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Research Paper

The influence of model frameworks in spatial planning of regional climate-adaptive connectivity for conservation planning

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HIGHLIGHTS

- Landscape connectivity model outputs may have low spatial agreement.
- Different frameworks and topographic, biotic, and climate inputs affect model outputs.
- Model selection should be based on the landscape variables and conservation criteria.
- A combination of connectivity modeling approaches may provide the best solution.

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ABSTRACT

Landscape connectivity improves species' capacity to adapt to climate change. These models are increasingly needed and available for climate-change conservation planning. However, their relative strengths and weaknesses are unclear. We asked how well do the spatial outputs from four connectivity models intended to support climate change conservation agree? To understand the implications of selecting one or several approaches, we compared various combinations of four connectivity models for ecoregions in California, U.S.A. Two models are based on landscape structure, Land Facet Corridors and Omniscape, while two other models, Meta-Corridor Approach and Network Flow Analysis (NFA), use focal species' range dynamics to determine connectivity. We also describe how each approach integrates climate-adaptive connectivity concepts. Variation in modeling methods, objectives, inputs, and landscape representations strongly affects the modeled connectivity patterns. For the region where all four models were run, almost three quarters of the landscape was selected by one or more models, but three or more agree for only 9.5% of the area, all of which is riparian. This emphasizes the importance of riparian areas for climate adaptation. We found NFA prioritized connections close to protected areas, while Meta-Corridor avoided higher cost agricultural and developed areas. The structural models agreed in areas with low human impact but Omniscape avoided areas of low topographic diversity and Land Facet Corridors avoided connections in areas with no protected areas.

Connectivity models should be selected based on the conservation objectives, such as spatial scale to be implemented, and a combination of models may be best.

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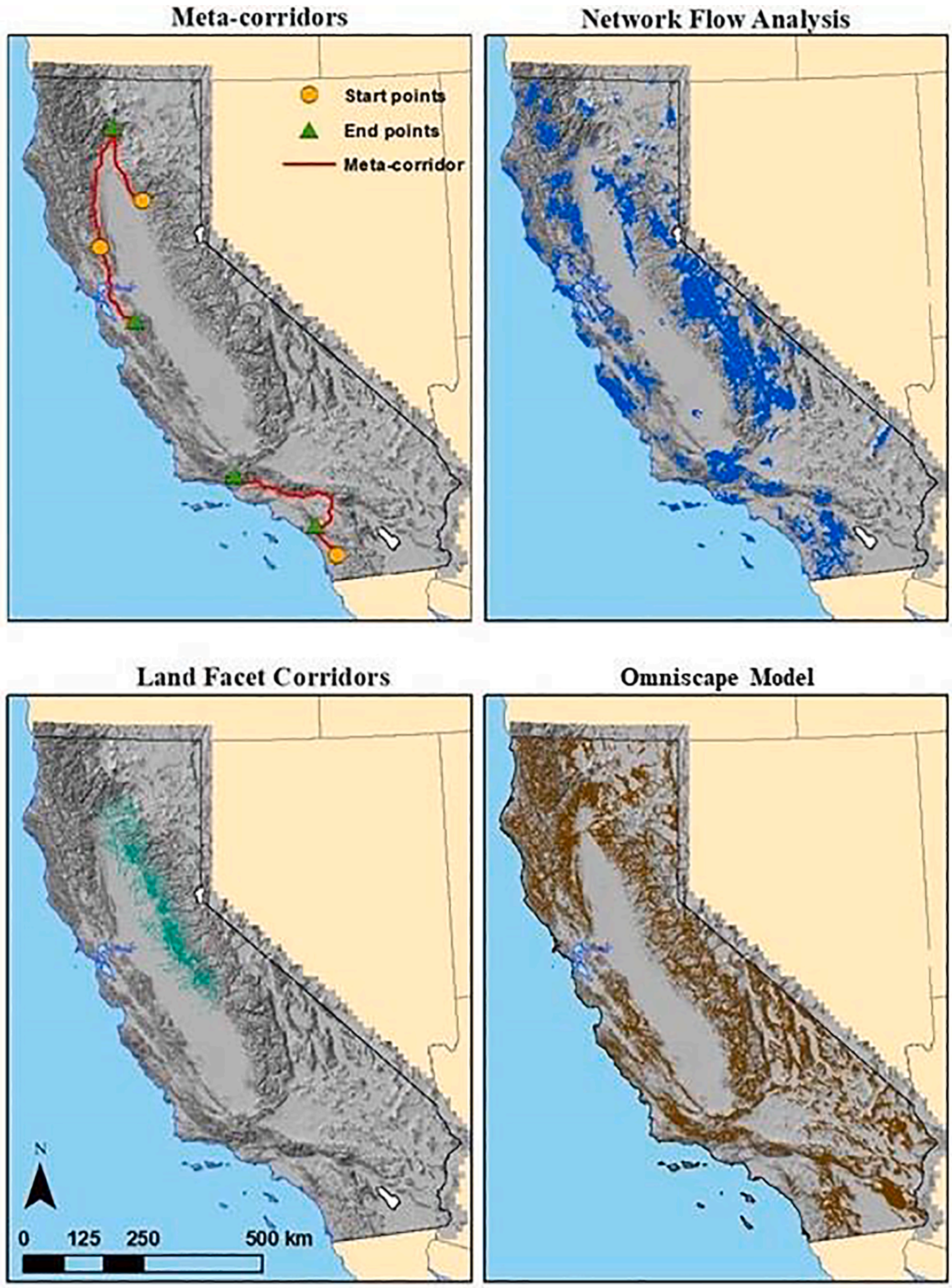

Fig. 1. Output of four connectivity planning approaches for regions in or the whole state of California. Meta-Corridor Approach and Network Flow Analysis use suites of focal species, while Land Facet Corridors and the Omniscape model structural connectivity.

1. Introduction

Adapting human use of landscapes to climate change is increasingly important for biodiversity conservation. Strategies include increasing the number and size of protected areas, preserving climate refugia (Thorne et al. 2020), managing habitats for climate resilience, restoring habitats with plants that will withstand climate change and other stressors, and increasing landscape connectivity (Heller & Zavaleta, 2009; Choe et al., 2018, 2020). Counteracting landscape fragmentation due to human land use by maintaining or restoring conservation corridors and by managing landscapes for permeability is essential to facilitate species movements to track suitable climates (Beier, 2012; NUÑEZ et al., 2013). While conserving landscape connectivity has been a conservation planning tool for several decades, conserving areas for climate-wise connectivity to facilitate species range shifts is relatively new (Keeley et al. 2018). There are several considerations when designing or prioritizing connectivity areas to support species range shifts under climate change. For example, selecting areas with high geographic heterogeneity ensures the presence of many microclimates in a small area, and may allow for species to find nearby climatically suitable sites. Delineating corridors along climate or moisture gradients similarly may enable species to find suitable climatic conditions close to their current occurrences. Matching sites with today's climate types to sites that may have similar climate in the future and ensuring connectivity between these climate analog sites may enable species to move beyond their current ranges (Choe et al. 2020). Species that can adapt to climate change by adjusting their ranges may be the best candidates for focal species connectivity modeling approaches. Accommodating the needs of species with short dispersal distances in corridor designs can facilitate movement over many generations (Beier et al. 2008).

