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Distribution and protection of climatic refugia in North America

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Abstract: *As evidenced by past climatic refugia, locations projected to harbor remnants of present-day climates may serve as critical refugia for current biodiversity in the face of modern climate change. We mapped potential climatic refugia in the future across North America, defined as locations with increasingly rare climatic conditions. We identified these locations by tracking projected changes in the size and distribution of climate analogs over time. We used biologically derived thresholds to define analogs and tested the impacts of dispersal limitation with 4 distances to limit analog searches. We identified at most 12% of North America as potential climatic refugia. Refugia extent varied depending on the analog threshold, dispersal distance, and climate projection. However, in all cases refugia were concentrated at high elevations and in topographically complex regions. Refugia identified using different climate projections were largely nested, suggesting that identified refugia were relatively robust to climate-projection selection. Existing conservation areas cover approximately 10% of North America and yet protected up to 25% of identified refugia, indicating that protected areas disproportionately include refugia. Refugia located at lower latitudes (≤40°N) and slightly lower elevations (approximately 2500 m) were more likely to be unprotected. Based on our results, a 23% expansion of the protected-area network would be sufficient to protect the refugia present under all 3 climate projections we explored. We believe these refugia are high conservation priorities due to their potential to harbor rare species in the future. However, these locations are simultaneously highly vulnerable to climate change over the long term. These refugia contracted substantially between the 2050s and the 2080s, which supports the idea that the pace of climate change will strongly determine the availability and effectiveness of refugia for protecting today's biodiversity.*

Keywords: climate analogs, climate-change adaptation, climate-change vulnerability, conservation, dispersal, protected areas

Distribución y Protección de los Refugios Climáticos en América del Norte

Resumen: *Los refugios climáticos pasados han evidenciado que las localidades proyectadas para albergar remanentes de los climas actuales pueden fungir como refugios importantes para la biodiversidad contemporánea de frente al cambio climático actual. Mapeamos los refugios climáticos potenciales en el futuro a lo largo de América del Norte, definidos como localidades con condiciones climáticas cada vez más raras. Identificamos estas localidades rastreando los cambios proyectados en el tamaño y distribución de los análogos climáticos en el transcurso del tiempo. Usamos umbrales derivados biológicamente para definir estos análogos y probamos los impactos de la limitación de la dispersión con cuatro distancias para limitar las búsquedas análogas. Identificamos, cuando mucho, el 12% de América del Norte como refugios*

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climáticos potenciales. La extensión de los refugios varió dependiendo del umbral análogo, la distancia de dispersión y la proyección climática. Sin embargo, los refugios estuvieron concentrados en elevaciones altas y en regiones complejas topográficamente en todos los casos. Los refugios que fueron identificados usando diferentes proyecciones climáticas estuvieron anidados en general, lo que sugiere que estos refugios identificados fueron relativamente sólidos con respecto a la selección de proyección climática. Las áreas de conservación existentes cubren aproximadamente el 10% de América del Norte y aun así protegieron hasta el 25% de los refugios identificados, lo que indica que las áreas protegidas incluyen desproporcionadamente refugios climáticos. Los refugios localizados a latitudes menores (≤40°N) y a elevaciones ligeramente menores (aproximadamente 2500 m) tuvieron una mayor probabilidad de no estar protegidos. Con base en nuestros resultados, una expansión del 23% de la red de áreas protegidas debería ser suficiente para proteger los refugios presentes en las tres proyecciones climáticas que exploramos. Creemos que estos refugios climáticos son de prioridad alta para la conservación debido a su potencial para albergar especies raras en el futuro. Sin embargo, estas localidades también son altamente vulnerables al cambio climático a largo plazo. Estos refugios se redujeron sustancialmente entre las décadas de 2050 y 2080, lo que refuerza la idea de que el paso del cambio climático determinará con fuerza la disponibilidad y efectividad de los refugios climáticos para proteger a la biodiversidad contemporánea.

Palabras Clave: adaptación al cambio climático, análogos climáticos, áreas protegidas, conservación, dispersión, vulnerabilidad ante el cambio climático

北美气候庇护所的分布及保护: 【摘要】 *过去的气候庇护所数据可以证明, 在现代气候变化的情况下, 那些被预测可以保留残存物种的地区可能是当前生物多样性的重要庇护所。我们绘制了北美地区未来潜在的气候庇护所地图, 对气候庇护所的定义是那些罕见气候条件日益增加的地区, 我们主要是通过追踪相似气候在大小和分布上随时间的预计变化确定了这些地区。我们用生物学的临界值来定义相似气候, 并通过分析四种不同扩散距离限制的影响来限定对相似气候的搜寻范围。本研究发现北美洲至多有12%的地区是潜在气候庇护所。庇护所的范围随相似气候的临界值、扩散距离和气候预测模型而变化。然而, 在所有案例中, 庇护所都集中在那些海拔高、地形复杂的地区。用不同气候预测模型确定的庇护所很大程度上是相互嵌套的, 这表明它们对气候预测模型的选择相对稳健。目前, 现有的保护地覆盖了北美约10%的地区, 保护着高达25%经确定的庇护所, 这说明保护地不成比例地囊括了庇护所, 而那些位于低纬度地区 (≤40°N) 和较低海拔 (约2500米) 的庇护所更有可能仍未受到保护。根据我们的结果, 保护地网络扩大23%就足以保护我们分析的三种气候预测模型下存在的庇护所。我们相信这些庇护所应得到优先保护, 因为它们有潜力在未来为珍稀物种提供栖息地。然而, 从长期来看, 这些地区同时非常容易受到气候变化的影响。它们可能在21世纪50到80年代大幅度缩小, 这支持了气候变化的速度将大大影响庇护所对于保护当前生物多样性的可用性及有效性的观点。***【翻译:胡怡思;审校:聂永刚】**

