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Connecting today's climates to future climate analogs to facilitate movement of species under climate change

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Abstract: *Increasing connectivity is an important strategy for facilitating species range shifts and maintaining biodiversity in the face of climate change. To date, however, few researchers have included future climate projections in efforts to prioritize areas for increasing connectivity. We identified key areas likely to facilitate climate-induced species' movement across western North America. Using historical climate data sets and future climate projections, we mapped potential species' movement routes that link current climate conditions to analogous climate conditions in the future (i.e., future climate analogs) with a novel moving-window analysis based on electrical circuit theory. In addition to tracing shifting climates, the approach accounted for landscape permeability and empirically derived species' dispersal capabilities. We compared connectivity maps generated with our climate-change-informed approach with maps of connectivity based solely on the degree of human modification of the landscape. Including future climate projections in connectivity models substantially shifted and constrained priority areas for movement to a smaller proportion of the landscape than when climate projections were not considered. Potential movement, measured as current flow, decreased in all ecoregions when climate projections were included, particularly when dispersal was limited, which made climate analogs inaccessible. Many areas emerged as important for connectivity only when climate change was modeled in 2 time steps rather than in a single time step. Our results illustrate that movement routes needed to track changing climatic conditions may differ from those that connect present-day landscapes. Incorporating future climate projections into connectivity modeling is an important step toward facilitating successful species movement and population persistence in a changing climate.*

Keywords: climate analogs, climate-change adaptation, connectivity, dispersal

La Conexión entre los Climas de Hoy y los Futuros Climas Análogos para Facilitar el Movimiento de las Especies bajo el Cambio Climático

Resumen: *Incrementar la conectividad es una estrategia importante para facilitarle a las especies cambios en su extensión y mantener a la biodiversidad de frente al cambio climático. Sin embargo, a la fecha pocos investigadores han incluido las proyecciones del futuro climático en los esfuerzos por priorizar áreas para incrementar la conectividad. Identificamos áreas clave con probabilidad de facilitar el movimiento de las especies inducido por el clima en América del Norte. Por medio de un análisis novedoso de ventana en movimiento basado en la teoría de los circuitos eléctricos, mapeamos las rutas potenciales de movimiento de las especies que enlazan las condiciones climáticas actuales con condiciones climáticas análogas en el futuro (es decir, futuros climas análogos) utilizando conjuntos de datos históricos del clima y las proyecciones del futuro climático. Además de rastrear los climas cambiantes, la estrategia tomó en cuenta la permeabilidad del paisaje y derivó empíricamente las capacidades de dispersión de las especies. Comparamos los mapas de conectividad generados con nuestra estrategia informada por el cambio climático con los mapas de conectividad basados solamente en el grado de modificación humana del paisaje. La inclusión de las proyecciones del futuro*

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climático dentro de los modelos de conectividad modificó y restringió sustancialmente las áreas prioritarias de movimiento a una porción más pequeña del paisaje que cuando no se consideraron las proyecciones climáticas. El movimiento potencial, medido como el flujo de corriente, disminuyó en todas las ecoregiones cuando se incluyeron las proyecciones climáticas, particularmente cuando la dispersión estuvo limitada, lo que hizo que los análogos climáticos fueran inaccesibles. Muchas áreas emergieron como importantes para la conectividad sólo cuando el cambio climático fue modelado en pasos de dos tiempos, en lugar de un paso de un sólo tiempo. Nuestros resultados ilustran que las rutas de movimiento necesarias para rastrear las condiciones climáticas cambiantes pueden diferir de aquellas que conectan a los paisajes hoy en día. La incorporación de las proyecciones del futuro climático dentro del modelado de conectividad es un paso importante hacia la facilitación del movimiento exitoso para las especies y la persistencia de las poblaciones en un clima cambiante.

Palabras Clave: adaptación al cambio climático, análogos climáticos, conectividad, dispersión

Introduction

Anthropogenic climate change is driving species range shifts on every continent (Parmesan & Yohe 2003). Paired with paleoecological evidence of species movements during past climate changes (Davis & Shaw 2001), these current trends strongly suggest that range shifts will continue under even the most modest of future climate-change scenarios (Settele et al. 2014). If species are unable to track shifting climatic conditions because of dispersal constraints or anthropogenic barriers to movement, they may experience declines in abundance or even extinction (Thomas et al. 2004; Sinervo et al. 2010; Kerr et al. 2015). Accordingly, increasing connectivity—the degree to which organisms can move through a landscape (Taylor et al. 1993)—is the strategy most frequently invoked to facilitate species range shifts and, more broadly, conserve species diversity in a warming world (Heller & Zavaleta 2009). However, incorporating future climate projections into efforts to both identify important movement routes and target areas for increasing connectivity remains a significant, unresolved challenge.

Species' Movement under Climate Change

Climate change challenges the effectiveness of traditional connectivity planning approaches that aim to facilitate movement between protected areas. Species' movements to track suitable climatic conditions may reduce the effectiveness of protected areas that are fixed in space, and species may encounter new anthropogenic barriers as they move (Peters & Darling 1985; Hannah 2011). Thus, maintaining or increasing connectivity under climate change may involve a temporal and directional consideration that strategies focused solely on connecting present-day landscapes do not necessarily require (e.g., movement corridors between existing protected areas) (Groves et al. 2012).

Future species distributions depend on myriad factors such as species-specific habitat requirements, biotic interactions, and species' capacities to adapt to changing climatic conditions in place. However, paleoecological records and observed species' movements in response to contemporary climate change indicate that many species will shift their ranges to track suitable climatic conditions (Davis & Shaw 2001; Parmesan & Yohe 2003). Future climate analogs (i.e., climatic conditions that are analogous to those that exist today [Ohlemüller et al. 2006; Carroll et al. 2015]) must therefore be within reach. Enhancing connectivity under climate change (e.g., with landscape corridors, stepping-stone reserves, or increased matrix permeability [Krosby et al. 2010]) would thus ideally accommodate the individualistic responses of multiple species simultaneously. In all cases, species' dispersal capabilities and, relatedly, the accessibility of suitable climatic conditions in the future will govern the effectiveness of connectivity-enhancing strategies (Urban et al. 2013).