There are many connectivity models that operationalize these concepts. Some approaches are species-specific, and use species distribution models and climate projections to connect modeled current and future species ranges (e.g., Williams et al., 2005; Phillips et al., 2008; Dilts et al., 2016; Leonard et al., 2017). Other connectivity models use landscape structure as the driving influence of identifying corridors, with the assumption that structure will capture the movement needs of most species that need to shift their ranges. Climate-wise models, which integrate climate conditions as well as landscape structure into the quantification of connectivity, include riparian corridors (Krosby et al. 2014), Land Facet corridors (Beier & Brost 2010), and connectivity areas based on high levels of natural landcover (McGuire et al. 2016). Designs to connect climate-analog locations have been explored in several studies (Littlefield et al., 2017; Carroll et al., 2018).

As landscape planners start including climate change concerns, an understanding of the methods, assumptions, and mapped outputs of different connectivity models is needed to select the appropriate model and approach (Diniz et al. 2020). The basic decision points on the selection of connectivity models have been identified (Keeley et al. 2018), but the differences in spatial outputs from different methods are just beginning to be examined.

We examined the spatial outputs of four landscape connectivity models developed for conservation and climate adaptation objectives in California, U.S.A. (Fig. 1). The models represent differing approaches to landscape connectivity and the incorporation of climate change considerations. Two models use suites of focal species, the Meta-Corridor Approach and the Network Flow Analysis; while the other two, the Land Facet Corridors and Omniscape, model the structural components of landscape connectivity. The Meta-Corridor Approach conceptually prioritizes climatically suitable corridors for use by multiple species (Choe et al. 2017). Network Flow Analysis (NFA) generates chains of connectivity needed to ensure stable habitat through all time steps for all focal species (Phillips et al. 2008). Land Facet Corridor models identify corridors with a continuity and diversity of landscape units defined by abiotic factors such as topography, geology, and soils which remain relatively constant under climate change (Beier & Brost 2010). Finally, the Omniscape Approach (McRae et al., 2012; Littlefield et al., 2017; Choe & Thorne, 2019) uses circuit theory (Dickson et al. 2019) to identify high flow areas connecting current climate locations to future analog climates, or along topographically diverse natural routes. Three of the models, NFA, Land Facet, and Omniscape were already in use for conservation planning and environmental regulatory processes in California, prior to this study. We aligned species, climate and other input data from the versions of the three models whose outputs we compared, and to create comparable output for Meta-Corridor model that we added to the analysis. The previous existence of the three connectivity model outputs is representative of situations that conservation planners in other regions may encounter, where they not only may have to construct new models, but also to evaluate existing ones.

We compared model assumptions and methods and used the spatial congruence (Seo et al. 2009) of areas selected by the four models to compare how their frameworks and inputs affect land area selection. All four models overlap in one region of California, which is the primary location for comparison of spatial outputs. However, we also compared the outputs of the two focal species-based approaches, the two structural connectivity approaches, and a region where focal-species-based approach and a structural connectivity approach overlap. The results can inform what criteria should conservation designers use in selecting connectivity models for their region. Since the goal of the paper is the comparison of the assumptions, methods and outputs of the connectivity models, we used a single global circulation model (GCM) and one future time period to control for uncertainty among climate models.

2. Methods

To standardize for model comparison purposes, we ran the Meta-Corridors model using the HadGEM2 global circulation model and RCP8.5 emissions scenario, on which the NFA and Omniscape results had been based, and modeled connectivity for 2070 (average for 2061–2080) (Fig. 1). The RCP8.5 is the most plausible scenario in the midcentury and 2100 under current policies (Schwalm et al. 2020).

The two focal species-based approaches, Meta-Corridor and NFA, used the same data set of the current and future distribution ranges of 2,235 California native and endemic plant species (Hannah et al. 2012). We applied a hierarchical cluster analysis to classify the plant's distribution ranges with similar spatial distribution patterns into 10 groups and applied the Meta-Corridor model to the two largest groups of species. In addition, because the Land Facet Corridor model was limited in extent, the focal landscape for the four-model comparison is limited to a specific ecoregion (see below). Below we briefly describe each of the four models. More details are given in the Appendix A.

2.1. Four connectivity modeling approaches

2.1.1. Meta-Corridor analysis

Based on the shifts in modeled species' climatic distributions, this approach identifies climate Meta-Corridors - potential pathways suitable for the range shifts of multiple species - by grouping species with similar current distribution patterns from the modeled results. Thus, it optimizes one corridor for many species under the assumption that species with similar distribution shifts could use the same routes (Choe et al. 2017), and addresses the need to prioritize conservation actions when faced with limited funding. While not meant to inform parcel-scale conservation action, the California Meta-Corridors can serve as a tool to draw attention to the importance of areas selected as potential options for native plant species to adapt to climate change through range shifts.

We applied a hierarchical cluster analysis to the set of plant species distributions and selected the two largest groups according to their current spatial distributions. These comprise 286 species mostly distributed in Southern California's Coast Ecoregion; and 282 species in Northern California's Sierra Nevada Foothills and Interior Coast Range. For each group, we selected the starting and ending points of corridors based on high species richness areas from current and future species ranges. We conducted a least-cost path analysis with species richness and landcover informing the resistance layer, on a landscape composed of grid cells with 2.5 arc-minute resolution. Least-cost modeling identifies a single path with the lowest cost distance from the source and the destination points (Diniz et al. 2020). In this study, a least-cost path was calculated between the selected areas for the two species sets.

2.1.2. Network flow analysis

The goal of Network Flow Analysis is to find the minimum area that ensures that connected, suitable habitat for a single species or a set of species through time as their ranges shift in response to climate change (Phillips et al. 2008). To identify the optimal areas that would need to be conserved to ensure the continued protection of native California plant species, we used an NFA results for 2,235 plant species across the statewide domain through 2070.

By modeling species distributions using the Maxent at several time steps and taking into account dispersal distances, chains of 2.5 arc-minute resolution grid cells are found that would allow species to persist and move to suitable climate through the decades. Models were fit in baseline climate (1960–1990) using the following climate variables: maximum temperature of the warmest month; minimum temperature of the coldest month; temperature seasonality, precipitation seasonality, and aridity index (the ratio of annual precipitation to potential evapotranspiration). Fitted models were projected into 2070 using the HadGEM2. Background pseudo-absences were generated from a random sample of 10,000 points from the statewide domain. Maxent

Table 1
Overview of four connectivity modeling approaches as operationalized for California.

