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Related documents of the Washington Wildlife Habitat Connectivity Working Group may be found at
http://waconnected.org/climate-change-analysis/ .

Connectivity Planning to Facilitate Species Movements in Response to Climate Change

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Abstract

Connectivity Planning to Facilitate Species Movements in Response to Climate Change

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Chair of the Supervisory Committee:
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As species begin to shift their ranges in response to climate change, the most frequently recommended strategy for conserving biodiversity is to increase ecological connectivity in human-fragmented landscapes. However, the models currently used to prioritize areas for connectivity do not consider climate-driven movements outside of species' present-day distributions. In my thesis I demonstrate an approach to prioritizing lands for conservation that specifically addresses climate-driven range shifts. This methodology identifies cost-distance based corridors between areas of low human impact along present-day spatial gradients of temperature or moisture, along which species are likely to move as the climate changes. Using data on current land use and climate patterns, I model a network of linkages in the Pacific Northwest of the United States. The resulting maps allow planners addressing climate change to focus on areas for connectivity for climate change. The approach I present here will be of value to local, regional, and continental-scale

connectivity conservation initiatives seeking to target their investments toward climate change adaptation.

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Acknowledgments

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Chapter 1 – Connectivity Planning to Facilitate Species Movements in Response to Climate Change

Introduction

Species have moved large distances in response to past climatic changes (Martinez-Meyer et al. 2004; Parmesan & Yohe 2003). It is likely that the ranges of both plants and animals will need to move even farther and faster in response to projected climate change in the 21st Century (Lawler et al. 2009; Thomas et al. 2004). Unlike the species of the past, however, today's species will encounter significant human impacts across a majority of the Earth's land surface (Sanderson et al. 2002). As a consequence, fewer species will be able to track shifting climates and more will experience range contractions or extinctions.

Unsurprisingly, increasing ecological connectivity is the most frequently recommended climate change adaptation strategy for conserving biodiversity (Heller & Zavaleta 2009). Connectivity models are used as planning tools to identify areas most likely to facilitate species movements or other ecological flows (Crooks & Sanjayan 2006). However, standard connectivity analyses only address movement within species' current distributions, and do not address the range shifts made necessary by climate change. Although it is legitimately argued that maintaining flows of genes and individuals within current distributions increases overall resilience to climate change (Minor & Lookingbill 2010), conservation planners are in need of models that help identify areas that will specifically facilitate climate-driven changes in distributions (Opdam & Wascher 2004).

Several approaches have been proposed to address connectivity for climate change, but none have directly used the spatial climate gradients that will influence how changing climates, and the species distributions associated with them, transition across a landscape (Ackerly et al. 2010). Here, we demonstrate an approach to identifying landscape linkages that promote movement along climate gradients. Ours is a coarse-filter approach that uses underlying climatic and anthropogenic land use patterns rather than focusing on specific species (Hunter et al. 1988; Noss 1987). Our approach begins with contiguous areas of land, or patches, with a high degree of naturalness relative to surrounding land uses. We then use present-day climate gradients to identify pairs of patches, which if connected, would allow species to move from warmer to cooler areas (Fig. 1). We then map corridors between linked patches, using a novel cost-distance modeling approach to find the route with the most unidirectional change in temperature between the patches (Fig. 2) while remaining within areas of lowest human impact.

This approach is based on several basic assumptions about organisms' responses to climate change. We focus on connecting natural areas with corridors that traverse less-impacted routes across landscapes because, in general, the species that are most sensitive to human activities are the ones that will have the most trouble shifting through converted landscapes. We link patches along present-day climate gradients because we assume that 1) many species will track climatic changes, 2) species will be less likely to move through unsuitable climates than they will be to move through suitable ones, and 3) although climates will change, climate gradients — particularly those driven by topography and latitude — will not change dramatically. If species need to move to track their current climates as temperatures warm, and if climatic gradients are conserved (e.g., as temperatures increase, higher elevations will still be cooler than lower elevations, even if both are warmer than they are presently), species can be expected to move from their present locations to nearby areas with relatively cooler current climates. Species that will be sensitive to climate change will likely avoid moving through areas that are much cooler or much warmer than the climates they currently inhabit. For example, an alpine species is less likely to move across a hot valley bottom to get to the next higher meadow and a lowland species is less likely to cross a high mountain range to get to a slightly cooler valley. Routes of unidirectional change in temperature between patches of different temperatures provide for a climatically-bounded transition.

We use this approach to identify potential linkages for facilitating climate-driven movements of biota in the Pacific Northwest of the United States. First, we describe the study area and input data (in the form of geographic information system maps) consisting of climate data, patches of natural lands, and an index of landscape naturalness. Second, we describe the process of selecting patches to link based on their relative locations along a temperature gradient. Third, we introduce a method of using a cost-distance model to identify corridors based on climate gradients. We use this method to identify two different sets of corridors between patches. The first map depicts corridors modeled using only temperature gradients. The second map depicts corridors that were modeled using land use patterns as well as temperature gradients. Although we focus on temperature in this paper, we also demonstrate how the approach can be applied to moisture gradients as well.

Methods

Study Area

Our study area covered 443,578 square kilometers including the State of Washington in the United States and extending several hundred kilometers into Idaho, Oregon, and British Columbia, Canada (Fig. 3a). The area includes 14 ecoregions in conifer forest, temperate broadleaf and mixed forest, temperate grassland, savannah and shrubland, and desert and xeric shrubland biomes (Olson et al. 2001). We selected the region because of data availability, for its steep and varying temperature and moisture gradients, and for the substantial differences in the anthropogenic fragmentation of its landscapes. On average, increases of 3.0°C by the 2080s for the Pacific Northwest are predicted by the models considered in the IPCC Fourth Annual Report, relative to the average from 1970 to 1999, with rates of warming ranging between 0.1 and 0.6°C per decade (Mote & Salathé 2009). Annual precipitation is only predicted to increase by 1 to 2 %, but some models predict larger seasonal changes in precipitation (Mote & Salathé 2009).

Natural Land-cover Patches

The patches we linked together in our analysis were previously identified by the Washington Habitat Connectivity Working Group (WHCWG) (Fig. 3a). We include in our analysis a total of 348 patches in the study area, varying in size from 4,047 hectares to 1,250,090 hectares. The WHCWG delineated these patches by identifying all contiguous areas over 4047 ha (10,000 acres) of land classified as native cover by the Northwest Regional Gap Analysis Program (Cassidy et al. 1997), and not crossed by major roads or converted to agriculture or built environments (WHCWG 2010). Because naturalness is a subjective concept this is a subjective measure, but it identifies areas in which human activities are the least prominent. Within the WHCWG patches, the density of low-use roads (calculated as the percentage of 100-meter pixels containing low-use roads in a square 20 by 20 pixel moving window) varies by ecoregion. Patches in the heavily-roaded Pacific Northwest Coast and the Willamette Valley – Puget Trough – Georgia Basin ecoregions include densities of low-use roads up to 20% and 30%, respectively, compared to 10% in all other ecoregions.

Temperature Data

We used mean annual temperature gradients to demonstrate our approach (Fig. 3b). Mean annual temperature gradients in the Pacific Northwest are broadly correlated with gradients of more direct ecological relevance, such as growing degree days, average temperature of the coldest month, and climatic moisture deficit. We used a map of the normal of mean annual temperatures from 1971-2000, derived at a 1 square kilometer scale using the ClimateWNA climate data tool (v4.61, Wang et al. 2006), which is based on the Parameter-elevation Regressions on Independent Slopes Model (PRISM, Daly et al. 2008).

Landscape Integrity for Mapping Corridors

We used "landscape integrity," a spatially explicit index of naturalness (Fig. 3c) developed by the WHCWG, to address ecological resistance to movement arising from human land uses (WHCWG 2010). The landscape integrity index was based on methods developed by NatureServe (Comer & Hak 2009), and is similar in its goals to other indices including the human influence index and landscape naturalness (Sanderson et al. 2002; Theobald 2010). The landscape integrity index ranks 100 meter pixels on a scale from 0.5 to 9.0 in order of increasing naturalness based on land cover, increasing human population density and proximity to roads (See Appendix, Supporting Table 1) (WHCWG 2010). Based on the assumption that decreasing naturalness reduces species movement, the WHCWG inverted the integrity ranks by subtraction from 10, resulting in a movement resistance index of 1 to 9.5. We exponentially transformed this resistance index to vary the degree of resistance from human land uses, producing three different land-use resistance maps. These gridded maps, also called surfaces, had a minimum resistance of 1 and maximum resistances of 25, 50, and 100. To transform the resistance index we identified the exponent required to raise 9.5 to the maximum resistance value (25, 50, or 100) by finding the $\log_{9.5}$ of the maximum resistance value. We then raised the landscape integrity value of each pixel by this exponent for each of the different maximum resistance values. To match the resolution of our climate data, we aggregated the 100 meter resolution landscape integrity data to a 1 kilometer resolution by taking the mean of the 100 meter values in each 1 kilometer cell.