Predicting Landscape Connectivity

Despite the acknowledged importance of these dynamics associated with connectivity for addressing climate change (e.g., Lister et al. 2015; Robillard et al. 2015), we know of no examples either in the literature or implemented in conservation efforts that specifically include future climate projections and the accessibility of suitable climatic conditions in predicting landscape connectivity. Specifically, 3 key elements of predicting connectivity under climate change have not been addressed simultaneously: climate analogs and their accessibility as constrained by landscape permeability due to human modification and species' dispersal capabilities.

Some studies bypass consideration of dispersal constraints by comparing the spatial overlap of current ranges with either projected future ranges or protected areas as an assessment of connectivity (e.g., Ordonez & Williams 2013; Vieilledent et al. 2013). Others incorporate more biological realism by comparing climate velocities with biotic velocities (e.g., Carroll et al. 2015) or with empirically derived species' dispersal rates (e.g., Schloss et al. 2012). Only a few studies that assess whether species will be able to track suitable climates also consider landscape permeability (e.g., Schloss et al. 2012; Lawler et al. 2013), which will largely dictate the success of species' movement. These studies, however, do not map specific routes and rely on data-intensive species distribution models. Furthermore, studies that incorporate climate projections, either to compute climate velocities or to generate species distribution models, often represent climate change as a single event (e.g., from a historical period to a point in the future), although climate change is a dynamic process that unfolds continuously.

Some connectivity efforts that consider landscape permeability and protected-area configuration do not rely on future climate projections but instead rely on the first principles that govern the distribution of climatic conditions, for example, the principle that higher latitudes and elevations will tend to remain relatively cooler than lower latitudes and elevations and that species may correspondingly shift uphill and poleward. Other studies have mapped connectivity in a manner that both accounts for human modification and tracks shallow climatic gradients (e.g., delineating routes with the most unidirectional change in present-day temperature [Nuñez et al. 2013; Burrows et al. 2014]). Still others connect basic elements of the landscape (e.g., land facets) as part of a geophysical-based approach that aims to conserve and connect arenas of biological activity under climate change (Anderson & Ferree 2010; Brost & Beier 2012).

Thus, a range of approaches has been used to assess the potential for successful species' movement under climate change. However, without simultaneously considering future climate projections, landscape permeability due to human modification, and dispersal capabilities, understanding of connectivity under climate change is limited. We sought to address some of these limitations through a novel approach based on electrical-circuit theory to map connectivity between historical and future climate analogs across a human-modified landscape. We defined climate analogs based on their multivariate similarity and constrained potential areas of connectivity by dispersal rates that reflect a range of taxa. We use multiple climate-change scenarios and 2 time steps to assess how varying degrees of climate change and the temporal resolution at which climate change is modeled affects inferences about potential species' movement.

Methods

Climate Data

We used historical climate data sets and future climate projections for western North America and areas therein that were downscaled using the ClimateNA version 5.10 software package (Wang et al. 2016). The software downscales the PRISM 4-km data (Daly et al. 2002) to 1-km gridded data sets and applies a dynamic lapse-rate adjustment that accounts for local spatial and temporal variability in lapse rates (Wang et al. 2016). We used the following 10 variables, with appropriate transformations to normalize their distributions (Supporting Information), mapped at 1-km resolution: mean annual temperature, mean temperature of the warmest month, mean temperature of the coldest month, difference between the mean temperature of the warmest and coldest months, mean annual precipitation, total summer precipitation, Hargreaves reference evaporation, summer heat-moisture index, number of frost-free days, and number of degree days above 5°C.

We used the 1961–1990 climate normal period for historical climate conditions. We used future climate projections for 2041–2070 and 2071–2100 (hereafter, the 2050s and the 2080s, respectively) downloaded from the CMIP5 multimodal data set (Taylor et al. 2012) and based on the business-as-usual representative concentration pathway (RCP) 8.5 scenario (IPCC 2013). We used the projections from 3 global circulation models (GCMs): INM CM4 (Volodin et al. 2010), which projects mild climate change for the study area; MIROC5 (Watanabe et al. 2010), which projects moderate change; and GFDL CM3 (Donner et al. 2011), which projects considerable change.

Climatic Niche Breadth and Climate Analogs

We identified climate analogs between historical and future climatic conditions based on their multivariate similarity (following Hamann et al. 2014). Using principal component analysis (PCA), we generated a multivariate measure of climate for each 1-km cell in the study area to reduce the dimensionality of the nine-variable data set and minimize the influence of highly correlated climate variables. The first and second principal components explained 87.5% of the variance in the initial data set (Supporting Information), and we applied the scores of these 2 components to each 1-km cell.

To define climate analogs, we established a similarity threshold below which 2 cells would be considered analogous. We determined this threshold by calculating climatic niche breadths of species ranges, which were based on digital range maps for 200 birds (Birdlife International 2014), 450 mammals (Patterson et al. 2007), 498 amphibians (IUCN 2014), and 24 tree species in North America (Roberts & Hamann 2012). To calculate niche breadth for each species, we plotted the geographic range in the two-dimensional principal component space, identified the median centroid of this distribution, and calculated the radius of a circle that would capture 75% of the points within the distribution to use as a niche breadth. The median niche breadth was narrowest for amphibians (0.9 PCA units) relative to trees, mammals, and birds (1.5 PCA). We selected the conservative 0.9 PCA unit threshold for identifying climate analogs between historical and future climatic conditions.