	Meta-Corridors	*Network Flow*	*Land Facet Corridors*	*Omniscape*
Objectives	Identify major pathways accommodating the range shifts of multiple plant species from a common geographic region.	Find the minimum number of grid cells that will support successive decadal range shifts predicted under climate change of many focal plant species.	Maximize the continuity and diversity of landscape units defined by topography.	Document ecological flow patterns as a function of landscape naturalness and topoclimatic diversity that connect current to future similar climate.
What is being connected?	Areas of high species richness and natural land cover	Current to predicted species ranges	Wildland blocks	Continuous core-free connectivity; flow between present-day climates and similar climates in the future in natural and semi-natural areas
Approach	Uses current species suitable habitat ranges to create species groups based on similar spatial distribution patterns; models climate Meta-Corridors for groups to permit current species-rich areas to link to future climatically suitable areas.	Finds connectivity chains by finding a continuous path or a set of pixels in which a species can disperse from currently suitable habitat through all time steps to future suitable habitat.	Uses cluster analysis to define land facets with respect to topographic variables and then applies least-cost analysis to design linkages between termini that include one corridor per land facet.	The landscape is treated as a circuit board with varying levels of resistance based on naturalness and topodiversity. Using a moving window approach, current flow is measured from all suitable cells within the circular window to the center cell and then summed across all windows.
Input	Plant occurrence information, current climate information, future climate scenarios, land cover map		Digital Elevation Map	Human modification, topoclimatic diversity layer, current climate and future climate projections
Output	Least cost paths and number of species overlapping the paths	Essential connectivity chains	Linkage design with corridor strands for each land facet	A continuous measure of wall-to-wall current flow
Assumptions	• Species will disperse more successfully through the areas containing suitable habitats • Species' interactions do not affect distributions strongly • Climate envelopes are constant, i.e., species cannot evolve to tolerate new climate regimes • Plant movement can be promoted by maintaining habitat connectivity		• Topography is a major driver of biodiversity	• Topoclimate diversity confers microclimate diversity and therefore is more likely to provide suitable climate options for species tracking coarser shifts in analogous climate. • Species will move directionally towards climate analog locations • Human modification will limit species movement
	• Grid cells with low species richness have a high cost for species to persist	• The rate of climate change is uniform through time • Distributions reach equilibrium with expectations from the models, i.e. within each of the 10-year time periods • Generation times approximate the 10-year time-slice duration • Constant dispersal rate for all species		

model features for each predictor were limited to linear, quadratic and product. Binary distributions were created using the maximum sensitivity plus specificity logistic threshold calculated from 30% of the initial occurrence records withheld for model testing and evaluation.

For California, plant species were included in the analysis if they have a minimum of 10 occurrence records, can form minimum chains, and need non-protected and undeveloped land to form these chains (Hannah et al. 2013). Thus, NFA found the set of chains that will need the least amount of currently unprotected area but still contain a minimum required area for each species. For all species, a universal dispersal distance of 1.5 pixels was assumed (the eight-neighbor rule). To determine the minimum number of chains required for a species, the IUCN minimum area threshold for endangered species of 100 km^2 (IUCN Standards and Petitions Committee, 2019) was increased by a factor of 10 because this is useful to elicit important regions for statewide temporal connectivity for a large number of plant species (Hannah et al. 2013).

2.1.3. Land Facet Corridors

Using topography and soil as surrogates for biodiversity (Brost and Beier, 2012a), the Land Facet Corridors connect land facets between two landscape blocks using a least cost approach (Brost and Beier, 2012b). Land facets are physical landscape units characterized by similar topography, such as high elevation, steep canyons, or low elevation gentle ridges. By focusing on landscape elements that constitute the physical foundation of species' habitats, which will remain constant potentially even under climate change, this approach aims to conserve connectivity for a diversity of species, including plants, through time, even if species assemblages change. Inclusion of riparian corridors and corridors where different land facet types are interspersed ensures the presence of topographic diversity and thus microclimate diversity in the corridors. California's Department of Fish and Wildlife (CDFW) has incorporated this approach into their landscape planning (Biogeographic Information and Observation System; https://wildlife.ca.gov/Data/BIOS; Hill et al. 2015). We used outputs from the ecoregion which they modeled, the western foothills of the northern Sierra Nevada Mountains. Three types of Land Facet Corridors were modeled to connect landscape blocks: ridge, slope, and canyon corridors; riparian corridors were additionally included (see Krause et al., 2015 for detailed methods).

2.1.4. Omniscape model

The Omniscape model identifies structural connectivity that facilitates species movement and thus range shifts between current climates and future similar climates. It assumes that areas of high naturalness allow movements of many species (McRae et al. 2016), and high microclimate diversity in a corridor may offer species climatic options at local scales enabling range shifts at regional scales. The Nature Conservancy built the Omniscape model for California (Schloss et al. 2019). The model prioritizes routes with little human modification to address the long temporal period that may be necessary to allow range shifts to happen. Connectivity was modeled between our baseline time period and HadGEM2 RCP8.5 (2070) climate analogs throughout California using Omniscape, is a moving window application of Circuitscape where electrical current flow, affected by the resistance of the landscape, is measured between all cells in the window and the target cell (McRae et al., 2016; Littlefield et al., 2017; Dickson et al., 2019). The resistance surface was created by combining topoclimate diversity-based with the

Table 2
Comparison of connectivity model input parameters.

	Meta-Corridors	*Network Flow*	*Land Facet Corridors*	*Omniscape*
GCMs & Emission Scenario	HadGEM2-ES RCP85	HadGEM2-ES RCP85	n/a	HadGEM2-ES RCP85
Time	2070	Decadal time steps until 2070	n/a	2041–2070
Spatial resolution	2.5 arc-minute resolution (~4 km)	2.5 arc-minute resolution (~4 km)	270*270 *m*	270*270 *m*
Climate variables	Temperature Seasonality, Max Temp of Warmer Period, Min Temp of Colder Period, Precipitation of Warmest Quarter, Precipitation of Coldest Quarter, Aridity Index	Temperature Seasonality, Max Temp of Warmer Period, Min Temp of Colder Period, Precipitation of Warmest Quarter, Precipitation of Coldest Quarter, Aridity Index	n/a	Mean annual temperature, mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), difference between MWMT and MCMT, mean annual precipitation, mean summer precipitation, mean winter precipitation, degree-days above 5 °C (growing degree days), the number of frost-free days, Hargreave's reference evaporation, and Hargreave'sclimatic moisture index
Which species included	282 species in the Sierra Nevada and 286 species in the Southern California Coast Ecoregion	Omit species that cannot form the minimum chains; omit species that meet minimum chains in protected areas	n/a	n/a
Dispersal	n/a	Universal dispersal of 1.5 (8-neighbor rule)	n/a	Climate analogs are within 50 km
Cost layers	Species richness (high species richness = low cost), combined with land cover cost	Protected areas, developed areas, non-developed areas	Cumulative cost raster for each land facet	Human footprint
Modeled domain	The Northern California Interior Coast Range and the Sierra Nevada Foothills, the Southern California Coast Ecoregion	California	The northern foothills of the Sierra Nevada Mountains	California

human modification-based resistance surfaces (Theobald 2012). By systematically moving the window across the landscape, current flow was measured to all target cells on the landscape to produce landscape-wide current flow map.

