Journal of Ecology and Toxicology

Combining physical and species-based approaches improves refugia identification

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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 suitabil- ity (Keppel et al. 2012). Identifying and protecting such refu- gia 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 identifed by various approaches, how they are spatially distributed, and the relative agreement among them.

Certain landscape characteristics may make a location more likely to serve as a refugium for a greater number of spe- cies. At the broadest level, latitude, elevation, distinctive land- forms, and large-scale atmospheric circulation patterns deter- mine 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 microcli- matic 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 refu- gium for any individual species depends on the range of cli- matic 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 con- cepts to identify such refugia: climatic exposure, environmen- tal diversity, and climate tracking over time and space. Climatic exposure approaches identify areas where projected 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 fne-scaled landscape features with regionally distinct climatic character- istics (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 condi- tions, 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-fiter") versions do not necessarily account for the climatic requirements of individ- ual species but do include measures of the rate at which hypo- thetical organisms must move to track suitable climatic condi- tions (ie climatic velocity; Loarie et al. 2009; Hamann et al. 2015), or locations that retain increasingly rare climatic con- ditions (ie rareclimate refugia; Michalak et al. 2018). In con- trast, species-based (or "fne-flter") 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 identifed 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-km2 resolution) and publicly available at the time of this study (WebPanel 1). We then explored the spa- tial agreement of refugia as interpreted from the datasets of these multiple studies, both within and across refugia classes. We also identifed landscape characteristics associated with each of the refugia datasets to better understand what factors are driving spatial similarities and differences.

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