Title

Targeting current species ranges and carbon stocks fails to conserve biodiversity in a changing climate: opportunities to support climate adaptation under 30x30

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ABSTRACT

Protecting areas for climate adaptation will be essential to ensuring greater opportunity for species conservation well into the future. However, many proposals for protected areas expansion focus on our understanding of current spatial patterns, which may be ineffective surrogates for future needs. A science-driven call to address the biodiversity and climate crises by conserving at least 30% of lands and waters by 2030, 30x30, presents new opportunities to inform the siting of new protections globally and in the U.S. Here we identify climate refugia and corridors based on a weighted combination of currently available models; compare them to current biodiversity hotspots and carbon-rich areas to understand how 30x30 protections siting may be biased by data omission; and compare identified refugia and corridors to the Protected Areas Database to assess current levels of protection. Available data indicate that 20.5% and 27.5% of identified climate adaptation areas (refugia and/or corridor) coincides with current imperiled species hotspots and carbon-rich areas, respectively. With only 12.5% of climate refugia and corridors protected, a continued focus on current spatial patterns in species and carbon richness will not inherently conserve places critical for climate adaptation. However, there is ample opportunity for establishing future-minded protections: 52% of the contiguous U.S. falls into the top quartile of values for at least one class of climate refugia. Nearly 27% is already part of the protected areas network, but managed for multiple uses that may limit their ability to contribute to the goals of 30x30. Additionally, nearly two-thirds of nationally identified refugia coincide with ecoregion-specific refugia suggesting representation of nearly all ecoregions in national efforts focused on conserving climate refugia. Based on these results, we recommend that land planners and managers make more explicit policy priorities and strategic decisions for future-minded protections and climate adaptation.

Keywords: Climate refugia, Climate corridors, Protected areas, Biodiversity conservation, Carbon mitigation

INTRODUCTION

The spatial heterogeneity of shifting climatic conditions presents challenges and opportunities for large-scale biodiversity conservation, as impacts to habitat and species can vary significantly across the landscape (Baldwin et al. 2018). In North America, nearly half of species are already undergoing local extinctions (Wiens 2016), which are, in part, due to increasing temperatures and decreasing precipitation (Roman-Palacios and Wiens 2020). In the contiguous U.S. (CONUS), the average annual temperature has risen 1.2-1.8 °C since the beginning of the 20th century, with the largest net increases occurring in western regions (Vose et al. 2017). Precipitation patterns are also shifting, with increases in central and northern United States and large reductions in the Southeast and West (Fei et al. 2017, Wuebbles et al. 2017). As the effects of climate change accelerate, local biodiversity will either need to adapt or make effective use of the changing landscape; species may find locations that serve as refugia from extreme or rapid climatic changes or shift their ranges to better-suited habitat (Neilson et al. 2005, Keppel and Wardell-Johnson 2012, Franks and Hoffman 2012, Román-Palacios and Wiens 2020). Identifying and conserving important refugia habitats and dispersal routes will be one critical step in jointly addressing the biodiversity and climate crises for the longer term (Pörtner et al. 2021). Therefore, it is important to understand what conservation planning opportunities exist in those areas where climate shifts are less extreme or more stabilized. While expansion of the U.S. protected areas network has been identified as an important solution to lowering extinction risk and overall ecosystem degradation (Stolton et al. 2015, Gray et al. 2016, Dinerstein et al 2017, 2019), efforts generally focus on present species distributions and may not effectively reflect future needs (Elsen et al. 2020, Maxwell et al. 2020).

Calls to address the joint biodiversity and climate crises by protecting at least 30% of Earth by 2030, known as “30x30” (Dinerstein et al. 2019), have been endorsed by government and conservation leaders at global (United Nations 2020), national (Biden 2021, U.S. DOI et al. 2021), and state levels (e.g., Newsom 2020). While the specifics of carrying out such a plan have yet to be established (Büscher et al. 2016, Rights and Resources Initiative 2020, Simmons et al. 2021), efforts would hypothetically conserve areas needed to sustain essential ecological services and reverse extinction trends (Locke 2013, Dinerstein et al. 2017). Translating these commitments into national policy may prove challenging since the protected areas network is incongruous with locations that could effectively maximize biodiversity conservation (Scott et al.

2001, Jenkins et al. 2015, Venter et al. 2018) or climate mitigation (Buotte et al. 2019, Melillo et al. 2015). However, it is unclear how well the current network and 30x30 goals can ensure the conservation of climate-resilient habitat in the coming decades as climate change continues to accelerate.

Climate-resilient habitat can largely be delineated into refugia and corridors. Generally, refugia protect native species and ecosystems from negative effects of climate change in the short term by remaining relatively buffered from climatic changes over time (Morelli et al., 2020). For example, steep canyons and north-facing slopes are sheltered from solar radiation and heat accumulation (Stralberg et al., 2020a) and wet areas like wetlands and riparian zones can remain moist during droughts (Morelli et al., 2016; Stralberg et al., 2020a). Refugia can be identified by various approaches which rely on at least one of three main concepts: topodiversity, climate exposure, and climate tracking (Michalak et al. 2020). Topodiversity models are based on physical habitat data and highlight regions with varied land cover, climate, soil, and topographic conditions, which may produce microrefugia (Ackerly et al. 2010, Groves et al. 2012, Carroll et al. 2018). Climatic exposure models are based on projected climatic changes and represent the degree of climate change likely to be experienced by a species or locale (Saxon 2011, Groves et al. 2012). Lastly, climate tracking models are based on one or more representative climate models and measure the proximity and accessibility of future suitable climatic conditions (Hamann et al. 2015, Michalak et al. 2018).

However, to survive in the face of ongoing and worsening climate change impacts, species may need to disperse longer distances to adapt and find more suitable habitat (Roman-Palacios and Wiens 2020). Climate corridors are relatively climate-stable areas that can facilitate long-distance dispersal (Stralberg et al., 2020b) by connecting current and future habitat. Network theory principles can be used to model climate corridors by delineating single paths or diffuse flow between climate analogs. Depending on model inputs, corridors may emphasize movement toward cooler latitudes and topographies, along rivers and streams, and/or through areas providing better habitat and less stress from disturbances (McGuire et al. 2016, Stralberg 2020b, Carroll et al. 2018, Littlefield et al. 2017).

Given the urgency of the biodiversity and climate crises, there is a pressing need to include potential climate refugia and corridors in the conservation planning process. However, some challenges exist. First, a growing body of available spatial data for identifying areas important for climate adaptation means that planners must reconcile a diversity of data (Carroll and Ray 2021). Previous research indicates that identified priority areas can be highly dependent on the datasets used as each represents different mechanisms and highlights different landscapes (Michalak et al. 2020, Carroll and Ray 2021). Second, the majority of prioritization frameworks for protected areas expansion focus on current spatial patterns in biodiversity, landscape connectivity and other key factors (Cushman et al. 2009, Lookingbill et al. 2010, Dickson et al. 2013, Belote et al. 2016, McClure et al. 2016). Focusing on the current state of the environment may result in critical omissions in protected areas siting for longer-term persistence of some target species (Monzón et al. 2011, Elsen et al. 2020). If this is the case, consideration of future conditions may complement efforts to preserve current biodiversity and ecosystem service hotspots, thereby reducing the threat of mass extinctions and accompanying biosphere degradation. Last, other omissions may occur if identification and prioritization of areas for climate resilience happen at a national scale: national-level analyses do not necessarily provide adequate representation of all natural ecoregions, communities, and species (e.g. Kraus and Hebb). Taking additional steps to identify refugia at multiple scales may help increase ecosystem representation and protections for the unique species assemblages and services they harbor.

Proper identification, protection, and management of climate-informed refugia and corridors are essential to ensuring greater opportunity for species conservation via migration and adaptation. While previous research and policy discussion surrounding the protected areas network has identified areas important to conserving the current state of biodiversity and natural carbon storage (Scott et al. 2001, Myers et al. 2000, Gray et al. 2016, Buotte et al. 2020), to our knowledge, there are no analyses of coincidence of these with areas important to species climate adaptation. To help close this knowledge gap, we:

1. identify areas in the contiguous U.S. critical to climate adaptation based on coincidence and complementarity among refugia (national and ecoregion-specific) and corridors models;
2. compare the spatial distribution of identified climate refugia and corridors with current biodiverse and carbon-rich areas; and
3. quantify the extent to which climate refugia and corridors are considered protected.

Step #2 guides our understanding of how protections siting under the 30x30 framework may be biased by data omission, and step #3 helps to assess the current level of protection for identified climate refugia and distinguish where stronger management might be needed. Our research contributes to a growing literature demonstrating the importance of incorporating climate-informed data in place-based land protection policy and practices and helping to identify specific areas for conservation. While these analyses are not meant to serve as a map of priority lands for conservation, they help frame a discussion on operationalizing 30x30 for strategic, future-minded conservation decisions.

