"No-regrets" pathways for navigating climate change: planning for connectivity with land use, topography, and climate

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Abstract. As both plant and animal species shift their ranges in response to a changing climate, maintaining connectivity between present habitat and suitable habitat in the future will become increasingly important to ensure lasting protection for biodiversity. Because the temporal period commensurate with planning for mid-century change is multi-generational for most species, connectivity designed to facilitate climate adaptation requires pathways with 'stepping-stones' between current and future habitat. These areas should have habitats suitable not only for dispersal, but for all aspects of species lifecycles. We integrated present-day land use, topographic diversity, and projections of shifting climate regimes into a single connectivity modeling approach to identify pathways for mid-century shifts in species ranges. Using Omniscape we identified climate linkages, or areas important for climate change-driven movement, as the areas with more current flow than would be expected in the absence of climate considerations. This approach identified connectivity potential between natural lands in the present climate and natural lands with future analogous climate following topo-climatically diverse routes. We then translated the model output into a strategic framework to improve interpretation and to facilitate a more direct connection with conservation action. Across modified landscapes, pathways important to climate-driven movement were highly coincident with the last remaining present-day linkages, reinforcing their importance. Across unfragmented lands, the presence of climate-adapted pathways helped inform the prioritization of conservation actions in areas where multiple connectivity options still exist. Many climate linkages follow major watercourses along elevational gradients, highlighting the importance of protecting or managing for these natural linear pathways that provide movement routes for climate adaptation. By integrating enduring landscape features with climate projections and present-day land uses, our approach reveals "no-regrets" pathways to plan for a connected landscape in an uncertain future.

Key words: California; Circuitscape; climate adaptation; climate analogs; climate change; connectivity; conservation planning; corridor; linkage; microclimate; range shifts; topographic diversity.

Introduction

Species have begun to shift their ranges in response to recent climate change (Moritz et al. 2008, Chen 2011). Maintaining a connected landscape to facilitate these range shifts, as species track the changes in suitable climates, is an important strategy for biodiversity conservation. In a review of climate adaptation strategies for biodiversity conservation, increasing connectivity was the most frequently cited parameter (Heller and Zavaleta 2009).

Several approaches for modeling connectivity have been proposed that explicitly account for climate adaptation and range shifts. These approaches have varying levels of uncertainty in model inputs and generality of planning approach (Keeley et al. 2018, Littlefield et al. 2019). These studies have evaluated: connectivity spanning elevation gradients along riparian corridors (Beier 2012, Fremier et al. 2015, Krosby et al. 2018); connectivity along uniform landscape features or across a diversity of landscape features (Beier 2012, Brost and Beier 2012); connectivity along climate gradients between warm and cool climates or between present climate and future analogous climates (Beier 2012, Nuñez et al. 2013, McGuire et al. 2016, Littlefield et al. 2017, Carroll et al. 2018); and connectivity between focal species current distributions and their projected future distributions (Williams et al. 2005, Phillips et al. 2008) (Table 1, Appendix S1).

TABLE 1.   Summary of proposed connectivity approaches for climate adaptations including the assumptions, potential benefits of the approach and tool and data requirements.

Approach	Riparian network	Land facets	Climate gradients and analogs	Projected suitable habitat
Corridor	Riparian areas that span temperature gradients, high canopy cover, high naturalness, low solar insolation	One linkage per unique land facet One interspersion linkage One riparian linkage	Monotonic climate gradients	Suitable habitat in small intermediate time-steps
Connects	Low elevations (warm) to high elevations (cool) Evaluated on ability to connect protected areas	Like land facets in landscape blocks	Warmer natural patches to cooler natural patches or current climate to future analogous climate	Current species habitat to future species habitat
Assumptions	N/A	Dispersal is only limited by unlike abiotic conditions and modified lands	Climate gradients remain the same over time Like climate space is equated to suitable habitat Dispersal only limited by temperature gradients and modified lands	Emissions GCMs Downscaling Climate envelope model Dispersal
Benefits	Multibenefit (high ecosystem service, habitat, movement value) Simplicity Existing policies in place	Avoids uncertainty of climate models and species response Fine scale Easily obtainable data	Avoids uncertainty of climate models and climate envelopes Species are likely to shift ranges on monotonic gradients	Fine-filter (species specific) Specifically addresses anticipated changes
Tools	GIS	Clustering approaches (GIS overlay, fuzzy c-means, k-means), least-cost path	Linkage Mapper, Least-cost modeling	Linear Programming; SDMs (GAMs, Random Forest, etc.)

