptation decision-making across broad regions.

1. Introduction

Maintaining resilient communities of diverse species and ecosystems across broad landscapes will require conservation efforts that explicitly account for the processes of climate change (Convention on Biological Diversity, 2016a; Hannah et al., 2002; Heller and Zavaleta, 2009; Settele et al., 2014). Among those conservation efforts, one key strategy for minimizing the impacts of climate change has been to broadly identify and conserve areas that potentially serve as climate change refugia, here defined as areas that buffer species and other conserved resources against long-term exposure to contemporary climate shifts (Ashcroft, 2010; Morelli et al., 2016; Pacifici et al., 2015). Though current limitations in the availability of fine-resolution climate data often restrict many efforts to those identifying macro-scale refugia, effective refugia conservation requires efforts at both broad and fine spatial scales (Ashcroft et al., 2009; Morelli et al., 2016).

Climate velocities – the rates at which organisms would have to move in order to maintain consistent climate conditions, given some predicted climatic change (Loarie et al., 2009) – offer a coarse-filter metric for approximating potential exposure to climate shifts and quantifying contrasting patterns of climate refugia (Brito-Morales et al., 2018; Carroll et al., 2015; Theobald et al., 2016). In practice, velocities can be calculated as the rate at which organisms must travel in order to a reach a location with similar climate conditions in the future ("forward climate velocity"), with areas of low forward climate velocity serving as potential candidates for the conservation of *in situ* refugia for species limited in their ability to disperse (Ashcroft, 2010; Carroll et al., 2015). Velocities can also be derived as a measure of how quickly organisms would have to move in order to reach a particular location from surrounding areas ("backward climate velocity"; Carroll et al., 2015). Areas with low backward climate velocity thus represent new areas that organisms could more easily colonize under novel climate conditions, potentially acting as *ex situ* refugia for species unable to continually occupy their current ranges (Ashcroft, 2010; Stralberg et al., 2018). Though climate velocities on their own can prove useful for quantifying exposure to climate-induced range shifts, their direct applicability to biological conservation could be further enhanced through consideration of the biotic elements of the landscape (Carroll et al., 2015).

Conservation efforts aimed at enhancing the resilience of biodiversity to climate change are inextricably embedded within a world of broader conservation practices (Game et al., 2011). To promote biologically meaningful climate change conservation, efforts must be made to integrate the use of climate velocities and other abiotic metrics of climate refugia to ongoing biological conservation practices (Brito-Morales et al., 2018). Perhaps foremost among those practices is the creation of protected areas (parks, reserves, wilderness areas, etc.) based on the representation of static biological, geophysical, and

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cultural resources (Convention on Biological Diversity, 2016b; Jones et al., 2016; Pressey et al., 2007). Primarily due to their largely static nature, traditional protected areas may be limited in their ability to adapt to dynamic climatic shifts, leaving the long-term persistence of their protected resources in question and necessitating innovative conservation solutions (Ban et al., 2012; Game et al., 2011; Marris, 2011; Virkkala et al., 2019).

Landscape conservation strategies for assessing the ability of protected areas to withstand future climate changes must make efficient use of limited resources (Hobbs et al., 2014), while also addressing the broader suite of factors that drive conservation decision-making and success (Game et al., 2013; Jones et al., 2016; Maxwell et al., 2016). Real-world conservation decision-making requires that abiotic metrics such as climate velocity be combined with other relevant biophysical and sociopolitical factors (Game et al., 2013), such as traditional protection targets for sensitive species or habitats. While a substantial body of research on prioritizing conservation based on climate change and its impacts exists, a relatively small proportion of these efforts have attempted to systematically account for a multitude of environmental factors, such as land use and human responses to climate change (Faleiro et al., 2013; Jones et al., 2016; Maxwell et al., 2016; Theobald et al., 2016). Acknowledging these additional factors and their potential contributions in conservation success is an important step toward an effective framework for adaptive conservation (Game et al., 2013), and can substantially improve the predicted performance of conservation actions (Hammill et al., 2016).

Here we present an approach that systematically integrates existing climate-adaptive management frameworks that aid in ongoing landscape protection and conservation efforts (Ball et al., 2009; Hamann et al., 2015; Schwartz et al., 2018). To demonstrate its utility, we apply this approach to the conservation of threatened terrestrial wildlife species in the Southern Rockies region, a vast, topographically diverse ecoregion spanning the western US states of Arizona, Colorado, Idaho, Nevada, New Mexico, Utah, and Wyoming (Southern Rockies Landscape Conservation Cooperative, 2018). We show how our process identifies the climate refugia that best conserve species ranges and further investigate the potential roles that current protected areas can play in maintaining biodiversity in the face of climatic shifts. Our results suggest that some currently protected areas may already include refugia against future temperature changes, particularly those areas that have high topographic diversity. We further show how climate refugia based on climate velocity can be subsequently integrated with patterns of biodiversity and environmental factors contributing to protected area success. The inclusion of biodiversity and environmental factors provides a more holistic, synergistic view of climate change conservation planning, highlighting the potential variability in conservation priority within protected areas when both processes and patterns are considered.

2. Materials & methods

2.1. Study region

We evaluated existing protected areas within the Southern Rockies region of the western United States (Fig. 1) on the basis of climate velocity and values of conservation priority derived from a combination of climate velocity, biodiversity distributions, and land modification. We defined the Southern Rockies study region using the boundary delineated by the Southern Rockies Landscape Conservation Cooperative (Southern Rockies Landscape Conservation Cooperative, 2018). The Landscape Conservation Cooperatives (LCC) Network were an association of 22 landscape-scale collaborative partnerships between governmental and non-governmental agencies and stakeholders that aimed to address conservation issues crossing jurisdictional boundaries within regions of broad ecological similarity (Landscape Conservation Cooperatives, 2014). Furthermore, LCCs were explicitly directed to facilitate transboundary adaptation to climate change at the landscape scale (US Department of the Interior, 2009), a process that may increase chances of success in shared landscape management (Epperly et al., 2018).