扩散: 保护, 气候变化适应, 气候变化脆弱性, 相似气候, 保护地

Introduction

As Earth's climate changes, many species will need to move to track changing conditions, potentially leading to a dramatic reorganization of biodiversity (Moritz & Agudo 2013). Such a reorganization has profound implications for species residing in protected areas. For example, the conservation value of a given protected area may decline if species of conservation concern migrate out of the area (Araújo et al. 2004), and the emergence of novel ecological communities could stress the management of resources in existing protected areas (Stralberg et al. 2009). Finally, shifting patterns of biodiversity may result in new priority areas for conservation (Groves et al. 2012), thus requiring the expansion of existing or establishment of new protected areas to harbor climatic refugia.

To identify appropriate conservation targets under future climatic conditions, conservation planners need to identify locations where species are at greatest risk and places where the species most threatened by climate change may concentrate in the future (Loarie et al. 2008). Because climate is a primary constraint on species occurrence, species and the ecological communities they form may be at significant risk if the climatic conditions to which they are adapted move too far, too fast, become rare, or disappear in the future (Williams et al. 2007; Loarie et al. 2009). Indeed, rare, small-ranged species are disproportionately found in locations with regionally rare climatic conditions (Ohlemüller et al. 2008). As a result, the contraction or disappearance of a set of particular climatic conditions from a given region could contribute to the decline or extinction of local populations (Jackson & Overpeck 2000; Stralberg et al. 2009).

Paleoecological records indicate that during past climatic changes regions of North America served as refugia during glacial and interglacial periods (Stewart et al. 2010). Species that persisted in these refugia then recolonized the landscape after favorable climatic conditions returned. Therefore, not surprisingly, one of the most promising suggestions for addressing the potential impact of climate change on biodiversity involves protecting climatic refugia (Groves et al. 2012)—locations to which species can retreat, and in which they can persist, despite regional or larger-scale changes in climate (Keppel et al. 2012).

Multiple definitions of modern climatic refugia have been suggested depending on both the scale and function of the refugia (Ashcroft et al. 2012; Morelli et al. 2016). Refugia may be places where climates are likely to remain suitable for a species, allowing it to persist in situ. Conversely, refugia may be places outside a species' current distribution (ex situ) to which individuals may move to track suitable conditions. In addition, macrorefugia consist of large areas that are projected to retain a set of regional climatic conditions that have become rare relative to their historical extent (Ashcroft 2010). At a finer spatial scale, topographic features may create microrefugia in which local climatic conditions are particularly stable relative to the regional climate (Dobrowski 2011). These microrefugia may also play a critical role in facilitating species persistence during periods of unfavorable climate (Ashcroft et al. 2012). However, their small size may make them less useful for species with larger area requirements and makes them more challenging to identify across larger extents.

Few researchers have explicitly mapped future climatic refugia (Loarie et al. 2008). Game et al. (2011) identified climatic refugia in Papua New Guinea as those locations projected to experience the least climate change. Both Loarie et al. (2008) and Stralberg et al. (2018) used species distribution models to identify species-specific climatic refugia. These authors identified macrorefugia as opposed to microrefugia. The resolution of downscaled climate-model projections is too coarse to identify microrefugia, and downscaling algorithms fail to incorporate important local dynamics that would create microrefugia (Gavin et al. 2014).

Locations with low climatic velocity and high levels of environmental diversity have also been proposed as potential climatic refugia (Carroll et al. 2017). However, velocity measures alone do not identify classic macrorefugia, which are defined as regions of the continent retaining climatic conditions that become increasingly rare (Ashcroft 2010). Ohlemüller and others (2012) calculated proportional change in analogous climate space to successfully identify historical climatic refugia in Europe during the Last Glacial Maximum. These historical refugia eventually generated source populations for postglacial recolonization of the European landscape. The demonstrated ability of this technique to identify historical climatic refugia suggests that such a species-independent technique may successfully identify potential macrorefugia under future climatic conditions. Whether these future refugia will be able to generate source populations is less certain because, in contrast to historical climate changes which were cyclical, projections of modern climate change indicate continued warming without a reversal to present-day climatic conditions. Even so, these future refugia may still facilitate biodiversity conservation by slowing the rate of species loss and facilitating range shifts (Hannah et al. 2014).

We quantified changes in the extent and distribution of multivariate climate analogs between historical and projected future climatic conditions to identify future climatic macrorefugia. We define *refugia* as regions of the continent projected to retain increasingly rare climatic conditions. These climatic macrorefugia are potentially important locations for conservation because they are likely to harbor species that are particularly threatened by climate change. Although climate rarity does not necessarily result in species rarity, the two are correlated (Ohlemüller et al. 2008). We also identified locations with current climatic conditions that will potentially contract in size or shift outside the imposed dispersal radius, effectively disappearing from the regional landscape in the future.