Linkage Selection

Because warming is projected in our study region, we wanted linkages to provide species access to cooler temperatures not already available in the patches they occupied in the present. To do this, we connected patches based on their coldest temperatures and between-patch distances, connecting patches if they differed in their coldest temperatures by at least 1°C and were 50 kilometers or less apart. We focused on the coldest temperatures in a patch because patches vary greatly in size and span different temperature ranges. If the climate is warming, the temperature of the coldest place within a patch indicates its capacity to continue to provide thermally suitable habitat as the climate changes (Fig. 1). To represent this coldest temperature, we used a value that was two standard deviations below the mean of the temperatures of the pixels in the patch. Although one could also use the temperature of the coldest pixel in the patch, our measure reduces the possible influence of single-pixel temperature outliers.

We linked patches that differed in their coldest temperatures by 1°C or more because we considered this difference likely to be ecologically significant in our study region. A difference of 1°C may be a conservative threshold for linking patches, given that the observed global warming of 0.76°C over the 20th century has provoked observable movements of flora and fauna, and that on average 3°C of warming is expected in the region in the next century (IPCC 2007; Mote & Salathé 2009; Parmesan & Yohe 2003).

We used 50 kilometers as a maximum edge-to-edge Euclidean distance between patches because this distance was sufficiently long to connect every patch in our region to at least one neighbor over the 1°C threshold. In other cases, it may not make sense to connect isolated patches if the distance to the nearest patch is unreasonably long. Because our grids had a 1 kilometer resolution, cell-to-cell cost-distance calculations were not possible for linkages less than 2 kilometers long, so we only included linkages over 2 kilometers.

Calculating corridors based on cost distance

We mapped corridors based on patterns of landscape integrity and current climate gradients, in a way that avoided developed areas while maintaining unidirectional change in temperature between patches. For comparison, we also mapped corridors that found the routes of most unidirectional change in temperature without avoiding developed areas.

We mapped these corridors using a cost-distance model, a practical and computationally efficient approach that is commonly used to identify the relative importance of areas between patches for ecological movements (Adriaensen et al. 2003). Cost-distance models use a gridded surface (in the form of a raster GIS layer) of costs, or resistances, associated with movement across a landscape (Adriaensen et al. 2003; Beier et al. 2008). From the cost surface, cost distances are calculated cell-by-cell outward from the edge of each patch by iteratively accumulating cell-to-cell cost distances using Dijkstra's algorithm (Dijkstra 1959). This produces an accumulative cost-distance surface from each patch across the study area. When the accumulative cost-distance surfaces of two different patches are added to each other, the resulting "corridor surface" indicates the cost distance incurred in using a particular cell to move between the two patches. The best routes for movement are those with the lowest cost-distance values on the corridor surface.

Cost-distance models traditionally used for connectivity modeling calculate costs isotropically, meaning that cost is the same regardless of the direction in which the pixel is crossed. Using a cost surface representing resistance associated with land use, cost distances are calculated from a focal cell to each of its 8 neighbors by multiplying the Euclidean distance from the focal cell to its neighbor by the mean of the cost of the focal cell and the cost of the neighbor (Equation 1, Fig. 4a, b). For diagonally neighboring cells, the distance from a focal cell to its neighbor is multiplied by √2 relative to directly adjacent neighbors (Fig. 4 a).

Equation 1: Focal-to-Neighbor Cost Distance = $((\text{Cost}_{\text{FOCAL}} + \text{Cost}_{\text{NEIGHBOR}})/2) \times$ Focal-to-Neighbor Euclidean Distance

Temperature gradient-based corridors

To identify corridors that find the route of most unidirectional temperature change between patches as in Figure 2, we use anisotropic cost calculations which calculate movement costs from an underlying gradient such as elevation, wind speed, or temperature (Frank et al. 1993). In the same way that hiking along the side of a mountain is energetically easier than climbing up it, anisotropic costs change depending on the direction in which the gradient is crossed. We use temperature as an underlying gradient, and calculate the cost of moving between two cells by multiplying a pre-determined distance-to-temperature ratio (in cost-distance units per unit change in temperature) and the focal-to-neighbor change in temperature, plus the Euclidean distance of moving between the cells (Equation 2, Fig. 4c). The distance-to-temperature ratio specifies how far in geographic distance a corridor should deviate from a straight Euclidean line in order to avoid a deviation of 1°C from a route of unidirectional temperature change between the two patches.

Equation 2: Focal-to-Neighbor Cost Distance = | Distance-to-Temperature Ratio × Focal-to-Neighbor Change in Climate Variable | + Focal-to-Neighbor Euclidean Distance

Using Equation 2, we calculated anisotropic cost distances from the raster of mean annual temperature using a distance-to-temperature ratio of 50 kilometers/1°C. We calculated accumulative cost outward from the edge of each patch across the entire study area using the r.walk tool in the GRASS GIS software package (GRASS 2010). We then added the two cost distance rasters of each linked pair of patches to create a corridor raster corresponding to that linkage. With anisotropic cost calculations on a temperature gradient, the routes on these corridor rasters with the lowest cost-distance values are those with the most unidirectional rate of change in temperature available between the two patches, producing the output illustrated in Figure 2. We then combined all of the corridors to produce a final map of the linkage network, following the approach in WHCWG (2010), using the Linkage Mapper tool for ArcMap 9.3.1 (McRae & Kavanagh 2011).

We chose the distance-to-temperature ratio of 50 km/1°C after first modeling corridors for 15 test linkages within the study area that were 40 kilometers long and crossed climate and land use gradients. On these test linkages we modeled distance-to-temperature ratios of 10, 25, 50, 100, and 200 km/1°C (Appendix, Supporting Fig. 1). We chose 50 km/°C because the corridors with this ratio maintained a largely unidirectional change in temperature without becoming unreasonably long. All of the corridors but one were robust to changes in the distance-to-temperature ratio at values over 25 km/°C.

Combined temperature gradient and land use-based corridors

To identify corridors that avoided developed areas while maintaining a unidirectional change in temperature between patches, we combined the anisotropic costs from moving across a temperature surface with the isotropic costs of crossing a resistance surface based on land use (Equation 3, Fig. 4d). We used an additive combination because it is simpler and more intuitive than alternative methods of combination.

Equation 3: Focal-to-Neighbor Cost Distance = $(((\mathrm{Cost}_{\mathrm{FOCAL}} + \mathrm{Cost}_{\mathrm{NEIGHBOR}})/2) \times$ Focal-to-Neighbor Euclidean Distance) + $\lvert$Distance-to-Temperature Ratio $\times$ Focal-to-Neighbor Change in Climate Variable$\rvert$

We used Equation 3 to calculate cost distances simultaneously from a raster of land-use resistance with a maximum resistance value of 100, and from a raster of mean annual temperature using a distance-to-temperature ratio of 50 km/°C. We chose this combination of distance-to-temperature ratios and land use resistances with the goal of identifying corridors that avoided areas with a landscape integrity value of less than 5 (urban, agricultural, and exurban lands; Appendix, Supporting Fig. 3), while keeping the temperature change relatively uniform in direction. We chose this combination of resistances by using the same set of test linkages as previously to explore all combinations of distance-to-temperature ratios and land-use resistances, using 25, 50, and 100 km/°C for temperature ratios and maximum land use resistances of 25, 50, and 100 (Appendix, Supporting Fig. 3). We combined all of the corridors to produce the linkage network across the entire study area as described above.

Results

Our analyses resulted in a network of patches connected by corridors along the Pacific Northwest's major temperature gradients (Fig. 5a, b). The warmest patches in the center of the study area are linked in stepwise fashion to ever-cooler patches, particularly west into the Cascade Mountains, north and east into the Rocky Mountains, and south into the Blue Mountains. Patches in the western portion of the study area either link to cooler patches in the Cascade Mountains, or to patches in the coastal ranges.

Areas with fewer patches, such as the western and central portions of the study area, have fewer, longer linkages that act as movement bottlenecks. In contrast, other areas have high densities of patches with many short, redundant linkages, or have very large patches that make corridors unnecessary barring further land conversion. To move from warmer patches to cooler patches along the linkages requires movements to the south, east, and west, as much as northward. This reflects the east-west and north-south orientation of mountain ranges in the region, and that at the scale of individual linkages topography has a large influence in the direction of temperature gradients relative to the influence of latitude.