Planning for habitat connectivity for climate adaptation is different from present-day connectivity planning in several ways. First, connectivity for climate adaptation will need to facilitate movement outside a species' present range (Keeley et al. 2018). Present-day connectivity is often designed to address movement between existing populations or habitats within the present ranges of species, whereas connectivity in a changing climate will need to additionally connect to future suitable habitats outside a species' present ranges (Groves, 2012, Schmitz, 2015). Second, while present-day connectivity is designed to accommodate movement in the order of days, weeks or months, and therefore can occur through habitat that may only need to be suitable for movement or feeding, connectivity for climate change-driven movement needs to facilitate movement over many generations and will therefore need to incorporate habitats that support feeding, cover, and reproduction over longer periods of time. Finally, connectivity planning for climate-driven movement should incorporate geophysical features such as topographic diversity. Geophysical features are likely to play an important role in facilitating connectivity in a changing climate, because terrain and soil features remain relatively constant as climate changes and a diversity of these features creates conditions that support a diversity of microclimates and habitats (Dobrowski et al. 2009, Anderson and Ferree 2010, Brost and Beier 2012). This habitat diversity on a fine

scale may facilitate dispersal for some types of species because it provides temporary refugia during periods of rapid climate change and may enable species with a slower pace of dispersal to track a quickly changing climate (Dobrowski 2011, Brost and Beier 2012, Hannah et al. 2014). Topographic diversity is also typically evaluated at a finer spatial resolution (e.g., 30–270 m) than even downscaled climate projections (>810 m) and therefore can capture a variety of climate options that could be important at the leading edge of a range shift that may be missed by the coarser climate models (Hannah et al. 2014).

We modeled connectivity between contemporary natural lands and their future climate analogs across a topoclimatically diverse landscape to model connectivity priorities for climate adaptation. This approach incorporates present-day impediments to movement, data on shifting climate regimes from two climate models, and topographic diversity. It is a structural, coarse-filter approach that explicitly incorporates human modification as a factor that will limit movement for species moving in response to climate change, as that has been shown to pose an additional threat to climate-driven movement (Parks et al. 2020). This approach also addresses the multiple scales at which suitable climates may drive species distributions by modeling connectivity between the broad shifts in coarsely defined climate "space" along routes with finer scale topoclimate

diversity. Finally, it accounts for the longer time frames and incremental movements necessary for multigenerational range shifts, by incorporating the likelihood of climate-driven movement across microclimate stepping stones.

Our approach includes the following assumptions:

1) Species will move toward locations where the future climate is analogous to the present-day climate they are experiencing.
2) Species range shifts often require multigenerational movements over a longer temporal period and, therefore, routes that provide microclimate stepping stones with habitat suitable for all phases of a species' lifecycle are needed.
3) Topoclimate diversity confers microclimate diversity and therefore is more likely to provide suitable climate options, facilitating dispersal for species tracking suitable climate.

This approach extends recent advances in both terrestrial connectivity modeling and methods for factoring climate change into connectivity planning. Our work leverages recent advances in connectivity modeling by implementing omnidirectional *Circuitscape*, or *Omniscape* (McRae et al. 2008, 2016, Littlefield et al. 2017, Dickson, 2019, Landau et al. 2021). Like other wall-to-wall approaches (Compton et al. 2007, Theobald et al. 2012, Pelletier et al. 2014, McClure and Dickson 2017), this moving window approach removes the constraint of defining source and destination habitat patches based on jurisdictional boundaries or subjective thresholds and enables the characterization of the relative connectivity and fragmentation of the entire landscape. Recently, *Omniscape* was used to connect climate analogs (Littlefield et al. 2017) and, separately, to develop a strategic framework for connectivity implementation (McRae et al. 2016; D. R. Cameron et al., *in preparation*). Carroll et al. (2018) applied a similar centrality approach (i.e. ranked evaluation of connectivity opportunities between all or multiple sites) to identifying connectivity for climate adaptation and evaluated the results within the context of land use and topographic factors.

In this paper, we build on this body of work using *Omniscape* to model connectivity that addresses the need for climate adaptation at multiple spatial scales. We explicitly incorporate land use, topographic complexity, and climate projections into a single modeling approach. We then translate the climate-adapted output into a strategic conservation framework for easier interpretation and to create a more direct connection between connectivity modeling and on-the-ground implementation. By integrating present-day habitat connectivity priorities with those for climate adaptation, this approach can provide a basis for "no-regrets" conservation investments that will provide enduring ecological benefits in the face of environmental change. We also add novel programmatic advances to *Omniscape*'s implementation by

scaling parameters, further reducing the model output's reliance on user-defined thresholds.

Study area – California

California provides an ideal socio-ecological system for climate-related conservation planning. It has a wide diversity of climates and ecosystems that together comprise a global biodiversity hotspot, is moderated by the marine influence of a 1,352 km coastline, and has steep elevation gradients. Although California has a strong history of environmentally progressive policies, it has a high rate of population growth and associated land conversion, including the greatest loss of natural land to urbanization in the western United States (Theobald et al. 2020). If this pattern of sprawl continues to accompany population growth, landscape connectivity and the associated climate adaptation potential it provides could become severely limited. Early identification of movement routes that will facilitate climate adaptation will be critical to communicate and incorporate into growth planning to maintain options for adaptation. Although there are regional examples of policies and funding to advance habitat connectivity in California, there is no statewide plan to ensure plants and animals can successfully migrate to suitable habitats. As such, California is representative of many fast-growing, biodiverse regions of the world with the inclination, if not the tools, to plan for climate-adapted biodiversity conservation.

