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opinion

There are many barriers to species' migrations

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Abstract. Temperature-change trajectories are being used to identify the geographic barriers and thermal 'cul-de-sacs' that will limit the ability of many species to track climate change by migrating. We argue that there are many other potential barriers to species' migrations. These include stable ecotones, discordant shifts in climatic variables, human land use, and species' limited dispersal abilities. To illustrate our argument, for each 0.5° latitude/longitude grid cell of the Earth's land surface, we mapped and tallied the number of cells for which future (2060–2080) climate represents an analog of the focal cell's current climate. We compared results when only considering temperature with those for which both temperature and total annual precipitation were considered in concert. We also compared results when accounting for only geographic barriers (no cross-continental migration) with those involving both geographic and potential ecological barriers (no cross-biome migration). As expected, the number of future climate analogs available to each pixel decreased markedly with each added layer of complexity (e.g. the proportion of the Earth's land surface without any available future climate analogs increased from 3% to more than 36% with the inclusion of precipitation and ecological boundaries). While including additional variables can increase model complexity and uncertainty, we must strive to incorporate the factors that we know will limit species' ranges and migrations if we hope to predict the effects of climate change at a high-enough degree of accuracy to guide management decisions.

Keywords. Species migrations, biomes, climate change, global warming, conservation biogeography, climate analogs, dispersal, extinction.

A recent study by Burrows et al. (2014) helps advance our understanding of the effects of global warming by identifying how temperatures will shift through geographic space. Burrows et al. also highlighted how the ability of species to track shifting temperatures can be limited by geographic barriers and thermal 'cul-de-sacs' (sensu Forero-Medina et al. 2011). However, translating geographic shifts in climate into predictions of species' migrations is complicated and we contend that there are several important issues that need to be addressed. Perhaps most notably, Burrows et al. only considered changes in temperature, despite the fact that climate change will encompass a multitude of other climate variables. Species' distributions can be strongly influenced by factors other than temperature, and therefore the inclusion of other climactic factors may greatly improve our ability to predict where and how species will migrate (McCain and Colwell 2011, Feeley

and Rehm 2012). In addition, there are many other abiotic (e.g. soil type and topography) and biotic (e.g., competition and predation) factors that can determine habitat suitability and species' distributions (Ibáñez et al. 2006). These factors may not change in concert with temperature, thus creating potential barriers to species migrations. In other words, we propose that climate cul-de sacs, or 'sinks', will be far more prevalent than indicated by Burrows et al. (2014), highlighting the need for more-realistic models to guide conservation policy.

To help illustrate the compounding effects of including additional climate variables and other potential barriers in predictions of species' migrations, we mapped and tallied the number of future climate analogs (i.e., number of pixels) associated with each 0.5°x 0.5° pixel of the Earth's land surface (Figure 1). We first considered only the predicted changes in mean annual temperature.

Current climate conditions were based on the WorldClim extrapolated climate database (Hijmans et al. 2005) and future climate conditions were predicted for the 2070s (mean of 2060–2080) using the CSIRO ACCESS1-0 General Circulation Model under the RCP8.5 emissions scenario. We next considered the predicted concomitant changes in both temperature and total annual precipitation. In identifying the future analogs under each of these two climate-change scenarios (i.e., changes of temperature alone vs. changes of temperature and precipitation), we accounted for (1) only geographic barriers, by restricting 'available' analogs to only those pixels that occur within the same continent as each focal pixel, and (2) both geographic and potential ecological barriers, by restricting available analogs to only those pixels that occur within the same continent and WWF biome (Olson et al. 2001) as each focal pixel. Biomes were included as a surrogate for ecological barriers because of their association with various environmental factors and the fact that they represent the distributional limits of many species (Olson et al. 2001). Biome boundaries may also be stable ecotones that will shift slowly or not at all under climate change, thereby limiting the ability of some species to track shifting climates (Salazar et al. 2007, Feeley and Silman 2010, Lutz et al. 2013).