We evaluated the degree to which the current protected-area network in North America will likely harbor climatic refugia and conversely where species in the network will potentially be at risk due to shrinking and disappearing climatic conditions. If the network already protects a large portion of potential climatic refugia, it may be poised to help protect species in the face of climate change. If, however, the network protects few refugia and is likely to experience extensive disappearing climatic conditions, it may be less well suited to protecting biodiversity in the future. Understanding where refugia are underprotected and which parks and reserves are likely to experience disappearing climates will help managers and planners address gaps and vulnerabilities in the current protected-area network.

Methods

We used climate-analog analysis (Ohlemüller et al. 2006; Williams & Jackson 2007; Hamann et al. 2015) to identify potential future macrorefugia and areas with climatic conditions at risk of regionally disappearing across North America. We identified locations (cells) with analogous climates for each focal cell on the landscape using a variant of the climate-change-velocity algorithm (Hamann et al. 2015). Our algorithm tallies the number of climate analogs in each alternative period in a given search radius (Fig. 1). We conducted two separate analog analyses. First, to identify potential refugia, we quantified the historical prevalence of projected future climatic conditions within the search radius for each focal cell (backward analogs). We considered locations with future climatic conditions that are less prevalent (by at least 25%) than they were historically (i.e., are projected to shrink relative to their historical distribution) to be potential climatic refugia (Table 1).

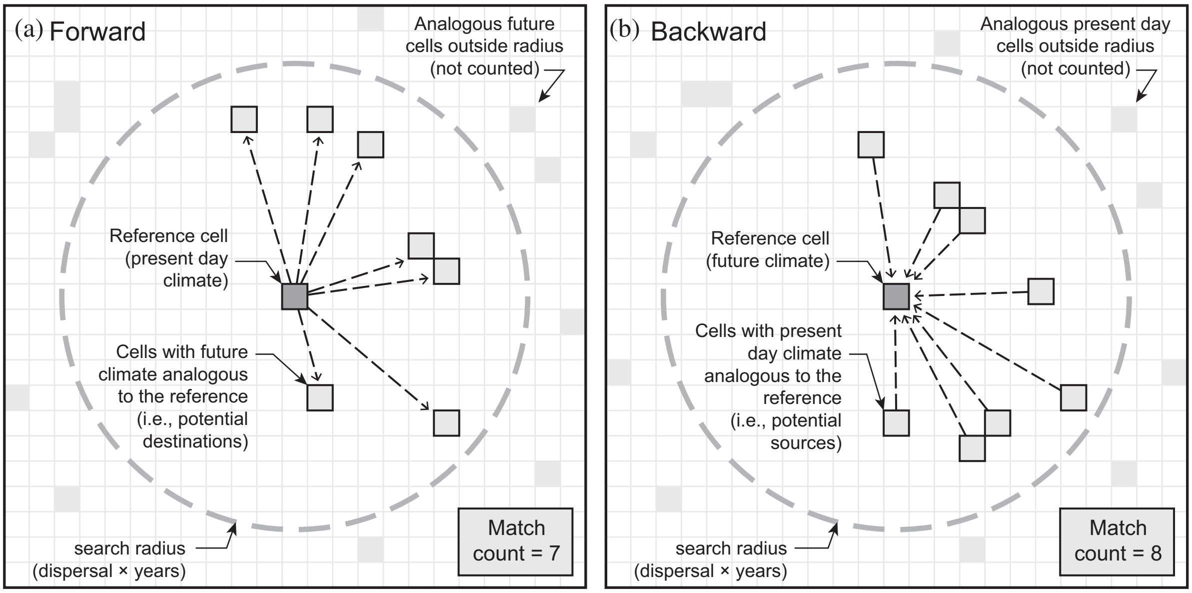

Figure 1. Conceptual diagram of the identification of forward and backward climate analogs (match, 2 cells with analogous climatic conditions; search radius, the maximum allowed distance from the reference cell to a climate analog; arrows, direction of movement from current climatic conditions to locations with analogous climatic conditions in the future).

For each cell classified as a refugium, we further designated it as in situ if the climatic conditions in the focal cell itself were analogous between the future and historical periods. If the climatic conditions in the focal cell itself changed so that the future conditions were not analogous to the historical conditions, we classified that refugium as ex situ. Finally, we quantified the future prevalence of current climatic conditions (forward analogs). With this analysis we sought to provide a prognosis for present-day climates at focal locations. If no future analogs were found in the search radius, we classified the focal cell as having regionally disappearing climatic conditions (Table 1).

Climate Data

Historical climatic conditions were averaged over 30 years (1961–1990). For future time periods, we used 30-year averages from 2041 to 2070 ("the 2050s") and 2071 to 2100 (hereafter the 2080s). Climate data were obtained from the AdaptWest Project (2015). We used the RCP8.5 emissions scenario and 3 climate models from the Coupled Model Intercomparison Project (CMIP) 5 family (Taylor et al. 2012): INM-CM4 (Donner et al. 2011), MIROC5 (Volodin et al. 2010), and GFDL-CM3 (Watanabe et al. 2010). These 3 models were selected to represent the range of variation in future projected climatic conditions across the 8 individual climate models provided by AdaptWest (Supporting Information). All historical climate data and future projections were topographically downscaled to 1-km resolution with ClimateNA software version 5.10 (Wang et al. 2016). All analyses were completed with R version 3.4.3.