Connecting Climate Analogs

We used Circuitscape (McRae et al. 2013) with a novel moving-window algorithm (McRae et al. 2016) to quantify potential species' movement—measured as current flow—between historical climates and their future analogs. Circuitscape models connectivity on the basis of electrical circuit theory, treating landscapes as conductive surfaces and replacing cells connected to their neighbors with nodes connected by resistors. Patterns of electrical current (in amperes [amps]) predict the movement patterns of random walkers between source and target cells across a landscape (here between pairs of cells with analogous historical and future climates), where walkers are proportionally more likely to move through intervening low-resistance cells than high-resistance cells. The result of the moving-window analysis is a continuous map of current flow across all possible routes between source and target cells (McRae et al. 2008; Lawler et al. 2013)—here across all possible routes between climate analogs. The more current (amps) flowing through a given cell, the more individuals or more individual movements one might expect to go through that cell.

We used the degree to which the landscape had been altered as a measure of resistance to movement. The values in the human-modification index ranged from 1 to 100 (Theobald 2013, 2016). We squared these values to produce a more effective and meaningful resistance layer. Given that such a transformation is somewhat arbitrary, we compared our results with those produced using an untransformed set of values and those produced using an alternative transformation (Supporting Information). Because we sought to model connectivity between the most natural areas on the landscape, we constrained sources and targets (i.e., climate analogs) to those cells with the lowest human modification index value (1). These included areas represented 84% (9,116,817 km^2) of the overall study area (Supporting Information).

Rather than treating the landscape as a conductive surface with a limited number of fixed source cells and target cells, the moving window iteratively enabled every cell that met our naturalness criteria to act as a target for current flowing from sources (i.e., matching historical climates) within the moving window (McRae et al. 2016). We summed the current within each moving window across the study area, thereby generating a continuous map that summarized movement probabilities between all source and target cells (i.e., between all historical and future climate analogs, respectively) (Fig. 1). Thus, high densities of current flow indicated important movement pathways between analogous historical and future climates. For comparison purposes, we also modeled connectivity more conventionally, without matching climate analogs, to see how their inclusion would shift patterns of current flow and hence movement pathways. In this case, without matching climate analogs, all cells within areas with the lowest human-modification value (1) could act as sources and targets.

Because species' dispersal capacities will constrain their ability to reach suitable climatic conditions, we limited potential analogs to those within specified sets of search radii. These radii were derived from reviews of maximum known dispersal distances for amphibians, mammals, and birds. Specifically, we used a 0.5-km annual dispersal distance, which represents the majority of amphibian species (Smith & Green 2005). We contrasted this limited dispersal capability with a 5-km annual dispersal distance, which represents most small mammals and dispersal-limited terrestrial birds (Sutherland et al. 2000; Bowman et al. 2002). These values were multiplied by the number of years in each period and then used as moving-window search radii. Dispersal distances of 0.5 and 5 km corresponded to radii of 40 and 400 km (historical to 2050s), 55 and 550 km (historical to 2080s), and 15 and 150 km (2050s to 2080s). When applied in the connectivity analyses, greater search radii values reflected increasing accessibility of distant climate analogs.

In summary, we modeled connectivity between climate analogs in a manner that reflects species-based climate-niche breadths, landscape resistance due to human modification, and empirically derived dispersal capacities. We summarized the resulting patterns of potential movement across level I and level III ecoregions (U.S. EPA 2010). We conducted model runs in Python version 2.7, used ArcGIS 10.3 for creating maps, and used R 3.2.3 for post hoc calculations and plotting results.

Results

Western North America's mountainous regions and narrow physiographic features consistently exhibited high current flow, and therefore are likely important pathways for potential species' movements. The importance of these areas increased as degrees of climate change increased. Under the mildest climate scenario, more climate analogs were within reach given that our moving-window search radius was designed to reflect dispersal constraints (0.5 km/year). Accordingly, there was some movement throughout most of western North America (INM CM4) (Fig. 2a), including within flat ecoregions (level I) such as the interior northern forests and parts of the Great Plains that were not heavily modified by humans. By contrast, potential movement was drastically curtailed and constrained to mountainous ecoregions and narrow features such as isthmuses and peninsulas (e.g., Baja

California) under the scenarios that portray moderate and considerable climate change (MIROC5 and GFDL CM3, respectively) (Figs. 2b & 2c). Even under moderate climate change (MIROC5), the flattest ecoregions (e.g., interior northern forests, taiga, and tundra) were predicted to have minimal current flow because climate analogs were not accessible (Fig. 3).

Potential movement was highest in ecoregions (level III) with intermediate ranges of elevation and slope (e.g., the Columbia Plateau, the eastern Cascades foothills) (Fig. 4). Ecoregions with extreme topographic complexity and therefore localized diversity in climatic conditions (e.g., the Alaska Range, the Sierra Nevada) showed a moderate amount of potential movement. By contrast, our model predicted minimal or no movement in flat ecoregions dominated by agriculture (e.g., central Great Plains, Willamette Valley).

