# Combining physical and species-based approaches improves refugia identification

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Climate-change refugia – locations likely to facilitate species persistence under climate change – are increasingly important components of conservation planning. Recent approaches for identifying refugia at broad scales include identifying regions that are projected to experience less severe changes (climatic exposure), that contain a diversity of physical and topographic features (environmental diversity), and that either retain or remain close to suitable climatic conditions (climate tracking, including both "species-neutral" and species-based approaches). We compared the degree of agreement between these approaches – with respect to their spatial coverage and other characteristics – across much of North America. This analysis found that approaches based on environmental diversity and species-neutral climatic gradients both favored topographically complex regions, whereas climatic exposure and species-based approaches identified regions with a range of topographic characteristics. Species-based approaches targeting specific habitat groups identified unique regions missed by other approaches, emphasizing the importance of asking the question "refugia for what?" when prioritizing refugia. Our results highlight the necessity of including climatic exposure and species-based information in addition to topographic diversity and climatic gradients in refugia analyses.

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Historically, many species have persisted through periods of climate change by occupying locations that retained suitable climates despite regional declines in climatic suitability (Keppel *et al*. 2012). Identifying and protecting such refugia has become a key focus of biodiversity conservation efforts (Groves *et al*. 2012; Carroll *et al*. 2017), but these efforts are challenged by the unique needs of individual species, varying definitions, and increasingly diverse approaches to mapping potential refugia (Ashcroft 2010; Reside *et al*. 2014). Incorporating refugia into conservation planning requires that managers understand the different types of refugia identified by various approaches, how they are spatially distributed, and the relative agreement among them.

## In a nutshell:

- We compared the spatial distribution of climate-change refugia identified by several new approaches at broad spatial scales
- Potential refugia were identified in most regions, although the types of refugia identified varied substantially across regions
- Many refugia identification approaches prioritize mountainous regions; the exceptions identify locations with relatively low climatic exposure or use species range-shift models
- Species-based refugia approaches may be uniquely important in flat regions
- As compared to using a single approach, pairing species-based with species-neutral approaches provides a more complete understanding of the potential for a region to provide refugia

Certain landscape characteristics may make a location more likely to serve as a refugium for a greater number of species. At the broadest level, latitude, elevation, distinctive landforms, and large-scale atmospheric circulation patterns determine which regions retain the coolest, warmest, driest, or wettest conditions on any continent (Stewart *et al*. 2010). Unique regional climatic characteristics, such as upwelling in large lakes or coastal air currents, may buffer the impacts of climate change, resulting in regions with relatively low climatic exposure (Stralberg *et al*. 2020). Landscape topography can also offset regional climatic exposure. Areas with complex topography have steep climatic gradients and diverse microclimatic conditions, including some that are cooler or wetter than the region at large (Ashcroft 2010; Dobrowski 2011). Ultimately, however, the ability of a location to serve as a refugium for any individual species depends on the range of climatic conditions that the species can tolerate (ie its climatic niche) and the degree to which the refugium provides those conditions despite broader climatic changes (Ashcroft 2010).

Several approaches to mapping potential climate-change refugia for biodiversity have recently been proposed (Carroll *et al*. 2017; Michalak *et al*. 2018; Stralberg *et al*. 2018). Each of these approaches relies on one or more of the following concepts to identify such refugia: climatic exposure, environmental diversity, and climate tracking over time and space. Climatic exposure approaches identify areas where projected

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**Table 1. Description of refugia classes and datasets**

| Refugia class | Conservation target | Regions identified | Dataset(s) | Priority regions |
|---|---|---|---|---|
| Environmental diversity | Physical landscape (species-neutral) | Physically diverse landscapes (eg diverse climatic, topographic, soil, and/or land-cover characteristics) | Land facet, current climate, and ecotypic diversity (Carroll *et al.* 2017) | Topographically complex regions, such as western North America and the Appalachian Mountains |
| Climatic exposure | Climate-based, no species information (species-neutral) | Regions where the degree of projected climate change is relatively low | Climatic dissimilarity (Belote *et al.* 2018) | West Coast and southern US |
| Climate tracking | Climate-based, no species information (species-neutral) | Regions where climatic conditions move more slowly across the landscape | Climate velocity (Carroll *et al.* 2017) | Topographically complex regions, such as western North America and the Appalachian Mountains |
| | | Regions that retain increasingly rare climatic conditions | Rare-climate refugia (Michalak *et al.* 2018) | High-elevation mountain tops and northern continental margins |
| | Climate-based with species information (species-based) | Regions where the current and projected future ranges of resident species overlap or remain physically close | Biotic velocity (Stralberg *et al.* 2018) | Variable depending on the species or groups of species selected |