To avoid collinearity in climate variables and to maintain reasonable computational requirements, all climate data were standardized and transformed with a principal component analysis (PCA), and only the first 2 principal components, explaining 89% of the variance in the climate data, were included in the analyses (Supporting Information). This process, also implemented by Hamann et al. (2015), creates a multivariate measure of climatic conditions that ensures highly correlated climate variables do not have an undue influence on defining analogs. Ten biologically relevant climate variables were included in the PCA: mean annual temperature, mean temperature of the warmest month, mean temperature of the coldest month, the difference between the mean temperature of the warmest and coldest months, mean annual precipitation, total summer precipitation, Hargreaves reference evaporation, Hargreaves moisture deficit, the number of frost-free days, and degree days above 5°C (Wang et al. 2016). This set of variables was chosen to best represent the climatic conditions driving the respective distributions of a broad diversity of plants and animals (Wang et al. 2016; Carroll et al. 2017).

Climatic Niche Breadth

We defined locations as being climate analogs if the multivariate climatic distance between them was less than a specified threshold. Previously, thresholds for defining analogs have been based on the range of values in the

Table 1. Definitions of disappearing, shrinking, and refugial climate types and associated ecological impacts and potential management responses.

Climate outcome	*Description*	*Landscape characteristics*	*Ecological implications*	*Management responses*
Disappearing	historical climate types with no analogs in the future (ratio of future area to current area = 0)	mountain tops, high latitudes, and plains	species in these locations (cells) are highly threatened and have no analogous climate space to move into within the defined dispersal radius	may require assisted migration to reach analogous climatic conditions outside dispersal capacity
Shrinking	historical climate types with less analogous climate space available in the future (ratio of future area to current area >0 and ≤0.75)	mid- to high elevations, high latitudes, and plains	species in these locations (cells) are threatened; analogous climate space to move into is smaller than historically available; reduced area of climatic suitability may translate to reduced habitat suitability and smaller population sizes	management and monitoring of potentially smaller populations; enhanced connectivity between small populations; identification of additional, possibly larger, areas of analogous climate space beyond specified dispersal radius
Refugia	future location of shrinking climate types (ratio of current area to future area ≥1.25)	high elevations, areas with high topographic complexity	locations (cells) are conservation priorities; species threatened by climate change due to a shrinking availability of analogous climate space likely to be concentrated in these areas	protect ecological integrity; ensure connectivity so species can reach refugia; manage expected influx of species to these locations

climatic data for the entire study area (Ohlemüller et al. 2006; Hamann et al. 2015) or within ecoregions (Williams & Jackson 2007). We developed biologically informed thresholds based on a measure of species climatic niche breadth for 200 birds (Birdlife International 2014), 450 mammals (Patterson et al. 2007), 498 amphibians (IUCN 2014), and 24 tree species in North America (Roberts & Hamann 2012). For each species, we measured the range of values for climate variables (principal components) within each current species' range. We identified the median centroid of the two-dimensional principal component distribution and calculated the radius of a circle that would capture 85% of the points within the species range. We refer to this radius as the species' climatic niche breadth. We then identified the median niche breadth values across all species within each taxonomic group to obtain a threshold for defining climate analogs. Median climatic niche breadths were 0.84 for amphibians, 1.34 for trees, 1.45 for mammals, and 1.64 for birds in unitless PCA values (Supporting Information). Because the values for the latter 3 groups were similar enough to result in functionally identical results, they were analyzed together under a single breadth of 1.5. For computational efficiency, amphibian niche breadth was conservatively rounded up to 0.9. For each location (cell) on the landscape, we defined alternative locations as climate analogs if the multivariate distance between them was less than these niche breadths.

Dispersal Radii

A species' vulnerability to climate change is based on its sensitivity to environmental change and its ability to respond and adapt to this change. Species that can disperse long distances can more easily track changing climatic conditions than those with limited dispersal capabilities. To evaluate the impacts of these limitations, we restricted climate analogs to those that fell within a specified dispersal radius of the focal location (cell). We chose 4 representative annual dispersal distances, 0.5, 1, 5, and 10 km, based on reviews of the maximum known dispersal distances for amphibians, birds, and mammals. One-half to 1 km/year represents most amphibians, some small mammals, and many plants. An annual dispersal distance of 5 km represents many small mammals and a few highly dispersal-limited birds (Sutherland et al. 2000; Bowman et al. 2002). Finally, a 10 km annual dispersal radius represents most small and a few midsized mammals and dispersal-limited birds (Sutherland et al. 2000; Bowman et al. 2002). To calculate a dispersal radius for each future period, dispersal distances were multiplied by the number of interim years between periods. For example, amphibians with a dispersal capacity of 0.5 km/year would have a dispersal radius of 40 km for the 2050s (0.5 × [2050 − 1970]) and 55 km for the 2080s (0.5 × [2080 − 1970]). The result is a generous estimate of dispersal capacity because the calculation is based on the assumption that individuals disperse, establish, and propagate a new generation ready to disperse again within 1 year.

Generic Species Types

We tallied analogous cells for each combination of analog threshold (narrow, 0.9 PCA units; wide, 1.5 PCA units) and dispersal radius (0.5, 1, 5, and 10 km annually), which provided results for 8 generic species types. Results based on these species types are intended to provide insight into how different abilities to tolerate climate change (as represented by the 2 climate-analog thresholds) and differential dispersal capabilities of species may affect the size, distribution, and availability of analogous climate space in the future. Results are reported for individual generic species types (i.e., results based on a particular combination of analog threshold and dispersal ability) and for all generic species types combined (i.e., any cell identified as a refugium for at least 1 of the generic species types was counted as a refugium for all species types combined).