METHODS

We used *Omniscape* to model connectivity through topographically diverse landscapes between natural lands with similar current and future climates. We then classified the continuous output to identify discrete climate linkages and overlaid these climate linkages with the present-day characterization of connectivity in California. We evaluated the results against ownership patterns.

Omniscape

There are three main data inputs to parameterize *Omniscape*: (1) the source layer identifies the locations where species came from and where they are moving to; (2) the resistance layer represents the degree to which land-use facilitates or impedes movement; and (3) the size of the moving window in which current flow is calculated. Fig. 1 shows the input data, workflow, and intermediate and final model output.

Source input data.—We used two inputs for the source layer: the similarity between present and future projected climate analogs and the degree of naturalness of the landscape:

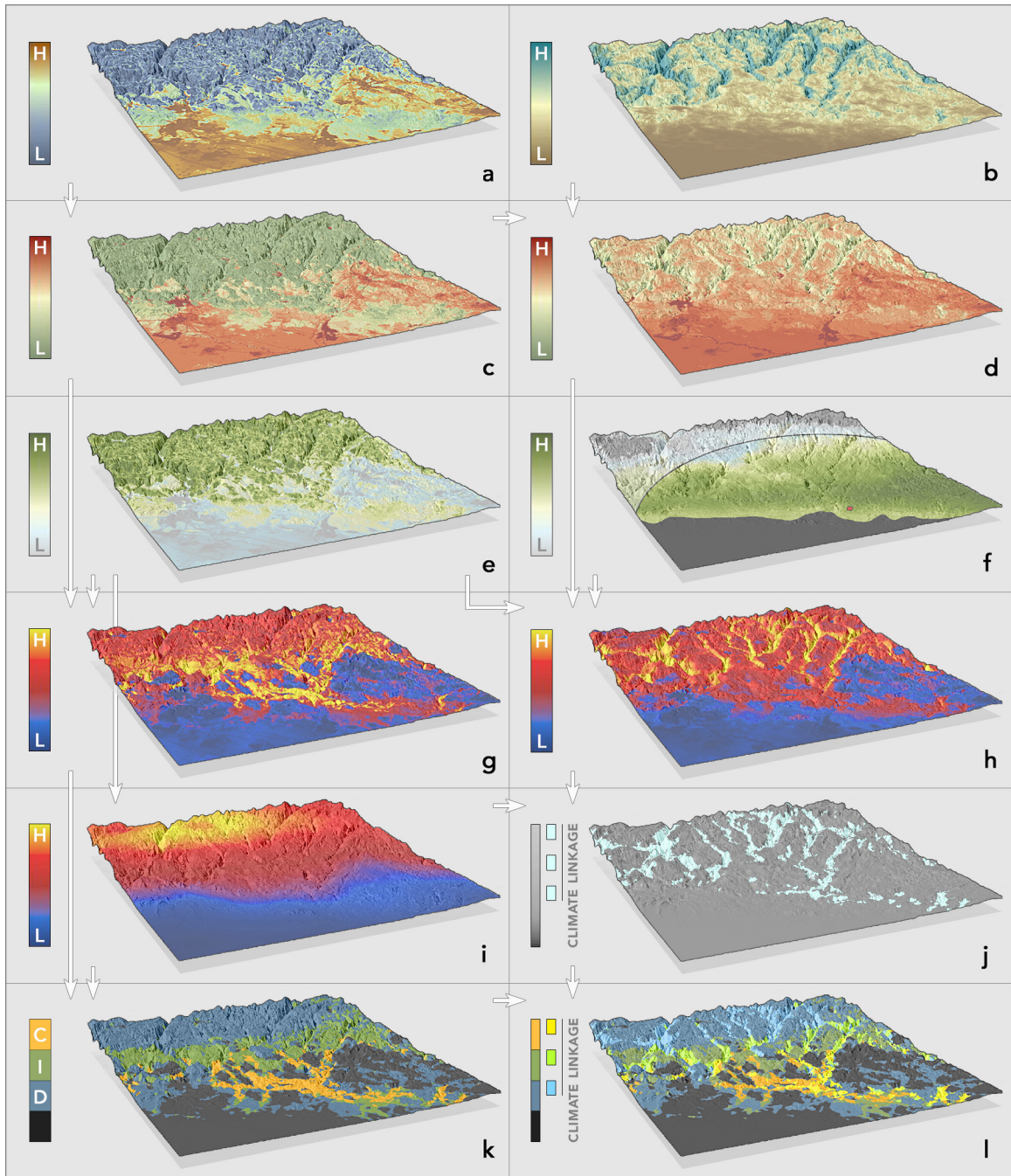*1. Climate analogs.*—We used the first two axes of a principal components analysis (PCA) of present-day