The Southern Rockies study region is characterized by high topographic and ecoregional diversity and varying levels of landscape management across 582,339 square kilometers, seven US states (Arizona, Colorado, Idaho, Nevada, New Mexico, Utah, and Wyoming) and more than a dozen distinct ecoregions. Ecoregions range between the hot, lowland Sonoran and Mojave deserts ($\sim 500-1200$ m elevation) and the sub-alpine and alpine highlands of the Southern Rocky Mountains ($\sim 1500-4400$ m elevation), though the semi-arid plateaus of Arizona, Colorado, New Mexico, and Utah are most widely represented ($\sim 1000-3200$ m elevation; Omernik and Griffith, 2014; Wang et al., 2016). Mean annual temperatures range between -4.5 °C and 20.6 °C and mean annual precipitation between 135 and 1764 mm (Wang et al., 2016). Overall, the region remains minimally developed, with only 1.02 % of the region consisting of urban land cover types and 1.48 % made up of agricultural land cover (Homer et al., 2015). While most of the region consists of lands under public management, these areas receive different levels of protection, allowing for varying degrees of management intensity, changes to ecological disturbance regimes, and extractive uses. Roughly 11.5 % of the region is listed under the USGS Protected Areas Database of the United States as being managed primarily for the protection of their biological resources (GAP Protection Status 1 and 2). This designation corresponds to the global definition of a “protected area” set by the International Union for Conservation of Nature (IUCN; USGS Gap Analysis Program, 2016). Management of these designated protected areas varies in whether natural disturbance regimes are largely maintained (GAP Protection Status 1) or altered through management interventions (GAP Protection Status 2), though extractive uses (timber harvest, mining) are not permitted in either type of protected area (USGS Gap Analysis Program, 2016).

For summarizing landscape characteristics within the study region, a 3km*3km planning unit grid was overlaid across the landscape (N = 66,135). Each of these planning units was then parameterized with its climate velocity values, the species distributions present, and the potential impact of human land development. Species of interest for prioritizing conservation consisted of all terrestrial vertebrate species within the study area that are listed under the Red List of the IUCN as either Near Threatened, Vulnerable, Endangered, or Critically Endangered (IUCN, 2016). Species distributions and seasonal ranges of all reptiles, amphibians, terrestrial mammals, and birds within the study region were obtained from the IUCN and BirdLife International (BirdLife International and Handbook of the Birds of the World, 2016; IUCN, 2016). The final distribution dataset consisted of the ranges of 31 terrestrial wildlife species (Table 1), with the greatest diversity of target species located in the southeastern corner of the study region (Fig. 2a). The amount of each species range represented within each planning unit was calculated and proportional conservation targets were then set as 20 % of each species range, providing a moderately strict set of conservation targets closely aligned with the 17 % terrestrial landscape conservation objective set through the Aichi Biodiversity Targets (Convention on Biological Diversity, 2016a). In order to represent the degree to which each species is endemic to the study region, we additionally calculated the percentage of each species range that is located within the Southern Rockies boundary (Table 1). While we recognize that different species will react differently to temperature shifts (Pacifici et al., 2015), species-specific assessments were not conducted due primarily to the lack of detailed information regarding the sensitivities of the target species. However, the exposure of each species to temperature shifts was considered.

To represent the potential impacts of human development, we assigned each planning unit a value of “risk” directly related to the current prevalence of anthropogenic landscape features (i.e. agriculture,

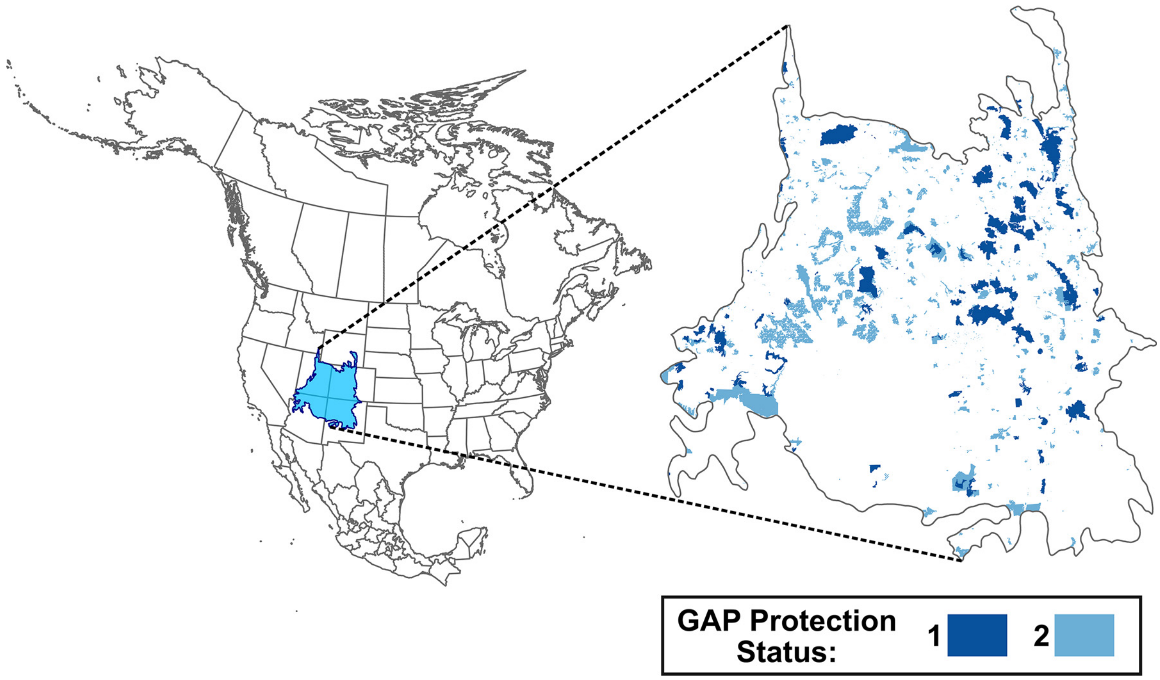

Fig. 1. The location of the Southern Rockies region and its protected areas. The protection statuses of individual land management units were assessed as part of the U.S. Geological Survey Gap Analysis Program (GAP) and data were obtained online from the Protected Area Database of the United States. Areas with GAP Protection Status 1 are managed for natural disturbance regimes, whereas GAP Protection Status 2 areas allow for management practices that alter disturbance. Neither grouping includes areas that permit resource extraction (e.g. timber harvest, mining).