Protected-Area Analyses

We used the International Union for Conservation of Nature (IUCN) World Database of Protected Areas (http://www.protectedplanet.net/) to assess the degree to which the current reserve network is likely to capture modern refugia. We included all protected areas in IUCN categories I through VI. These categories include strict nature preserves, wilderness areas, national parks, national monuments or features, and habitat and species management areas. We determined how much of the protected-area network as a whole was classified as containing refugia or disappearing climatic conditions. We calculated the percentage of protected and unprotected climatic refugia and characterized their distribution by latitude, elevation, and ecoregion. We also calculated how many individual protected areas (limited to those greater than 100 km^2 in area) are projected to include at least some (≥10 km^2) area classified as having disappearing or refugial climates.

Results

Climatic Refugia

Climatic macrorefugia covered a small proportion of North America. Total refugia area was largest under the mildest climate-change projection (INM CM4, 2050s). This this case, refugia for all species types combined covered 12% of North America (Table 2). Refugia were often, but not always, identified in areas with high elevation relative to the surrounding landscape and in areas with greater topographic complexity (Fig. 2d and Supporting Information). From the 2050s to the 2080s, refugia area shrank by, on average, 5–21% depending on the climate projection (Supporting Information).

For any individual generic species type, refugia covered on average 2% and at most 9% of North America (Supporting Information). Species types with stronger dispersal capabilities (10 km/year) had refugia up to 9 times larger than those for similar species types with more limited dispersal capacity (0.5 km/year). Conversely, the total area of refugia identified for species types with a narrow climatic niche breadth was 10–140% larger than the area refugia for comparable species types with a wider climatic niche breadth. This is because climatic conditions are more likely to shrink, triggering a refugia designation, if the analog threshold is narrow.

The majority of refugia for all species types in the 2050s and those with a relatively larger climatic niche breadth in the 2080s were classified as in situ refugia (Supporting Information). However, by the 2080s, for species with a narrow climatic niche, only 14–40% of all identified refugia were in situ. The remaining refugia were places with future climatic conditions that were not analogous to historical condition within the focal cell itself (i.e., ex situ refugia).

Depending on the climate projection, 16–25% of identified refugia (i.e., cells identified as a refugium for at least 1 of the generic species types) fell within current projected area boundaries. This coverage is disproportionately large given that only approximately 10% of North American land area is currently protected and refugia covered at most only 12% of North America (Fig. 2, Table 2). For all generic species types combined, 30–49% of protected areas over 100 km^2 contained at least some (≥10 km^2) refugia depending on the climate projection (Table 2); nearly one-third of parks had an average of 20% of their area classified as refugia in the 2050s (Supporting Information).

Although the current protected-area system disproportionately included identified refugia, 75% or more of potential refugia were unprotected. Refugia located at lower elevations (2500 m) and lower latitudes (south of 40° N) were more likely to be unprotected (Supporting Information). Under a mild climate projection (INM CM4, 2050s),

Table 2. Extent of disappearing and refugial climate types in North America and the current system of protected areas.

		Disappearing				*Climatic refugia*			
Period	*General circulation model (GCM)*	*% North America[a]*	*% protected areas system[b]*	*% protected areas with >10 km[2,c]*	*% protected areas with >50%[d]*	*% North America[a]*	*% protected by the current system[e]*	*% protected areas with >10 km[2,c]*	*% protected areas with >50%[d]*
2050s	INM CM4	0.02	0.04	0.72	0	12.03	19.19	48.96	22.53
	MIROC5	30.54	24.53	21.03	10.94	7.64	22.97	43.16	16.54
	GFDL CM3	44.52	54.53	44.27	26.17	5.23	22.51	38.15	13.02
2080s	INM CM4	18.53	24.44	22.01	6.51	12.33	16.15	41.28	17.64
	MIROC5	69.35	60.18	64.65	44.6	5.32	24.64	34.31	12.24
	GFDL CM3	77.92	73.49	77.67	59.51	3.66	23.81	29.56	10.29

[a]*Percentages represent total area identified as disappearing or climatic refugia for all 8 representative species types combined.*
[b]*Percentage of the entire protected areas system classified as disappearing or climatic refugia*
[c]*Percentage of individual protected areas with at least 10 km^2 of the area within their boundaries classified as disappearing or climatic refugia.*
[d]*Percentage of individual protected areas with over 50% of the area within their boundaries classified as disappearing or climatic refugia.*
[e]*Percentage of identified climatic refugia covered by current protected-area system.*

when refugia were most extensive, 29 ecoregions were identified as having a relatively high percentage of their area classified as refugia (>10%) and a relatively low percentage (<10%) of those refugia protected. By contrast, under a warmer climate projection, only 8 ecoregions are classified similarly (GFDL CM3, 2080s). Three ecoregions in Mexico, Chiapas Highlands, Sierra Madre Occidental, and the Hills and Sierras and 1 in the United States, the Wyoming Basin, contained consistently high percentages of unprotected refugia (Supporting Information).

Protecting all potential refugia identified under any climate projection would require roughly doubling the size of the current network. However, focusing on the most robust refugia for the 2050s (i.e., those identified as refugia in all 3 climate projections) would require increasing the protected areas network by 25%. Refugia identified under the warmest climate-change projection (i.e., GFDL CM3) were largely nested within locations identified under milder climate projections (i.e., INM CM4). For example, 82% of refugia locations identified under the high-change projection for the 2080s were also classified as refugia under the other 2 climate-change projections.