METHODS

For this analysis, we focus on spatial datasets based on climate models or topography to identify areas that could serve as important refugia or migration routes for the contiguous U.S. (CONUS; Table 1). All datasets using climate models are informed by an ensemble of three to seven General Circulation Models (GCMs) for emission scenario Representative Concentration Pathway (RCP) 4.5 and projected for the time period 2071-2100. RCP 4.5 requires that carbon dioxide (CO_2) emissions start declining by approximately 2045 to reach roughly half of the levels of 2050 by 2100 (IPCC 2014). Recent studies suggest that near-term CO_2 emissions - an indicator of likely outcomes under current policies - agree more closely with RCP 4.5 than more extreme scenarios (e.g., RCP 8.5, International Energy Agency 2019, Hausfather and Peters 2020). All datasets have been resampled and aligned at 1km resolution. We combined datasets for refugia (n = 8) and corridors (n = 2) separately, accounting for differences in underlying mechanisms in modeling method and landscape conservation principles.

Climate refugia

We initially analyzed relationships between datasets through a principal components analysis where each component helps define a refugia class. As with principal components, datasets were assigned to a class based on the sign and size of the eigenvector. However, to avoid a tradeoff in refugia identification within a single class, all datasets within the class were required to load together and in the same direction on a principal component. In addition to presenting three separate classes, we weighted datasets based on their principal component loadings and combined them in a single dataset so that no one refugia class has a greater weight in identifying climate refugia locations. All datasets were normalized to a scale of 0 to 1 prior to being combined. Based on the relationships between refugia datasets, the weighted combination was calculated as:

$$\begin{aligned}
&Combined\ Refugia \\
&= Z_{Bird\ Macrorefugia} + Z_{Current\ Climate\ Diversity} + Z_{Ecotypic\ Diversity} \\
&+ Z_{Land\ Facet\ Diversity} + Z_{Landscape\ Diversity} + \left(Z_{Climatic\ Dissimilatiry} * 2.5\right) \\
&+ \left(Z_{Climate\ Velocity} * 2.5\right) + \left(Z_{Tree\ Macrorefugia} * 5\right)
\end{aligned}$$

We analyzed locations in the 80^{th} percentile (i.e., the top 20% of values) of the distribution of values for the combined data and for each refugia class separately. Additionally, we quantified the degree of overlap in refugia classes.

In addition to CONUS-level analyses, we extracted refugia values for each ecoregion separately (EPA level II; EPA 2006), classifying the locations that fell into the top 20% of the distribution as areas of interest. The result was a map of ecoregion-specific refugia, ensuring equal representation of all ecoregions relative to size. Results from the national- and ecosystem-scale analyses were compared and contrasted using spatial overlays.

Climate corridors

We extracted raw data values on connectivity and climate flow (The Nature Conservancy 2020) for areas that were identified as ‘climate-informed’ corridors based on the categorical connectivity and climate flow dataset (The Nature Conservancy 2020). The remaining values were rescaled to fall between 0 and 1. A second climate corridor dataset (Carroll et al. 2018) was similarly rescaled. We then combined these two datasets and analyzed locations in the 80^{th} percentile of the distribution of combined values.

Analyses

We used spatial overlay analysis to describe the extent to which the current protected areas network covers identified climate refugia (based on national- and ecoregion-scales) and corridors in CONUS. We quantified the extent to which identified refugia would be protected by the 30x30 framework if it were to solely focus on current areas of high imperiled species biodiversity and ecosystem carbon. Data on protected areas are from the PADUS 2.1 database (USGS 2020). We use U.S. Geological Survey's Gap Analysis Program (GAP) codes, which are specific to the management intent to conserve biodiversity. GAP 1 and 2 areas are managed in ways typically consistent with conservation. Areas assigned a GAP 3 code are governed under multiple-use mandates that may include biodiversity priorities but may also include incompatible activities such as forestry and mining, and GAP 4 areas lack any conservation mandates or such information is unknown as of 2020. As such, GAP codes are a natural system for identifying possible policy paths to achieving 30x30 and advancing wildlife conservation in the United States. Imperiled species richness was assessed from publicly available range data (USGS GAP, International Union of Conservation of Nature - IUCN, and U.S. Fish and Wildlife Service) for species defined as 'imperiled' (1,923 species). These include species that are listed or under consideration for listing under the ESA, have a NatureServe G1-3 status and/or are in critically endangered, endangered or vulnerable IUCN categories. Modeled total ecosystem carbon is based on a high-resolution map of global above- and below-ground carbon stored in biomass and soil (Soto-Navarro et al. 2020). We used ArcPro v2.5 (ESRI, USA) to produce maps and run analyses, with maps using the Albers Equal Area Conic projection. All area statistics are based on GIS estimates using this projection.

RESULTS

Identifying refugia and corridors

Climate refugia datasets generally correlated well with others of similar methodology or concept; three resulting classes generally represent topodiversity, climatic stability, and tree macrorefugia (Tables 1 & S1). The main exception was for climate-based datasets with species information, where bird macrorefugia correlated with datasets based on topodiversity, but tree macrorefugia was the sole dataset in its class (Table S2). The three refugia classes exhibited very little overlap with one another at the national scale: while 52% of CONUS falls into at least one of the refugia classes, 7.5% falls into refugia identified by 2 or more classes (approx. 568,000 km^2, Fig. S1). Additionally, two classes (tree macrorefugia and climatic stability) were strongly and negatively correlated with one another. Locations in the combined refugia layer that were within the top 20% of the distribution of values represent these overlaps and are used for reporting the remainder of statistics here.

34% of CONUS is identified as a climate refugia or corridor under one or more datasets (approx. 2,652,000 km^2, Fig. 1). Climate refugia generally follow the Appalachian, Rocky, and Cascade Mountain Ranges with additional refugia in the Ozarks, Ouachitas, southern Sierra Nevadas and along the California coast. Climate corridors are somewhat complementary to national-scale refugia, with 28.9% of their area (444,501 km^2) overlapping identified refugia locations. Overlaps occur in the central Appalachians, Pacific Northwest, and portions of the Rockies, Sierra Nevadas and Ozarks. Corridors that do not overlap with refugia are key in connecting parts of the Great Plains and Mexico borderlands to refugia and in connecting refugia to northern locales, particularly in New England, Midwest, Crown of the Continent and between northern California and the Cascades.

Using a stratified ecoregion approach resulted in refugia that were highly coincident with lands identified in the national scale analysis, with 63% of all national refugia overlapping with ecoregion refugia (Fig. 2). Overlaps between the two cover 12% of CONUS total land area (approx. 949,000 km^2). All refugia combined (both from national and ecoregion-specific analyses) equal 26% of the total CONUS land area (approx. 2.1 million km^2). Locations that were emphasized in the ecoregion-specific approach include temperate and semi-arid prairies and places along the eastern coast.

Comparison to 30x30 objectives: biodiversity and carbon

Refugia and corridors are generally complementary on the landscape to areas of current high biodiversity and carbon storage values (Fig. 3a&b). There is some overlap between current biodiversity hotspots (i.e., top quartile of imperiled species richness values) and identified national-scale refugia (36.8%) and corridors (9.3%; Table 2). Overlaps are generally concentrated in western California and Appalachia/Ozarks regions. Overlap between carbon-rich areas is greater in extent overall (refugia overlap = 32.5% and corridor overlap = 27.2%) and similar in spatial pattern with greater overlap in northern areas: northern Appalachians, Crown of the Continent and Pacific Northwest. When combining the two objectives (biodiversity and/or carbon), 45.0% (approx. 1,000,000 km^2) of the land area representing at least one of these objectives is also identified as part of a climate refuge or corridor.

Taking an ecoregion-specific approach to comparing refugia, corridors, biodiversity, and carbon results in less coincidence in current and future values: 22.0% and 21.7% of stratified refugia overlap with ecoregion-specific biodiversity hotspots and carbon-rich areas, and 17.5% and 26.1% of corridors overlap with ecoregion-specific biodiversity hotspots and carbon-rich areas, respectively (Fig. 3c&d; Table 3).

Current protections for refugia and corridors

Overall, 12.5% of the combined network of refugia and corridors is managed consistently with biodiversity conservation (i.e., GAP 1 or 2; 4.2% of CONUS or approx. 325,000 km^2; Fig. 4). The rest of this network falls on GAP 3 (26.5%) or GAP 4 (69.3%) lands, which represents 29.2% of CONUS (approx. 2,280,000 km^2). Proportions are similar when analyzing protection of national-scale climate refugia and corridors separately (Table 2). Ecoregion-specific refugia fall more heavily in GAP 4 categories with 12.2% of area on lands managed for biodiversity conservation and 19.6% on those managed for multiple uses (Fig. 4, Table 3). Finally, the entire set of CONUS lands representing either biodiversity conservation (GAP 1 or 2) or 30x30 objectives (biodiversity hotspots and/or carbon-rich areas) coincides with 44.5% of the national climate refugia and corridor network.