climatic changes are relatively small, presumably reducing impacts on local species (Groves *et al.* 2012). Approaches focusing on environmental diversity highlight regions with varied land cover, climate, soil, and topographic conditions, which often contain features like deep valley bottoms or shaded slopes that may produce microrefugia, or fine-scaled landscape features with regionally distinct climatic characteristics (Ackerly *et al.* 2010; Lawler *et al.* 2015; Carroll *et al.* 2017). Approaches based on climate tracking measure the proximity and accessibility of future suitable climatic conditions, identifying both in situ refugia (locations that remain suitable) and ex situ refugia (suitable climatic conditions in new locations) (Ashcroft 2010). There are two versions of climate-tracking approaches: species-neutral or species-based. Species-neutral (or "coarse-filter") versions do not necessarily account for the climatic requirements of individual species but do include measures of the rate at which hypothetical organisms must move to track suitable climatic conditions (ie climatic velocity; Loarie *et al.* 2009; Hamann *et al.* 2015), or locations that retain increasingly rare climatic conditions (ie rare-climate refugia; Michalak *et al.* 2018). In contrast, species-based (or "fine-filter") versions are based on the distance between individual species' projected future and current ranges over a given time period (ie biotic velocity). Locations where future ranges overlap or are near the species' current range are considered to have low velocities and therefore to be potential refugia for that species (Serra-Diaz *et al.* 2014; Carroll *et al.* 2015; Stralberg *et al.* 2018).

We identified published refugia datasets, each of which spanned most of North America; belonged to one of three classes (climatic exposure, environmental diversity, or climate tracking); and were broad-scale (≥1-km$^2$ resolution) and publicly available at the time of this study (WebPanel 1). We then explored the spatial agreement of refugia as interpreted from the datasets of these multiple studies, both within and across refugia classes. We also identified landscape characteristics associated with each of the refugia datasets to better understand what factors are driving spatial similarities and differences.

## Methods

A total of 11 refugia datasets covering the majority of North America were identified and grouped into one of three classes: (1) climate-exposure refugia (one dataset [Belote *et al.* 2018]), (2) environmental diversity-based refugia (three datasets [Carroll *et al.* 2017]), and (3) climate tracking-based refugia (including two species-neutral datasets [Carroll *et al.* 2017; Michalak *et al.* 2018] and five species-based datasets [including refugia indices for forest, woodland, grassland, and scrub songbirds and trees from Stralberg *et al.* 2018]) (Table 1; WebPanel 1). All data were originally available at 1-km$^2$ resolution, except for the species-based climate-tracking refugia. To match the species-based refugia, we resampled other layers to 10-km$^2$ resolution. The geographic extent of the smallest dataset limited our study area to the continental US and most of Canada. All processing of spatial data was performed using the *raster* package in R (v3.4.3; R Core Team 2018).

For refugia that incorporated projected future climatic conditions, we used mid-century (2041–2070) and end-of-century (2071–2100) projections (hereafter, the 2050s and 2080s, respectively) as well as Representative Concentration Pathway (RCP) 8.5, which assumes relatively high levels of atmospheric greenhouse-gas emissions (Riahi *et al.* 2011). All the 11 refugia datasets we considered provided a continuous measure of refugia value for each site, except for one that was binary (refugium/non-refugium). We evaluated the overall correlation among continuous refugia datasets using the Spearman rank correlation coefficient ($\rho$). We used generalized additive models (GAMs) to evaluate relationships between each refugia dataset and latitude, elevation, and topographic complexity (WebPanel 1).