The test linkages we modeled were largely robust to changes in distance-to-temperature ratios. For temperature-only linkages, for which we modeled distance-to-temperature ratios of 10, 25, 50, 100, and 200 km/°C, at values over about 25 km/°C, increases in the distance-to-temperature ratio generally did not result in major changes in corridor shape (Appendix, Supporting Fig. 1). In the combined land-use and temperature model, where we modeled all combinations of distance-to-temperature ratios of 25, 50, and 100 km/°C and land use maximum resistances of 25, 50, and 100, as long as the ratio between maximum land use cost and the distance-to-temperature ratio was between 1:1 and 3:1, urban and agricultural areas were avoided by the corridors without switching the direction of the underlying climate gradient within the corridor (Appendix, Supporting Fig. 2, 3).

The corridors calculated using only temperature gradients have cost distances that increase more rapidly in mountainous regions with steep climate gradients, resulting in corridors that are narrower and more constrained than in flatlands (Fig. 5a). In part, this arises because temperature differences are larger between patches. In addition, the temperature-only corridors often pass directly through urban or agricultural regions (Fig. 6a). This suggests that species whose movements are restricted by human activities will not be able to directly track climatic conditions as the climate changes. In comparison, corridors calculated using both temperature and land use inputs necessarily avoid areas of heavy land use (Fig. 6b). This caused the Linkage Mapper algorithm to reroute or drop some linkages and replace them with others compared to the temperature-only corridors.

Discussion

Our approach provides a much-needed framework for prioritizing areas to increase landscape permeability in the face of climate change. Resource managers and others addressing climate adaptation can apply this approach as a coarse-filter model as we have demonstrated it here, or tailor it to more specific needs. Our methods can be incorporated into existing cost-distance connectivity planning efforts using previously identified patches and land-use resistance surfaces. As a result, it may be useful for a number of regional conservation planning efforts that have used cost-distance models to develop connectivity networks in the past decade. In addition, it may be useful for major, continental-scale connectivity initiatives including Yellowstone to Yukon in North America, the Natura 2000 Network in Europe and the Alps to Atherton corridor in Australia, all of which include climate adaptation among their primary goals (Graumlich & Francis 2010; Taylor & Figgis 2007; Vos et al. 2008). To this end, we are integrating the tools used to model connectivity along climate gradients with Linkage Mapper, an open source cost-distance connectivity tool for ArcGIS (McRae & Kavanagh 2011).[1]

Compared to standard connectivity modeling methods, our methods highlight areas specifically relevant for connectivity for climate change. Whereas standard connectivity models typically connect patches to many neighbors on the basis of adjacency and cost distance (Spencer et al. 2010; WHCWG 2010), the patches in our results are only connected to each other if they are separated by a substantial difference in climate. Using our approach there are fewer linkages across major changes in the spatial orientation of temperature gradients (such as the bottoms of large valleys), because these changes reduce the difference in temperature between nearby patches.

Several approaches have been proposed to address climate connectivity, but ours is the first to design a comprehensive coarse-filter linkage network that provides for movement along climate gradients. In general, coarse-filter approaches focus on using community-level, geophysical, or anthropogenic patterns in conservation prioritization (Hunter et al. 1988). Fine-filter approaches in turn focus on individual species. Fine-filter approaches to connectivity modeling for range shifts have used bioclimatic envelope models to model small

[1] http://www.circuitscape.org/linkagemapper/LinkageMapper.html

numbers of vertebrates (Vos et al. 2008) and plant species (Phillips et al. 2008; Rose & Burton 2009; Williams et al. 2005) by projecting distributions into the future and connecting present and future distributions through time. These models are limited by the uncertainty associated with greenhouse-gas emissions scenarios, global circulation model projections, downscaling approaches, species distribution models, and assumptions about species dispersal abilities, particularly at the fine spatial scales of conservation planning (Beier & Brost 2010). It is also difficult to imagine combining individual bioclimatic envelope connectivity networks for all species in a region into a single network that managers can implement. Even connectivity models designed without climate change in mind struggle with combining corridor networks made for different species (Beier et al. 2008; WHCWG 2010). However, bioclimatic envelope approaches for species of particular ecological importance may be a useful complement to a coarse-filter approach. In these cases, our approach to identifying continuous corridors could be used to link current and projected future bioclimatic niches on a species-specific basis, as an alternative to the stepwise approach presently used.

In contrast to bioclimatic envelope models, our approach addresses the issue of uncertainty in future climatic changes by relying solely on the basic assumptions described in the introduction and elaborated upon below. This does not eliminate the uncertainty, but avoids multiplying it across component models. Decisions in our approach about thresholds governing which patches to link together are still informed by global circulation model outputs regarding the projected direction and magnitude of regional climatic trends, but these outputs are more robust than projections downscaled to fine resolutions (Salathé et al. 2009). In this way, our approach to linking patches can be adapted to regions where increased precipitation or cooling are expected rather than drying or warming. The relative simplicity of our approach makes it more transparent, but reduces its precision. It identifies corridors of natural lands that cross climate gradients – a concept that is easily understood – but does not predict the precise movements of individual species distributions.

In an approach that does not rely on projections of future climate but is still species-specific, Vos et al. (2010) modeled networks of present-day wetland habitats based on species-specific habitat needs and dispersal distances, and identified areas on the landscape that the highest number of species had to move through. Others have proposed more coarse-filter approaches. In a precursor to the approach we offer, Rouget et al. (2003) proposed corridors for ecosystem processes in changing climates via simple 1-kilometer wide corridors, based on land use, between areas of different elevations with correspondingly different climates. Beier & Brost (2010) propose connecting areas with uniform topographic and soil attributes, called land facets, with a cost-distance modeling approach. This creates a connected "stage" of similar topographic and geological characteristics for species to occupy or move through as the climate changes. Although the land facets approach does not incorporate information about climate gradients, it complements our approach, which does not address substrate, fine-scale topography and geology.

The utility of our approach is determined by how well our simplifying assumptions about organisms, climate gradients, and their respective responses to climate change hold under different circumstances. Our first assumption, that species ranges will move to track suitable climates, is documented in paleoecological studies and in observations of species responses to recent climate changes. Trees, other plant species, insects, and mammals have all tracked climate gradients in response to recent climatic warming (Beckage et al. 2008;

Chen et al. 2009; Lenoir et al. 2008; Moritz et al. 2008). Species whose range limits are not directly limited by climatic conditions may instead be limited by interactions with other species that are. For example, snow depth impacts the competitive interactions and distributions of coyotes and lynx (Bayne et al. 2008).

Our model can accommodate regional differences in which climatic variables exert the most control on species distribution patterns. For example, in boreal systems, the number of growing degree days or the mean temperature of the coldest month best predicts plant distributions, whereas in warmer, arid systems, climatic moisture deficit is more important (Wang & Price 2007). In our approach the underlying climatic gradient used to identify corridors can be tailored to regional sets of patches. Doing this could allow the model to better reflect the predominant driver in an area, and different gradients could be used in different portions of the same network. To demonstrate this flexibility, we modeled the same corridor network as above, but used annual climatic moisture deficit instead of mean annual temperature (Appendix, Supporting Fig. 4). Interestingly, the moisture deficit-based network was largely similar to the mean annual temperature network, reflecting the role of topography in driving both gradients in our region.

Our second major assumption, that climatic *gradients* between patches will remain largely constant even though the climate is changing in absolute terms, sets important constraints on the scales at which our approach may be used. We base this assumption on evidence that temperature and moisture gradients at scales between several kilometers and several hundred kilometers are driven largely by topography and other physiographic features (including the influences of elevation, cold air pooling, rain shadows, proximity to water bodies and wind patterns) (Daly 2006). Primarily because topography itself is unchanging, we assume that the shape of climate gradients will not change substantially at these scales. This same assumption is also present in many downscaled projections of future climate commonly used in climate envelope models (Ashcroft et al. 2009).