DISCUSSION

Currently, the U.S. protected areas network and emerging conservation policy objectives largely fail to represent valuable climate refugia and corridors. While there is some overlap with 30x30 objectives, solely using recent imperiled species ranges and carbon stores as conservation criteria will not inherently protect climate-resilient lands. In the most protective situation - if all biodiversity hotspots and carbon-rich areas were to be considered for strong conservation mandates (e.g., GAP 1 or 2 protections) - a majority (55.5%) of identified climate refugia or corridors would still be left unprotected. The omission of landscapes for climate adaptation from planning initiatives could inhibit the potential for longer-term conservation successes. As decision makers evaluate protected areas expansion, it will be important to prioritize lands and waters that will allow species to adapt and persist in a changing climate. While simply protecting currently biodiverse or carbon-rich areas may not ensure the preservation of climate corridors and refugia, conserving corridors and refugia will benefit imperiled species in biodiversity-rich hotspots and promote carbon sequestration. This is particularly true in parts of the country (e.g., Appalachia and western California) where hotspots are not directly covered by climate corridors, but adjacent to them, providing opportunities for migration to refugia or future climate analogs.

With over half of the contiguous U.S. identified as at least one type of climate refugia (topodiversity, climatic stability, or tree macrorefugia), many opportunities exist for decision makers interested in future-minded conservation. Our analysis supports previous work suggesting potential trade-offs in using one refugia type over other in refugia identification: approaches based on topodiversity favor environmentally complex regions, whereas climatic exposure and tree macrorefugia highlight lands beyond mountain ranges and areas of similar complexity (Michalak et al. 2020). Through our ensemble approach to refugia identification we both highlight the complementary information provided by these approaches (Belote et al. 2018) and simplify varied complex datasets for greater interpretability. A weighted combination of the datasets puts less pressure on the user to choose between mechanisms and on the decision maker to have a deep understanding of the methodology when interpreting maps. However, clarification of a specific refugia type may help states or local municipalities working at varying scales to set different priorities for contributing to national refugia protections based on local environments and community needs. In addition, taking a combined approach results in high overlap with an ecoregion-stratified approach, suggesting representation of nearly all ecoregions in national efforts focused on conserving climate refugia.

Currently unprotected climate refugia and corridors represent 29.2% of CONUS, of which 38% is federally managed. Given the extent and distribution of land managers, protecting valuable climate adaptation areas can help contribute to the 30% target numerically and meaningfully. However, there will need to be a concerted effort by land managers in all jurisdictions and leadership across jurisdictional boundaries.

Lands Administered by Government and Tribal Entities

Public lands can make significant contributions to achieving 30x30. The federal lands estate is particularly expansive (20% of CONUS, 86% of PADUS; CRS 2020, Rosa and Malcom

2020) and federal land management agencies are required to varying degrees to prioritize wildlife and habitat conservation. Currently, the majority (86%, representing 18.4% of CONUS) of GAP 3 lands are managed by federal agencies, suggesting that substantial gains can be made in focusing on existing statutory authorities to advance climate-smart conservation on these lands. Refugia with GAP 3 coverage present abundant opportunities to strengthen management mandates for climate adaptation, also adding to achievability of full linkage protection. Of GAP 3 lands, over half are managed by the Bureau of Land Management (BLM) and another third by the U.S. Forest Service (Rosa and Malcom 2020). Both agencies are guided by multiple use management mandates that empower them to designate and manage lands to enhance protection of areas recognized as having important conservation values (respectively, the Federal Land Policy and Management Act of 1976, National Forest Management Act of 1976). The agencies can capitalize on existing land and water designation authorities - like wilderness designation and BLM "areas of critical environmental concern" - to increase protection for climate refugia and corridors.

Expansion of GAP 1 and 2 lands to cover more refugia and corridors can also ensure greater conservation for climate adaptation. The U.S. Fish and Wildlife Service manages the National Wildlife Refuge System (NWRS) to conserve and restore wildlife, fish, and plants and their native habitats. Because refuge lands are expressly managed to conserve species and habitat, they offer a high level of federal land protection. Pursuing the acquisition of lands fundamental to species' survival and sustainability, including climate refugia and climate corridors, to establish new refuges would be consistent with the purview of NWRS, future-minded conservation and 30x30 objectives. However, since federal land acquisition and management decisions are often politically contentious, this may be a less feasible option for conserving the additional 440 million acres of land needed to reach the 30% target.

State governments also manage significant acreage (approximately 4% of the U.S.), including state forests, wildlife management areas, game lands, and natural area preserves. State parks, or portions thereof, may also contribute to conservation refugia and corridors, but are often categorized as GAP 4 (i.e., absent or unknown mandates for conservation). States can contribute to 30x30 by upgrading GAP status and management of undeveloped state lands that can contribute to climate adaptation. Furthermore, through the State Wildlife Action Planning

(SWAP) process, each state is required to describe "locations and relative condition of key habitats and community types essential to conservation of species" (USFWS & AFWA 2017). Results from this and other studies can help inform this process, and be a resource as states increasingly update their SWAPs to include climate changes (NFWPCAN 2021).

Tribal nations hold over 56 million acres in trust by the Bureau of Indian Affairs and may manage their lands in ways that afford more substantive protections for lands and species given their lower rates of habitat modification (Lee-Ashley et al. 2019). As many indigenous peoples are deeply connected to local culturally important resources such as plant and animal species, they are also impacted by climate-driven alterations in ecosystem processes and biodiversity (Jantarasami et al. 2018). A long history of managing and observing their lands has provided many indigenous communities with valuable knowledge and experience to inform land management and planning for climate adaptation and resilience (BIA 2018). Respectful inclusion of indigenous systems of knowledges and perspectives "can inform our understanding of how the climate is changing and strategies to adapt to climate change impacts" (NFWPCAN 2021). As such, government-to-government relationships will be important in addressing climate adaptation needs for species and peoples and may include cross-landscape management, tribal involvement in federal and state planning, and more. The Landscape Conservation Cooperative (LCC) program developed by Interior offers one such mechanism to advance landscape-scale protections and coordinate climate-related land conservation activities among Tribal Nations, federal agencies, state, local, and tribal governments, and other stakeholders (NASEM 2016).

Private and Non-Governmental Organization Lands

As most land in the United States is privately owned, conservation efforts on private lands will be critical to expanding protected areas. 62% of the refugia and 56% of corridors fall outside of the protected areas network (GAP 4), but this only represents 20% of CONUS. This suggests that well-targeted, voluntary acquisitions and easements could translate to large gains in private lands conservation. Land trusts are uniquely positioned to scale up conservation on private lands to achieve the 30x30 target and, when strategic with land protections, help protect these areas and fill important gaps in the nation's 30x30 network.

In addition to the role of land trusts, private working lands also have an important role to play in achieving 30x30 (Garibaldi et al. 2020, American Farmland Trust 2021). The Farm Bill conservation programs administered by the U.S. Department of Agriculture will be particularly important to achieving these goals (Theoharides 2014). For instance, the Agriculture Conservation Easement Program (ACEP) could be targeted to lands identified as climate refugia or connectivity areas and specify sensitive wetland habitats and riparian areas as eligible lands for wetland easements, as these will be increasingly valuable for supporting wildlife and ecosystem services as the climate changes (Theoharides 2014, Lewis et al. 2019). Longer-term (30 year) ACEP contracts that offer a commitment to consider re-enrollment of the same or similar land at contract expiration should be encouraged to ensure enduring conservation measures. Additionally, Environmental Quality Incentives Program (EQIP) and the Conservation Stewardship Program (CSP) can better reflect climate adaptation needs by assigning higher ranking points practices designed to build resilient natural resources, promote ecosystem services, and increase the adaptive capacity of the entire agro-ecosystem to climate change (Theoharides 2014).

Limitations

In order to enhance species' resilience in the face of growing climate and biodiversity crises, corridors and refugia must be preserved across both lands and waters. Due to some limitations of data and our analyses, we recommend against siting protections based on the coincidence of current biodiversity/carbon hotspots and climate refugia/corridors alone. For one, complementarity of species assemblages is not accounted for in using species richness. As a result, there may be biases toward conserving certain taxa. Additionally, while we included aquatic species in our biodiversity metric, and wetland/riparian areas are part of some topographic measures of refugia/corridors, we did not explicitly include aquatic refugia. At this time, there is no complete national dataset to represent aquatic refugia. Because cold-water aquatic organisms like salmon, trout, hellbenders, spring salamanders, and various macroinvertebrates are among the most vulnerable taxa to climate change, future analyses should focus on identifying freshwater refugia and corridors in regions where sufficient data exists (e.g., brook trout refugia in the northeast U.S. (Letcher et al., 2017), stream temperature scenarios in the western U.S. (Isaak et al., 2016), and Springs Online (https://springsdata.org), a collaborative database of spring locations and spring-dependent species in the Western U.S. and northern Mexico). Like terrestrial refugia, protection and restoration (where needed) of these areas should be focused at multiple scales, including protecting recharge areas, forests, and wetlands in the watershed (Stranko et al., 2008; Doyle and Shields, 2012; Jayakaran et al., 2016; Merriam et al., 2019), and restoring floodplains, riparian buffers and stream geomorphology (Sullivan and Watzin, 2009; Sweeney and Newbold, 2014; Favata et al., 2018; Merriam et al., 2019). Given the international scope of 30x30 and the benefits of larger-scale connectivity, future work on climate adaptation in 30x30 implementation should look beyond terrestrial habitats and political boundaries to cover all ecosystems of North America.