Maps connecting climate analogs within a human-modified landscape highlighted different areas as being important for potential movement than maps that did not take climate analogs into account (Fig. 5 & Supporting Information). Human modification largely determined the underlying permeability of the landscape and thus which parts of the landscape species could traverse, but including climate projections de-emphasized the importance of some pathways. For example, when we did not consider climate analogs, there was connectivity throughout an extensive lattice of narrow natural areas in places that were otherwise extensively cultivated (i.e., channeled scablands of southeastern Washington) (Fig. 5b). In contrast, connecting climate analogs funneled current through a smaller proportion of the landscape and highlighted mountainous regions (Fig. 5c). Thus, some areas that appeared important for species' movement in the absence of climate change were less important for climate-induced movements, and new pathways became

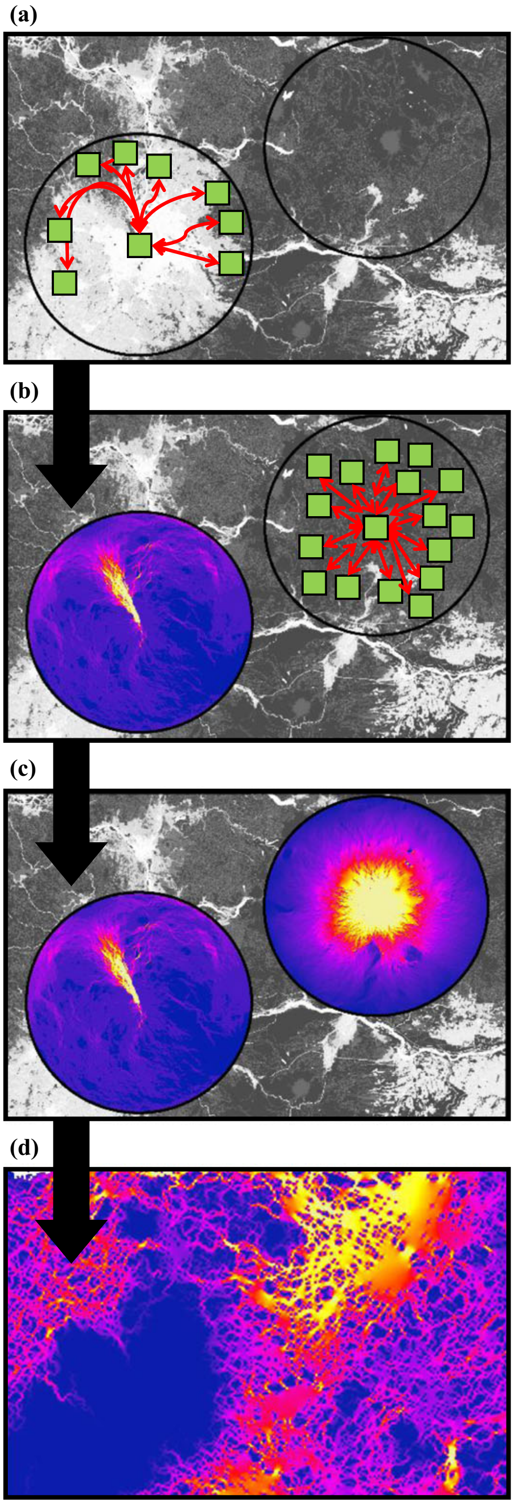

Figure 1. Conceptual illustration of the mapping of connectivity between where current climate conditions occur and where those conditions will occur in the future (i.e., climate analogs) based on electrical circuit theory. Maps are of the Portland, Oregon (U.S.A.) metropolitan area on the left and the more natural area surrounding Mt. Adams in Washington State on the right (i.e., landscapes with varying degrees of human modification; the darker the shading, the more natural the area); green squares, analogous climates in natural areas [enlarged for illustrative purposes]; central green square, future climate analog [i.e., the target]; other green squares, historical climate analogs [i.e., sources]). One amp of electrical current is injected into each source and flows (a) between the climate analogs following low-resistance paths (red arrows) in the human-modified landscape and (b, c) in a circular moving window across the landscape in a spatially continuous manner (windows are separated for illustrative purposes). (d) Continuous map of connectivity between historical and future climate analogs derived from the sum of potential movement within each moving window (low values of potential movement, measured as current flow in amps, in blue and high values in yellow).

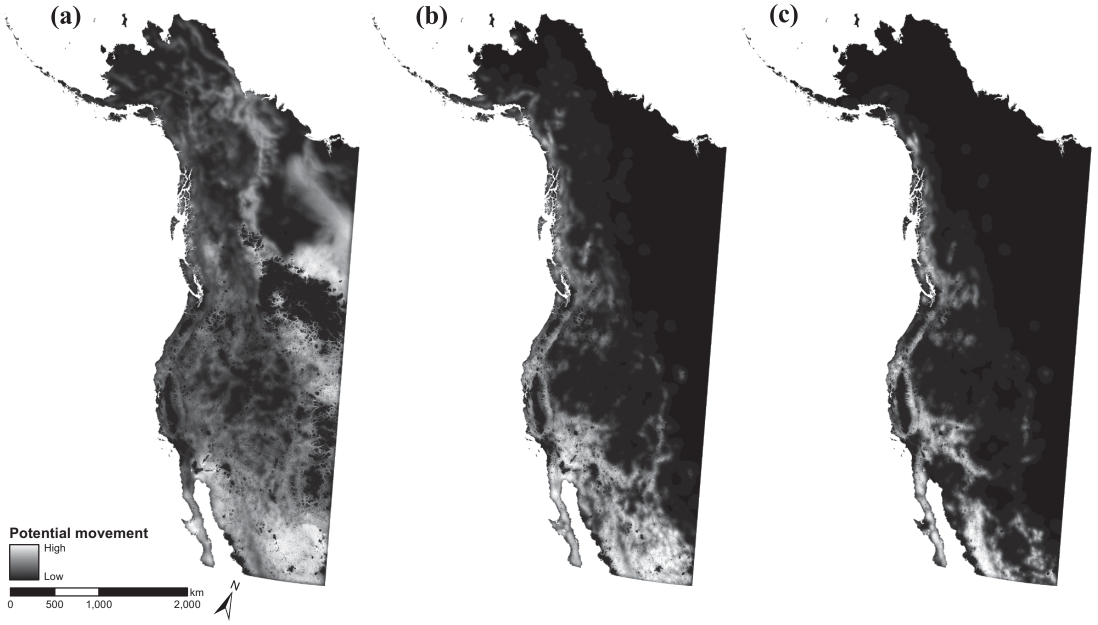

Figure 2. Potential species' movements (measured as current flow in amps) between areas of historical climates and their 2080s climate analogs under representative concentration pathway 8.5 as implemented in 3 global circulation models (GCMs): (a) INM CM4, (b) MIROC5, and (c) GFDL CM3 (IPCC 2013; Volodin et al. 2010; Watanabe et al. 2010; Donner et al. 2011). Dispersal rate is 0.5 km/year. Shading reflects the values of potential movement for each GCM (maximum values: 2,645,580 amps for INM CM4; 1,250,170 amps for MIROC5; and 830,863 amps for GFDL CM3).