To identify regional patterns in refugia characteristics, we created three composite refugia layers representing locations with high values for each refugia class. To combine the layers, we first identified all locations with values at or above the 75th percentile for each continuous refugia dataset and reclassified these locations as potential refugia. The composite refugia layers designated any location identified as potential refugia by at least one dataset within each class as potential refugia for that class. We overlaid each composite layer to identify regions with high refugia value for one or more classes.

## Results

The level of agreement among refugia datasets varied widely. Results for the 2050s (presented in the main text) and the 2080s (presented in WebFigures 1 and 2) were qualitatively similar. Environmental diversity datasets were highly correlated (0.62 ≤ ρ ≤ 0.72) and moderately correlated with one of the two species-neutral climate-tracking datasets (climatic velocity, 0.39 ≤ ρ ≤ 0.48). Correlation coefficients between the remaining datasets were moderate to low (–0.32 ≤ ρ ≤ 0.45). Refugia values based on climatic exposure and one of the climate-tracking approaches (grassland bird refugia) were largely uncorrelated with values based on other approaches (mean ρ = –0.02 for both) (WebTable 1).

Mountainous regions were identified as potential refugia by the greatest number of datasets (WebFigure 3), as refugia value increased with elevation and topographic complexity for most approaches (WebFigure 1). However, the strength of this relationship varied. One environmental diversity approach (current climate diversity) and four climate-tracking approaches (climatic velocity, tree, forest bird refugia, and woodland bird refugia) resulted in values that increased with elevation. In contrast, the potential for scrub bird and grassland bird refugia increased only slightly at higher elevations, and areas with low climatic exposure were most common at mid-elevations. The potential for climate-exposure refugia declined with increasing latitude (WebFigure 1c), whereas little to no relationship was found between the other two refugia approaches and latitude.

Collectively, 86% of the study area was identified as potential refugia for at least one refugia class (Figure 1a). Locations identified as having both high environmental diversity and low climatic exposure were rare, accounting for only 10% of potential refugia locations. Consequently, only 7% of the study area, primarily along the West Coast, within the southwestern US, and in the southern Appalachian Mountains, was identified as potential refugia for all three classes.

Areas with potential climate-tracking refugia covered 77% of the study area and included most areas identified by environmental diversity or climate-exposure approaches (Figure 1a). The two species-neutral climate-tracking approaches (climatic velocity and rare-climate refugia) overlapped substantially with each other and with environmental diversity-based refugia (Figure 1b). Species-based refugia alone identified potential refugia in the flat central regions of the continent (Figure 1c).

Geographic variability across the different refugia classes resulted in regions with distinct refugia characteristics (Figure 1). Mountainous western North America scored high for all refugia classes, except for climatic exposure. The Southeastern Coastal Plain in the US had low environmental diversity but also low climatic exposure and high climate-tracking refugia potential. Plains regions in the middle of the continent had low refugia values across most datasets but relatively high refugia potential for grassland birds, and to a lesser extent scrub birds (WebFigure 4). Only 14% of the study area, mostly in Canada's flat boreal region and sections of the North American Great Plains, had low refugia value for all classes (Figure 1).