Our analysis demonstrates the need to make climate adaptation a more explicit objective in conservation planning for addressing the biodiversity crisis. Without direct consideration for climate refugia and corridors, a 30x30 implementation focused on current species ranges and carbon stocks may be ineffective for the longer term persistence of species. The key to operationalizing 30x30 and subsequent efforts will be growing a protected areas network that ensures a long-term commitment to biodiversity and climate. By incorporating climate refugia and corridors, the U.S. can work to protect places that will continue to serve wildlife and human populations now and in the future.

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DATA AVAILABILITY

The data that support the findings of this study are all publicly available. Those directly generated by this work can be downloaded from the following OSF repository: https://osf.io/jksyx/

LITERATURE CITED

Ackerly, D. D., Loarie, S. R., Cornwell, W. K., Weiss, S. B., Hamilton, H., Branciforte, R., & Kraft, N. J. B. (2010). The geography of climate change: Implications for conservation biogeography: Geography of climate change. *Diversity and Distributions*, *16*(3), 476–487. https://doi.org/10.1111/j.1472-4642.2010.00654.x

AdaptWest Project. (2015). Gridded climatic velocity data for North America at 1km resolution. https://adaptwest.databasin.org/pages/adaptwest-velocitywna/

American Farmland Trust. (2021). Agriculture's Role in 30x30: Partnering with Farmers and Ranchers to Protect Land, Biodiversity, and the Climate. American Farmland Trust. https://s30428.pcdn.co/wp-content/uploads/2021/04/AFT_-_Agricultures_Role_in_30x30_-_4-5-2021.pdf

Baldwin, R. F., Trombulak, S. C., Leonard, P. B., Noss, R. F., Hilty, J. A., Possingham, H. P., Scarlett, L., & Anderson, M. G. (2018). The Future of Landscape Conservation. *BioScience*, *68(2)*, 60–63. https://doi.org/10.1093/biosci/bix142

Belote, R. T., Dietz, M. S., McRae, B. H., Theobald, D. M., McClure, M. L., Irwin, G. H., McKinley, P. S., Gage, J. A., & Aplet, G. H. (2016). Identifying Corridors among Large Protected Areas in the United States. *PLOS ONE*, *11(4)*, e0154223. https://doi.org/10.1371/journal.pone.0154223

Belote, R. T., Carroll, C., Martinuzzi, S., Michalak, J., Williams, J. W., Williamson, M. A., & Aplet, G. H. (2018). Assessing agreement among alternative climate change projections to inform conservation recommendations in the contiguous United States. *Scientific Reports*, *8*(1), 9441. https://doi.org/10.1038/s41598-018-27721-6

Biden, J.R. (2021). Executive Order on Tackling the Climate Crisis at Home and Abroad. https://www.whitehouse.gov/briefing-room/presidential-actions/2021/01/27/executive-order-on-tackling-the-climate-crisis-at-home-and-abroad/

Buotte, P. C., Law, B. E., Ripple, W. J., & Berner, L. T. (2020). Carbon sequestration and biodiversity co-benefits of preserving forests in the western United States. *Ecological Applications*, *30(2)*, https://doi.org/10.1002/eap.2039

Bureau of Indian Affairs (BIA). (2018). National Climate Assessment: Indigenous Peoples' Resilience Actions. https://biamaps.doi.gov/nca/

Büscher, B., Fletcher, R., Brockington, D., Sandbrook, C., Adams, W. M., Campbell, L., Corson, C., Dressler, W., Duffy, R., Gray, N., Holmes, G., Kelly, A., Lunstrum, E., Ramutsindela, M., & Shanker, K. (2017). Half-Earth or Whole Earth? Radical ideas for conservation, and their implications. *Oryx*, *51(3)*, 407-410.https://doi.org/10.1017/S0030605316001228

Carroll, C., Roberts, D.R., Michalak, J.L. et al. (2017). Scale-dependent complementarity of climatic velocity and environmental diversity for identifying priority areas for conservation under climate change. Global Change Biology Early View. https://doi.org/10.1111/gcb.13679

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

Carroll, C., & Ray, J. C. (2021). Maximizing the effectiveness of national commitments to protected area expansion for conserving biodiversity and ecosystem carbon under climate change. *Global Change Biology*, gcb.15645. https://doi.org/10.1111/gcb.15645

Cushman, S. A., McKelvey, K. S., & Schwartz, M. K. (2009). Use of Empirically Derived Source-Destination Models to Map Regional Conservation Corridors. *Conservation Biology*, *23(2)*, 368–376. https://doi.org/10.1111/j.1523-1739.2008.01111.x

Dickson, B. G., Roemer, G. W., McRae, B. H., & Rundall, J. M. (2013). Models of Regional Habitat Quality and Connectivity for Pumas (Puma concolor) in the Southwestern United States. *PLoS ONE, 8(12),* e81898. https://doi.org/10.1371/journal.pone.0081898

Dinerstein, E., Vynne, C., Sala, E., Joshi, A. R., Fernando, S., Lovejoy, T. E., Mayorga, J., Olson, D., Asner, G. P., Baillie, J. E. M., Burgess, N. D., Burkart, K., Noss, R. F., Zhang, Y. P., Baccini, A., Birch, T., Hahn, N., Joppa, L. N., & Wikramanayake, E. (2019). A Global Deal For Nature: Guiding principles, milestones, and targets. *Science Advances, 5(4),* eaaw2869. https://doi.org/10.1126/sciadv.aaw2869

Dinerstein, Eric, Olson, D., Joshi, A., Vynne, C., Burgess, N. D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E. C., Jones, B., Barber, C. V., Hayes, R., Kormos, C., Martin, V., Crist, E., … Saleem, M. (2017). An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. *BioScience, 67(6),* 534–545. https://doi.org/10.1093/biosci/bix014

Doyle, Martin W. & F. Douglas Shields. (2012). Compensatory Mitigation for Streams Under the Clean Water Act: Reassessing Science and Redirecting Policy. *Journal of the American Water Resources Association (JAWRA) 48(3),* 494-509.

Elsen, P. R., Monahan, W. B., Dougherty, E. R., & Merenlender, A. M. (2020). Keeping pace with climate change in global terrestrial protected areas. *Science Advances, 6(25),* eaay0814. https://doi.org/10.1126/sciadv.aay0814

Environmental Protection Agency (EPA). (2006). Ecoregions of North America. https://www.epa.gov/eco-research/ecoregions-north-america

Favata, C. A., A. Maia, M. Pant, V. Nepal, & R. E. Colombo. (2018). Fish assemblage change following the structural restoration of a degraded stream. *River Research and Applications 34(8),* 927-936.

Fei, S., J. M. Desprez, K. M. Potter, I. Jo, J. A. Knott & C. M. Oswalt. Divergence of species responses to climate change. (2017). *Science Advances 3(5)*, e1603055. https://doi.org/10.1126/sciadv.1603055

Franks, S. J., & Hoffmann, A. A. (2012). Genetics of Climate Change Adaptation. *Annual Review of Genetics*, *46(1)*, 185–208. https://doi.org/10.1146/annurev-genet-110711-155511

Garibaldi, L. A., Oddi, F. J., Miguez, F. E., Bartomeus, I., Orr, M. C., Jobbágy, E. G., Kremen, C., Schulte, L. A., Hughes, A. C., Bagnato, C., Abramson, G., Bridgewater, P., Carella, D. G., Díaz, S., Dicks, L. V., Ellis, E. C., Goldenberg, M., Huaylla, C. A., Kuperman, M., … Zhu, C. (2021). Working landscapes need at least 20% native habitat. Conservation Letters, 14(2). https://doi.org/10.1111/conl.12773

Gray, C. L., Hill, S. L. L., Newbold, T., Hudson, L. N., Börger, L., Contu, S., Hoskins, A. J., Ferrier, S., Purvis, A., & Scharlemann, J. P. W. (2016). Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nature Communications, 7(1),* 12306. https://doi.org/10.1038/ncomms12306

Groves, C. R., Game, E. T., Anderson, M. G., Cross, M., Enquist, C., Ferdaña, Z., Girvetz, E., Gondor, A., Hall, K. R., Higgins, J., Marshall, R., Popper, K., Schill, S., & Shafer, S. L. (2012). Incorporating climate change into systematic conservation planning. *Biodiversity and Conservation*, *21*(7), 1651–1671. https://doi.org/10.1007/s10531-012-0269-3

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

Hausfather, Z., & Peters, G. P. (2020). RCP8.5 is a problematic scenario for near-term emissions. *Proceedings of the National Academy of Sciences*, *117(45)*, 27791–27792. https://doi.org/10.1073/pnas.2017124117

International Energy Agency (IEA). (2019). World Energy Outlook 2019. https://www.iea.org/reports/world-energy-outlook-2019

Intergovernmental Pannel of Climate Change (IPCC). (2014). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland. https://www.ipcc.ch/report/ar5/syr/

Isaak, D.J.; Wenger, S.J.; Peterson, E.E.; Ver Hoef, J.M.; Hostetler, S.W.; Luce, C.H.; Dunham, J.B.; Kershner, J.L.; Roper, B.B.; Nagel, D.E.; Chandler, G.L.; Wollrab, S.P.; Parkes, S.L.; Horan, D.L. (2016). NorWeST modeled summer stream temperature scenarios for the western U.S. Fort Collins, CO: Forest Service Research Data Archive. https://doi.org/10.2737/RDS-2016-0033.