At scales larger than several hundred kilometers, changes in global circulation patterns arising from climate change may make gradients unstable as the climate changes (Daly 2006). At scales finer then several kilometers, emerging research, including Fridley (2009) and Daly et al. (2010), suggests that local temperature gradients may change in slope with climate change due to local atmospheric decoupling, particularly in climatically complex landscapes. In addition, the developers of the PRISM model, which we used to derive present-day climate gradients, urge caution in applying it at scales below 4 kilometers (Daly et al. 2008). For these reasons, we discourage using patterns in the cost-distance corridor rasters that are smaller than several kilometers to prioritize areas for corridors. Despite these caveats, we do not expect changes in gradients to result in major changes for our modeled corridors as long as the direction and shape of the gradient remain constant. Because most conservation linkages are longer than several kilometers but rarely reach several hundred kilometers, these scale constraints are less problematic for our approach than might be expected. Using individual linkages of these sizes, networks of any extent can be modeled. However, regional differences in which climate variables most drive ecological patterns require caution when crossing biome boundaries.

Our third assumption, that species will move most easily through areas with climates similar to those that they currently inhabit, targets our approach at species limited by climate in their dispersal and colonization ability. Similarly, our fourth assumption, that species will move most easily through natural lands, tailors the model to species that are limited by human land uses. These are the species that will have the most difficulty moving through converted landscapes in a changing climate and the most appropriate targets for conservation actions. At the same time, our approach is sufficiently flexible that it can be tailored further to address species with more specific movement needs or climatic associations. For example, a network for small mammals sensitive to thermal extremes but able to live in agricultural landscapes would assign higher movement costs to temperature gradients and lower costs to movement through agricultural lands.

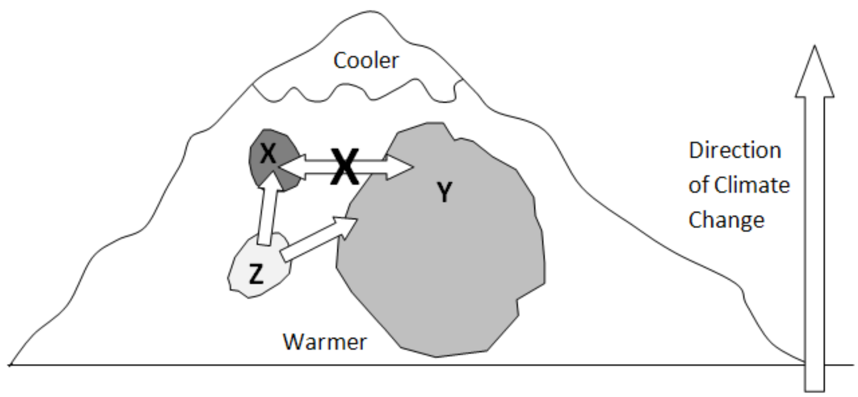
Although the generality of our approach is useful, it results in several limitations. As with most cost-distance modeling in conservation planning (Beier et al. 2008), our approach is inherently subjective in the way it is parameterized. The temperature threshold used to determine if patches are climatically different, and the resistances applied to land use and changes in temperature in modeling corridors, depend on the modeler's judgment. In this analysis, we used an iterative process of modeling different potential resistance values. We selected the combination used in the final model based on which cost values resulted in corridors that kept the rate of temperature change in the corridor uniform in direction, and avoided areas of agricultural, urban, and exurban land uses. In this way, we let the land use and temperature gradient patterns in our region determine the appropriate combination of resistances. Although subjective, this parameterization approach provides a rigorous, transparent, and repeatable way of assessing the impacts of different factors. As noted in the results, corridor locations were largely robust to changes in the resistances assigned to temperature and land use within the bounds that we explored using test linkages.

There are other connectivity needs in a changing climate that are missed by our approach. Riparian corridors may be important for movement during periods of environmental change (Decamps 1993). Topographical or geological factors are also likely to be important. Maintaining connectivity for long-distance migrations of birds, ungulates, and other organisms, as well as wetlands and aquatic systems, are not addressed by the climate gradients approach. These dimensions of connectivity could be analyzed separately and merged with a climate gradients-based network.

Conservation planning in a changing climate faces the fundamental challenge of developing strategies that are robust to uncertainty while still identifying the best investments of limited conservation resources. Our approach seeks to strike this balance. Without making uncertain predictions of the precise routes of range shifts, our approach significantly improves the field's ability to focus on connectivity that will help species to shift their ranges. Although increasing connectivity has been identified as a key climate adaptation strategy, existing connectivity models do not differentiate between linkages that help maintain resilient populations and ecosystems in the present and those that facilitate movements in response to climate change. Our approach improves the effectiveness of a key adaptation strategy in an analytically sophisticated way that meets the needs of practitioners.

Figures

(a)



(b)

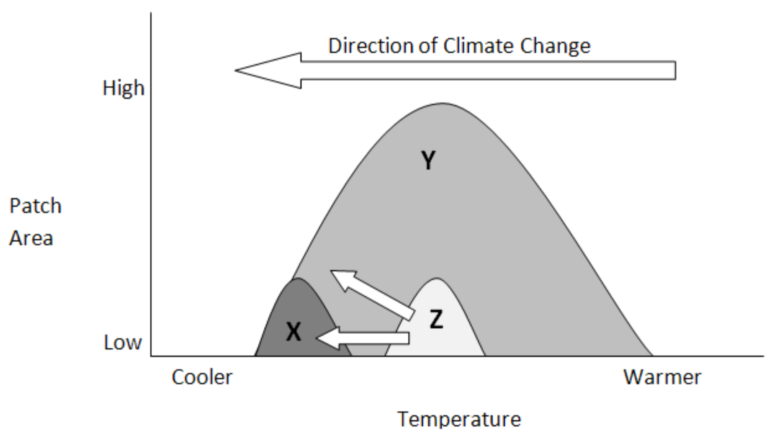


Figure 1. (a) Graphic representation of three differently-sized patches on the side of a mountain. Species found in Patch Z, a warmer area, can shift their ranges into cooler areas in Patches X and Y. Linking X and Y does not provide for access to cooler areas not already available to species in X and Y. (b) Histogram of the area of the patches in (a) showing that linking Z with X and Y helps species in Z move to a cooler climate.

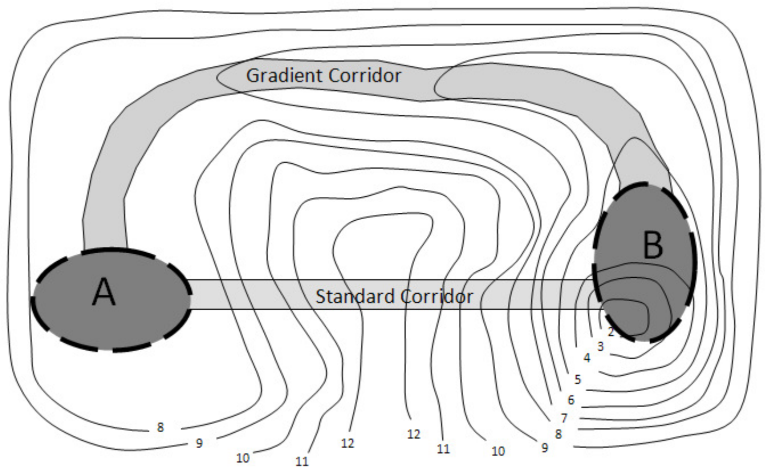


Figure 2. Map of two potential corridors traversing a temperature gradient (represented by contour lines) between patches A and B. Patch A can be connected to Patch B by a standard cost-distance corridor, which finds the shortest path (all else being equal) between the patches, or by a "climate gradient" corridor, which minimizes the total change in the underlying climate gradient between A and B.