2.2. Comparisons of four connectivity approaches

We conducted four spatial comparisons to evaluate how the different connectivity models select area. We compared the four connectivity model approaches for their objectives, corridor definitions, methods, inputs, outputs and assumptions (Table 1). We also compared their input parameters (Table 2). We then compared spatial outputs in four ways:

(1) We assessed the spatial convergence of the four model approaches in the northern Sierra Nevada Foothills by identifying areas that are selected by one, two, three, or all four approaches.
(2) We compared the two focal-species oriented models which used the same set of plant species distribution models (NFA and Meta-Corridors). We summed the area of Meta-Corridors for the two geographic species groups and calculated overlap with pixels that contain Network Flow chains.
(3) We compared the output of the two structural connectivity approaches (Land Facet Corridors and the Omniscape model) in a specific ecoregion, the northern Sierra Nevada Foothills and calculated the area of overlap. The Omniscape model assigns each grid cell a current flow value. We limited the output of this analysis to all areas in California in the top 25% of current flow ("high-flow") for the purpose of comparing this output to the discrete linkage areas of the other methods. We determined overlap between these high-flow areas and the four types of land facets. In addition, we analyzed how well the high-flow areas function to connect protected areas by calculating the percent overlap between high-flow areas and Land Facet Corridors for 11 pairs of protected areas throughout the study area. For these 11 pairs, we calculated overlap in buffers created by drawing a straight line between the centroids of two neighboring protected areas and buffering it by ½ the length of the straight line. We also visually determined which neighboring protected areas are connected by high-flow Omniscape connectivity and calculated the percent of neighbors connected.
(4) We compared the outputs of two models that were run for the entire state, the Omniscape and NFA models by calculating the overlapped percent of high-flow cells (270x270 m) from Omniscape that fell within each 4x4 km cell identified by NFA in California. To determine whether area selected by connectivity models differed according to the degree of human modification or number of species present, for each California ecoregion (Hickman 1993), we measured the area selected by Omniscape and NFA, and the mean human footprint extent (Theobald et al. 2012). We also calculated the number of focal species distributed in each ecoregion by summing the stacks of species' presence layers. We tested for correlation by calculating Pearson's correlation coefficient (Pearson's r) between percent of the landscape selected by the Omniscape and NFA models, human footprint scores, and number of focal species.

Table 3
The area and percentage of the northern Sierra Nevada ecoregion selected by zero to four modeling approach.

The number of modeling approaches selecting the same grid	Area (km^2)	Percentage (%)
0	790.62	25.37
1	1161.68	37.27
2	868.20	27.86
3	269.70	8.65
4	26.58	0.85

3. Results

Spatial overlap between the areas prioritized for connectivity conservation by the three climate-incorporating connectivity and one model connecting landscapes with similar topography is low overall, even with a relatively large percentage of the landscape being prioritized by one approach or another (Fig. 1). However, the four approaches showed high agreement along riparian corridors. The individual comparisons below highlight differences between the areas prioritized by the focal

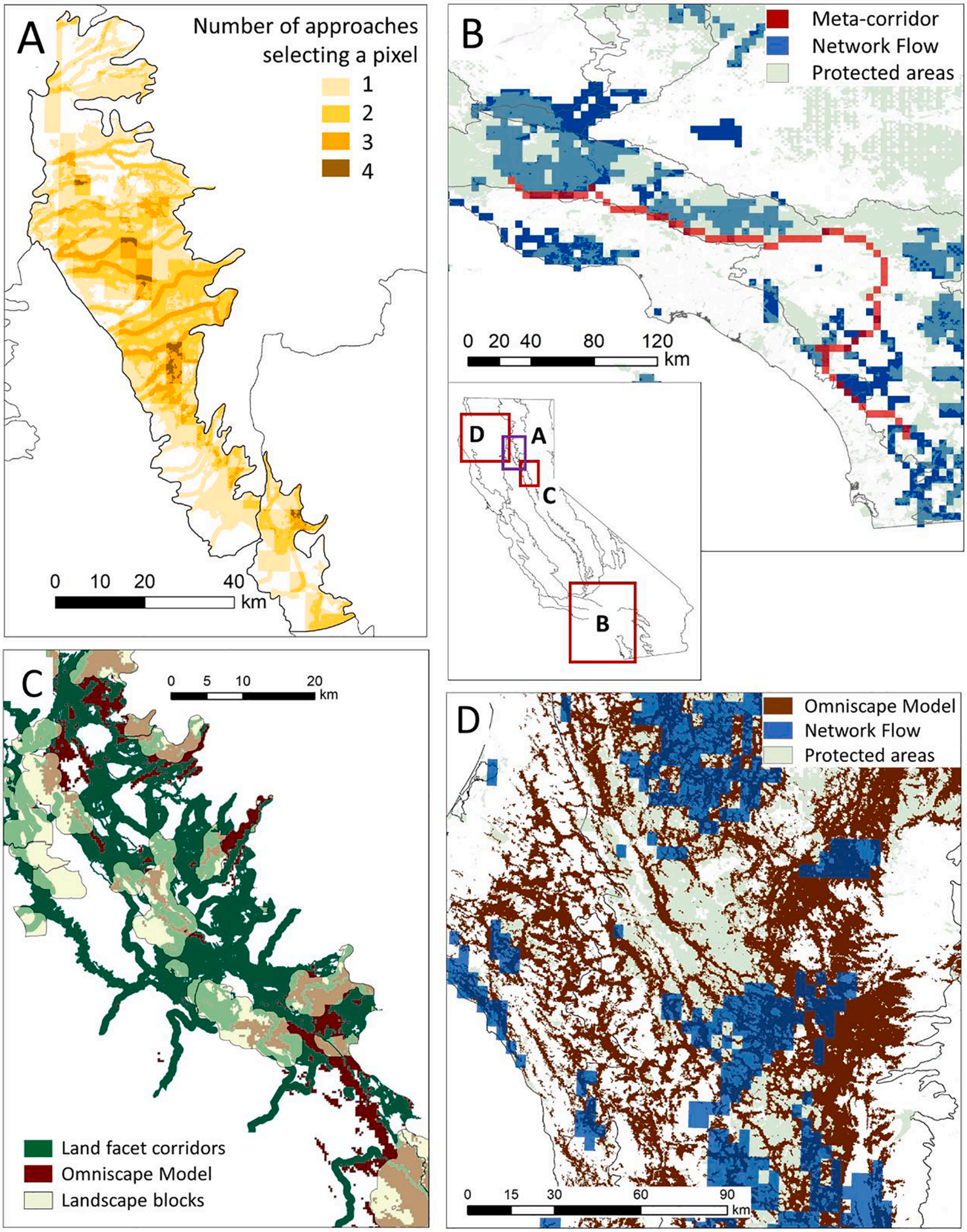

Fig. 2. Maps showing areas prioritized by (A) all four approaches, (B) Network Flow and Meta-Corridor approaches, (C) Omniscape and Land Facet Corridor analyses, and (D) Network Flow and the Omniscape.

connectivity modeling approaches.