urbanization, roads) within each individual planning unit (Fig. 2b). In the absence of predictive data about the spatial distribution of future land development, we found the extensive, formal assessment of risk due to future development to be outside the scope of this study. Instead, we estimated the distribution of current risk to each planning based from the relative presence of human-modified 2011 land cover types as designated by the National Land Cover Database for the United States (Homer et al., 2015). We quantified each planning unit's overall modification intensity by aggregating the percentages of all agricultural and developed lands, including pasture, hay, cultivated crops, and lands with variable intensities of development. These percentages of current land modification (hereafter referred to simply as *land modification*) were then treated as the probabilistic risk of planning unit failure - i.e. the likelihood that the planning unit will not be primarily used for conservation of biodiversity – within Marxan (Ball et al., 2009).

2.2. Climate velocity

We calculated forward and backward climate velocities based on analogs of current and projected mean annual temperature across all of North America (Carroll et al., 2015; Hamann et al., 2015). Spatial data depicting the current and projected climate conditions across North America at a ~1 km spatial resolution were obtained online from the climate database of the AdaptWest Project (AdaptWest Project, 2015). Current climate conditions represent average recorded values from a 1981–2010 reference climate period. Future climate data were depicted by a 15-model ensemble projection for the 2041–2070 time period under a "middle of the road" representative concentration pathway (RCP 4.5; Thomson et al., 2011; IPCC, 2014; AdaptWest Project, 2015). All calculations of climate velocities were conducted in R (R Core Team, 2018), using code adapted from open-source R script algorithms produced by Hamann and colleagues (2015; available online at https://adaptwest.databasin.org/pages/adaptwest-velocitywna).

We based our climate velocity analyses on projected changes in mean annual temperature, due its role as an indicator variable for a suite of other temperature-based metrics, and its ecological importance in the study region (Jones and Kelly, 1983; Mathys et al., 2016). In addition, climate model projections of temperature have relatively lower levels of uncertainty compared to precipitation (Flato et al., 2014). Analogs in mean annual temperature were set using a match threshold of ± 0.2 °C, though we additionally tested climate velocities within the study region across a range of threshold values. This sensitivity analysis revealed that smaller thresholds led to increased velocities, with more rapid increases below the 0.2 °C threshold, consistent with previous analyses of climate velocity for North America (Hamann et al., 2015) and is depicted in the Appendix (Fig. A1). Although changes in temperature thresholds resulted in different absolute magnitudes of climate velocity, the spatial patterns of relative velocities remained similar across thresholds. We produced average values of climate velocity within each 3 km planning unit using the Zonal Statistics tool from the Spatial Analyst extension for ArcMap 10.4 (Environmental Systems Research Institute, Redlands, California).

2.3. Spatial prioritization

We identified ecologically-relevant climate refugia by integrating climate velocities and the distributions of species of interest into an existing conservation prioritization framework. We quantified the priority of conserving each planning unit using Marxan, a systematic landscape planning software program that aims to meet a series of predetermined targets subject to the minimization of a continuous variable (Ball et al., 2009). We directed Marxan to construct potential reserve networks that achieved representation of all species conservation targets while additionally minimizing climate velocities and accounting for land modification. Marxan initiates each of its runs by selecting a group of planning units at random. Through a process of simulated annealing, planning units are iteratively added and subtracted from the network in an attempt to meet the predetermined targets. This selection process additionally seeks to minimize a specified value while considering the likelihood of a planning unit failing to help meet the targets (in the current analysis, this likelihood was defined using the current extent of modified land cover types). We used 100

Table 1
List of the 31 terrestrial wildlife species of interest found in the Southern Rockies region and used for setting conservation targets in our Marxan analyses. Endemism was calculated as the percent of each species full range that is located within the study region.

Binomial	Class	Order	Common Name	IUCN Status (as of 2016)	Endemism (%)
Lithobates onca	Amphibia	Anura	Relict Leopard Frog	Endangered	35.065122
Lithobates chiricahuensis	Amphibia	Anura	Chiricahua Leopard Frog	Vulnerable	7.776248
Plethodon neomexicanus	Amphibia	Caudata	Jemez Mountains Salamander	Near Threatened	100.00
Anthus spragueii	Aves	Passeriformes	Sprague's Pipit	Vulnerable	0.01939965
Calcarius ornatus	Aves	Passeriformes	Chestnut-collared Longspur	Near Threatened	9.40060424
Calidris pusilla	Aves	Charadriiformes	Semipalmated Sandpiper	Near Threatened	0.89764059
Centrocercus minimus	Aves	Galliformes	Gunnison Grouse	Endangered	99.9995699
Centrocercus urophasianus	Aves	Galliformes	Greater Sage Grouse	Near Threatened	12.73987157
Chaetura pelagica	Aves	Caprimulgiformes	Chimney Swift	Near Threatened	0.06936585
Charadrius montanus	Aves	Charadriiformes	Mountain Plover	Near Threatened	10.93786865
Charadrius nivosus	Aves	Charadriiformes	Snowy Plover	Near Threatened	0.43247531
Colinus virginianus	Aves	Galliformes	Northern Bobwhite	Near Threatened	0.24964717
Contopus cooperi	Aves	Passeriformes	Olive-sided Flycatcher	Near Threatened	1.51364257
Euphagus carolinus	Aves	Passeriformes	Rusty Blackbird	Vulnerable	0.05498096
Gymnogyps californianus	Aves	Cathartiformes	California Condor	Critically Endangered	7.65200292
Gymnorhinus cyanocephalus	Aves	Passeriformes	Pinyon Jay	Vulnerable	36.23618813
Haemorhous cassinii	Aves	Passeriformes	Cassin's Finch	Near Threatened	16.30715938
Melanerpes erythrocephalus	Aves	Piciformes	Red-headed Woodpecker	Near Threatened	2.04969312
Strix occidentalis	Aves	Strigiformes	Spotted Owl	Near Threatened	13.38566535
Toxostoma bendirei	Aves	Passeriformes	Bendire's Thrasher	Vulnerable	32.05058406
Vireo bellii	Aves	Passeriformes	Bell's Vireo	Near Threatened	0.55785258
Bison bison	Mammalia	Cetartiodactyla	American Bison	Near Threatened	6.8653476
Cynomys parvidens	Mammalia	Rodentia	Utah Prairie Dog	Endangered	70.6357094
Dipodomys spectabilis	Mammalia	Rodentia	Banner-tailed Kangaroo Rat	Near Threatened	17.3664698
Spilogale putorius	Mammalia	Carnivora	Eastern Spotted Skunk	Vulnerable	0.2056444
Sylvilagus cognatus	Mammalia	Lagomorpha	Manzano Mountain Cottontail	Endangered	99.9923680
Aspidoscelis neotesselata	Reptilia	Squamata	Colorado Checkered Whiptail	Near Threatened	12.94886692
Heloderma suspectum	Reptilia	Squamata	Gila Monster	Near Threatened	2.80652167
Kinosternon sonoriense	Reptilia	Testudines	Sonoyta Mud Turtle	Near Threatened	2.37586458
Pseudemys gorzugi	Reptilia	Testudines	Rio Grande Cooter	Near Threatened	0.03793824
Terrapene ornata	Reptilia	Testudines	Ornate Box Turtle	Near Threatened	32.40859605