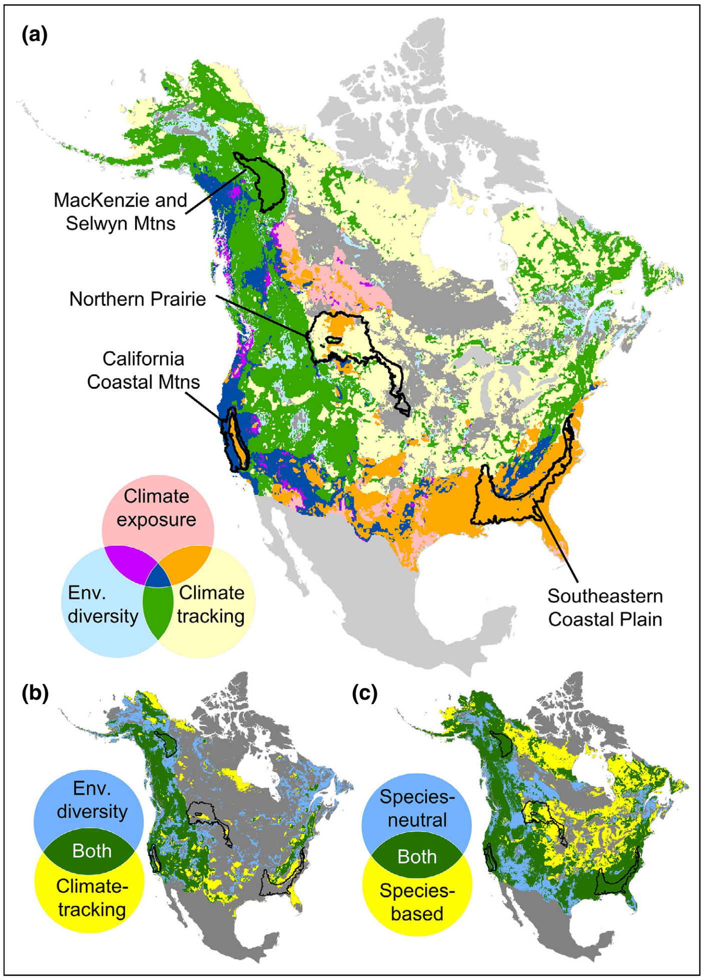

**Figure 1.** Spatial distribution and overlap of refugia approaches for the 2050s: (a) climatic exposure, environmental diversity, and climate-tracking approaches; (b) environmental diversity and species-neutral climate-tracking approaches; and (c) species-neutral and species-based approaches. Single colors indicate locations with potential refugia (≥75th percentile) for one or more datasets within each class; overlapping colors indicate potential refugia according to more than one approach, with colors as shown in the Venn diagrams. Boundaries for case study ecoregions are in black.

## Discussion

We compared the spatial distribution of climate-change refugia identified by several new approaches at broad spatial scales. Only 7% of the study area (ie the continental US and most of Canada) was classified as potential refugia for all three refugia classes (climatic exposure, environmental diversity, and climate tracking), although 86% was classified as refugia for at least one of the three classes. This discrepancy indicates that some approaches for identifying refugia were more relevant in particular regions depending on physical landscape characteristics.

Topography was a key determinant of potential refugia based on environmental diversity, species-neutral climate-tracking, and some species-based climate-tracking approaches. These approaches identified regions with rugged topography (Figure 1b; WebFigures 4 and 5), emphasizing that such regions are likely to provide multiple types of refugia (Reside *et al*. 2014). By contrast, latitude, not topography, heavily influenced the distribution of climate-exposure refugia due to more rapid warming at the poles, creating potential climate-exposure refugia in the Southeastern Coastal Plain and along the West Coast (Figure 1). The lack of geographic overlap between climatic exposure refugia and the more topographically determined environmental diversity or species-neutral climate-tracking approaches does not indicate uncertainty but rather highlights the complementary information provided by these approaches (Belote *et al*. 2018).

Species-based approaches add another level of information critical to refugia identification because they account for the climatic requirements of individual species. Raw measures of climatic exposure, general climate shifts, or topography alone may over- or underestimate refugia potential because individual species tolerate greater or lesser degrees of climate change. We found that species-based approaches, when subdivided by habitat groups, identified the greatest diversity of regions, including some that were not prioritized by other approaches. For example, maps of species-based refugia targeting grassland birds – a highly vulnerable species group (Wilsey *et al.* 2019) – prioritized the Northern Prairie despite both low environmental diversity and moderate climatic exposure in this region (WebFigure 4). Consequently, species-based approaches are widely applicable and may be uniquely important in some regions.

Although species-based approaches provide unique information, there are trade-offs between species-neutral and species-based refugia approaches. Species-neutral approaches rely on readily available datasets, can be widely implemented, and do not require species-specific information (Beier and Brost 2010; Carroll *et al*. 2017). In addition, environmental diversity approaches are both species-neutral and avoid the uncertainty introduced by climate projections (but see Lawler and Michalak [2017]). Species-based approaches, on the other hand, rely on data-intensive range-shift models with numerous limitations, which raises concerns about their validity (Pearson and Dawson 2003). Despite these concerns, such models approximate recent shifts in species distributions well (Araújo *et al*. 2005; Comte and Grenouillet 2015). Notably, range-shift models are generally available only for well-studied taxonomic groups, such as the tree and four bird groups analyzed here. Given these limitations – and as with traditional conservation planning frameworks (eg Groves *et al*. 2002) – combining species-neutral and species-based approaches in refugia identification may result in more comprehensive biodiversity protection than relying on a single approach.