Disappearing Climates

The extent of regionally disappearing climates for all generic species types combined varied (0.02–78% of North America) depending on the projected degree of climate change (Table 2 & Supporting Information). Latitude and topography were strong drivers of disappearing climates; relatively higher latitudes and flatter regions had greater losses (Supporting Information). However, the large geographic extent of locations with disappearing climates was driven primarily by the most sensitive species types, those with both a narrow climatic niche (0.9 PCA units) and limited dispersal radius (0.5 or 1 km) (Fig. 3). For these highly vulnerable species types, up to 78% of North America was classified with regionally disappearing climatic conditions (Supporting Information). By contrast, species types with either greater dispersal capacity or a wider climatic niche were able to find analogous climatic conditions throughout most of the continent, regardless of the climate projection (Fig. 3). For species types with these more flexible characteristics, disappearing climatic conditions covered at most 33% of the continent (Supporting Information).

Discussion

We produced a comprehensive map of climate macrorefugia for North America. We found the protected-area system disproportionately protected climatic refugia relative to the general landscape. A substantial proportion, 25–50%, of current protected areas potentially harbor at least some refugia—defined as locations with increasingly rare climatic conditions—in the future. This finding indicates that many current protected areas have an important role to play in conserving species adapted to increasingly rare climatic conditions. In addition, refugia management is likely to be an important aspect of protected-area management in the future.

Protected areas disproportionately covered climatic refugia because, in part, refugia are predominantly located in areas of high elevation (Fig. 2d) and high topographic complexity (Supporting Information). Previous research shows that protected areas tend to disproportionately represent higher elevations, which were historically less easily developed or farmed (Joppa & Pfaff 2009). Although this tendency has limited the ability of the current reserve network to capture today's biodiversity, it may facilitate the protection of climatic refugia (Loarie et al. 2008; Carroll et al. 2010).

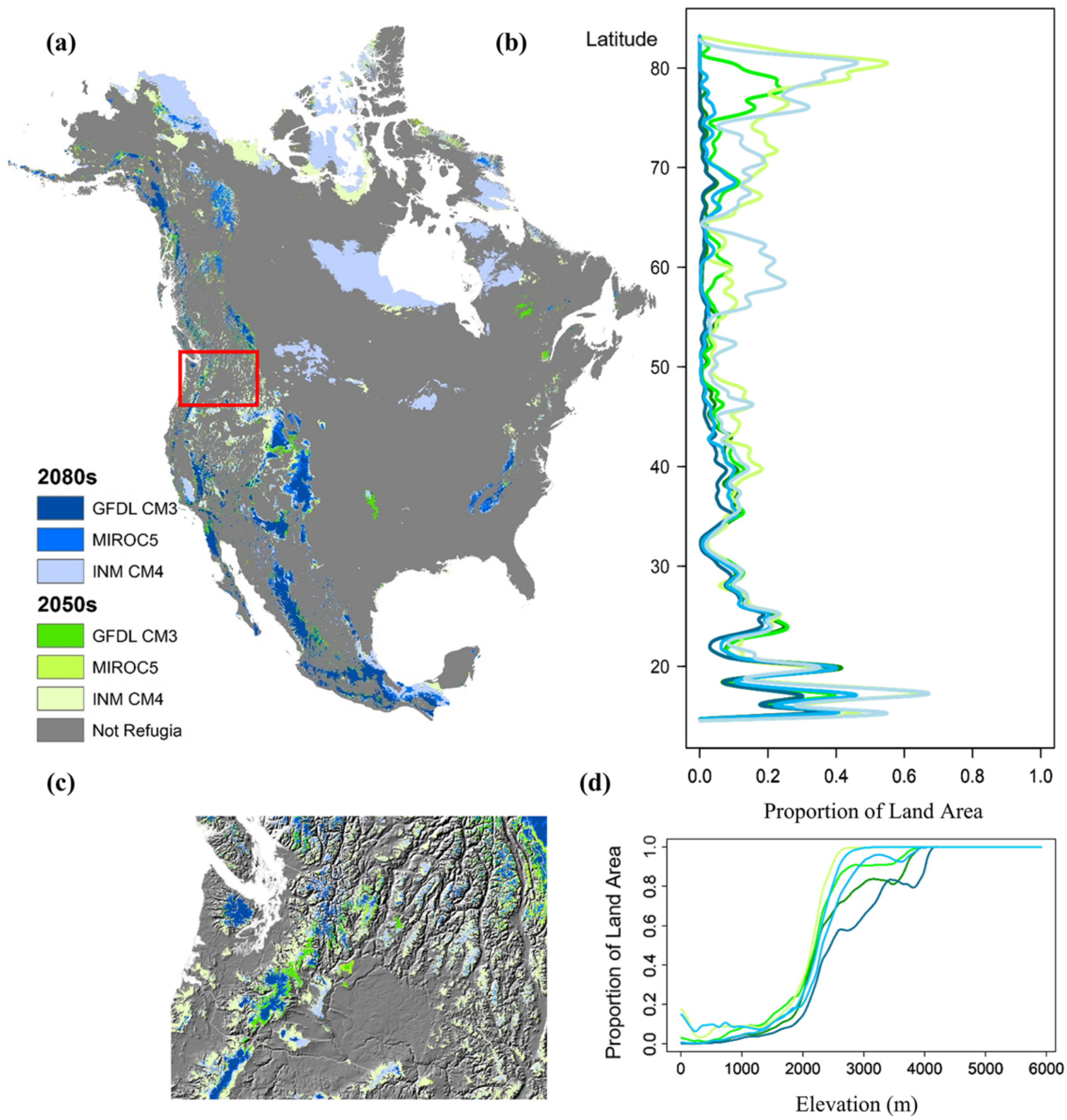

Figure 2. Map of climatic refugia for all 8 generic species types combined with locations for the 2050s (green) and 2080s (blue) for each general circulation model (GCM) for (a) North America and (c) Washington State (U.S.A.) (inset) as an example to show more detail of a topographically complex landscape. The darker the color the greater the changes in warming and precipitation projected by that GCM. Graphs show the proportion of land area classified as climatic refugia within (b) latitudinal and (d) elevational bands.