Marxan runs of 1,000,000 iterations each. We defined values of conservation priority as the frequency with which an individual planning unit was selected for conservation across all 100 runs – the *selection frequency*, or irreplaceability. Separate Marxan analyses minimizing forward and backward climate velocities were conducted, corresponding to two alternative scenarios for prioritizing velocity-based climate refugia conservation efforts. To assess the possible influence of land modification on conservation priority, we used Spearman's rank-order correlations to evaluate associations between land modification, species richness, and forward and backward priority and examined differences in these metrics between high priority areas and the overall region.

2.4. Protected area evaluation

We classified each planning unit as currently protected if more than 50 % of its area lay in areas with a designated protected areas from the USGS Protected Areas Database of the United States (Fig. 1; USGS Gap Analysis Program, 2016), giving a total of 7,225 protected planning units. Individual protected areas were subsequently represented by contiguous groupings of protected planning units (N = 358) and account for roughly 10.98 % of the entire study region. We first evaluated the role of protected areas as climate refugia in the study region by comparing their values of both forward and backward temperature-based climate velocity. Mean climate velocities across all currently protected planning units (refugia or not) were then directly compared to mean velocities across all planning units. To assess individual protected areas, we calculated summary values of climate velocity among each protected area's planning units, which were subsequently compared with the regional mean. 'Abiotic climate refugia' were designated as the planning units with the lowest 5 % climate velocity values. Current protection of these refugia was measured as the percentage of aggregated refugia area located within the extent of protected areas.

'Priority refugia' were designated as the top 5 % highest priority planning units in our Marxan analyses for each of the two conservation scenarios – forward refugia priority and backward refugia priority. Following the same processes for analyzing climate velocities, values of conservation priority within protected areas were summarized across

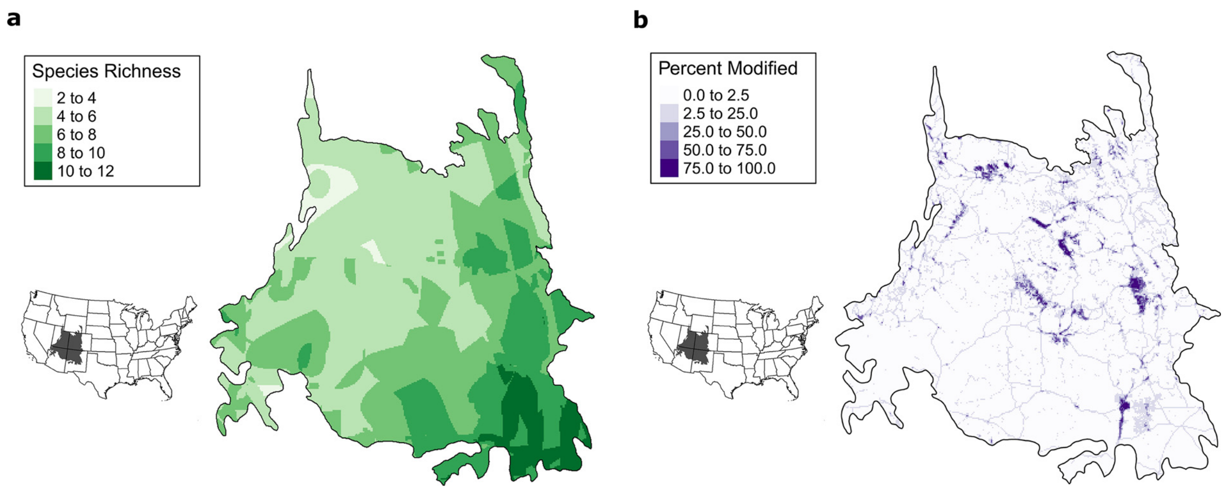

Fig. 2. Spatial distributions of species richness and land modification within the Southern Rockies region. (a) Richness of wildlife species of interest, derived from the number of overlapping species ranges from the IUCN Red List and BirdLife International; (b) prevalence of human-modified land cover types within planning units, derived from the National Land Cover Database for the United States (Homer et al., 2015).

the protected area network and within individual protected areas, with mean values being directly compared to those across the all of the region's planning units. As with abiotic climate refugia, the overall protection of priority climate refugia was evaluated as the percentage of refugia area located within currently protected areas. We additionally assessed the percentage overlap between priority refugia and abiotic climate refugia. Lastly, we averaged the priorities from the two conservation scenarios and separated the top 5 % of planning units, producing a map of 'aggregated priority refugia' depicted in the Appendix (Fig. A2).