The approaches analyzed here focus on identifying continental regions that may act as potential refugia. However, none of the compared approaches are designed to identify specific fine-scale refugial features such as incised valleys (Dobrowski 2011), or hydrologic refugia like springs or lakeshores (McLaughlin *et al*. 2017; Cartwright *et al*. 2020). In addition, old-growth forests (Betts *et al*. 2018), peat-forming wetlands (Stralberg *et al*. 2020), fine-scale (<10 m) terrain characteristics, and tree-canopy effects (Lenoir *et al*. 2017; De Frenne *et al*. 2019) can influence climate, potentially creating local refugia. As such, finer-scaled approaches to identify specific refugia sites would complement the broad-scale methods explored here.

## Regional examples and management implications

Regional physical (including climatic) characteristics influence both the types of climate changes that affect an area (Garcia *et al*. 2014) and the potential refugia that may be present. Applying complementary refugia mapping approaches that capture these different characteristics offers a more complete understanding of regional refugia, facilitating more tailored management actions. A few regions, such as the California Coastal Mountain region (Figure 2a), contain high refugia values across all three refugia classes (Figure 3). Climatic exposure in this region is buffered by the California Current, which cools the area and generates coastal fog (Petterssen 1938). The California Coastal and Sierra Nevada mountain ranges contain steep elevational gradients, which create diverse microclimates and reduce the rates at which species will need to move to track suitable climates (Ackerly *et al*. 2010). Our study found high macrorefugia potential in this region for woodland, grassland, and scrub birds, as well as for trees, adding to the region's potential to serve as a refugium for endemic plants (Loarie *et al*. 2008). This region has a dense human population and contains many rare and endemic species; therefore, protecting potential refugia from development and preserving climatic connectivity may help to maintain biodiversity in this area as the climate changes (Carroll *et al*. 2018).

Most regions, were not identified as potential refugia by all approaches. For example, in the Mackenzie and Selwyn Mountains of the Yukon and Northwest Territories (Figure 2b), steep terrain creates large climatic gradients that increase climate-tracking potential. Microrefugia created by complex topography may protect vulnerable species or systems (eg by mitigating tree invasion of alpine meadows; Zald *et al*. 2012). Nevertheless, polar amplification of climate change increases climatic exposure in this region (Figure 3), and mountain

M McBay

Sahtu Wildlife

A Cressler

B Snyder

**Figure 2.** Example ecoregions illustrating variation in regional refugia characteristics: (a) California Coastal Mountains, (b) MacKenzie and Selwyn Mountains, (c) Southeastern Coastal Plain, and (d) Northern Prairie.

geometry limits high-elevation range shifts (Elsen and Tingley 2015). Complex topography may also increase cumulative exposure to unsuitable conditions as species move to track suitable climates (Dobrowski and Parks 2016). Careful monitoring in such regions may help to identify and mitigate lags in species' range shifts.

Ecoregions with low topographic relief, such as the Southeastern Coastal Plain (Figure 2c) and the Northern Prairie (Figure 2d), may seem to have poor refugia potential due to low environmental diversity and limited climate-tracking potential (Figure 3). Yet the Southeastern Coastal Plain also has relatively low climatic exposure, as well as potential to provide tree and forest bird refugia; this region also served as a refugium during previous climate shifts (Noss *et al.* 2015). Projected climatic exposure is somewhat higher in the Northern Prairie region but, again, a species-specific approach identifies the region as containing potential grassland bird refugia. In these regions, topography may be less important in supporting fine-scale refugia than hydrologic features such as springs, riparian areas, and lakeshores, which influence soil moisture and surface water availability (McLaughlin *et al.* 2017; Anderson *et al.* 2018). Furthermore, because relatively flat, fertile landscapes are commonly dominated by intensive land uses (eg row-crop agriculture), refugia locations may be constrained by habitat quality and availability.