With each added layer of complexity, the number of future climate analogs corresponding to each focal pixel decreased markedly (Figure 1). In our most realistic model that included both temperature and precipitation, and that ac-
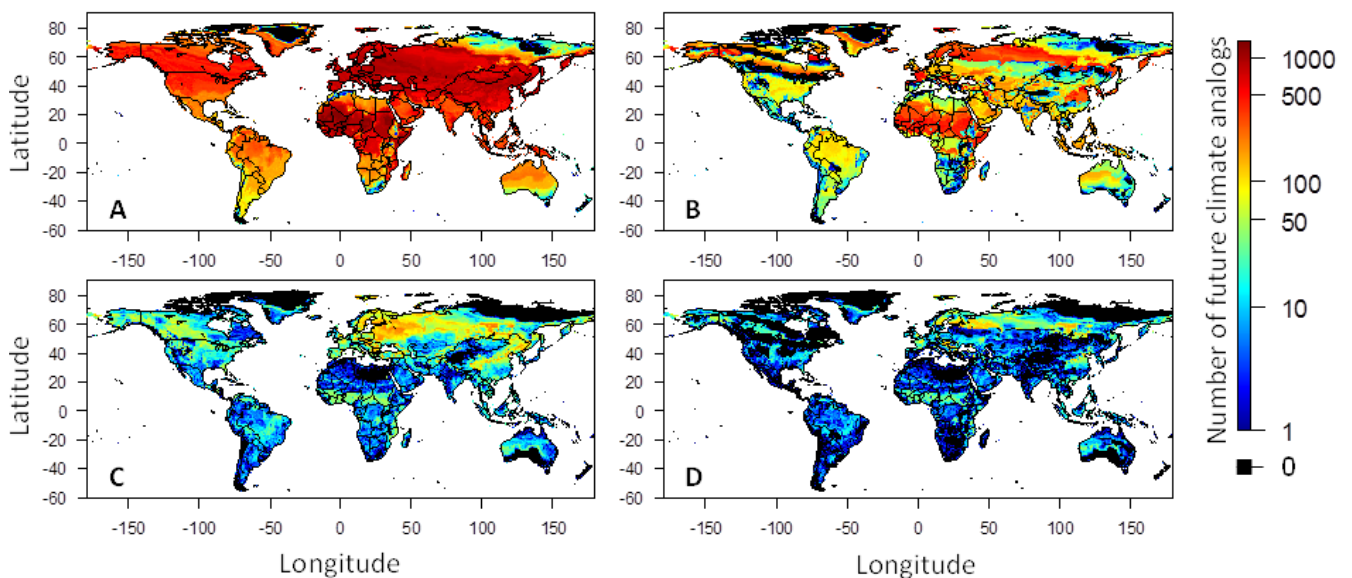

Figure 1. Maps showing the number of future terrestrial pixels that are 'available' analogs of the current climate occuring at each pixel of the Earth's land surface (pixels are 0.5^o latitude/longitude resolution or approximately 55 x 55 km at the equator). In panels A and B, available future climate analogs were identified and tallied as all cells where the future mean annual temperature is predicted to be within ±0.5^{o}C of the focal pixel's current temperature. In panels C and D, available climate analogs were identified and tallied as the cells where the future temperature is predicted to be within ±0.5^{o}C of the focal pixel's current temperature *and* the future total annual precipitation is predicted to be within ±10% of the focal pixel's current precipitation. In panels A and C, we assumed geographic barriers by counting only those climate analogs that are located within the same continent as the focal pixel [continents were North and Central America (including Caribbean), South America, Eurasia (including Southeast Asian Islands), Africa (including Madagascar), Australia, and Oceania]. In panels B and D, we accounted for both geographic and ecological barriers by only counting the future climate analogs that are located within the same continent *and* the same biome as the focal pixel (biomes were defined based on WWF classifications). Current climate conditions were based on the WorldClim high resolution climate database and future climate conditions were based on predictions for the 2070s (average of 2060–2080) from the CSIRO ACCESS1-0 General Circulation Model under the RCP 8.5 emissions scenario downscaled to a spatial resolution of 0.5^o based on the delta method using the WorldClim current climate as baseline conditions.

counted for both geographic and ecological barriers, the number of potential future analogs was reduced by a median of 99% relative to when only temperature and geographic barriers were considered. Furthermore, the proportion of land area without any future climate analogs ('disappearing climates' sensu Williams et al. 2007) increased from just 3% to over 36% with the inclusion of both precipitation and biome boundaries. The number of reachable climate analogs would be reduced even further if we followed climate-change trajectories and thus included interior climate sinks sensu Burrows et al. (2014). Also, even our most complex model is clearly still overly simplistic. The estimated number of reachable analogs would decrease further if we considered other important barriers to species migrations such as human land use (Feeley and Rehm 2012) or the limited dispersal capability of many species (Corlett and Westcott 2013). For example, even if climate analogs are available and connected via climate-change trajectories, many species may be incapable of migrating the required distances at sufficient speeds to keep pace with environmental changes. Finally, even within biomes, there are likely to be many other potential ecological barriers to the distributions and movements of species, such as soil type and edaphic conditions (Ibáñez et al. 2006, Higgins et al. 2011).

It is important to note that both the current analysis (Figure 1) and the analyses of Burrows et al. (2014) are based only on the predicted changes in the geographic distributions of climates; both studies implicitly assume that species will be forced to respond to shifting climates through migration. In reality, it remains unclear how important climate is in determining the current distributions of species and/or whether species' current distributions are at equilibrium with climate (Sax et al. 2013). Correspondingly, it is unknown whether species will be forced to migrate in the future, or whether they will be able to tolerate climate change in situ (Feeley et al. 2012).

The study by Burrows et al. (2014) is a major step forward in predicting the paths that species may follow if they need to migrate to remain at equilibrium with changing climates, as well as some of the potential barriers that migrating species may run into along the way. However, we clearly need to incorporate additional realism if we hope to eventually predict the responses of species to future climate change at a high-enough degree of accuracy to guide management decisions.

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