3. Results

3.1. Climate velocity

Climate velocities based on mean annual temperature showed high heterogeneity across the Southern Rockies study region, with the highest forward velocity areas corresponding to locations of extreme high elevations (Fig. 3a). In contrast, backward climate velocities were found to be highest at low elevations (Fig. 3b). We found that the protected areas of the region have slightly lower climate velocities than the region as a whole (Fig. 3c and d) and encapsulate a disproportionately large amount of potential climate refugia. Mean forward climate velocities were 3.93 % lower and mean backward climate velocities 33.83 % lower in currently protected planning units than the means across the entire region (Table 2). However, this slightly lower velocity masks the variation present within the current protected area network. Climate velocities also varied considerably between protected areas, with 74 % of the individual protected areas having average forward climate velocities lower than the regional average and 70 % having lower backward climate velocities (Fig. 3e and f). We found that protected areas already include 26.95 % of the total abiotic climate refugia based on forward climate velocity and 39.19 % of abiotic climate refugia based on backward climate velocity, despite only covering 10.98 % of the area. These results demonstrate that existing, traditional protected areas may already contain a greater number of low climate velocity areas than expected by chance, potentially making their ecological features more resistant to climate shifts than unprotected resources.

3.2. Spatial prioritization

Areas identified as having high conservation priority through Marxan generally corresponded to areas with the lowest forward and backward climate velocities, though the simultaneous influence of species ranges and land modification were also apparent (Fig. 4a and b). Approximately 71.10 % of priority refugia for minimizing forward climate velocity were located within the areas with the lowest forward climate velocities, indicating widespread overlap between the two. Similarly, 70.52 % of priority refugia for minimizing backward climate velocity overlap with areas with low backward climate velocities. Such similarities and differences in patterns respectively represent the synergies and trade-offs between the dual strategies of managing for the processes of climate change (minimizing vulnerability to range shifts) and managing for patterns of ecological value (threatened species diversity). Priority refugia and other planning units of high conservation priority were additionally located in areas where the diversity of target species was slightly higher, such as the southern and eastern portions of the region. Values of species richness in priority refugia based on forward climate velocity ($\bar{x}$ = 6.61, SE = 0.03) and those based on backward climate velocity ($\bar{x}$ = 6.45, SE = 0.03) were 7 % and 5 % greater than the regional average ($\bar{x}$ = 6.15, SE = 0.01, respectively. While land modification was not found to be strongly correlated with conservation priority based on forward climate velocity ($\rho = -0.0402$), it demonstrated a slight association with priority based on backward climate velocity ($\rho = -0.2411$). The regional average level of land modification ($\bar{x}$ = 2.93, SE = 0.04) was 2.4 times higher in the priority areas identified using forward velocity, and 9.9 times higher than the priority areas for backward climate velocity ($\bar{x}$ = 1.21, SE = 0.07 for forward; $\bar{x}$ = 0.30, SE = 0.02 for backward). These degrees by which land modification was lower in priority refugia were lesser than the degrees by which forward and backward climate velocities were lower in priority refugia relative to the entire study region (6.3 and 10.1 times lower, respectively), suggesting that climate velocity had a stronger impact on the selection of protected areas than land modification.

We further used our modeled values of conservation priority to evaluate the potential resistance of current protected areas to climate shifts, again finding that current protected areas may already be aiding in reducing the impacts of future change. Mean conservation priorities across the currently protected planning units were 27.48 % higher than the regional average when derived from forward climate velocities and 53.01 % higher when derived from backward climate velocity (Table 2; Fig. 4c and d). Different protected areas demonstrated variable priorities (Fig. 4e and f), with 47 % of individual protected areas having greater average forward priorities and 38 % having greater backward priorities, relative to their respective regional means. 22.89 % of high forward priority refugia and 33.11 % of high backward priority refugia fell within currently protected areas, which cover only 10.98 % of the