Jantarasami, L.C., Novak, R., Delgado, R., Marino, E., McNeeley, S., Narducci, C., Raymond-Yakoubian, J., Singletary, L., and K. Powys Whyte. (2018). Tribes and Indigenous Peoples. In Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment, Volume II [Reidmiller, D.R., Avery, C.W., Easterling, D.R., Kunkel, K.E., Lewis, K.L.M., Maycock, T.K., & Stewart, B.C. (eds.)]. U.S. Global Change Research Program, Washington, DC, USA, pp. 572–603. doi: 10.7930/NCA4.2018.CH15

Jayakarana, A.D., Z.T. Smoot, D.M. Park, and D.R. Hitchcock. (2016). Relating stream function and land cover in the Middle Pee Dee River Basin, SC. *Journal of Hydrology Regional Studies, 5,* 261–275.

Jenkins, C. N., Van Houtan, K. S., Pimm, S. L., & Sexton, J. O. (2015). US protected lands mismatch biodiversity priorities. *Proceedings of the National Academy of Sciences, 112(16),* 5081–5086. https://doi.org/10.1073/pnas.1418034112

Keppel, G., & Wardell-Johnson, G. W. (2012). Refugia: Keys to climate change management. *Global Change Biology*, *18(8)*, 2389–2391. https://doi.org/10.1111/j.1365-2486.2012.02729.x

Kraus, D., & Hebb, A. (2020). Southern Canada's crisis ecoregions: Identifying the most significant and threatened places for biodiversity conservation. *Biodiversity and Conservation*, *29(13)*, 3573–3590. https://doi.org/10.1007/s10531-020-02038-x

Lee-Ashley, M., Rowland-Shea, J. & Richards, R. (2019). The Green Squeeze. Washington, D.C., Center for American Progress. https://www.americanprogress.org/issues/green/reports/2019/10/22/476220/the-green-squeeze/

Letcher, B., et al. (2017). Brook Trout Probability of Occurrence. Northeast U.S. North Atlantic Landscape Conservation Cooperative.

Lewis, K. E., Rota, C. T., Lituma, C. M., & Anderson, J. T. (2019). Influence of the Agricultural Conservation Easement Program wetland practices on winter occupancy of Passerellidae sparrows and avian species richness. PLOS ONE, 14(1), e0210878. https://doi.org/10.1371/journal.pone.0210878

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

Locke, H. (2013). Nature needs half: A necessary and hopeful new agenda for protected areas. *PARKS*, *19(2)*, 13–22. https://doi.org/10.2305/IUCN.CH.2013.PARKS-19-2.HL.en

Lookingbill, T. R., Gardner, R. H., Ferrari, J. R., & Keller, C. E. (2010). Combining a dispersal model with network theory to assess habitat connectivity. *Ecological Applications, 20(2),* 427–441. https://doi.org/10.1890/09-0073.1

Maxwell, S. L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A. S. L., Stolton, S., Visconti, P., Woodley, S., Kingston, N., Lewis, E., Maron, M., Strassburg, B. B. N., Wenger, A., Jonas, H. D., Venter, O., & Watson, J. E. M. (2020). Area-based conservation in the twenty-first century. *Nature*, *586*(7828), 217–227. https://doi.org/10.1038/s41586-020-2773-z

McClure, M. L., Hansen, A. J., & Inman, R. M. (2016). Connecting models to movements: Testing connectivity model predictions against empirical migration and dispersal data. *Landscape Ecology*, *31(7),* 1419–1432. https://doi.org/10.1007/s10980-016-0347-0

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

Melillo, J. M., Lu, X., Kicklighter, D. W., Reilly, J. M., Cai, Y., & Sokolov, A. P. (2016). Protected areas' role in climate-change mitigation. *Ambio*, *45(2),* 133–145. https://doi.org/10.1007/s13280-015-0693-1

Merriam, E. R., J. T. Petty, & J. Clingerman. (2019). Conservation planning at the intersection of landscape and climate change: brook trout in the Chesapeake Bay watershed. *Ecosphere, 10(2),* e02585.

Michalak, J. L., Lawler, J. J., Roberts, D. R., & Carroll, C. (2018). Distribution and protection of climatic refugia in North America: Climatic Refugia. *Conservation Biology*, *32*(6), 1414–1425. https://doi.org/10.1111/cobi.13130

Michalak, J. L., D. Stralberg, J. M. Cartwright, & J. J. Lawler. (2020). Combining physical and species-based approaches improves refugia identification, *Front Ecol Environ 18(5)*, 254–260.

Monzón, J., Moyer-Horner, L., & Palamar, M. B. (2011). Climate Change and Species Range Dynamics in Protected Areas. *BioScience, 61(10),* 752–761. https://doi.org/10.1525/bio.2011.61.10.5

Morelli, T. L., C. Daly, S. Z. Dobrowski, D.M. Dulen, J. L. Ebersole, & S. T. Jackson, et al. (2016). Managing climate change refugia for climate adaptation. *PLoS ONE, 11(8),* e0159909.

Morelli, T. L., C. W Barrows, A. R. Ramirez, J. M. Cartwright, D. D. Ackerly, T. D. Eaves, J. L. Ebersole, et al. (2020). Climate-change refugia: biodiversity in the slow lane. *Front Ecol Environ, 18(5),* 228–234.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature, 403(6772),* 853–858. https://doi.org/10.1038/35002501

National Fish, Wildlife, and Plants Climate Adaptation Network (NFWPCAN). (2021). Advancing the national fish, wildlife, and plants climate adaptation strategy into a new decade. Association of Fish and Wildlife Agencies, Washington, DC. https://www.fishwildlife.org/application/files/4216/1161/3356/Advancing_Strategy_Report_FINAL.pdf

National Academy of Sciences, Engineering, and Medicine (NASEM). (2016). A review of the Landscape Conservation Cooperative. Washington, DC: The National Academies Press. https://doi.org/10.17226/21829

Nature Conservancy, The. (2020). Resilient Land Mapping tool. https://maps.tnc.org/resilientland/

Neilson, R. P., Pitelka, L. F., Solomon, A. M., Nathan, R., Midgley, G. F., Fragoso, J. M. V., Lischke, H., & Thompson, K. (2005). Forecasting Regional to Global Plant Migration in Response to Climate Change. *BioScience*, *55(9)*, 749. https://doi.org/10.1641/0006-3568(2005)055[0749:FRTGPM]2.0.CO;2

Newsom, G. (2020). Executive Order N-82-20. https://www.gov.ca.gov/wp-content/uploads/2020/10/10.07.2020-EO-N-82-20-signed.pdf

Pörtner, H.O., Scholes, R.J., Agard, J., Archer, E., Arneth, A., Bai, X., Barnes, D., Burrows, M., Chan, L., Cheung, W.L., Diamond, S., Donatti, C., Duarte, C., Eisenhauer, N., Foden, W., Gasalla, M. A., Handa, C., Hickler, T., Hoegh-Guldberg, O., Ichii, K., Jacob, U., Insarov, G., Kiessling, W., Leadley, P., Leemans, R., Levin, L., Lim, M., Maharaj, S., Managi, S., Marquet, P. A., McElwee, P., Midgley, G., Oberdorff, T., Obura, D., Osman, E., Pandit, R., Pascual, U., Pires, A. P. F., Popp, A., ReyesGarcía, V., Sankaran, M., Settele, J., Shin, Y. J., Sintayehu, D. W., Smith, P., Steiner, N., Strassburg, B., Sukumar, R., Trisos, C., Val, A.L., Wu, J., Aldrian, E., Parmesan, C., Pichs-Madruga, R., Roberts, D.C., Rogers, A.D., Díaz, S., Fischer, M., Hashimoto, S., Lavorel, S., Wu, N., Ngo, H.T. (2021). IPBES-IPCC co-sponsored workshop report on biodiversity and climate change; IPBES and IPCC. DOI:10.5281/zenodo.4782538

Rights and Resources Initiative. (2020). Rights-Based Conservation: The path to preserving Earth's biological and cultural diversity? Washington, DC: Rights and Resources Initiative.