(1) Almost three quarters (74.63%) of the northern Sierra Nevada ecoregion is selected by one or more of the four approaches. Out of an area of 3,117 km^2, Meta-Corridor selected 404 km^2 (13%); NFA selected 982 km^2 (32%); Land Facet corridors selected 1,113 km^2 (36%); and Omniscape selected 1,314 km^2 (42%). This indicates considerable suitable conditions for connectivity in the area. However, the areas selected by all four approaches are only 0.85% of the total area (Table 3), and they are all riparian (Fig. 2A). Most of the areas in which any of the three results overlapped (8.65%) among the four approaches also occur in riparian areas.
(2) The Meta-Corridors for the Sierra Nevada and Southern California Coast Ecoregion species' groups cover 2,000 km^2 and 1,344

Table 4
Percent overlap of high-flow Omniscape connectivity areas in protected areas and connecting Land Facet corridors.

	% overlap with high-flow Omniscape Connectivity areas		% overlap between Land Facet corridor and high-flow Omniscape Connectivity areas
	Protected area 1	Protected area 2	
Pair 1	7.4	24.9	0.1
Pair 2	44.3	0.0	8.7
Pair 3	0.0	0.0	0.0
Pair 4	66.7	20.7	15.1
Pair 5	41.5	0.7	6.9
Pair 6	52.0	66.0	40.0
Pair 7	0.0	0.0	0.0
Pair 8	0.0	0.0	0.0
Pair 9	14.9	55.0	10.8
Pair 10	0.2	9.1	0.0
Pair 11	18.1	33.9	17.6
Pair 12	17.8	0.0	4.0

km^2, respectively. In each Meta-Corridor, 28% of the grid cells overlap with pixels that contain Network Flow chains (Fig. 2B).

(3) Overlap between high-flow Omniscape connectivity areas and Land Facets in the northern Sierra Nevada Foothills does not differ much between the different types of Land Facet Corridors (Fig. 2C). Average overlap between ridge, canyon, slope, and riparian corridors and the top 25% of the high-flow Omniscape areas ranges from 19 to 27%. Only 23% of neighboring protected areas are connected by high-flow Omniscape connectivity areas. When two adjacent protected areas overlapped well with high-flow areas, overlap between Land Facet Corridors connecting these protected areas and high-flow areas is relatively high. However, overlap is low when one or both protected areas are not in high-flow areas (Table 4).

(4) Statewide, of 4,038 NFA grid cells, 17.68% contain more than 75% high-flow Omniscape area (median 34.42%, average 37.95%, standard deviation 32.19). The two approaches perform differently in ecoregions with different characteristics (Fig. 3). The Omniscape selects more area in ecoregions with a lower mean human footprint (Pearson's $r = -0.636$, $p = 0.007$), whereas NFA is not correlated with the human footprint (Pearson's $r = -0.286$, $p = 0.161$). Thus, in ecoregions with a high degree of human modification, NFA selects more area than the Omniscape (e.g., Southern California Coast). For both approaches, there is a positive correlation between the number of focal species in an ecoregion and the percent area selected (Omniscape: Pearson's $r = 0.525$, $p = 0.027$; NWF: Pearson's $r = 0.642$, $p = 0.066$).

4. Discussion

The spatial outputs of the four models in the northern Sierra Nevada ecoregion overlapped very little, even while each model selected a large proportion of the landscape. This shows how the variations in model objectives, approaches, inputs, and landscape representations, strongly affects their output, resulting in low spatial congruence of areas prioritized for connectivity. Therefore, it is important that planners have clear landscape conservation objectives and that they use those to help evaluate and select the connectivity modeling approach or approaches that best fit their objectives. Since each of the four connectivity approaches has strengths and weaknesses (Table 5), it is necessary to understand them and the specific spatial results of each approach for the real-world applications. This discussion uses the comparative analyses to help identify some of the suggestions landscape planners may wish to consider.

The large percentage of area selected by one or more of the approaches in the Sierra Nevada ecoregion is a consequence of the different objectives and input data that result in prioritization of different parts of the landscape for connectivity conservation. However, areas of high agreement among the approaches tend to be in riparian areas, even though only one of the approaches prioritized riparian areas specifically in its objectives. This emphasizes the important value of riparian corridors for climate adaptation. Riparian plants are more resilient to extreme climate events such as flooding or drought, and riparian areas provide microclimates by absorbing heat against extreme temperatures (Seavy et al. 2009). Riparian corridors may function as climate gradient corridors that can limit future development along rivers because of their unique soils and diverse topography (Beier 2012).

Coarse-grained connectivity conservation models such as the Meta-Corridor and NFA should serve as a vision map or decision support tool and can inspire or guide finer-scaled planning efforts and conservation actions (Beier et al. 2011). Fine-grained connectivity conservation plans, such as those resulting from Land Facet Corridor or Omniscape models, can recommend protection of specific areas with parcel-scale guidance to implementers. Both fine-grained approaches we discuss here design structural connectivity which is a coarse filter approach to connectivity conservation that may need to be complemented with corridor designs specific for species with special connectivity needs to enhance the effectiveness of the application (Krosby et al. 2015).

While the two focal-species based approaches used the same data, they had different objectives, and consequently prioritized different parts of the landscape. The NFA algorithm finds chains of grid cells that promote connectivity through time, avoids prioritizing already protected areas, and prioritizes grid cells close to protected areas. As a result, it selects pixels that, when protected, would increase the size of existing protected areas. Meta-Corridors, on the other hand, prioritize regional pathways along which a large number of focal plant species may be able to shift their ranges because their current and future ranges intersect the modeled pathway. In addition to prioritizing cells with high species richness, the cost raster informing the Meta-Corridor least cost path analysis assigns a higher cost to cells with more developed or agricultural areas than natural areas. This ensures that the Meta-Corridors will preferentially pass through natural areas including current protected areas, resulting in a 28% overlap of Meta-Corridors with NFA cells despite very different objectives.

We found spatial congruence between the two landscape structural modeling approaches to be high in areas with a low human footprint, that have high topographic diversity, and that contain isolated protected areas. Conversely, overlap was low in areas where there are either no protected areas (lack of Land Facet Corridors), that have a high human footprint, or low topographic diversity (lack of high flow Omniscape Corridors). The lower elevations of the Sierra Nevada Foothills exemplify the latter. Due to lower topographic diversity and a higher human footprint than the upper elevations, Omniscape corridors selected few areas in this environment compared to the Land Facet Corridors, which were designed to connect existing protected areas. Therefore, if the objective is to ensure that protected areas will remain connected, an approach that is specifically designed to connect protected areas is more appropriate or additional model settings for protected areas are required.