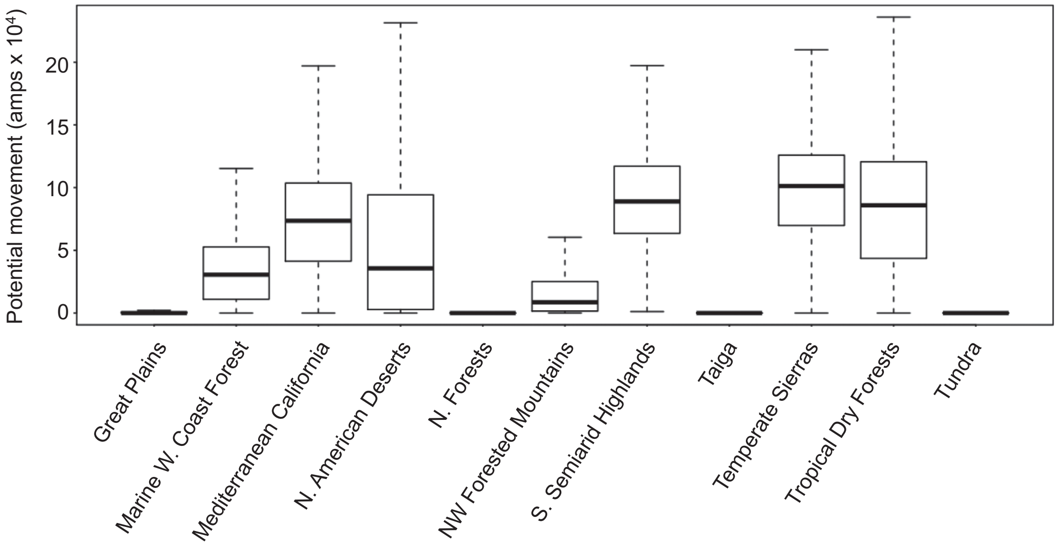

Figure 3. Potential species' movements by ecoregion (level I) (U.S. EPA 2010) between areas of historical climates and their 2080s climate analogs under representative concentration pathway 8.5 as implemented by MIROC5, which projects moderate climate change for the study area (Watanabe et al. 2010; IPCC 2013). Dispersal rate is 0.5 km/year (boxes, 25th and 75th percentiles of values; horizontal lines, median; whiskers, most extreme data points [i.e., potential movement value in a pixel within that ecoregion] that are ≤1.5 times the interquartile range from the box). Unplotted outliers do not exceed 10 × 10^4 amps for Northern Forest, Taiga, or Tundra; outliers for Great Plains, Mediterranean California, North American Deserts, Northwestern Forested Mountains, Southern Semiarid Highlands, Temperate Sierras, and Tropical Dry Forests range from 50 × 10^4 amps to 75 × 10^4 amps; and outliers for Marine West Coast Forest are up to 105 × 10^4 amps.

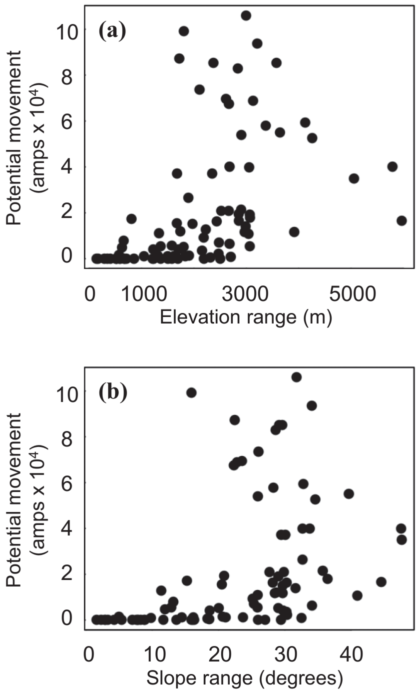

Figure 4. Average potential movement between areas of historical climates and their 2080s climate analogs in ecoregions (level III) (U.S. EPA 2010) versus the ranges of (a) elevation and (b) slope therein. Potential species' movements are between historical climates and their 2080s climate analogs under representative concentration pathway 8.5, as implemented by MIROC5 (Watanabe et al. 2010; IPCC 2013). Dispersal rate is 0.5 km/year.

increasingly important under climate change (Fig. 5d). More broadly, human modification severely restricted potential movement (Fig. 5a vs. Fig. 5c).

Modeling climate change in a single time step (i.e., historical to 2080s) obscured pathways that emerged as important for connectivity when we analyzed climate change in 2 time steps (i.e., historical to 2050s then 2050s to 2080s) (Fig. 6). For example, some bottlenecks where movement was concentrated in the 2 shorter time steps were missed in the single time step (e.g., in the westernmost foothills of the Cascades). Relative to a dispersal rate of 0.5 km/year, a rate of 5 km/year resulted in greater maximum movement across the landscape. Modeling climate change in a single time step and using this greater dispersal capability did not de-emphasize narrow pinch points that were highlighted in the 2 shorter time steps.