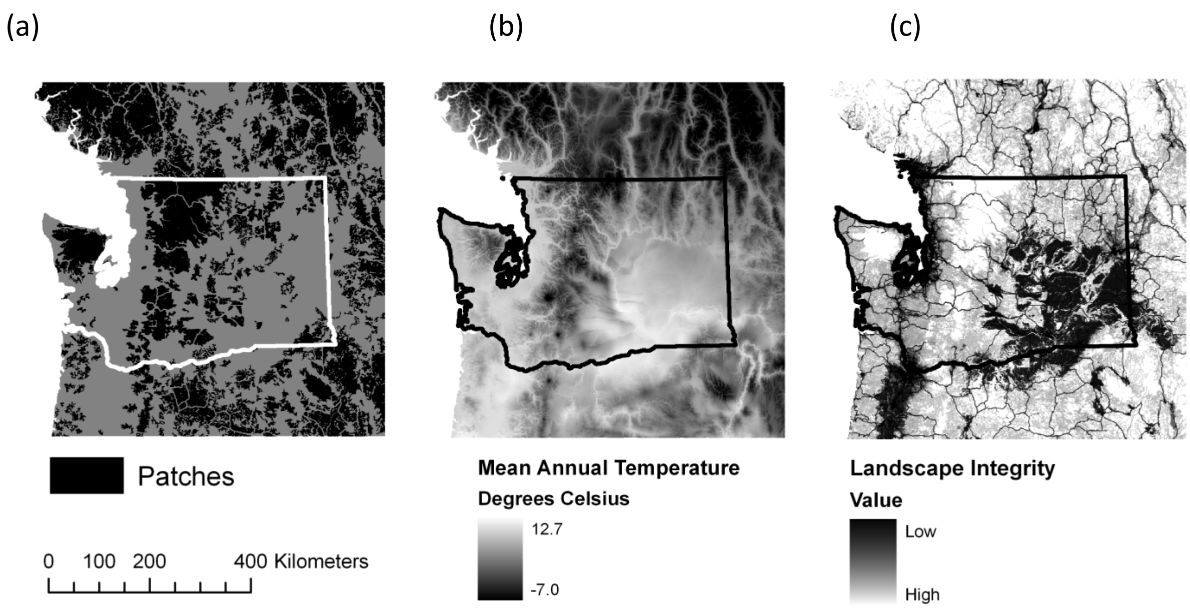


Figure 3. (a) Study area and patches of most "natural" lands over 4047 hectares in size. (b) 30-year normal of mean annual temperatures from 1971-2000. (c) Landscape integrity index, a metric of "naturalness" incorporating data on urban areas, distance to roads, agriculture, and other land uses.

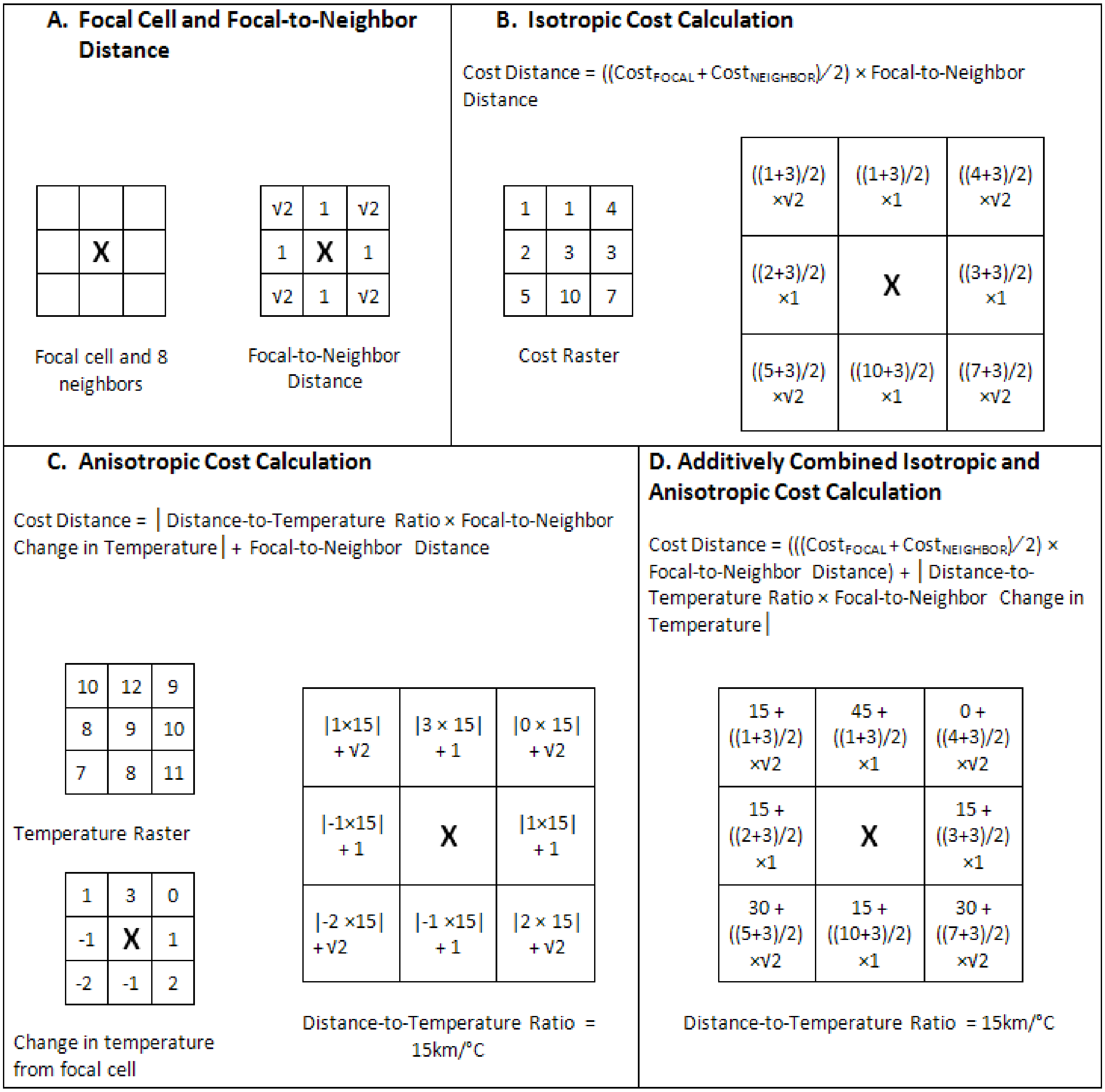


Figure 4. (a) Cost distance calculations start from each focal cell and use the focal-to-neighbor distance shown here. (b) Cost distance is calculated isotropically from each focal cell based on an underlying cost raster. (c) Cost distance is calculated anisotropically from each focal cell based on an underlying gradient, shown here using a distance-to-temperature ratio of 15 km / °C. (d) Anisotropic and isotropic cost distance calculations are combined additively.

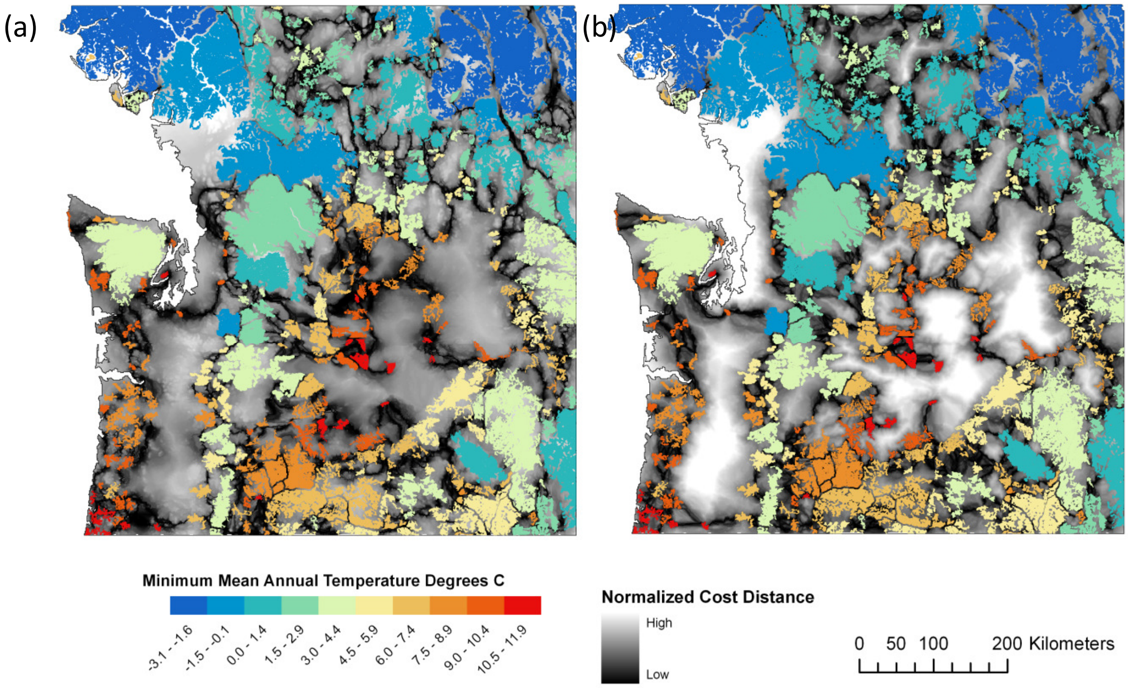


Figure 5. (a) Corridors between warmer and cooler patches of unidirectional change along the temperature gradient, and (b) of unidirectional change along the temperature gradient while also remaining in areas of lowest human impact. Lower normalized cost distances represent routes of more constant temperature change or higher naturalness.