Fɪɢ. 1. *Omniscape* model inputs, modeled current flow, and classified connectivity for the present-day (left column) and for climate change adaptation (right column). Arrows indicate stepwise model inputs and outputs. *First row:* The input data for the resistance surfaces included (a) human modification and (b) topographic diversity. *Second row:* The resistance surfaces for (c) present-day connectivity based only on human modification and (d) connectivity for climate change adaptation based on the fuzzy sum combination of human modification and topographic diversity. *Third row:* Source of flow (e) for present-day connectivity based on naturalness (one minus human modification) and (f) between the present-day climate of the target cell and the similarity of future climate within 50 km of the target cell under the HADGEM-ES climate model (alternative run with CNRM-CM5 not shown). *Fourth row:* Omniscape-modeled current-flow outputs (g) for the present-day and (h) parameterized to account for climate-driven movements (i.e. with similarity of future analogous climate in the source and the inverse of topographic diversity in the resistance). *Fifth row:* (i) *Omniscape*-modeled current flow for the "null" connectivity model parameterized with only a uniform resistance surface and the present-day source and (j) climate linkages where climate connectivity current flow from either climate model is 1.3 times greater than the current flow from the null model. *Bottom row:* Present-day connectivity classified as C – Channelized; I – Intensified; and D – Diffuse; and (k) present-day classified connectivity overlaid with climate linkages (l).

climate (1981–2010) modeled from 11 bioclimatic variables (Carroll et al. 2015, Hamann et al. 2015) to represent present climate space at 1 km resolution. The PCA included mean annual temperature, mean temperature of the warmest month, mean temperature of the coldest month, difference between MCMT and MWMT, mean annual precipitation, mean summer (May to Sep) precipitation, mean winter (Oct to Apr) precipitation, degree days above 5°C (growing degree days), the number of frost-free days, Hargreave's reference evaporation, and Hargreave's climatic moisture index. The first two axes were dominated by annual temperature (axis 1) and annual precipitation (axis 2). To represent future climate space, we used the PCA applied to climate projections for mid-century (2041–2070) for unmitigated emissions and high population growth (Representative Concentration Pathway (RCP) 8.5) and two Global Climate Models (GCMs), CNRM_CM5 (Voldoire et al. 2013) and the HADGEM2-ES (Bellouin et al. 2011). We chose these GCMs because they were available from AdaptWest's climate adaptation planning resources (Carroll et al. 2015) and were recommended models from California's Fourth Climate Change Assessment. They represent a range in climate scenarios from a warmer-wetter (CNRM_CM5) to a hotter-drier (HADGEM2-ES) future in California.

We developed novel features in *Omniscape* to scale the amount of current flow relative to the degree of similarity between the current climate of the target pixel and future climates of the source pixels (Fig. 1f). This decreased the influence of the user-defined threshold that differentiates analogous climates from non-analogous climates. In addition to scaling the flow based on similarity, we used 1.5 principal component units as a dissimilarity threshold after which climates would no longer be considered analogous. In an analysis of niche breadths in North America, 1.5 PCA units were the median threshold for birds, reptiles, and trees (Littlefield et al. 2017). Also, 1.5 was inclusive of the median interquartile range for each PCA axis for 64 habitat types in California (0.47 and 1.02 for PCA 1 and PCA2 respectively). To determine the impact of our choice of a dissimilarity threshold, we conducted a sensitivity analysis to test the resulting current flow from a threshold ranging from more restrictive (0.9) to more permissive (10) (Appendix S2). We found that the more permissive the threshold the more similar the results were to present-day connectivity results and the more restrictive the threshold the stronger the influence of climate analogs.

2. Naturalness.—We used an estimate (H) of the degree of human modification (Theobald 2013, Theobald et al. 2020) to measure the amount of influence humans have exerted on the landscape (Fig. 1a). As described in Appendix S3, the source weightings were calculated using the naturalness (N) values which is the complement of human modification: $N = 1 − H$ (Fig. 1e). This means that more natural cells have relatively higher source flow, making the model more likely to try to connect such cells.

Resistance.—We created a resistance surface using both a multiscalar measure of topographic diversity and a measure of human modification (Fig. 1a–d):

1. Topographic diversity.—We used a measure of topographic diversity to quantify the variety of temperature and moisture conditions available to species as local habitat options, following the logic that a higher variety of topo-climate niches should support higher habitat diversity and provide options for species to persist despite climatic change.

To estimate topographic diversity (Fig. 1b), we combined two indices presumed to be primary factors in explaining the variation of topoclimate diversity (Dobrowski 2011, Anderson and Clark 2016). First, we used a modification of the Topographic Position Index (TPI) to measure hillslope position that is a dominant control of soil moisture. We used TPI because it allows multiscale parameterization, avoids challenges of an extremely skewed distribution, is computationally efficient, and minimizes artifacts (Salo and Theobald 2016). We calculated T as the average TPI value found at multiple resolutions of 30, 90, 270, 810, and 2,430 m (Riitters et al. 2002). Second, we used a modification of the Heat Load Index (McCune and Keon 2002) called Continuous Heat and Insolation Load Index (CHILI) (Theobald et al. 2015) that accounts for latitude shifts on a continuous basis, as well as moving the aspect of maximum heat load to south-southwest (202.5 clockwise from 0 north) to better approximate patterns found in empirical estimates of thermal south (Theobald et al. 2015). We calculated C as the standard deviation of CHILI values at multiple resolutions (the same as those used with TPI).