Discussion

Incorporating climate projections in connectivity models substantially changed the roadmap for species' movement. Connectivity maps that accounted for climate change highlighted a smaller number of specific locations where conservation efforts could be focused. By contrast, connectivity maps based solely on landscape permeability depicted more options for movement. Thus, excluding climate projections from connectivity models may result in an overly optimistic view of landscape connectivity and undervalue specific important connections. Furthermore, representing climate change in one time step obscured some critical pathways for dispersal-limited species that otherwise emerged when climate change was modeled incrementally in 2 time steps. These results suggest that simplifying the temporal resolution of climate change may miss some important links for climate-induced species' movement and that approaches that go beyond a single time step—or even 2 time steps—to explore climate change as more of a continuous process are likely warranted.

Drivers of Potential Movement

Because certain areas of the landscape consistently emerged as key pathways across multiple climate-change scenarios, we can have confidence in their conservation importance, despite inherent uncertainties in climate projections. The consistent importance of mountainous regions in our results reflects lower climate velocities therein (Hamann et al. 2014; but see Dobrowski & Parks 2016) and thus greater accessibility of analogous climates.

Ecoregions (level III) with the most extreme ranges of elevation and slope contain a diversity of climates such that species can make smaller spatial adjustments to track suitable climatic conditions. These areas also tend to have minimal human modification such that there are numerous movement routes. Thus, according to our model, these areas will likely have many small, successful movements but only moderate levels of overall movement. In some cases, however, cold climates in the highest terrain will have no analogs in the future and will likely disappear (Williams & Jackson 2007). Species that need to track such conditions will face climatic cul-de-sacs at the highest elevations and are therefore disproportionately vulnerable to climate change (Ohlemüller et al. 2008; Carroll et al. 2015). Furthermore, the extreme topographic relief of some mountainous regions may hinder movement or introduce intervening climatic conditions in some potential pathways that render them impassable for some species (Dobrowski & Parks 2016).

Ecoregions with intermediate ranges of elevation and slope (e.g., mountain range foothills, high deserts) may harbor accessible climate analogs, but these are separated by greater distances (i.e., source and target cells are farther apart in our models). These greater distances required more overall movement and accordingly resulted in higher mapped current flow in our models. By contrast, minimal to no movement was predicted for the lowest and flattest ecoregions, where climate velocities

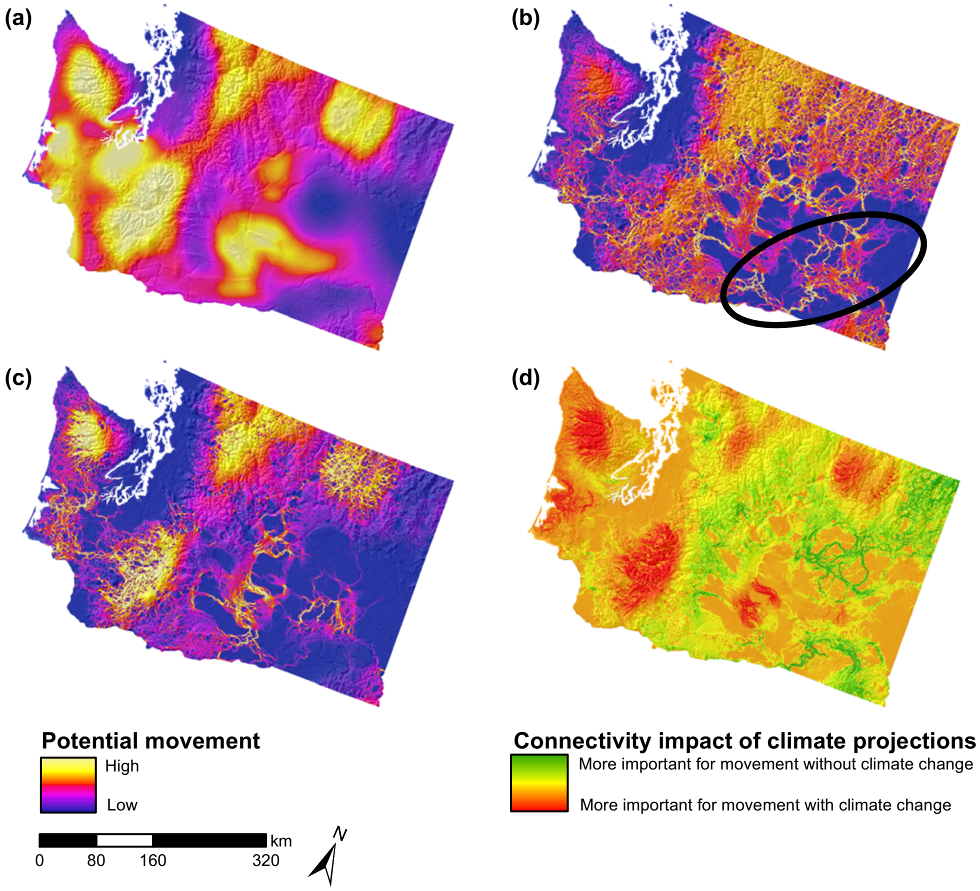

Figure 5. Potential species' movement in Washington State based on electrical circuit theory (a) between areas of historical climates and where those conditions will occur in the future (i.e., climate analogs) without considering human modification (i.e., a uniform resistance value of 1 across the study area and no naturalness criteria applied to climate analogs); (b) across a human-modified landscape but not including climate analogs (i.e., within a given moving window, Circuitscape injects current from all natural cells—not only matching climate analogs—that may then flow to the central target cell) (oval, channeled scablands of southeastern Washington); and (c) between climate analogs across a human-modified landscape (as per methods described in the text). The connectivity impact of climate projections (d) was computed by normalizing potential movement values that do (c) and do not (b) link climate analogs and then subtracting the former from the latter. Sources and targets for connectivity (i.e., climate analogs) were constrained to only the most natural areas, except in (a). The color ramp of (a–c) reflects the low and high values of potential movement for each frame. Thus, colors are not directly comparable across frames and results should be interpreted with regards to the relative importance of specific areas for potential movement. Analogous climates are defined for the historical period and the 2080s with MIROC5 projections under representative concentration pathway 8.5 (Watanabe et al. 2010; IPCC 2013). Dispersal rate is 0.5 km/year.