Román-Palacios, C., & Wiens, J. J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences, 117(8),* 4211–4217. https://doi.org/10.1073/pnas.1913007117

Rosa, L. & J. Malcom. (2020). Getting to 30x30: Guidelines for decision makers. Defenders of Wildlife. https://defenders.org/sites/default/files/2020-07/getting-to-30x30-guidelines-for-decision-makers.pdf

Saxon, E. (2008). Noah's Parks: A partial antidote to the Anthropocene extinction event. *Biodiversity*, *9*(3–4), 5–10. https://doi.org/10.1080/14888386.2008.9712901

Scott, J. M., Davis, F. W., McGhie, R. G., Wright, R. G., Groves, C., & Estes, J. (2001). Nature reserves: Do they capture the full range of America's biological diversity? *Ecological Applications*, *11(4)*, 999–1007. https://doi.org/10.1890/1051-0761(2001)011[0999:NRDTCT]2.0.CO;2

Soto-Navarro, C., Ravilious, C., Arnell, A., de Lamo, X., Harfoot, M., Hill, S. L. L., Wearn, O. R., Santoro, M., Bouvet, A., Mermoz, S., Le Toan, T., Xia, J., Liu, S., Yuan, W., Spawn, S. A., Gibbs, H. K., Ferrier, S., Harwood, T., Alkemade, R., … Kapos, V. (2020). Mapping co-benefits for carbon storage and biodiversity to inform conservation policy and action. Philosophical Transactions of the Royal Society B: Biological Sciences, 375(1794), 20190128. https://doi.org/10.1098/rstb.2019.0128

Simmons, B. A., Nolte, C., & McGowan, J. (2021). Delivering on Biden's 2030 conservation commitment [Preprint]. *Ecology*. https://doi.org/10.1101/2021.02.28.433244

Stolton, S., Dudley, N., Çokçalışkan, B. A., Hunter, D., Ivanić, N., Kanga, E., Kettunen, M., Kumagai, Y., Maxted, N., Senior, J., Wong, M., Keenleyside, K., Mulrooney, D., & Withaka, J. (2015). Values and benefits of protected areas. In *Protected Area Governance and Management*. ANU Press.

Stralberg, D., Carroll, C., Pedlar, J. H., Wilsey, C. B., McKenney, D. W., & Nielsen, S. E. (2018). Macrorefugia for North American trees and songbirds: Climatic limiting factors and multi-scale topographic influences. *Global Ecology and Biogeography*, *27*(6), 690–703. https://doi.org/10.1111/geb.12731

Stralberg, D., D. Arseneault, J. L. Baltzer, Q. E. Barber, E. M. Bayne, Y. Boulanger, et al. (2020a). Climate-change refugia in boreal North America: what, where, and for how long? *Front Ecol Environ 18(5)*, 261–270.

Stralberg, D., C. Carroll, & S. E. Nielsen. (2020b). Toward a climate-informed North American protected areas network: Incorporating climate-change refugia and corridors in conservation planning. *Conservation Letters*, e12712.

Stranko, S. A., R. H. Hilderbrand, R. P. Morgan II, M. W. Staley, A. J. Becker, A. Roseberry-Lincoln, E. S. Perry, & P. T. Jacobson. (2008). Brook Trout Declines with Land Cover and Temperature Changes in Maryland. *North American Journal of Fisheries Management, 28,* 1223-1232.

Sullivan, S. M. P. & M. C. Watzin. (2009). Stream–floodplain connectivity and fish assemblage diversity in the Champlain Valley, Vermont. *Journal of Fish Biology, 74,* 1394–1418.

Sweeney, B. W. & J. D. Newbold. (2014). Streamside Forest Buffer Width Needed to Protect Stream Water Quality, Habitat, and Organisms: A Literature Review. *Journal of the American Water Resources Association (JAWRA), 50(3),* 560-584.

Theoharides, K. (2014). Seeds of Resilience: Safeguarding Wildlife and Habitat from Climate Change through the Farm Bill Conservation Programs. Defenders of Wildlife. https://defenders.org/sites/default/files/publications/seeds-of-resilience-safeguarding-wildlife-and-habitat-from-climate-change-through-the-farm-bill-conservation-programs.pdf

United Nations Environment Program Convention on Biological Diversity (2020). Zero draft of the post-2020 global biodiversity framework. https://www.cbd.int/doc/c/efb0/1f84/a892b98d2982a829962b6371/wg2020-02-03-en.pdf

U.S. Fish and Wildlife Service (USFWS) & Association of Fish and Wildlife Agencies (AFWA). (2017). Guidance for Wildlife Action Plan Review and Revision. https://fawiki.fws.gov/download/attachments/5931146/2017%20Guidance%20on%20Wildlife%20Action%20Plan%20Review%20and%20Revision.pdf?version=1&modificationDate=1512664258000&api=v2

U.S. Geological Survey (USGS) Gap Analysis Project (GAP). (2020). Protected Areas Database of the United States (PAD-US) 2.1. U.S. Geological Survey data release, https://doi.org/10.5066/P92QM3NT.

U.S. Departments of Interior (DOI), Agriculture, Commerce, and the Council on Environmental Quality. (2021). Conserving and Restoring American the Beautiful. https://www.doi.gov/sites/doi.gov/files/report-conserving-and-restoring-america-the-beautiful-2021.pdf

Venter, O., Magrach, A., Outram, N., Klein, C. J., Possingham, H. P., Di Marco, M., & Watson, J. E. M. (2018). Bias in protected-area location and its effects on long-term aspiration of biodiversity conventions. Conservation Biology, 32(1), 127-134. https://doi.org/10.1111/cobi.12970

Vose, R. S., Easterling, D. R., Kunkel, K. E., LeGrande, A. N., & Wehner, M. F. (2017). Ch. 6: Temperature Changes in the United States. Climate Science Special Report: Fourth National Climate Assessment, Volume I. U.S. Global Change Research Program. https://doi.org/10.7930/J0N29V45

Wiens, J. J. (2016). Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. *PLOS Biology*, *14(12)*, e2001104. https://doi.org/10.1371/journal.pbio.2001104

Wuebbles, D. J., Fahey, D. W., Hibbard, K. A., Dokken, D. J., Stewart, B. C., & Maycock, T. K. (2017). Climate Science Special Report: Fourth National Climate Assessment, Volume I. U.S. Global Change Research Program. https://doi.org/10.7930/J0J964J6

TABLES AND FIGURES

Table 1. Description of refugia datasets. Classes are based on results from a principal components analysis where component 1 (topodiversity) explained 33.8%, component 2 (climate stability) explained 15.9% and component 3 (tree macrorefugia) explained near 13.8% of variation. See SI for additional details.

Refugia Class	Dataset	Description	Source
Topodiversity	Current Climate Diversity	*Climate-Based.* Based on 11 bioclimatic variables using climate data for a 30-year climate normal period (1981-2010).	Carroll et al., 2017
	Ecotypic Diversity	*Landscape-based and climate-based.* Derived from edaphic, climatic, and landcover data.	Carroll et al., 2017
	Land Facet Diversity	*Landscape-based.* Incorporated elevation, latitude-adjusted elevation, topographic position index, slope, modified heat load index, and soil.	Carroll et al., 2017
	Landscape Diversity	*Landscape-based.* Described the diversity of microhabitats and climatic gradients. Microclimates were measured by quantifying elevation range, the variety of small-scale landforms, and the density and configuration of wetlands in a 100-acre neighborhood.	The Nature Conservancy, 2020
	Bird Macrorefugia	*Climate-based and species-based.* Focused on regions where the current and projected future species ranges overlap. Input based on current species niches for 268 songbird species; climate velocity based on 4 representative GCMs, RCP 4.5, 2080s.	Stralberg et al., 2018
Climatic Stability	Climatic Dissimilarity	*Climate-based.* Described how different the future climate at a location will be from its current climate. Measured in terms of multivariate climate characteristics, via a principal components analysis (PCA) of 11 biologically-relevant temperature and precipitation variables, RCP 4.5, 2080s.	Belote et al., 2018
	Climate Velocity	*Climate-based.* Velocity was calculated by dividing the rate of climate change by the rate of spatial climate variability to focus on regions where climatic conditions move more slowly across the landscape. Input based on A2 emissions scenarios implemented by seven GCMs of the CMIP3 multimodel dataset, RCP 4.5, 2080s.	AdaptWest Project, 2015
Tree Macrorefugia	Tree Macrorefugia	*Climate-based and species-based.* Focused on regions where the current and projected future species ranges overlapped. Input based on current species niches for 324 tree species; climate velocity based on 4 representative GCMs, RCP 4.5, 2080s.	Stralberg et al., 2018

Table 2. Overlays of national-level datasets representing protected areas, carbon stores, biodiversity, climate refugia, and climate corridors. Values represent the percent of each top line item (column) that falls within each row. Values in parentheses are the percent of total CONUS area represented by the overlay.