To combine the two indices, we max-normalized each index, and then calculated the fuzzy sum which allows for some additive effect but asymptotes at 1.0:

$$D = 1 − ((1 − T') \times (1 − C'))$$

For this component of the resistance surface, we calculated the complement of topographic diversity (1 minus topographic diversity) to incentivize movement through more topographically complex regions.

2. Anthropogenic resistance.—We used the same human modification base data (Fig. 1a) described for the source input, but we scaled and transformed it to represent resistance to movement (Fig. 1c) as described in Appendix S3. These changes served to accentuate the influence of areas with higher human modification and to reduce the influence of low levels of modification on movement.

3. Combining resistance variables.—To calculate resistance values (R), we combined our estimate of topographic diversity and naturalness (Fig. 1d), as

$$R = 1 - ((1 - D) \times (1 - N)).$$

We used fuzzy sums as the combinatorial operator (Theobald 2013) so the maximum would never exceed one (as it would using addition), would never be less than the resistance of either of the inputs (as it would using multiplication), and would still account for the influence of both variables on species movement (as the maximum would not have).

We evaluated rescaling topographic diversity to maximum values ranging between 0.3 and 1 to adjust the degree to which topographic diversity influenced the resistance surface (Appendix S4). With topographic diversity rescaled to a maximum of 1, flat areas impose as much resistance to movement as high density urban areas. With topographic diversity rescaled to 0.3, flatter areas only limit movement to a similar degree as row crops. We chose 0.3 because it still would permit movement through flat areas but would provide enough resistance so that modeled movement would preferentially follow topographically complex routes when multiple options exist.

Window size.—We used a 50-km radius moving window in which to model flow and identify climate analogs. The 50-km radius includes the need to connect larger distances to accommodate a longer period of time (McRae et al. 2016) and still is representative of the short distances that are likely to characterize movements of smaller less mobile species and are more tractable for connectivity implementation (Beier 2012). Linkage patterns longer than 50 km can still arise due to the overlapping search radii in a moving window algorithm. We buffered all input data to 50 km beyond the border of California to mitigate edge effects at the State's boundaries.

Classification

To classify these raw climate connectivity results (Fig. 1h) into conservation-relevant categories within the context of the present-day connectivity landscape, we compared it both to a null connectivity model (i.e. *Omniscape*-derived current flow without any resistance or climate considerations) (Fig. 1i) (McRae et al. 2016) and to the present-day connectivity model (i.e. includes resistance surfaces, but without climate specific parameterizations such as topographic diversity and climate analogs) (Fig. 1k). We divided the climate connectivity raw current flow (Fig. 1h) by the null model current flow (Fig. 1i) to evaluate places in which the inclusion of human modification, topography, and climate analogs resulted in more flow than would be expected in the absence of those factors. We used a quotient of 1.3 as a minimum threshold to identify these 'climate linkages' (Fig. 1j). We then used the present-day connectivity model from D. R. Cameron et al. (in preparation) to provide a contemporary context

in which to evaluate the climate linkages. This present-day connectivity model used the same input data and methodology as the climate connectivity model but without topography as a factor in resistance or climate analogs incorporated into the source. The present-day connectivity model (Fig. 1g) was also divided by the null model (Fig. 1i) to classify connectivity into areas with more flow, as much flow, or less flow than expected when considering land-use barriers to movement (Fig. 1k). D. R. Cameron et al. (in preparation) classified the landscape into four main present-day classes. *Channelized* areas have much more flow than expected (i.e. a quotient greater than 1.7) where connectivity options are constrained to potentially a single remaining route through a modified environment. *Intensified* areas have more flow than expected (i.e. a quotient between 1.3 and 1.7) where land use, infrastructure and water bodies have reduced the options for movement. *Diffuse* areas have as much flow as expected (i.e. quotient between 0.7 and 1.3) where there are many options for movement through mostly natural lands with fewer barriers. *Impeded* areas and *Areas with limited movement potential* are areas where land uses restrict movement (i.e. quotient < 0.7 or a low flow diffuse with human modification >0.2 respectively). We combined the climate linkages with the spatial data on present-day climate connectivity categories with the assumption that areas that impeded present-day movement would also impede movement along a climate linkage (Fig. 1l).

To help interpret strategic opportunities for climate connectivity conservation, we compared this final connectivity landscape against ownership patterns and protection status (CCED 2016, CPAD 2017, The Nature Conservancy, unpublished data), topographic diversity patterns (Theobald et al. 2015), and the riparian network (McKay et al. 2012).

RESULTS

Climate linkages

Climate linkages in California largely follow east–west pathways up elevational gradients (Fig. 2a). Climate linkages are more likely to follow riparian valleys than present-day linkages. Climate linkages within the Channelized and Intensified categories were an average of 535 m closer to rivers than those same linkage classes that did not explicitly incorporate climate-driven movement. Topographic diversity was also notably higher in areas that contributed to climate-driven movements across all present-day connectivity classes.