were too high for climate analogs to be within reach. Humans have the largest effect on landscape permeability in the lowest-lying areas (e.g., due to coastal cities and agriculture [Seto et al. 2011]). As such, these heavily human-dominated areas contained few source and target cells (i.e., climate analogs) that could be connected, given our model parameterization.

Missed Connections

Human modification already restricts species' movement across landscapes, and the added constraint imposed by climate change highlighted a further reduced set of areas as important movement pathways. Indeed, prioritizing areas for connectivity enhancement based on human modification alone would miss some areas projected to be important for climate-induced movement.

Overlooking the fact that climate change is a dynamic process that unfolds continuously in time may also miss critical pathways. Most studies that model where species may find suitable climate conditions in the future (e.g., species-distribution models) either model climate change as a single event or average projected changes over

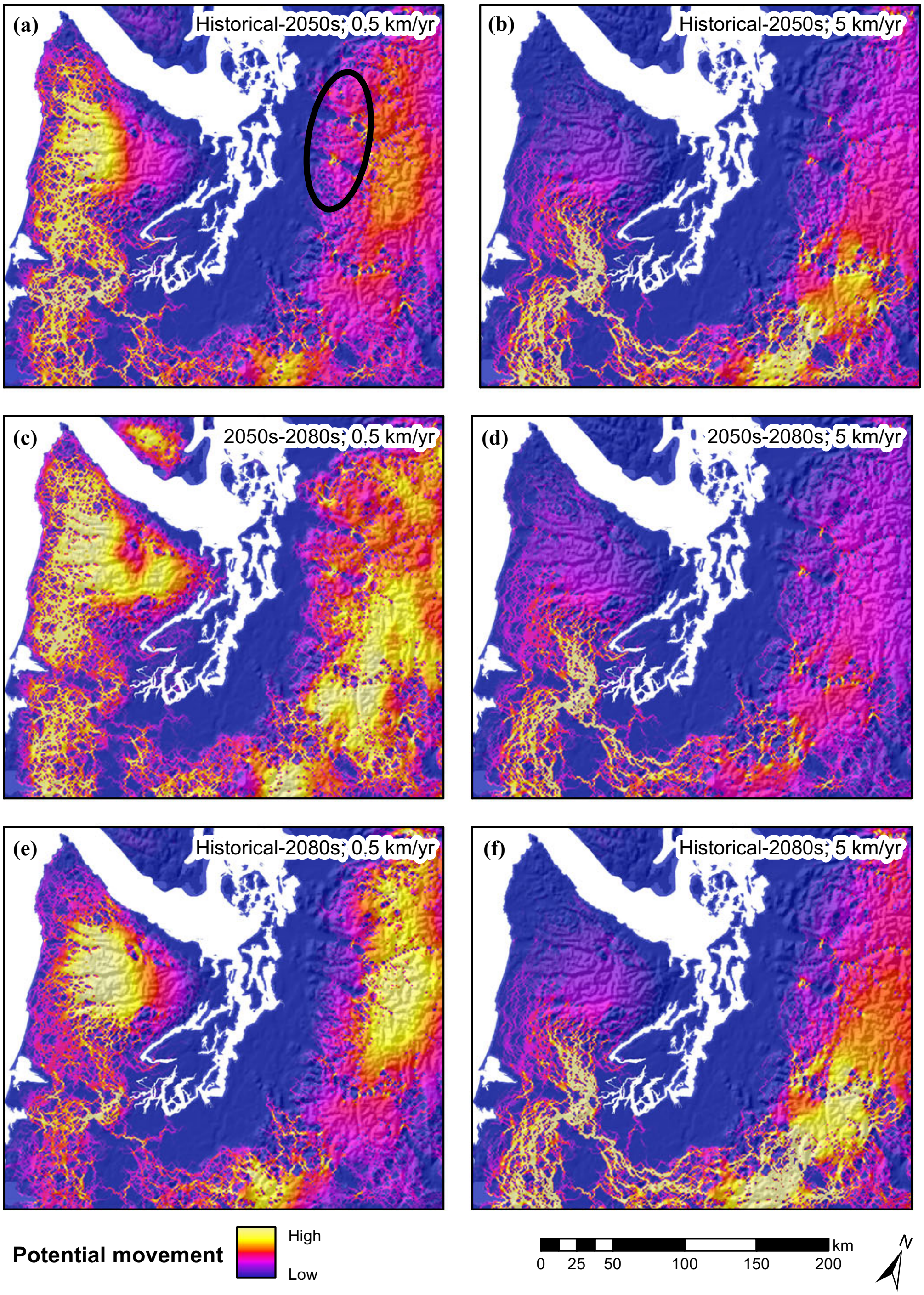

Figure 6. Potential species' movements in 2 time steps for 2 different dispersal capacities across a human-modified landscape: (a, b) potential movement between areas of historical climates and their 2050s climate analogs (oval, western-most foothills of the Cascade Mountains); (c, d) potential movement between projected climate conditions in the 2050s and their 2080s climate analogs; and (e, f) potential movement between areas of historical climates and their 2080s climate analogs (i.e., 1 extended time step). Analogous climates were defined using MIROC5 projections under representative concentration pathway 8.5 (Watanabe et al. 2010; IPCC 2013). Sources and targets for connectivity (i.e., climate analogs) are constrained to only the most natural areas. The color ramp reflects values of potential movement for each frame. Thus, colors are not directly comparable across frames and results should be interpreted with regards to relative importance of specific areas for potential movement.

multiple years. Realistically, climate change will be highly dynamic with fluctuations above and below the dominant directional change that unfolds over long periods (Easterling et al. 2000; Early & Sax 2011). The ability of species to reach suitable climatic conditions in the future will also strongly depend on population dynamics and dispersal processes that play out continuously through time (Keith et al. 2008; Early & Sax 2011).