% of top line items that fall into each of the following:	**GAP 1 & 2**	**GAP 3**	**Top 20% Carbon**	**Top 20% Biodiversity**	**Top 20% Refugia**	**Top 20% Climate-Informed Corridors**
GAP 1 & 2	100 (7.5)	0.0 (0.0)	12.7 (2.4)	3.7 (0.7)	13.3 (2.6)	13.8 (2.7)
GAP 3	0.0 (0.0)	100 (16.6)	20.2 (3.9)	5.1 (1.0)	25.0 (4.8)	30.4 (6.0)
Top 20% Carbon	32.8 (2.4)	23.3 (3.9)	100 (20.0)	28.8 (5.6)	32.5 (6.2)	27.2 (5.4)
Top 20% Biodiversity	12.3 (0.7)	8.7 (1.0)	32.0 (5.6)	100 (20.0)	30.8 (5.9)	11.2 (1.8)
Top 20% Refugia	34.2 (2.6)	29.0 (4.8)	32.8 (6.2)	36.8 (5.9)	100 (20.0)	28.7 (5.7)
Top 20% Climate-Informed Corridors	36.5 (2.7)	36.3 (6.0)	25.8 (5.4)	9.3 (1.8)	29.6 (5.7)	100 (20.0)

Table 3. Overlays of ecoregion-specific datasets representing protected areas, carbon stores, biodiversity, climate refugia, and climate corridors. Values represent the percent of each top line item (column) that falls within each row. Values in parentheses are the percent of total CONUS area represented by the overlay.

% of top line items that fall into each of the following:	GAP 1 & 2	GAP 3	Top 20% Carbon	Top 20% Biodiversity	Top 20% Refugia	Top 20% Climate-Informed Corridors
GAP 1 & 2	100 (7.5)	0.0 (0.0)	1.1 (2.2)	8.6 (1.5)	12.2 (2.4)	13.8 (2.7)
GAP 3	0.0 (0.0)	100 (16.6)	17.9 (3.5)	17.7 (3.1)	19.6 (3.8)	30.4 (6.0)
Top 20% Carbon	29.8 (2.2)	21.2 (3.5)	100 (20.0)	28.0 (4.9)	21.7 (4.2)	26.1 (5.2)
Top 20% Biodiversity	18.4 (1.5)	17.5 (3.1)	26.4 (4.9)	100 (20.0)	22.0 (4.2)	17.5 (3.3)
Top 20% Refugia	31.4 (2.4)	22.7 (3.8)	21.3 (4.2)	24.2 (4.2)	100 (20.0)	25.9 (5.1)
Top 20% Climate-Informed Corridors	36.5 (2.7)	36.3 (6.0)	26.3 (5.2)	18.8 (3.3)	26.7 (5.1)	100 (20.0)

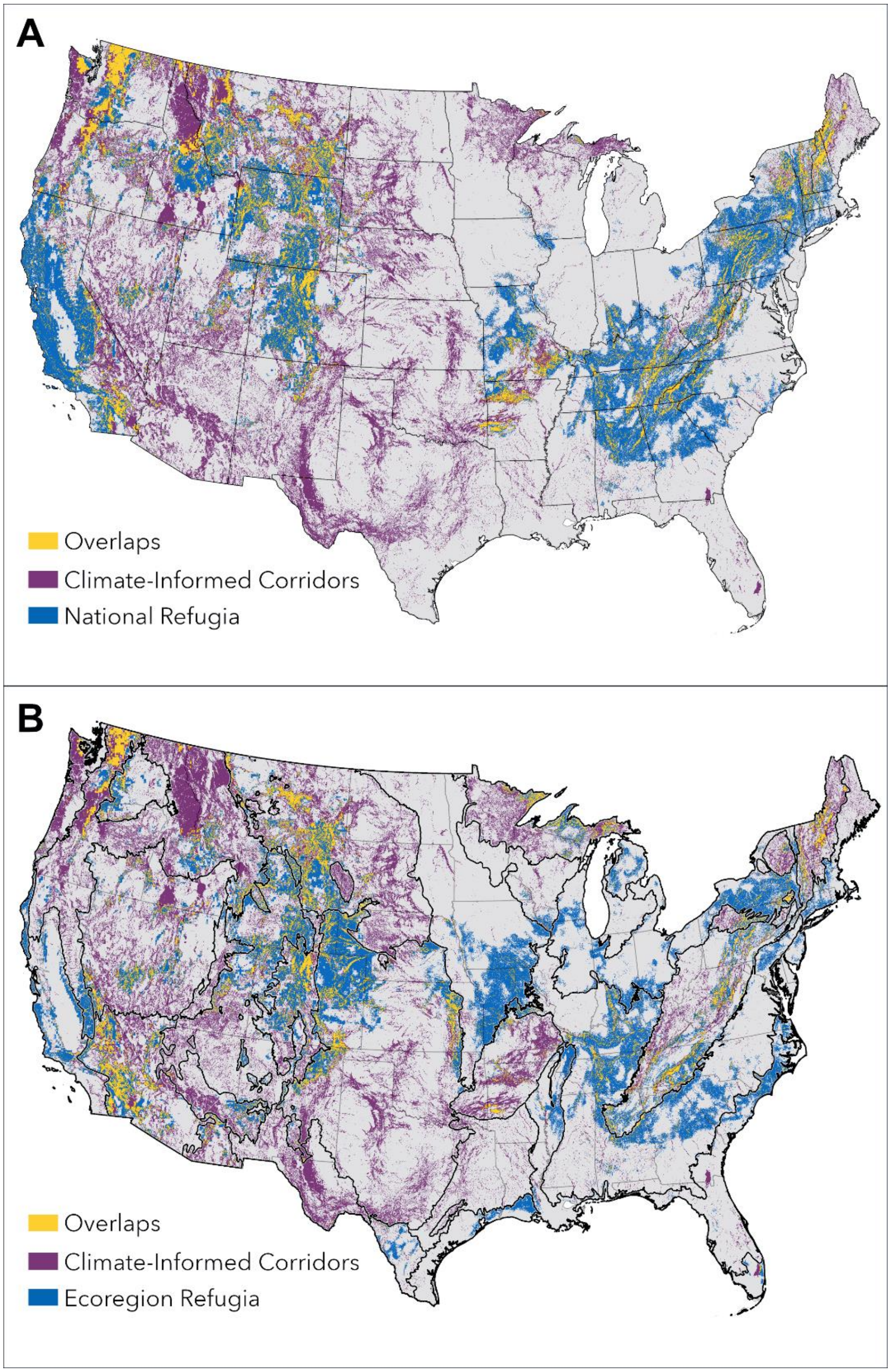

Figure 1. A) National-scale and B) ecoregion-specific refugia (top 20% of all three refugia classes combined) with climate-informed corridors (ecoregions are outlined in black). The full raster datasets were used to identify refugia in national analyses. Ecoregion-specific analyses employ a stratified approach, where refugia are identified for each ecoregion separately before combining them together. Ecoregions are outlined in black in map B.