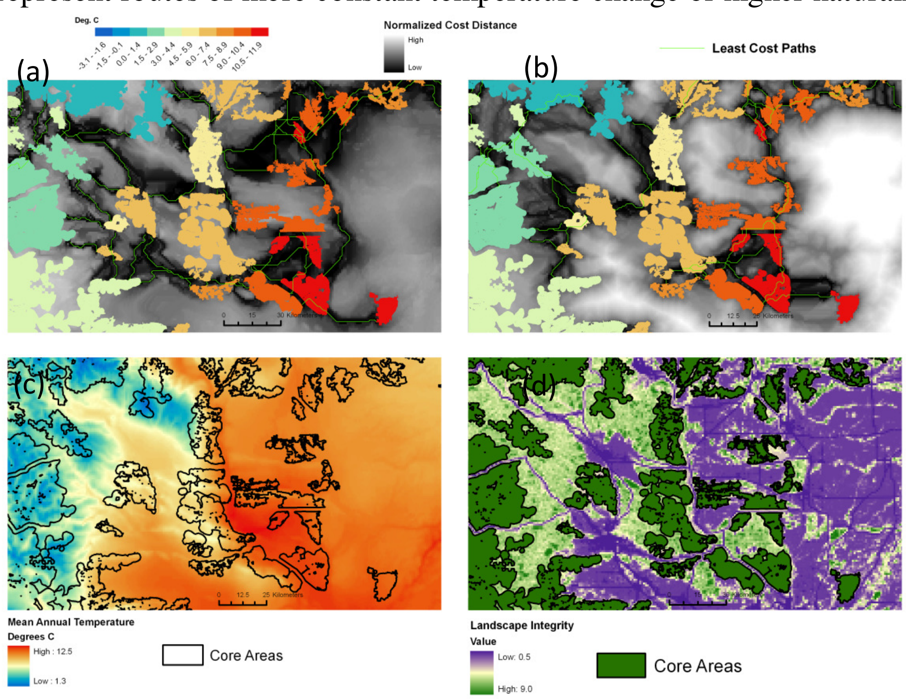


Figure 6. (a) Sample area of Fig. 5a showing corridors of most constant change in temperature. (b) Sample of Fig. 5b showing corridors of constant temperature change and low human impact. (c) Mean annual temperature gradient. (d) Landscape Integrity index. Least cost paths are used only to illustrate the lowest-cost section of each cost-distance corridor.

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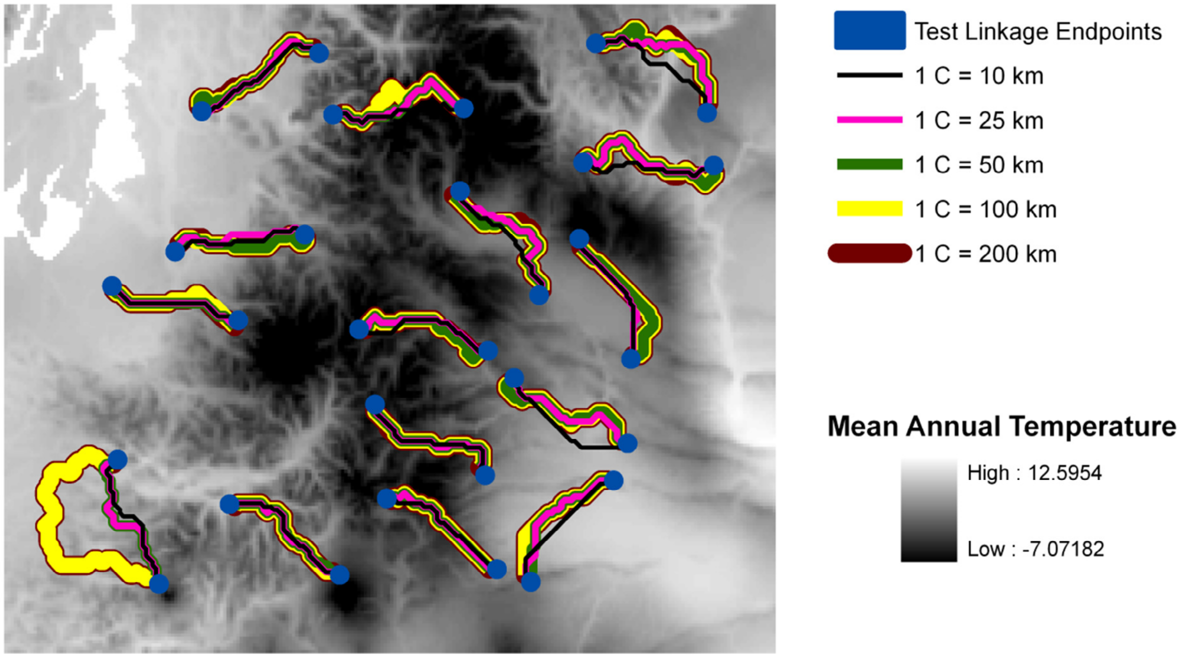
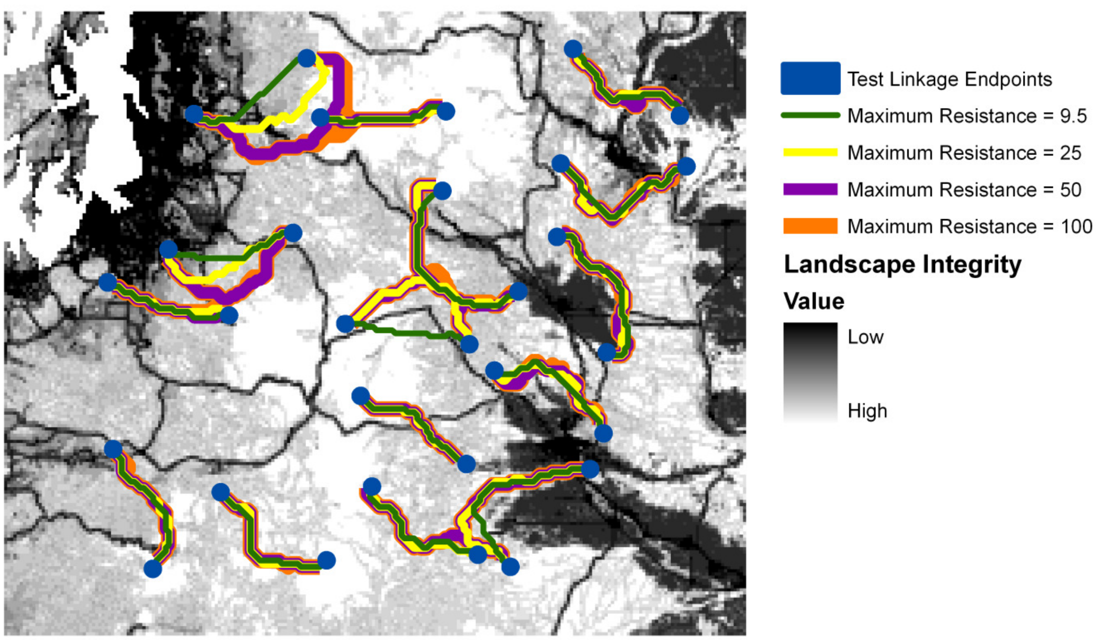
Appendix

Land cover data type	Category	Landscape Integrity Value
Land cover / land use	urban/developed	0.5
	agricultural lands	3.0
	water	5.0
	all other land cover	9.0
Housing density	≤ 10 acres per dwelling unit	0.5
	> 10 to ≤ 40 acres per dwelling unit	5.0
	> 40 to ≤ 80 acres per dwelling unit	6.0
	> 80 acres per dwelling unit	9.0
Freeways and major highways	centerline	0.5
	> 0 – 500 meter buffer	3.0
	> 500 – 1000 meter buffer	7.0
Secondary highways	centerline	2.0
	> 0 – 500 meter buffer	3.0
	> 500 – 1000 meter buffer	7.0
Local roads	centerline	5.0
	>0 – 500 meter buffer	8.0