Eighty-two percent of climate linkage areas were identified in both climate models, HADGEM2-ES and CNRM_CM5. The level of agreement in results between climate models was consistent for climate linkages across all present-day connectivity classes (i.e. 81.3% within present-day Channelized areas, 80.7% within present-
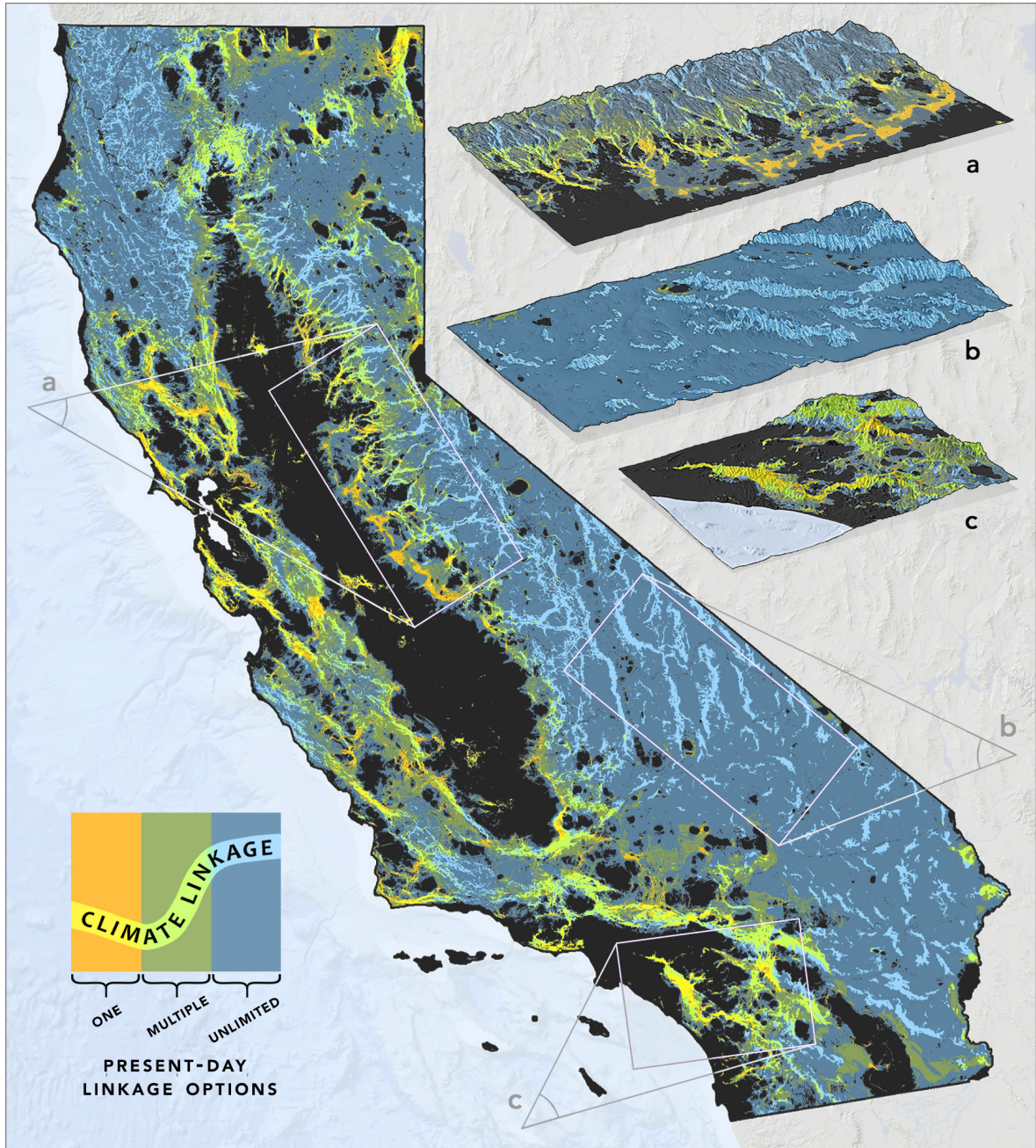
Fig. 2. Connectivity for climate adaptation in California overlaid on present-day connectivity classes statewide (a), the foothills to the Sierra east of Sacramento between Lassen Volcanic National Park and Stockton (b), the California Mojave desert (c), and the linkage between the Santa Ana and Palomar Mountains southeast of Los Angeles.

day Intensified areas, and 82.4% agreement in climate linkage areas within present-day Diffuse areas). The differences in the connectivity results between climate models did not result in new or different linkages, but rather in expanded linkages in the eastern slopes of the North Coast range (HADGEM2-ES) and in the western slopes of the northern Sierra Nevada (CNRM_CM5).