Climatic velocity studies also identify mountainous regions as being potential climatic refugia (Carroll et al. 2017). However, we measured not only distance to the nearest climate analog but also change in total area of analogous climate space. For the majority of North American mountain ranges land area declines as elevation increases, starting at low to mid (0–2000 m) elevations (Elsen & Tingley 2015). Our results show that the likelihood that locations are identified as refugia increases rapidly above 2000 m, regardless of the climate-change projection (Fig. 2d). If climatic velocity alone is considered, mountainous regions may be considered more resilient to climate change because analogous climatic conditions are nearby (but see Dobrowski & Parks 2016). However, the declining area of analogous climate space we measured indicates these regions are simultaneously highly vulnerable to climate change. These locations may have particularly high rates of species turnover (Langdon & Lawler 2015), potentially destabilizing community dynamics (Grimm et al. 2013).

These area limitations have particularly important implications for protected-area management because the long-term viability of these macrorefugia is challenged by the rapid pace of projected change. As climate change progresses, refugia contract and occupy ever-smaller areas at higher elevations (Fig. 2c, d). Historically, species

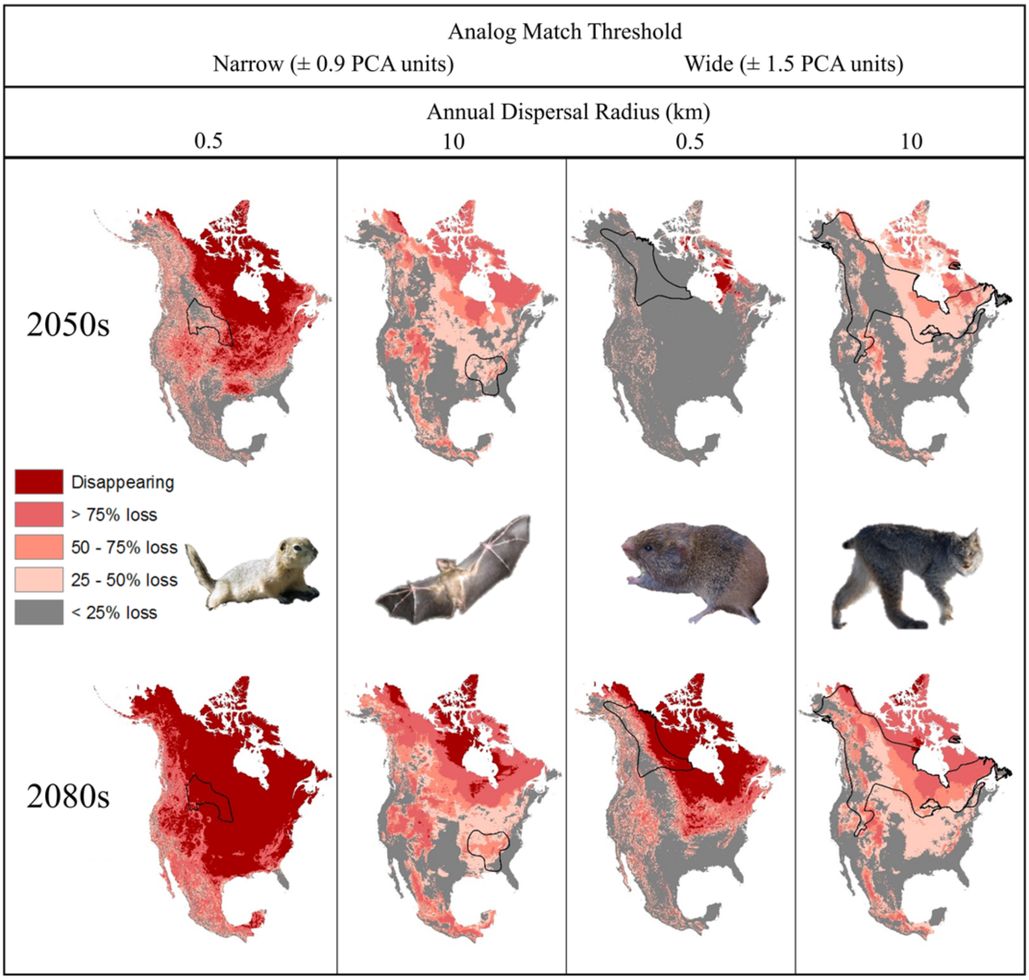

Figure 3. Proportional change in the ratio of future to current analogous climate space for 4 generic species types under a moderate (MIROC5) climate-change projection: species with narrow (0.9 principal component analysis [PCA] units) versus moderate (1.5 PCA units) climatic niche breadths and limited (0.5 km/year) versus strong (10 km/year) dispersal abilities. Example species with these niche breadths and dispersal characteristics are shown with the species' current range outlined in black (from left to right): Richardson's ground squirrel (Spermophilus richardsonii)*, gray myotis* (Myotis grisescens)*, taiga vole* (Microtus xanthognathus)*, and Canada lynx* (Lynx canadensis) *(red, climate disappears within the timeframe specified; pink, climate shrinks to the degree specified).*