## Conclusions

Ultimately, the climate refugia potential of a location depends on interactions between the physical landscape, the degree of climatic change, and the ecological tolerances of the species present. To date, approaches to mapping refugia at broad scales have focused primarily on landscape characteristics and general measures of climatic conditions. However, methods incorporating species-specific climatic tolerances, which are overlooked by species-neutral approaches, can produce more nuanced depictions of the value of regional ecological refugia. Asking the question "refugia for what?" and incorporating species-specific information into refugia planning may therefore be essential to better understand and manage for refugia, especially in areas lacking topographic complexity.

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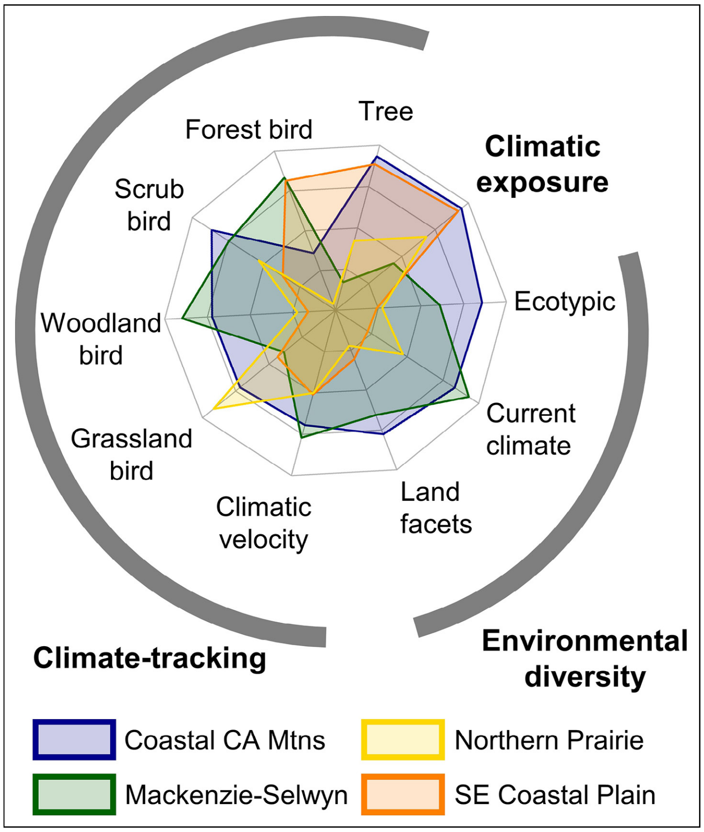

**Figure 3.** Radar chart showing standardized values for 10 refugia datasets with continuous values, grouped by refugia class (in bold), for each case study region. Values closer to the center of the plot indicate lower refugia potential according to that dataset. The rare-climate refugia dataset was omitted because the values are binary. See Table 1 for dataset descriptions.

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## Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2207/suppinfo

FrontiersEcoPics

### Get off my lawn!

As arguably the world's most venomous spider, the Sydney funnel-web spider (*Atrax robustus*) has a reputation for being a spider to avoid. Pictured here is a classic example of a threat display, with front legs raised and fangs exposed.

This male was found under a log during a university BioBlitz. Males are often very quick to react, with this one responding immediately to a gentle poke. The purpose of the display is to make the spider look bigger and to show off their most feared assets: their large, powerful fangs. This display is a warning, an unequivocal sign to back off or risk a bite.

Sydney funnel-web venom, which contains an ion-channel inhibitor called delta atracotoxin, is highly toxic to humans and other primates but has little to no effect on most other mammals. This is intriguing as, aside from humans, no other primate species live in Australia where the spider is found. Does the Sydney funnel-web therefore represent the only species that has evolved a toxin exclusively to defend itself from humans? Or is the fact its venom works so effectively against humans just a bizarre coincidence in a species that mostly feeds on large invertebrates? The venom is actually adapted to rapidly paralyze millipedes, one of the funnel-web's typical prey, and researchers agree that its effects on humans are purely coincidental.

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