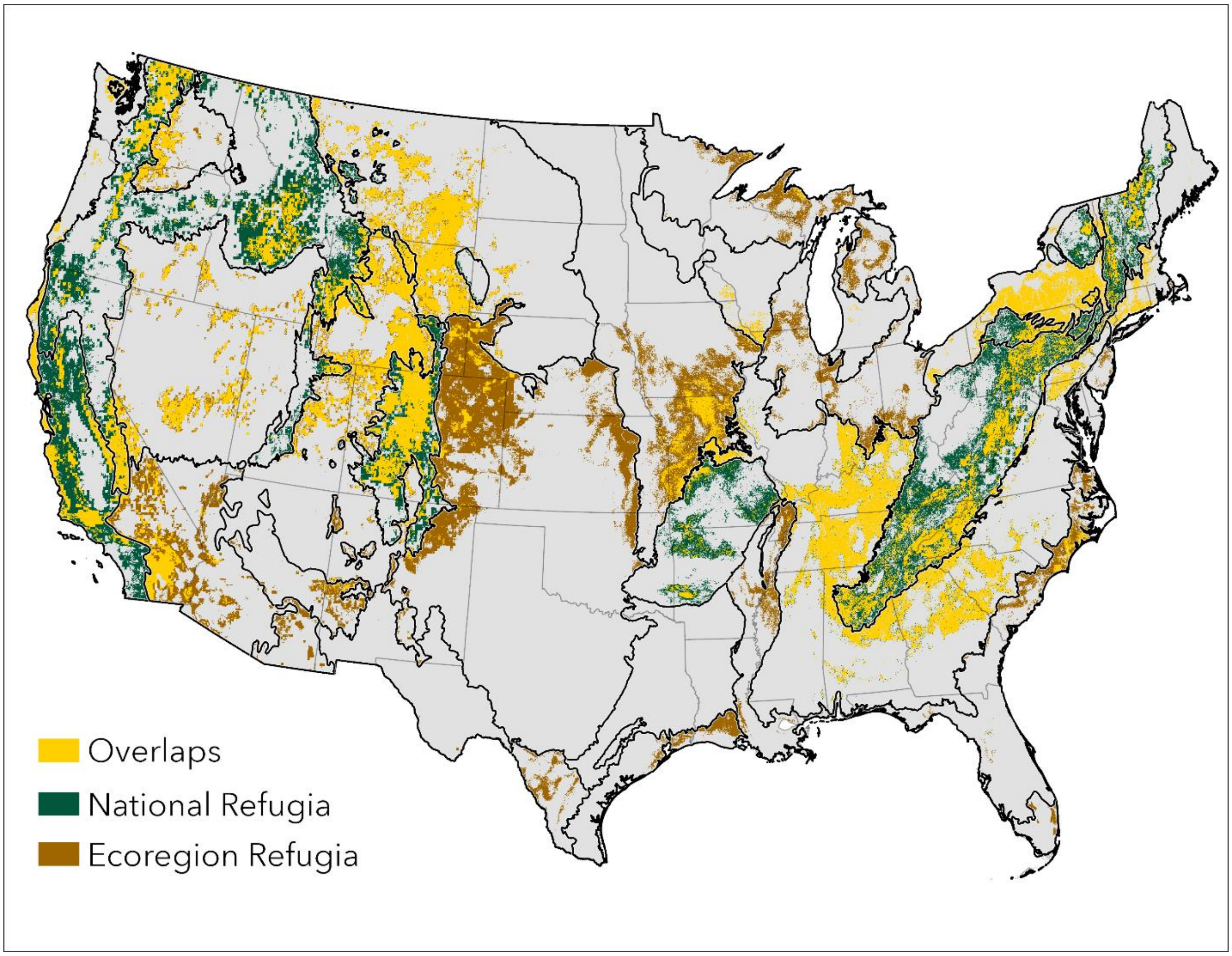

Figure 2. Coincidence between national-scale and ecoregion-specific refugia. The full raster datasets were used to identify refugia in national analyses. Ecoregion-specific analyses employ a stratified approach, where refugia are identified for each ecoregion separately before combining them together. Ecoregions are outlined in black.

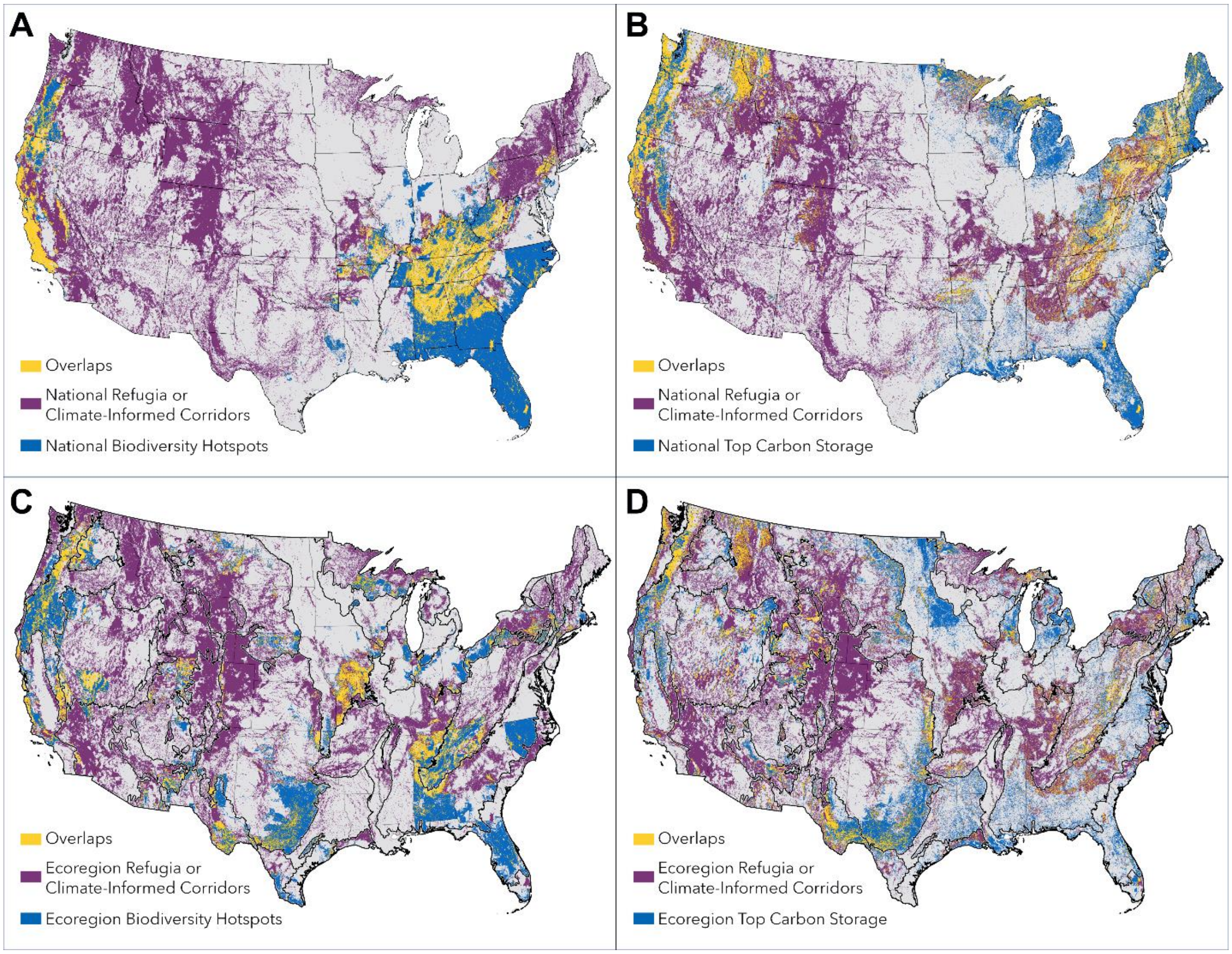

Figure 3. Overlap between national-scale (A,B) and ecoregion-scale (C,D) refugia and corridors with carbon stocks (B,D) and biodiversity hotspots (A,C). The full raster datasets were used to identify refugia in national analyses. Ecoregion-specific analyses employ a stratified approach, where refugia are identified for each ecoregion separately before combining them together. Ecoregions outlined in black in maps C and D.

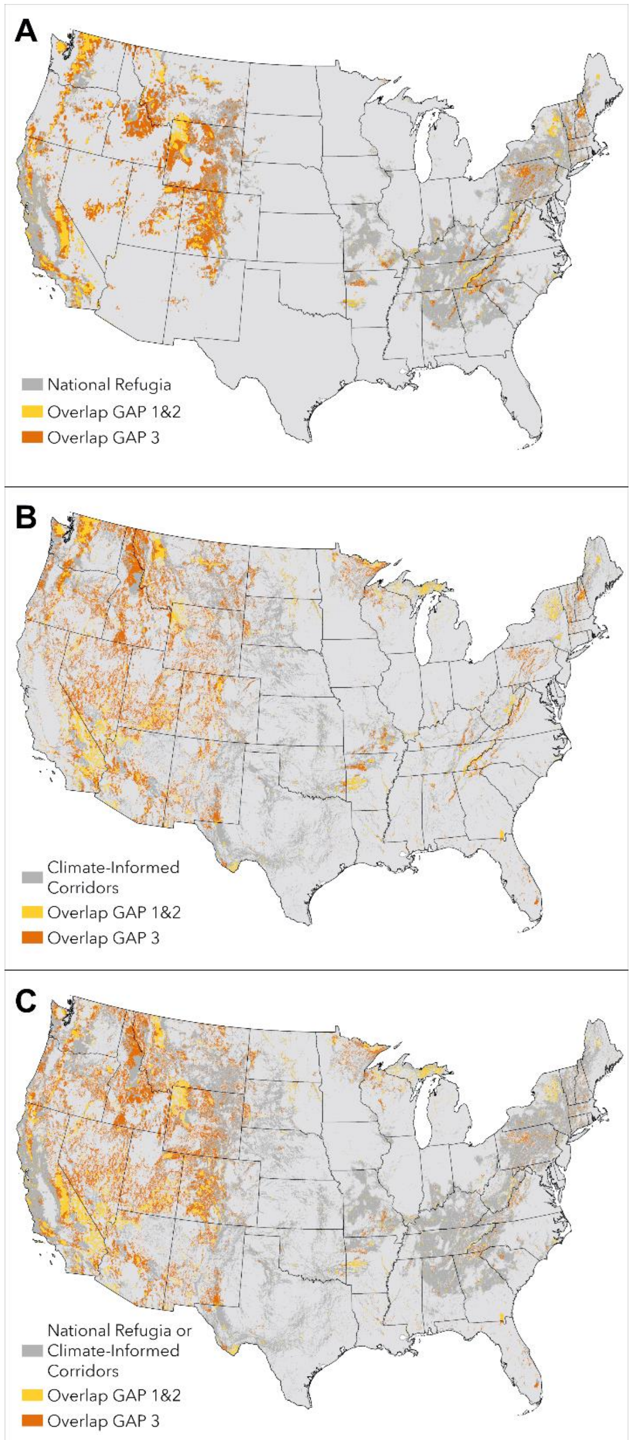

Figure 4. Overlap between national-scale refugia (A), climate corridors (B), and either refugia or corridors (C) with the protected areas database of the US (PADUS). GAP codes are specific to the management intent to conserve biodiversity; GAP 1 and 2 areas are managed in ways typically consistent with conservation and GAP 3 areas are governed under multiple-use mandates that may include biodiversity priorities but may also include incompatible activities.