The two models that were run for all of California, NFA and Omniscape, performed differently in different types of ecoregions (Fig. 3).

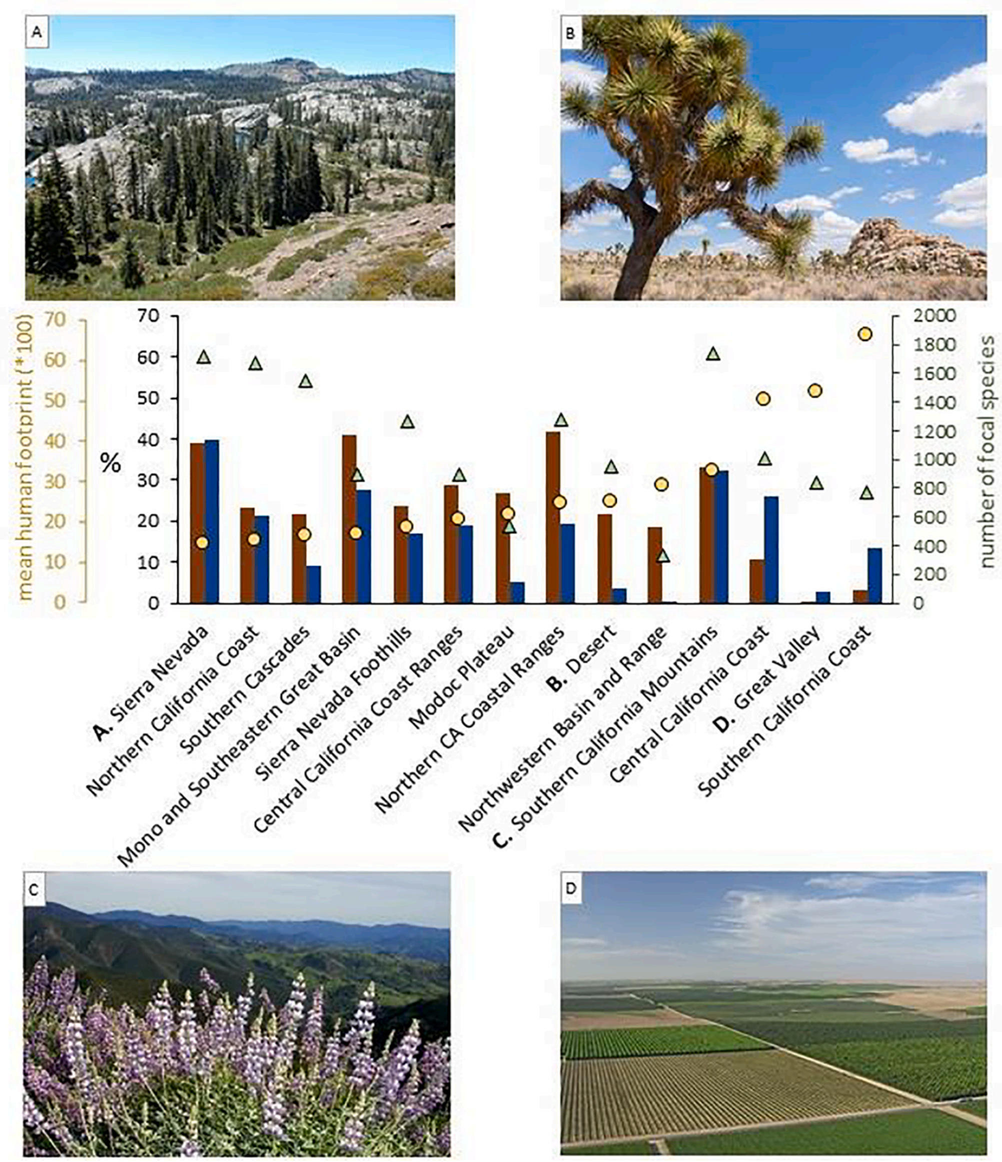

Fig. 3. Percent of high-flow Omniscape connectivity areas (brown bars) and Network Flow area (blue bars) in each California ecoregion. Green triangles represent the number of focal species, yellow circles indicate the mean human footprint. (For additional information on the ecoregions of California, please see the following link: https://doi.org/10.3133/ofr20161021. Photos by A. Brian Keeley; B. National Park Service; C. U.S. Forest Service; D. Conservation Biology Institute.) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Both approaches selected a large proportion of the landscape in ecoregions with lower human modification and a larger number of focal species (e.g. Sierra Nevada, Fig. 3A). In several ecoregions, a large percentage of the landscape is prioritized under the Omniscape model, compared with a smaller proportion by the NFA. This might be due either to low focal species numbers (e.g. the Modoc Plateau), or to a very low human footprint (e.g., Northern California Coast Ranges). For the Mojave Desert ecoregion (Fig. 3B), another possible explanation is that the climate will become unsuitable for many of the focal plant species and the NFA algorithm was not able to form consecutive dispersal chains through the end of the century. However, the Omniscape model does not consider intermediate time steps and may find analogous climate up to 50 km away.

The NFA prioritizes more area for connectivity than the Omniscape model in ecoregions with a high human footprint and high plant species diversity such as the Central California Coast (Fig. 3C; Thorne et al., 2009; Burge et al., 2016). By selecting a certain group of species as focal species, NFA prioritizes connectivity for this group. The Omniscape model on the other hand, is a structural connectivity approach, and therefore may miss important areas for certain groups of focal species. How well Omniscape will perform for the conservation of different groups of species needs to be determined.

Because of a high human footprint, low geodiversity, and few natural sites large enough to support temporal connectivity for the focal plant species, California's intensively farmed Central Valley ecoregion had a very limited area selected by either Omniscape or NFA (Fig. 3D). This may indicate that NFA is more appropriate in regions that are not dominated by human use and that still have natural areas available for species to move across and as destinations. However, the Omniscape model could be adjusted to reflect more subtle differences in land use in human dominated landscapes, allowing current flow through less intensely used areas. This can be accomplished by increasing the radius of the moving window or by assigning agricultural land covers lower resistance values.

In regions that are characterized by a high degree of naturalness, NFA cells have a clumped distribution, while high-flow climate-analog connectivity areas are distributed throughout the landscape (Fig. 2D). This demonstrates the tendency of NFA to select cells in the vicinity of existing protected areas and minimize the number of cells that will need to be protected, while the Omniscape model prioritizes flow areas throughout the landscape. In highly urbanized regions (Fig. 2B), NFA finds temporal corridors in natural areas in and around cities, revealing

Table 5
Benefits and caveats of four approaches to connectivity modeling. General caveats focus on the general approach; specific caveats consider the connectivity model run for California.