Overlap of climate linkages and present-day connectivity

There was a high degree of overlap between climate linkage areas and present-day Channelized areas. Forty-seven percent of Channelized areas were also classified as climate linkages in at least one climate model. In contrast, only 29% of areas in the Intensified category were also classified as climate linkages even though these two

classes shared a minimum quotient threshold for categorization (1.3).

Despite the high degree of overlap of climate linkages and Channelized areas, 61% of all climate linkage areas occurred on Diffuse lands in the present-day connectivity analysis. In these largely unfragmented landscapes with few barriers to movement, incorporating climate considerations provided an additional lens for prioritizing, managing, and protecting pathways for species moving in response to climate change.

Protection status and ownership

Climate linkages had relatively high levels of protection from permanent conversion (71.2% in public ownership or with a conservation easement). Within each present-day connectivity class, areas that also serve as climate linkages were better protected than those that only facilitated present-day movement (average difference in protection of 15.8%; Fig. 3). Climate linkages within the Channelized category had the lowest degree of protection of climate linkages in any present-day connectivity class (54% protected). Climate linkages in the Diffuse category had the highest levels of protection at 78% protected. Of the 2.05 million acres of climate linkage areas in the Diffuse category that were unprotected, 35% occurred in the North Coast and Klamath ecoregions and are largely managed as timber lands and 18% occurred on United States Department of Defense lands.

DISCUSSION

Considering climate-driven connectivity needs explicitly refined priority areas in lands that were uniformly Diffuse or Intensified in the present-day. Specifically,
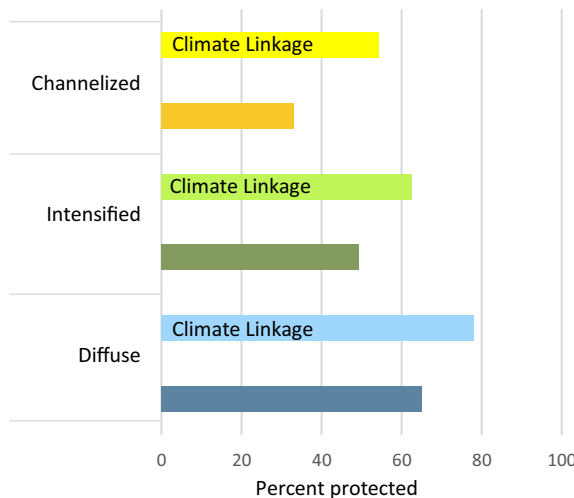
incorporating topographic diversity and connecting climate analogs elevated the importance of complex terrain with steep climate gradients through natural landscapes. In fact, topographic diversity was very influential to linkage design despite its relatively minor weighting in the resistance surface. However, within modified landscapes, the high degree of overlap of climate linkages and Channelized areas indicated that, in areas with a single remaining linkage, land use probably was more of a dominant driver in route selection (Fig. 2c). Channelized areas that were not distinguished as climate linkages probably connected current and future climates that were too dissimilar and/or had limited topoclimatic diversity. Although not connecting analogs, these Channelized areas are still important for climate adaptation as they often represent the last remaining natural linkage for maintaining connections between present populations and connect flatter lowlands to more topographically complex uplands.

We did not explicitly model movement from, to, or along riparian corridors (*sensu* Krosby et al. 2018). However, the climate linkages we identified still tended to follow riparian valleys, especially in the western foothills of the Sierra Nevada (Fig. 2a). Protecting and restoring riparian corridors is an often cited and appealing strategy for enhancing connectivity for climate adaptation because they provide natural linear pathways that connect warmer to cooler areas and are often protected to some extent by existing policies (Fremier et al. 2015). Maintaining or enhancing natural cover along riparian corridors can also have water quality and flood risk attenuation benefits that could help to leverage partnerships and funding sources for implementing connectivity actions in these areas.

The climate linkages in the Mojave desert appeared to deviate from the east–west movement characteristic in the Sierra foothills, however, these seemingly north–south patterns actually probably arose from short east–west upward movements on the steep eastern slopes from the valleys to the ridgelines that run north–south (Fig. 2b).

Addressing climate at multiple scales

This analysis is an early broad-scale application of *Omniscape* (McRae et al. 2016, Littlefield et al. 2017). It also includes a novel approach to address the multiple spatial and temporal scales at which species respond to climate change. The inclusion of climate analogs addressed the longer time period over which a species may shift its range and the coarser spatial scale of climate change projections. The inclusion of topographic diversity addressed the finer spatial scale at which individuals experience and respond to surface temperatures and moisture availability in addition to the shorter temporal scale at which individual dispersal events will take place. Previous studies have addressed temporal connectivity for species or ecosystems by modeling functionally

FIG. 3. The percentage of connectivity classes that are already protected through fee or easement.

connected distributions at different time periods (Rose and Burton 2009, Early and Sax 2011, Pellat et al. 2012), this analysis uses a structural approach to identify the stepping stones that are likely to provide habitat options during periods of projected climate change. The inclusion of topographic diversity also addressed the shortcomings of using coarse climate projections, because microclimate niches, important for movement at the leading end of a species range for some species, are missed by coarser climate models (Hannah et al. 2014). In combination, the use of climate analogs and topographic diversity addressed the short distance movements that better reflect how individuals actually disperse, the microclimate niches important for range expansion, and the longer term trends that will ultimately result in species-wide range shifts.