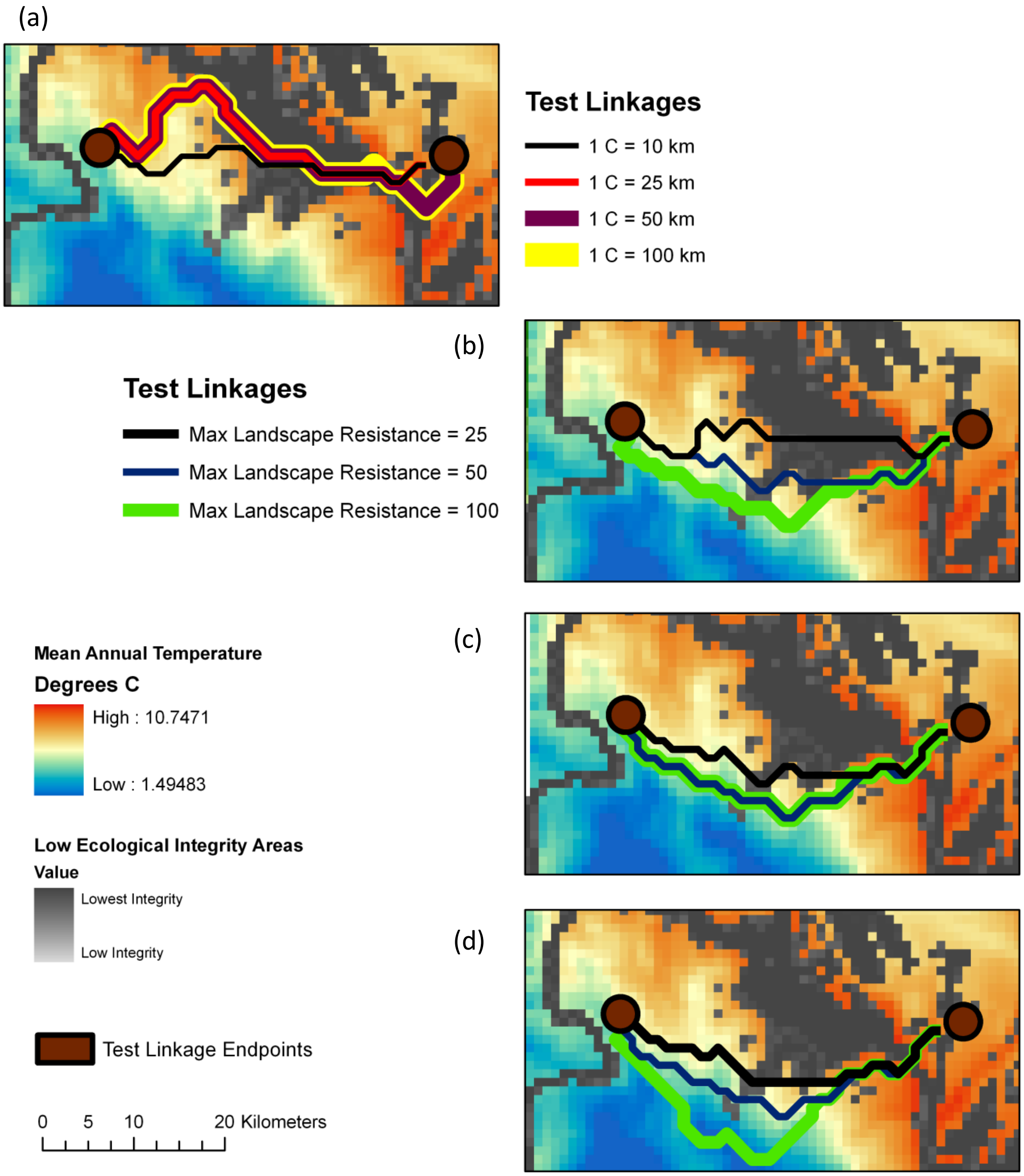
Supplementary Table 1. Landscape integrity values based on land cover used to develop the landscape integrity map. Reproduced from WHCWG (2010).



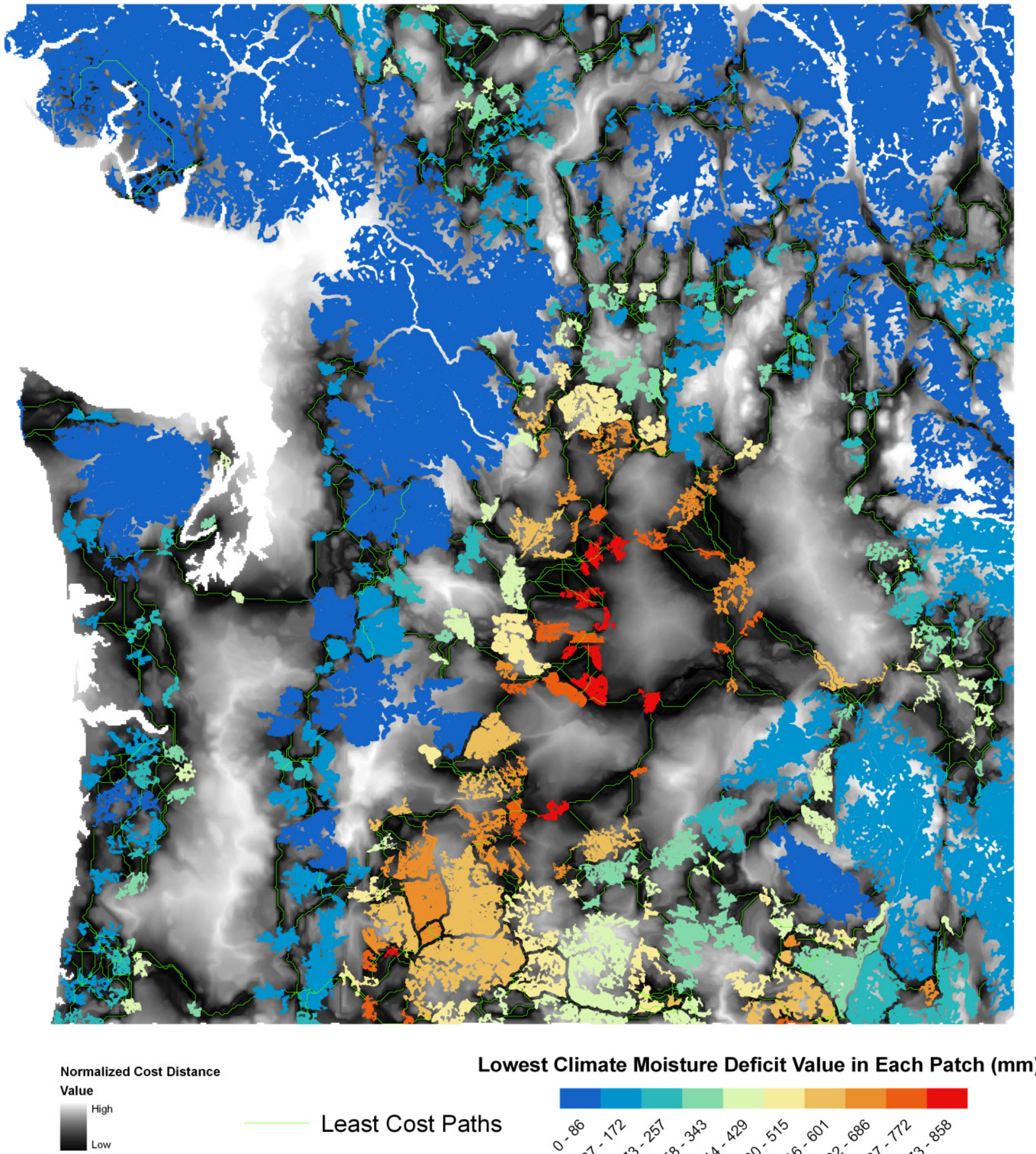
Supplementary Figure 1. Sensitivity of least cost paths to changes in distance-to-temperature ratio associated with temperature change using 40 km long test linkages. All least cost paths are one 1-kilometer pixel wide but are displayed with different widths in order to show overlaps.