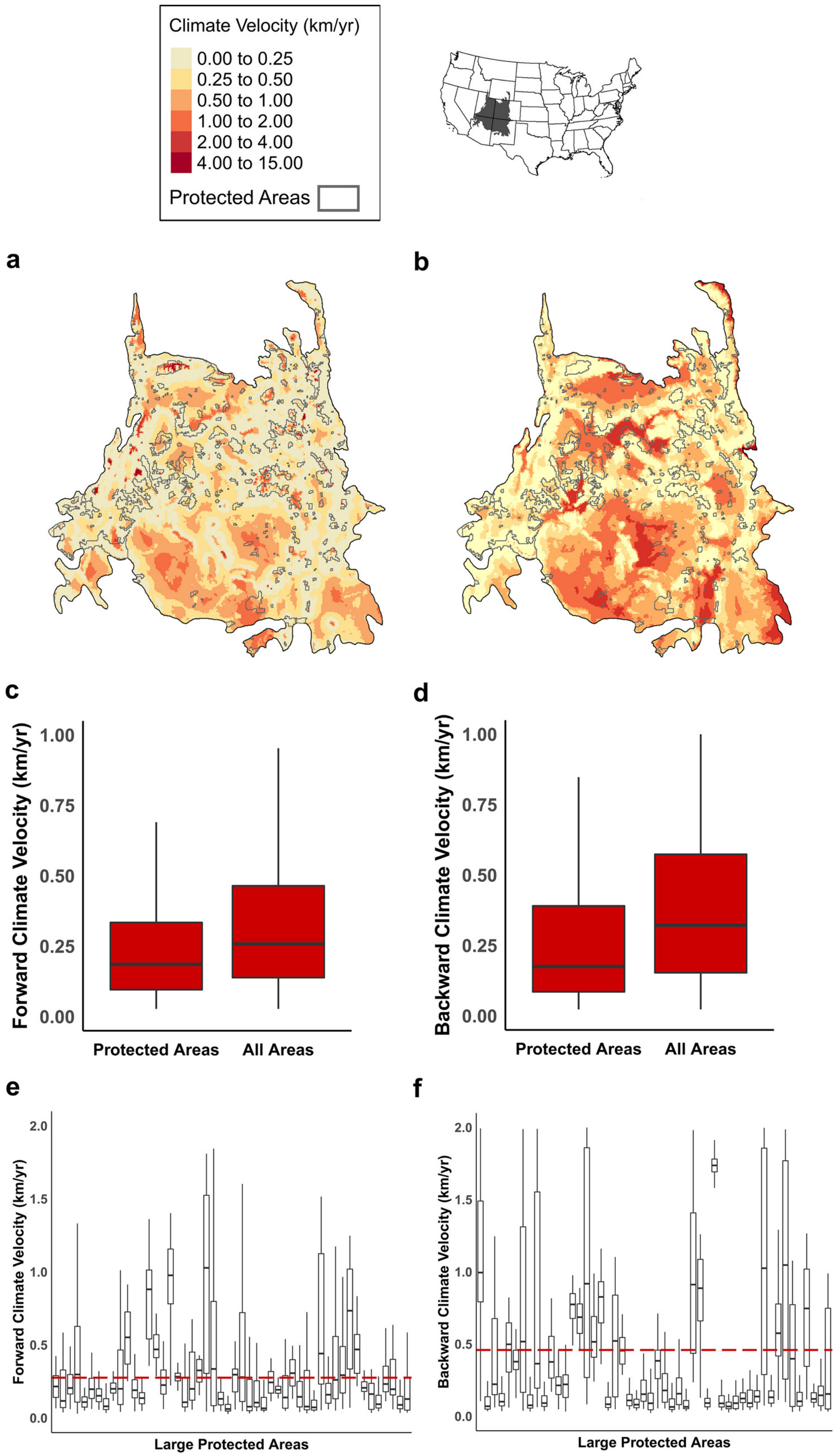

Fig. 3. Climate velocities within the Southern Rockies region. (a) Spatial distributions of forward climate velocity calculated using mean annual temperature; (b) spatial distribution of backward climate velocities; (c) forward climate velocities of protected areas vs. all areas; (d) backward climate velocities of protected areas vs. all areas; (e) forward and (f) backward climate velocities within the 50 largest individual protected areas (each with an area over 250,000 km^2). Dashed red line represents the median velocity across the whole region. Lower and upper box hinges correspond to the 25th and 75th percentiles of values, respectively.

Table 2
Mean and standard error (SE) values of climate velocities and conservation priorities across all areas of the Southern Rockies region and across only its current protected areas.

Extent	Forward Climate Velocity (km/yr)		Backward Climate Velocity (km/yr)		Conservation Priority derived from Forward Climate Velocity (% selection frequency)		Conservation Priority derived from Backward Climate Velocity (% selection frequency)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
All Areas	0.3891	0.0016	0.6735	0.0025	20.0760	0.0752	19.8816	0.0822
Protected Areas Only	0.3738	0.0067	0.4457	0.0054	25.5925	0.2423	30.4209	0.2723

region (Fig. 5). While each type of climate velocity generated separate patterns of refugia corresponding to distinct conservation priorities (protecting *in situ* vs. *ex situ* refugia), a 16.8 % overlap between the two sets of refugia did occur (Fig. 5), reflecting that some areas represent priority locations regardless of whether forward or backward velocities are considered (Fig. A2).

4. Discussion

Efforts must be made to improve the way that climate change is explicitly accounted for when identifying priority areas for conservation (Jones et al., 2016; Reside et al., 2018). Historically, protected areas have largely been established to conserve the geological, biological, and cultural resources in a given place, a strategy that may seem ill-suited to dealing with the dynamic impacts of climate change on biodiversity (Game et al., 2011; Marris, 2011; Settele et al., 2014). In order to understand how the placement of future protected area systems could be improved to cope with climate change impacts, one must first assess how well current areas already achieve that purpose (Gonzalez et al., 2018; Virkkala et al., 2019). We have shown that many protected areas within the Southern Rockies region may already include large refugia buffering species against pressures to shift their ranges due to climate change. Additionally, many other priority refugia seemingly may exist outside of the areas that are currently managed as traditional protected areas. It is possible that the identification of potential climate refugia in those areas with lower levels of protection and higher levels of human land modification may lead to reassessments of their conservation value and aid in the selection of new priority areas for management.

Overall, our temperature-based climate velocities demonstrate spatial alignment with the geographic characteristics that drive climatic patterns, particularly elevation and slope. For example, we found high forward climate velocities within the highest elevation areas of the Southern Rockies study region. This pattern of high mountaintop velocities likely arises from the fact that the nearest location with analogous climate under future predicted increases in temperature may be located on an entirely different mountain range with higher elevations or a more poleward latitude (Engler et al., 2011; Settele et al., 2014). Conversely, the high temperature-based backward climate velocities found in the lowest elevation, hottest parts of the region are likely the consequence of organisms having to eventually arrive from distant locations with high temperatures in the present. Promisingly, both types of climate velocities were lowest on mountain slopes and in places with high topographic diversity, where species need only move a short distance uphill to maintain their temperature envelope, emphasizing the disproportionate vulnerability of communities to climate shifts in topographically homogenous areas (Bertrand et al., 2011). For species whose ranges are restricted to those areas with less topographic variation, alternative management approaches such as assisted migration may be necessary to cover the large distances required to find future climate matches (Hamann et al., 2015; McLachlan et al., 2007). Our identification of the importance of topography also echoes previously raised concerns about the applicability of velocity-based metrics of climate exposure to conservation in regions with relatively low topographic diversity and high climate velocity and few potential climate refugia, such as lowland tropical forests (Loarie et al., 2009), the North American Great Plains (Hamann et al., 2015), and coastal marine systems (Burrows et al., 2014). The similarities and differences between patterns of forward and backward climate velocities further highlight how conceptual approaches for quantifying the magnitude of climate velocity are best not taken in isolation (Carroll et al., 2015). With these factors in mind, we recommend that future work explore how diverse assessments of climate exposure could contribute to conservation efforts across a wider range of systems.