"No-regrets" pathways

Many approaches to planning for climate adaptation avoid the inclusion of climate projections due to the concern for allocating limited conservation resources to plans based on uncertain climate models. However, the high degree of agreement in climate linkage areas offers "no-regrets" pathways for planning, even for alternative futures. This high degree of agreement between connectivity models based on different climate projections probably resulted from the moderating influence of the static parameters for topographic diversity and human modification. Minor differences in output were further diminished from the classification of the results to define "climate linkages," muting any differences that were not substantial enough to cross the threshold for that designation. These moderating factors helped to alleviate uncertainties in the climate projections, while still explicitly addressing climate change as a driver for species movement. Although topodiversity is one factor that moderates the uncertainty of climate projections, the adaptive advantage it provides to species moving in response to climate change remains nascent.

Implementing climate adaptation today

This is the first approach that brings climate connectivity directly into a comprehensive present-day connectivity framework, enabling a clearer understanding of the entire landscape's contribution to both present-day connectivity and to climate adaptation potential. This strategic framework can help to guide restoration, improved infrastructure crossing, management, policy, and protection decisions. Most climate linkages exist within relatively unfragmented landscapes that are largely protected or under consolidated ownership for timber production or as United States Department of Defense lands. In these areas, climate linkages can be maintained and enhanced through stewardship of public lands or protected through forestry policies or incentives.

Many unprotected climate linkages are threatened by near-term development based on recent land-use trends (U.S. Environmental Protection Agency 2016). In these urbanizing landscapes, incorporation of information on connectivity in the early stages of regional growth planning, to integrate overpasses or underpasses within transportation infrastructure planning, and to enact policies supporting compact growth, could avoid severing important climate linkages. Land protection may also be an important strategy for preserving climate linkages in areas that are experiencing high development pressure and where existing protection is limited.

Caveats and assumptions

This study describes a structural, coarse-filter modeling approach to represent connectivity. As such, it best represents movement opportunities for species that generally avoid anthropogenic land uses and for which movement in response to climate change is a necessary and a feasible adaptation strategy. It does not model species-specific habitat requirements and so should not be applied to species whose movement is limited to specific habitats.

This study is also limited in depicting connectivity options in the flatter, more modified, Central Valley. First, because the present-day connectivity context formed the foundation for identifying movement routes for climate adaptation, modified landscapes with limited movement potential were also considered to be limited in their potential to support movement for climate adaptation. In this region, where connectivity is already lost for wide-ranging wildlife, our approach will not highlight restorable linkages.

Although not in the California study area, this approach is also unlikely to be applicable in uniformly flat, unmodified, landscapes where microclimate options for movement do not exist and cumulative climate exposure to movement is low (Dobrowski and Parks 2016).

A major assumption in this work is that topographic diversity will facilitate climate adaptation. Specifically, we assumed that topographic diversity would lead to a diversity of microclimates and microhabitats and that these additional habitat options would suffice as stepping stones between climate analogs. Also, incorporation of topographic diversity resulted in some climate linkages with steep elevation and climatic gradients, as in the Mojave desert, which may be too extreme for species to move through (Nuñez et al. 2013, Dobrowski and Parks 2016, Carroll et al. 2018). Even outside these steep linkages, topodiversity may alternatively prove to be maladaptive. Dobrowski and Parks (2016) suggest that movement through topographically diverse landscapes may not be ideal because it may lead to higher cumulative climate exposure.

This analysis also failed to classify the important pathways between low flat lands and the topographically complex areas as climate linkages and therefore requires the inclusion of the present-day Channelized areas for a comprehensive understanding of connectivity potential for climate adaptation.

It is important to note that not all species will move in response to climate change. Some species will be able to

tolerate or adapt to changing conditions (Román-Palacios and Wiens 2020) or will be able to redistribute locally into microclimate niches without regional movement (Virkkala et al. 2020). For other species, the combination of the pace of climatic changes, dispersal limitations, and habitat fragmentation patterns will make movement an infeasible adaptation strategy (Schloss et al. 2012, Román-Palacios and Wiens 2020).

Conclusions

Planning for connectivity today provides more adaptation benefit in general by avoiding fragmentation. This analysis provides "no-regrets" priorities in an interpretable framework that can be communicated to land-use planners early in planning processes. A majority of pathways for most efficient climate-driven movements are already in public land or conservation ownership. Monitoring networks and conservation strategies to ensure that these lands are managed in compatible ways is an important implementation strategy and makes conservation action for the remaining connectivity priorities more tractable. This work is the first study to model connectivity for climate adaptation that combines topography, land use, and climate change projections into a single model parameterization and, as such, can be a model for other jurisdictions that implement similar planning efforts.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2468/full

Open Research

Data (Schloss et al. 2021) are available from the Dryad digital repository: https://doi.org/10.5061/dryad.d7wm37q1m