	Benefits	Caveats
Meta-Corridors	general • optimizes corridors for many possible futures and species	general • uncertainty in SDM and climate projections • uncertainty in species responses • does not consider dispersal limitations • clear Meta-Corridors may not exist for all species groups • does not consider plants' soil requirements specific • clear Meta-Corridors were found for only 2 of the 10 species groups identified for California • large grid cells make it less applicable for on-the-ground conservation
Network Flow	general • incorporates climate connectivity concepts (temporal connectivity) • considers short temporal time-steps which reflects the need for species to gradually shift their ranges with climate change • detects which species may not be able to keep pace with climate change; conservation targets can be adjusted to capture these species • supports planning when wanting to enlarge existing protected areas to accommodate for plant species persistence	general • uncertainty in SDM and climate projections • does not provide solutions for species that cannot disperse fast enough to keep up with climate change • computationally intensive specific • study did not include soil requirements • study used simplistic cost surfaces • study assumed same dispersal distances for all species • tradeoff between grid cell size and number of species included in the optimization
Land Facets	general • using topography and soil as surrogates avoids the uncertainties associated with climate change and biotic responses • locates best potential habitat and movement paths under climate change for low dispersal species and for species whose distribution is strongly influenced by topography and soil specific • connects protected areas which is important for protected area management	general • as a structural connectivity approach, it is designed to provide connectivity to the majority of species; however, as all coarse filter approaches, species with special connectivity requirements will need to be considered separately • does not consider refugia specific • study did not include soil data • corridor strands with interspersed land facets were not included
Omniscape	general • examines existing connectivity of entire landscape • incorporates climate-wise connectivity concepts (connecting climate analogs) • using a node-less approach eliminates necessity to define areas of high naturalness specific • incorporates topoclimatic diversity	general • as a structural connectivity approach, it will not provide connectivity for species with special requirements. specific • high-flow was subjectively set to be the top 25% of current flow • prioritizes areas with a low human footprint when possible and therefore generally does not consider restoration opportunities • does not consider protected areas and connections between them

the importance of these areas for plant persistence under climate change. The parameterization of the Omniscape model does not prioritize many areas in or around cities; however, lowering thresholds that determine the high-flow in identifying linkages (currently top 25% of current flow) does identify linkages that skirt the cities.

For our comparison study, we chose only one climate model output from each approach, and used it in all the climate-incorporating models, to isolate the effect the different connectivity models have so we could determine how the models themselves perform. Each connectivity model also had specific parameter choices that are not specific to the general approaches described (for example, the exclusion of soils in the Land Facet Approach or the inclusion of topographic diversity in the Omniscape). Considering the uncertainty of future climate change (Ando et al. 2018), the use of various global climate models and emission scenarios could increase insights for planning connectivity corridors in the real world. Therefore, we are not suggesting that the map outputs from the four approaches should be implemented for conservation in their current form. Instead, we suggest the analysis illustrates the variability and potential complementarity of the different connectivity models.

5. Conclusion

Landscape planners need clear conservation objectives in order to select the best-matching connectivity model. Landscape connectivity models have been developed to identify climate-stable corridors, corridors connecting current to future suitable habitat, or conservation networks for focal species (e.g., Howard & Schlesinger, 2013; Alagador et al., 2016; Dilts et al., 2016). However, while most climate-incorporating connectivity designs are based on sound ecological concepts, monitoring is needed across large taxonomic, spatial and temporal extents, to test their effectiveness in facilitating range shifts. To evaluate the functionality of each approach's assumptions and effectiveness (Table 1), long-term data on species movements and physical environments of moving locations are required. Migration tracking systems will be helpful to calculate species' dispersal rates. We could employ a citizen-science approach as one way of regular surveying over large areas, or a targeted monitoring approach (Furnas 2020). Future studies on the effectiveness of climate-adaptive corridors using survey results within the corridors could provide important information for climate change adaptation.

CRediT authorship contribution statement

Hyeyeong Choe: Conceptualization, Methodology, Software, Writing - original draft, Writing - review & editing. **Annika T.H. Keeley:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **D. Richard Cameron:** Resources. **Melanie Gogol-Prokurat:** Resources, Writing - review & editing. **Lee Hannah:** Resources. **Patrick R. Roehrdanz:** Resources, Writing - review & editing. **Carrie A. Schloss:** Resources, Writing - review & editing. **James H. Thorne:** Conceptualization, Methodology, Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

The detailed explanation of four connectivity models. Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2021.104169.

References

Alagador, D., Cerdeira, J. O., Araújo, M. B., & Anderson, B. (2016). Climate change, species range shifts and dispersal corridors: An evaluation of spatial conservation models. *Methods in Ecology and Evolution, 7*(7), 853–866.

Ando, A. W., Fraterrigo, J., Guntenspergen, G., Howlader, A., Mallory, M., Olker, J. H., & Stickley, S. (2018). When portfolio theory can help environmental investment planning to reduce climate risk to future environmental outcomes—and when it cannot. *CONSERVATION LETTERS, 11*(6). https://doi.org/10.1111/conl.2018.11.issue-610.1111/conl.12596.

Beier, P. (2012). Conceptualizing and designing corridors for climate change. *Ecological Restoration, 30*(4), 312–319.

BEIER, P., & BROST, B. (2010). Use of land facets to plan for climate change: Conserving the arenas, not the actors. *Conservation Biology, 24*(3), 701–710.

Beier, P., Majka, D. R., & Spencer, W. D. (2008). Forks in the road: Choices in procedures for designing wildland linkages. *Conservation Biology, 22*, 836–851.

Beier, P., Spencer, W., Baldwin, R. F., & McRAE, B. (2011). Toward best practices for developing regional connectivity maps. *Conservation Biology, 25*, 879–892.

Brost, B. M., & Beier, P. (2012a). Comparing Linkage Designs Based on Land Facets to Linkage Designs Based on Focal Species. *PLOS ONE, 7*(11), e48965. https://doi.org/10.1371/journal.pone.0048965.

Brost, B. M., & Beier, P. (2012b). Use of land facets to design linkages for climate change. *Ecological Applications, 22*(1), 87–103.

Burge, D. O., Thorne, J. H., Harrison, S. P., O'Brien, B. C., Rebman, J. P., Shevock, J. R., … Barry, T. (2016). Plant diversity and endemism in the California Floristic Province. *Madroño, 63*(2), 3–206.

Carroll C, Parks SA, Dobrowski SZ, Roberts DR. 2018. Climatic, topographic, and anthropogenic factors determine connectivity between current and future climate analogs in North America. Global change biology.

Choe, H., & Thorne, J. H. (2019). Omnidirectional connectivity of urban open spaces provides context for local government redevelopment plans. *Landscape and Ecological Engineering, 15*(3), 245–251.

Choe, H., Thorne, J. H., Hijmans, R., Kim, J., Kwon, H., & Seo, C. (2017). Meta-corridor solutions for climate-vulnerable plant species groups in South Korea. *Journal of Applied Ecology, 54*, 1742–1754.

Choe, H., Thorne, J. H., & Hollander, A. (2020). From disappearing climates to climate hubs, the five classes of climate risk for wildlife refuges. *Landscape Ecology, 35*(10), 2163–2177.