In this study, we chose to identify potential climate refugia using both forward and backward climate velocities separately, showing multiple possible approaches for applying climate velocities to systematic landscape conservation. Under these multiple scenarios, we find consistent evidence that protected areas within the Southern Rockies encapsulate a disproportionately large area of potential climate change refugia, in contrast with recent assessments of broader protected area networks (Gonzalez et al., 2018). However, efforts to prioritize conservation require a deeper understanding of the ecological processes that determine the consequences of climate change for species on the landscape. For instance, high priority areas identified by minimizing backward climate velocity indicate where conservation efforts could most easily aid organisms from nearby regions in finding climatic refuge in the future (*ex situ* refugia). Conversely, focusing on low forward climate velocities prioritizes places where the current community of conservation targets at a given area will be least exposed to shifting climate (*in situ* refugia). Both of these approaches have the potential to be valid for distinct efforts of climate change-driven conservation planning, so the alternative scenarios may best be considered independently. However, conservation efforts do not exist in isolation and their efficiency could be enhanced by further exploring the areas where priorities overlap, which may act as both *in situ* and *ex situ* refugia (Ashcroft, 2010).

Further consideration of details regarding interspecific variation in climatic vulnerabilities and connectivity has the potential to greatly enhance outcomes of future systematic conservation planning processes. Our refugia prioritization study featured a relatively coarse approach integrating the overlapping ranges of key species of potential conservation concern with broad metrics of exposure to temperature range. However, variation in the vulnerabilities of individual species and different species groups to climatic shifts is widely recognized as a vital consideration in climate-based conservation (Pacifici et al., 2015) and such variation has the potential to influence our results in some manner. Particularly in dealing with climate-induced range shifts, differences in dispersal ability between species and plasticity within populations can strongly influence assessments of vulnerability (Schloss et al., 2012; Settele et al., 2014). Furthermore, spatial heterogeneity in the landscape factors that contribute to the relative vulnerabilities of species responding to climate change continues to play a prominent role climate conservation decision-making (Theobald et al., 2016). The ecological realism of velocity-based climate exposure metrics would be greatly improved by emerging methods for integrating climate refugia

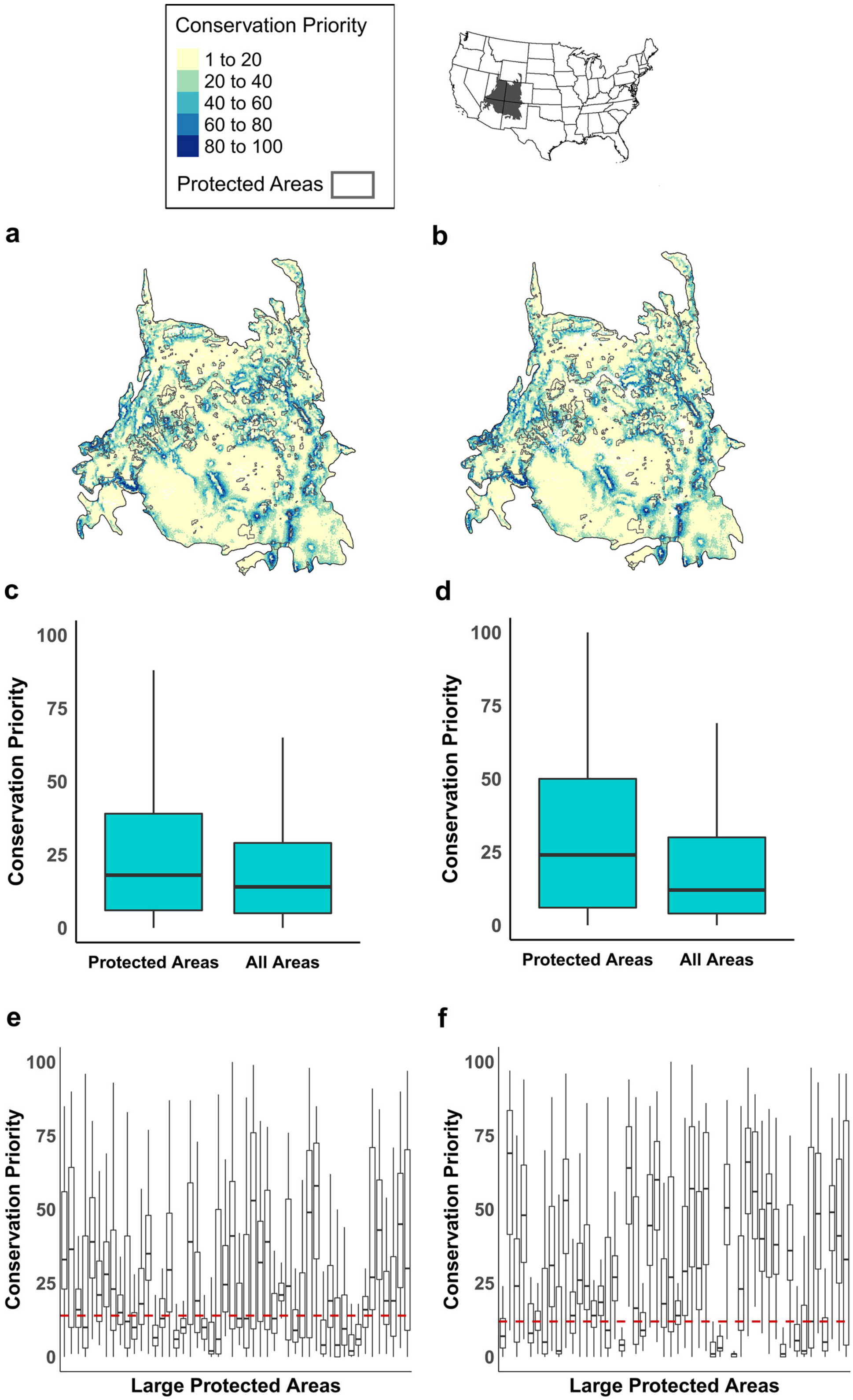

Fig. 4. Conservation within the Southern Rockies region estimated using Marxan. (a) Spatial distribution of conservation priorities within the region based on (a) forward climate velocities, (b) backward climate velocities, distribution of species, and land modification; Priority of protected areas vs. all areas separately derived from (c) forward climate velocities and from (d) backward velocities; and Priority derived from (e) forward climate velocity and (f) backward climate velocity within the 50 largest individual protected areas (each with an area over 250,000 km^2). Dashed red line represents the median priority across the region. Lower and upper box hinges correspond to the 25th and 75th percentiles of values, respectively.

identification with the measures of functional connectivity between core refugia (Carroll et al., 2018; Littlefield et al., 2019, 2017). Although logistical limitations warrant the development of additional methods for simultaneously accounting for numerous complexities associated with climate-based landscape conservation, methods based on principles of systematic planning (Jones et al., 2016; Wilson et al., 2006) likely warrant further investigation.