persisted in paleoecological refugia for millennia due to both the slower pace of climate change and the cyclical nature of warming and cooling phases. By contrast, according to our analysis, future refugia disappear rapidly within the next 100 years under moderate (MIROC5) and severe (GFDL-CM3) climate-change projections. As a result, these refugia are likely holdout refugia that may prolong range shifts and facilitate gene adaptation and transfer. Management activities that mitigate pressure from predators or competitors may extend refugia benefits for particular species targets (Hannah et al. 2014). However, high elevations can also become climatic sinks or traps (Burrows et al. 2014), leading to the possibility that assisted migration may be required to facilitate further range shifts (Corlett & Westcott 2013).

In contrast to the patterns we found in mountainous regions, velocities are large across flat plains (Hamann et al. 2015), but our results indicate the total area of analogous climate space does not, in general, contract. As a result, we identified few refugia in these regions. This is because for species with high dispersal capacity (5–10 km/year) or a moderately wide climatic niche breadth, the area of analogous climatic conditions within their general dispersal radius does not change substantially, although the location may shift. Most mammals and birds easily exceed these dispersal and climatic niche thresholds. Furthermore, evidence suggests, species inhabiting plains regions are more likely to have larger geographic ranges, potentially in response to high historical climatic velocities, whereas the opposite is true in topographically complex regions (Ohlemüller et al. 2008; Sandel et al. 2011). Thus, species adapted to areas with fewer climatic refugia may be less dependent on them. In these regions, rapid dispersal is likely critical to allow species to keep pace with climate change. The radii we used in this analysis did not account for landscape conditions that can change the effective distance between any 2 locations. Maintaining landscape connectivity is likely necessary to ensure that these species types can track climate changes as needed (Littlefield et al. 2017).

The presence of suitable climatic conditions does not ensure the existence of habitat, which depends on additional ecological factors such as soils, vegetation, and other food and reproductive resources. This concern is theoretically less significant for locations identified as in situ refugia. The majority of refugia we identified for the 2050s were in situ. As a result, these refugia could theoretically protect species in place as well as provide destinations for species from the surrounding landscape. These locations are arguably very high priorities for conservation given their potential to retain relict populations. However, by the 2080s, for species with a narrow tolerance for climate change (i.e., narrow climatic niche breadth), 60–86% of refugia were ex situ. The value of ex situ refugia is far less certain because these locations may not have the necessary habitat conditions to support a given species. The functional benefits of these locations depends on whether adequate habitat conditions are present, or could be facilitated by managers, to support in-coming species. Adequate landscape connectivity is needed for species to reach these locations. For both in situ and ex situ refugia, the size of the refugium will also be significant in determining whether the location can sustain a viable population.

It is important to note that the climatic refugia we identified represent only one type of macrorefugia and that other types of refugia are also likely to be important. These include areas uniquely buffered from the most intense climatic changes (Morelli et al. 2016), locations where particular species or communities may persist despite climate change (Loarie et al. 2008), and fine-scaled microrefugia (Dobrowski 2011). Furthermore, the refugia we identified are based on the assumption that conservation targets are adapted to the climatic conditions in which they are currently found. In reality, a species may be able to tolerate a wider range of climatic conditions than those within their current observed range in the absence of factors such as predation or competition (HilleRisLambers et al. 2013).

Our results indicate that existing protected areas are well situated to conserve climatic macrorefugia. Conserving these sites represents a potentially important strategy for protecting biodiversity in the face of climate change because they retain increasingly rare climate conditions and therefore may provide the only habitat for species adapted to those conditions. Still, a significant number of potential refugia sites remain unprotected. These sites may face less development pressure because refugia tend to be in high-elevation, topographically complex areas. Consequently, including them in the protected-area network may require a comparatively modest investment. The shrinking size of refugia under increasingly severe climate-change projections suggests that rapid climate change may substantially challenge the adaptive capacity of dispersal-limited and climate-sensitive species. Consequently, the rate of climate change will be critical, driving the extent to which species can track changing conditions and the availability and size of climatic refugia. As warming continues, more climates will disappear entirely and climatic refugia will contract as well, determining for many species whether or not they will have somewhere to move in the future.

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Supporting Information

Maps of PC1 and PC2 values for North America (Appendix S1), a biplot of the PCA analysis (Appendix S2), a summary of measured species' climatic niche breadths (Appendix S3), portrayal of the relationship between refugia and topographic complexity (Appendix S4), a map of protected areas projected to contain refugia or disappearing climatic conditions (Appendix S5), distribution of protected and unprotected refugia by elevation (Appendix S6), latitude (Appendix S7), and ecoregion (Appendix S8), maps of the extent and distribution of disappearing climates across North America (Appendix S9), summary of General Circulation Model information (Appendix S10), principle component loadings (Appendix S11), summary of refugia results for each generic species type (Appendix S12), relative distribution of in situ versus ex situ refugia (Appendix S13), summary of results of disappearing climates for each generic species type (Appendix S14), and summary of refugia by ecoregion (Appendix S15) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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