Choe, H., Thorne, J. H., Huber, P. R., Lee, D., Quinn, J. F., & Scherer, L. (2018). Assessing shortfalls and complementary conservation areas for national plant biodiversity in South Korea. *PloS one, 13*(2), e0190754. https://doi.org/10.1371/journal.pone.0190754.

Dickson, B. G., Albano, C. M., Anantharaman, R., Beier, P., Fargione, J., Graves, T. A., … Theobald, D. M. (2019). Circuit-theory applications to connectivity science and conservation. *Conserv. Biol., 33*(2), 239–249.

Dilts, T. E., Weisberg, P. J., Leitner, P., Matocq, M. D., Inman, R. D., Nussear, K. E., & Esque, T. C. (2016). Multiscale connectivity and graph theory highlight critical areas for conservation under climate change. *Ecological Applications, 26*(4), 1223–1237.

Diniz, M. F., Cushman, S. A., Machado, R. B., & De Marco Júnior, P. (2020). Landscape connectivity modeling from the perspective of animal dispersal. *Landscape Ecol., 35*(1), 41–58.

Furnas, B. J. (2020). Rapid and varied responses of songbirds to climate change in California coniferous forests. *Biological Conservation, 241*, 108347. https://doi.org/10.1016/j.biocon.2019.108347.

Hannah L, Roehrdanz PR, Soong O, Ikegami M, Tyner M. 2013. Advanced modeling of the biological effects of climate change and land use planning in California. California Energy Commission. Publication number: CEC-500-2014-056.

Hannah L, Shaw MR, Ikegami M, Roehrdanz PR, Soong O, Thorne J. 2012. Consequences of Climate Change for Native Plants and Conservation. California Energy Commission. Publication number: CEC-500-2012-024.

Heller, N. E., & Zavaleta, E. S. (2009). Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological conservation, 142*(1), 14–32.

Hickman JC. 1993. The Jepson Manual: Higher Plants of California. University of California Press, Berkeley, CA, USA.

Hill R, Hill S, Gogol-Prokurat M. 2015. ACEII Version 2. https://databasin.org/datasets/d5ae610954114029acae112386eee8c9/.

Howard TG, Schlesinger MD. 2013. Wildlife habitat connectivity in the changing climate of New York's Hudson Valley. Annals of the New York Academy of Sciences.

IUCN Standards and Petitions Committee. 2019. Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Committee. Downloadable from http://www.iucnredlist.org/documents/RedListGuidelines.pdf.

Keeley, A. T. H., Ackerly, D. D., Cameron, D. R., Heller, N. E., Huber, P. R., Schloss, C. A., … Merenlender, A. M. (2018). New concepts, models, and assessments of climate-wise connectivity. *Environmental Research Letters, 13*, Article 073002.

Krause CM, Gogol-Prokurat M, Bisrat S. 2015. Wildlife connectivity across the northern Sierra Nevada foothills. Technical report to the California Wildlife Conservation Board on the northern Sierra Nevada foothills fine-scale connectivity analysis.

Krosby, M., Breckheimer, I., John Pierce, D., Singleton, P. H., Hall, S. A., Halupka, K. C., … Schuett-Hames, J. P. (2015). Focal species and landscape "naturalness" corridor models offer complementary approaches for connectivity conservation planning. *Landscape Ecol., 30*(10), 2121–2132.

Krosby M, Norheim R, Theobald D, McRae B. 2014. Riparian climate-corridors: Identifying priority areas for conservation in a changing climate, Climate Impacts Group, University of Washington, Seattle.

Leonard, P. B., Sutherland, R. W., Baldwin, R. F., Fedak, D. A., Carnes, R. G., & Montgomery, A. P. (2017). Landscape connectivity losses due to sea level rise and land use change. *Animal Conservation, 20*(1), 80–90.

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. *Conservation Biology, 31*(6), 1397–1408.

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 of the United States of America, 113*(26), 7195–7200.

McRae, B. H., Hall, S. A., Beier, P., Theobald, D. M., & Merenlender, A. M. (2012). Where to Restore Ecological Connectivity? Detecting Barriers and Quantifying Restoration Benefits. *PLoS ONE, 7*(12), e52604. https://doi.org/10.1371/journal.pone.0052604.

McRae BH, Popper K, Jones A, Schindel M, Buttrick S, Hall K, Unnasch RS, Platt J. 2016. Conserving nature's stage: Mapping omnidirectional connectivity for resilient terrestrial landscapes in the Pacific Northwest., The Nature Conservancy, Portland Oregon. 47 pp. Available online at: http://nature.org/resilienceNW, last accessed April 22, 2021.

NUÑEZ, T. A., LAWLER, J. J., MCRAE, B. H., PIERCE, D. J., KROSBY, M. B., KAVANAGH, D. M., … TEWKSBURY, J. J. (2013). Connectivity Planning to Address Climate Change. *Conservation Biology, 27*(2), 407–416.

Phillips, S. J., Williams, P., Midgley, G., & Archer, A. (2008). Optimizing dispersal corridors for the Cape Proteaceae using network flow. *Ecological Applications, 18*(5), 1200–1211.

Seo, C., Thorne, J. H., Hannah, L., & Thuiller, W. (2009). Scale effects in species distribution models: Implications for conservation planning under climate change. *Biology Letters, 5*(1), 39–43.

Schloss C, Cameron D, Rindlaub N, Shank C. 2019. Available online at: https://www.scienceforconservation.org/products/connectivity-web-tour, last accessed April 22, 2021.

Schwalm, C. R., Glendon, S., & Duffy, P. B. (2020). RCP8.5 tracks cumulative CO_2 emissions. *Proceedings of the National Academy of Sciences, 117*(33), 19656–19657.

Seavy, N. E., Gardali, T., Golet, G. H., Griggs, F. T., Howell, C. A., Kelsey, R., … Weigand, J. F. (2009). Why climate change makes riparian restoration more important than ever: Recommendations for practice and research. *Ecological Restoration, 27*(3), 330–338.

Theobald, D. M., Reed, S. E., Fields, K., & Soule, M. (2012). Connecting natural landscapes using a landscape permeability model to prioritize conservation activities in the United States. *Conservation Letters, 5*, 123–133.

Thorne, J. H., Choe, H., Boynton, R. M., & Lee, D. K. (2020). Open space networks can guide urban renewal in a megacity. *Environmental Research Letters, 15*(9), 094080. https://doi.org/10.1088/1748-9326/ab9fad.

Thorne, J. H., Viers, J. H., Price, J., & Stoms, D. M. (2009). Spatial patterns of endemic plants in California. *Natural Areas Journal, 29*(4), 344–366.

WILLIAMS, P., HANNAH, L., ANDELMAN, S., MIDGLEY, G., ARAÚJO, M., HUGHES, G., … PEARSON, R. (2005). Planning for climate change: Identifying minimum-dispersal corridors for the Cape proteaceae. *Conservation Biology, 19*(4), 1063–1074.