4.1. Conclusion

Utilizing systematic processes for identifying climate refugia generates opportunities for integrating heterogeneous climate change impacts into existing landscape management contexts at broad scales (Game et al., 2013; Schwartz et al., 2018). While the identification of refugia does not itself amount to a comprehensive conservation

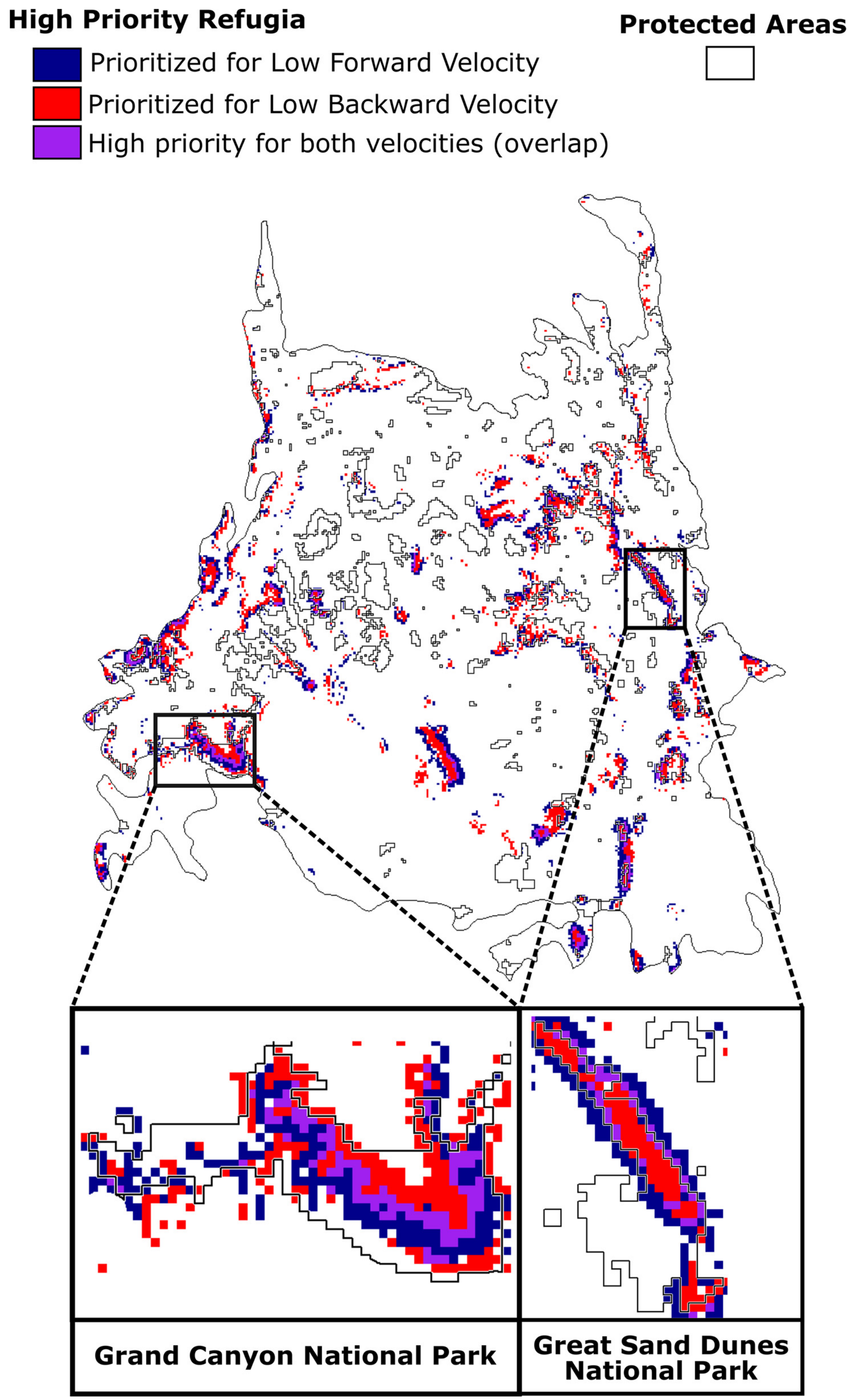

Fig. 5. Prioritized climate refugia extents relative to existing protected areas. High priority refugia were designated as the top 5 % of planning units in terms of conservation priority derived by minimizing forward climate velocity (blue) and priority derived by minimizing backward climate velocity (red). The two sets of high priority climate refugia (purple) overlap by 16.8 % of their individual area. Insets depict two examples of protected areas containing large amounts of high priority climate refugia: Grand Canyon National Park and Great Sand Dunes National Park.

planning strategy, we believe that it is a key early step in producing the data that can inform better climate-driven decision-making. Success in conserving a region's ecological diversity depends on many factors in addition to the direct impacts of climate change, such as risks associated with the modification of natural landscapes for anthropogenic uses. Importantly, human values and actions – including our own adaptations to climate change (Faleiro et al., 2013) – will continue to be the primary factor in the likelihood of conservation success under any climate (Game et al., 2013; Jones et al., 2016; Reside et al., 2018). Effective climate-based conservation requires careful and nuanced assessments of the ecological and social factors contributing to conservation success, tasks for which systematic approaches may prove particularly well-suited.

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None of the funding sources for this manuscript had any role in the included analyses.

Author Contributions

JH wrote the manuscript and conducted the spatial analyses. EH aided in the development of ideas and in the writing of the manuscript.

Declaration of Competing Interest

The authors declare no conflicting interests. This manuscript is the original research of its authors, who both agree with its contents and submission to *Biological Conservation*. This research has not been published, nor is it currently in consideration for publication, in any form elsewhere. All funding sources have been acknowledged in the manuscript and we declare no direct financial benefits from its publication.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2019.108258.

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