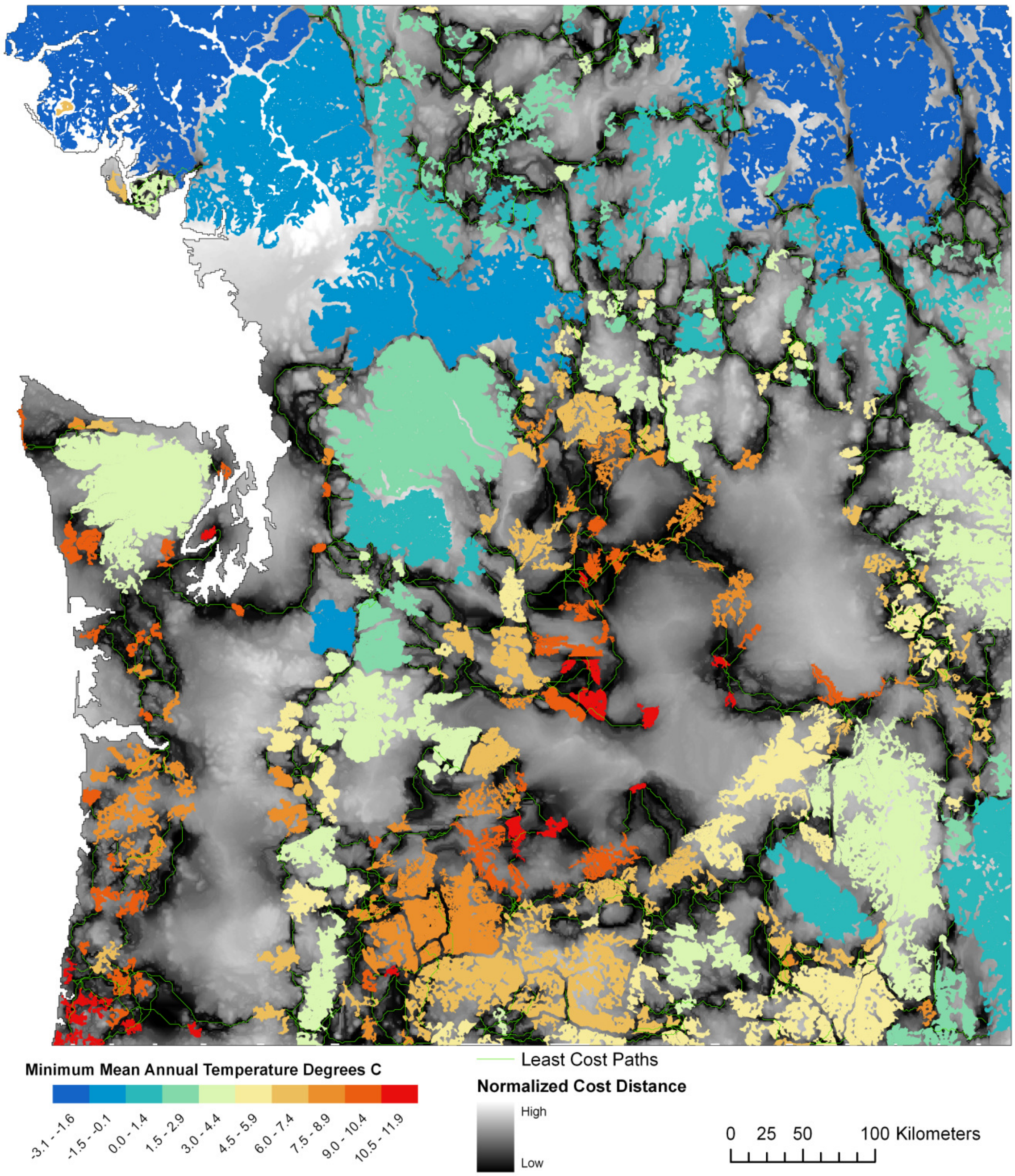
Supplementary Figure 2. Sensitivity of least cost paths to changes in scaling of landscape integrity resistance. For the test linkages shown here, areas of least resistance have a resistance value held constant at 1, while areas of higher resistance are changed so that maximum resistances are 9.5, 25, 50, and 100, respectively. All least cost paths are one 1-kilometer pixel wide but are displayed with different widths in order to show overlaps.



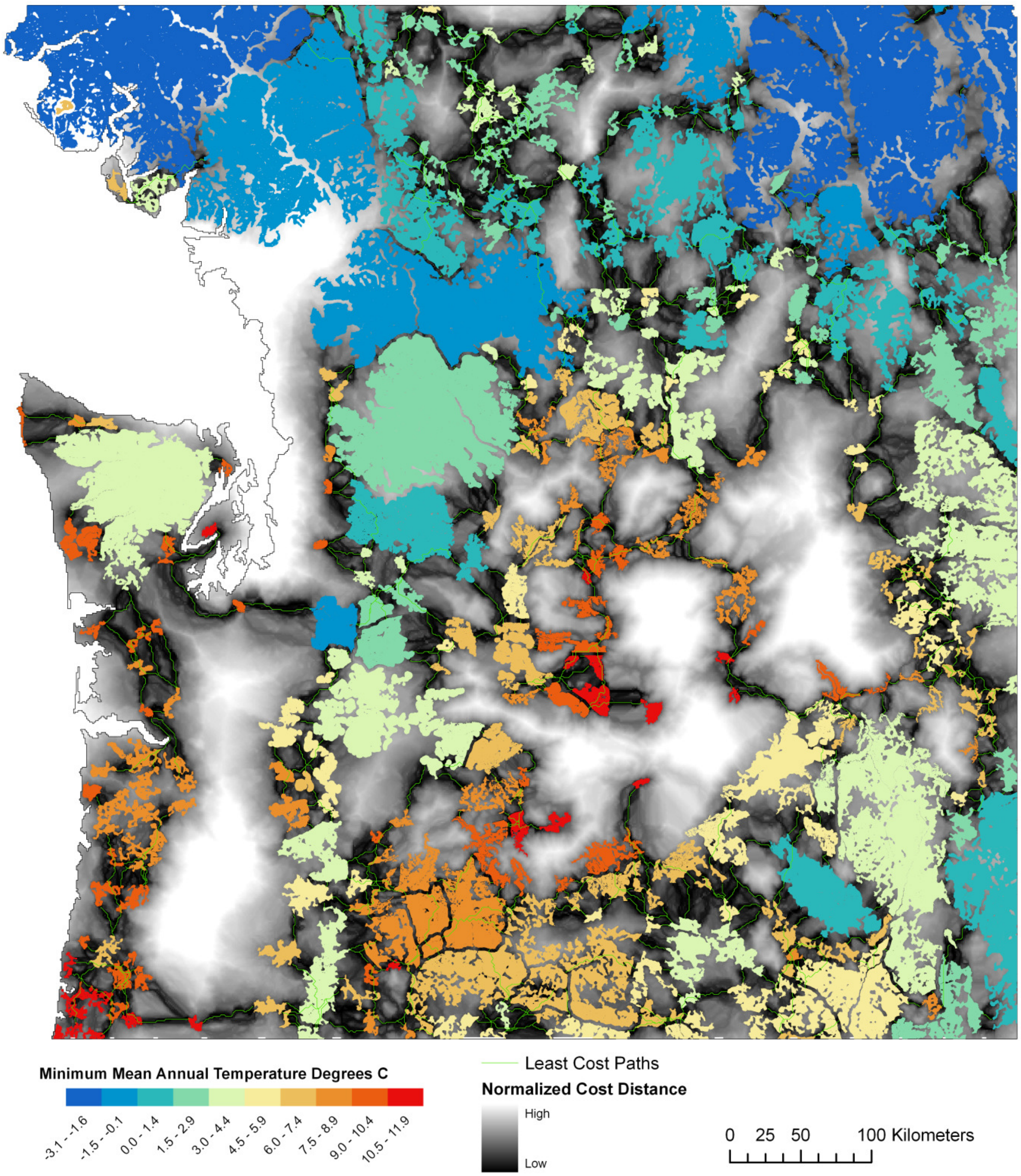
Supplementary Figure 3. (a) A test linkage showing different least cost paths using four different distance-to-temperature ratios (1°C = 10, 25, 50, and 100 km) without incorporating landscape integrity resistances. (b), (c), and (d) show least cost paths using landscape integrity maximum resistances of 25, 50, 100, with a distance-to-temperature ratio of 1°C = 100 km (b), 1°C = 50 km (c), and 1°C = 25 km (d), respectively. Grayscale represents areas of agricultural, exurban, and urban land covers, corresponding to landscape integrity index values less than 5 on a scale from 0.5 (low integrity) to 9.0 (high integrity).



Supplementary Figure 4. Corridors calculated using climatic moisture deficit. Annual climatic moisture deficit is calculated by subtracting annual precipitation from Hargreaves' reference evapotranspiration (Wang et al. 2006). Least cost paths are used only to illustrate the lowest-cost section of each cost-distance corridor, and are not meant to be used in conservation prioritization.



Supplementary Figure 5. Same as Figure 5a, corridors between warmer and cooler patches that find the route of most unidirectional change along the temperature gradient. Lower normalized cost distances represent routes of more constant temperature change or higher naturalness. Least cost paths are used only to illustrate the lowest-cost section of each cost-distance corridor, and are not meant to be used in conservation prioritization.



Supplementary Figure 6. Same as Figure 5b, corridors of most unidirectional change along the temperature gradient that also remain in areas of lowest human impact. Lower normalized cost distances represent routes of more constant temperature change or higher naturalness. Least cost paths are used only to illustrate the lowest-cost section of each cost-distance corridor, and are not meant to be used in conservation prioritization.