In our models, mapping connectivity in a single time step obscured pathways that were important for dispersal-limited species when 2 successive time steps were used and that occurred in areas more susceptible to human modification (e.g., low-elevation coastal zones). In some cases, narrow pinch points where movement is funneled between climate analogs in 2 time steps, were downplayed in the single, extended time step. We attribute this difference to the fact that modeling climate change in one longer time step entailed a larger search radius (due to the potential for longer movements over that longer period) and hence more analogs to be connected. There were also more, alternative routes between analogs when a larger search radius was used, so movement may not be restricted to narrow pinch points. Thus, conservation prioritization decisions based on a single, extended time step will likely miss important movement areas, particularly over short periods and for dispersal-limited species for which intermediate stepping stones will be important (Hannah et al. 2014). Instead, using multiple time steps could help identify such stepping stones or siting of movable targets for conservation that could be shifted in space over time. Our models did not represent climate change continuously, but they suggest a broader need in conservation decision-making contexts to consider climate change as a dynamic process that unfolds continuously.

Model Limitations

Our framework represents an important advance in incorporating future climate projections, human modification of the landscape, and dispersal capabilities into modeling connectivity under climate change. However, as have others modeling connectivity, we made several simplifying assumptions. First, the pathways between climate analogs may have traversed either intervening climatic conditions that would not be suitable for some species (Nuñez et al. 2013; Dobrowski & Parks 2016) or physiographic barriers (e.g., mountain ranges) that, in reality, may constrain movement. Therefore our models likely overestimated the potential for movement in some places. In the inverse, our approach did not take fine-scaled topoclimate processes into account, which may provide climate microrefugia to dispersing species (Dobrowski 2011; Hannah et al. 2014). We also used a static map of human modification of the landscape even though human population will continue to grow and human land-use patterns will continue to change.

Our approach is biologically informed (i.e., with climatic niche breadths and dispersal abilities), but it is not a species-specific approach. Although one could apply the approach to an individual species, we argue that there are merits to both species-specific and more generalized connectivity modeling approaches. Recent reviews suggest conservation planners use a suite of modeling methods that span a range of complexity, including both species-specific approaches and approaches that are not species specific (Gillson et al. 2013; Schmitz et al. 2015). Ours is a coarse-filter approach that identifies areas through which a diversity of species may need to move to track suitable climates. This approach may capture the movements of many species for which building individual models would be difficult if not impossible (e.g., due to lack of data necessary to define landscape resistances or dispersal abilities). One could imagine complementing our approach with species-specific models for species with specialized habitat needs, restricted-range species with isolated remnant populations, or other species that might fall through a coarse filter.

We applied our approach over a relatively broad extent to model connectivity across western North America. Such an application relies on general climatic patterns (e.g., latitudinal gradients, elevation-driven gradients, and marine influences), and it likely missed some of the more localized patterns driven by unique or relatively infrequently occurring drivers. One could apply the same approach to a smaller region to highlight more fine-scale, region-specific movement routes. By modeling a large spatial extent, we minimized the relative influence of edge or boundary effects and captured broad-scale potential movements. Nonetheless, our results are less meaningful at the inland edges of the study area, where connections to places outside the study area may be as important or more important than connections within it, and our results are less meaningful in locations with unique climatic gradients.

Planning for Species' Movements

Conservation actions in response to climate change are challenged by considerable uncertainty surrounding the rates, magnitudes, and ecological consequences of climate change (Kujala et al. 2013). Despite these uncertainties, conservation planners are necessarily prioritizing areas to protect with the aim of facilitating species' movement and persistence under climate change (e.g., Ayebare et al. 2013; Anderson et al. 2014). Although some planners may avoid models that include future climate projections due to their uncertainty, our results suggest that in doing so planners may overlook critical locations for facilitating climate-induced movement.

Some existing networks of protected areas may be sufficiently connected de facto to facilitate species persistence and movement (Mazaris et al. 2013), whereas others may not (Scriven et al. 2015; McGuire et al. 2016). For example, in the United States alone, only 41% of natural land area may be sufficiently connected to ensure that plants and animals can successfully track suitable climatic conditions (McGuire et al. 2016). Similarly, we show that human modification of the landscape and the accessibility of climate analogs severely restrict movement options for species responding to climate change. Thus, prioritizing areas for enhancing connectivity in a climate-informed manner will be critical for facilitating species' movement and the protection of biodiversity under a changing climate. This is particularly true because few other viable options (e.g., translocation) exist for many species. Specifically including future climate projections and the accessibility of suitable climatic conditions, given human modification of the landscape and dispersal capacities, will make these prioritization decisions more robust in an uncertain future of inevitable climatic and land-use change.

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Supporting Information

Transformations and PCA loadings of climate variables (Appendix S1), summary statistics of PCA component values (Appendix S2), ecoregion areas and degrees of human modification (Appendix S3), comparison of resistance value transformations (Appendix S4), and the connectivity impact of including climate projections for all of western North America (Appendix S5) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. Data associated with this paper are available from Adaptwest Climate Adaptation Planning Project.

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