

Connectivity Planning to Address Climate Change

TRISTAN A. NUÑEZ,*†‡ JOSHUA J. LAWLER,* BRAD H. MCRAE,‡ D. JOHN PIERCE,§
MEADE B. KROSBY,** DARREN M. KAVANAGH,‡ PETER H. SINGLETON,††*
AND JOSHUA J. TEWKSBURY**

*School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98115, U.S.A.

†Department of Environmental Science, Management, and Policy, University of California, Berkeley, Berkeley, CA 94720, U.S.A.

‡The Nature Conservancy, 1917 1st Avenue, Seattle, WA 98101, U.S.A.

§Washington Department of Fish and Wildlife, Olympia, WA 98501, U.S.A.

**Department of Biology, University of Washington, Seattle, WA 98115, U.S.A.

††USDA Forest Service, Pacific Northwest Research Station, 1133 N. Western Avenue, Wenatchee, WA 98801, U.S.A.

Abstract: As the climate changes, human land use may impede species from tracking areas with suitable climates. Maintaining connectivity between areas of different temperatures could allow organisms to move along temperature gradients and allow species to continue to occupy the same temperature space as the climate warms. We used a coarse-filter approach to identify broad corridors for movement between areas where human influence is low while simultaneously routing the corridors along present-day spatial gradients of temperature. We modified a cost-distance algorithm to model these corridors and tested the model with data on current land-use and climate patterns in the Pacific Northwest of the United States. The resulting maps identified a network of patches and corridors across which species may move as climates change. The corridors are likely to be robust to uncertainty in the magnitude and direction of future climate change because they are derived from gradients and land-use patterns. The assumptions we applied in our model simplified the stability of temperature gradients and species responses to climate change and land use, but the model is flexible enough to be tailored to specific regions by incorporating other climate variables or movement costs. When used at appropriate resolutions, our approach may be of value to local, regional, and continental conservation initiatives seeking to promote species movements in a changing climate.

Keywords: adaptation, climate gradients, coarse-filter approach, conservation planning, corridors, reserve design

Planificación de Conectividad para Atender el Cambio Climático

Resumen: A medida que cambia el clima, el uso de suelo por humanos puede impedir que las especies encuentren áreas con climas adecuados. El mantenimiento de la conectividad entre áreas con temperaturas diferentes permitiría que los organismos se muevan a lo largo de gradientes de temperatura y permitiría que las especies continúen ocupando el mismo espacio de temperatura a medida que el clima cambia. Utilizamos un método de grano grueso para identificar corredores para el movimiento entre áreas con baja influencia humana y simultáneamente trazando los corredores a lo largo de gradientes de temperatura actuales. Modificamos un algoritmo de costo-distancia para modelar estos corredores y probamos el modelo con datos sobre el uso de suelo y patrones climáticos actuales en el Noroeste de Estados Unidos. Los mapas resultantes identificaron una red de parches y corredores en los que las especies se pueden mover a medida que el clima cambia. Es posible que los corredores sean robustos a la incertidumbre en la magnitud y dirección del cambio climático futuro porque están derivados de gradientes y patrones de uso de suelo. Los supuestos que aplicamos en nuestro modelo simplificaron la estabilidad de los gradientes de temperatura y las respuestas de las especies al cambio climático y uso de suelo, pero el modelo es lo suficientemente flexible para ser adaptado a regiones específicas mediante la incorporación de otras variables climáticas o costos de movimiento. Cuando se utiliza en resoluciones apropiadas, nuestro método puede ser valioso para iniciativas de conservación locales, regionales y continentales que buscan promover el movimiento de especies en un clima cambiante.

##email tristan.nunez@gmail.com

Paper submitted February 14, 2012; revised manuscript accepted July 24, 2012.

Palabras Clave: Adaptación, corredores, diseño de reservas, gradientes de clima, método de grano grueso, planificación de la conservación

Introduction

In the past, species moved great distances relatively unimpeded in response to climatic change (Parmesan & Yohe 2003; Martinez-Meyer et al. 2004). Given the rate of projected future climate change, it is likely species will need to move farther in the 21st century (Schloss et al. 2012), and they may encounter substantial anthropogenic barriers that were not present in the past (Sanderson et al. 2002). Thus, maintaining connectivity—the degree to which a landscape facilitates the movement of organisms (Tischendorf & Fahrig 2000)—is the most frequently recommended strategy for conserving species diversity in a changing climate (Heller & Zavaleta 2009). However, traditional connectivity models are used to identify areas that facilitate species movements at one point in time between their current habitats and within their current distributions (Crooks & Sanjayan 2006; Hannah 2011). Thus, these models cannot identify areas that would allow species to track climate-driven range shifts of key attributes of their habitats. We focused instead on connectivity that enables species—and their component populations—to move among suitable areas and to newly suitable areas over time as climate changes (Hannah 2011).

We developed a connectivity model that targets climate change by building a series of linked assumptions about fauna whose movements are restricted by anthropogenic barriers, about the habitats of these species, and about the spatial dynamics of climate change. From these assumptions, we used spatial patterns of temperature and human land use, rather than species-specific habitat models, to develop a coarse-filter approach to identifying linkages that facilitate species range shifts in response to climate change (Noss 1987; Hunter et al. 1988). Although our logic in developing this corridor modeling approach came from a focus on nonvolant terrestrial fauna, the locations identified by our approach may also assist other biota to shift their ranges.

We started by assuming, for simplicity, that species distributions depend only on temperature. As have others (e.g., Loarie et al. 2009), we assumed spatial temperature gradients will maintain their geographic orientations as climate changes. For example, as temperatures increase, higher elevations will still be cooler than lower elevations, even if both are warmer, except in areas where inversions or cold-air pooling reverse this general relation.

To identify areas to connect, we assumed species restricted by human-created barriers would be most prevalent in large natural areas. If natural patches of different

temperatures are linked along climatic gradients, species living in them can move to the nearest areas with relatively cooler present-day climates as the climate warms and continue occupying the same temperature space. Implicit in this is the assumption that the necessary components of habitat will exist in these cooler areas, which may depend on the ability of plant species to disperse and whether the plants encounter appropriate conditions of soil composition and moisture. This network of linked patches of different temperatures would enable species to move varying distances along the temperature gradient, offering flexibility if the climate warms more or less than projected.

To identify corridors between patches, we assumed species will have the most success dispersing (potentially over many generations) through areas less modified by humans and areas where temperatures transition smoothly from one patch to another. For example, an alpine species would fare better moving along a ridge to get to the next cooler meadow than it would crossing a hot valley floor.

We applied this model of linked assumptions by identifying patches with a high degree of naturalness (i.e., low degree of human modification) relative to the surrounding landscape. We identified pairs of these patches that, if connected, would allow species to move from warmer to cooler areas. We then mapped corridors between linked patches with a cost-distance model that delineated routes with the most unidirectional changes in present-day temperature between the patches (Fig. 1), avoided extreme deviations in temperature, and remained within areas of lowest human influence. We used this method to identify corridors with the potential to facilitate climate-driven movements of biota in the Pacific Northwest of the United States.

Methods

Study Area

Our study covered 443,578 km² centered on the state of Washington and extending into Idaho and Oregon in the United States, and British Columbia in Canada. The region has steep and varying temperature and moisture gradients and varying intensities of land use. On average, climate models project increases of 3.0 °C by the 2080s for the Pacific Northwest and rates of warming ranging from 0.1 to 0.6 °C/decade (Mote & Salathé 2009). Annual precipitation is projected to increase by 1–2%, but some models projected larger seasonal changes in precipitation (Mote & Salathé 2009).

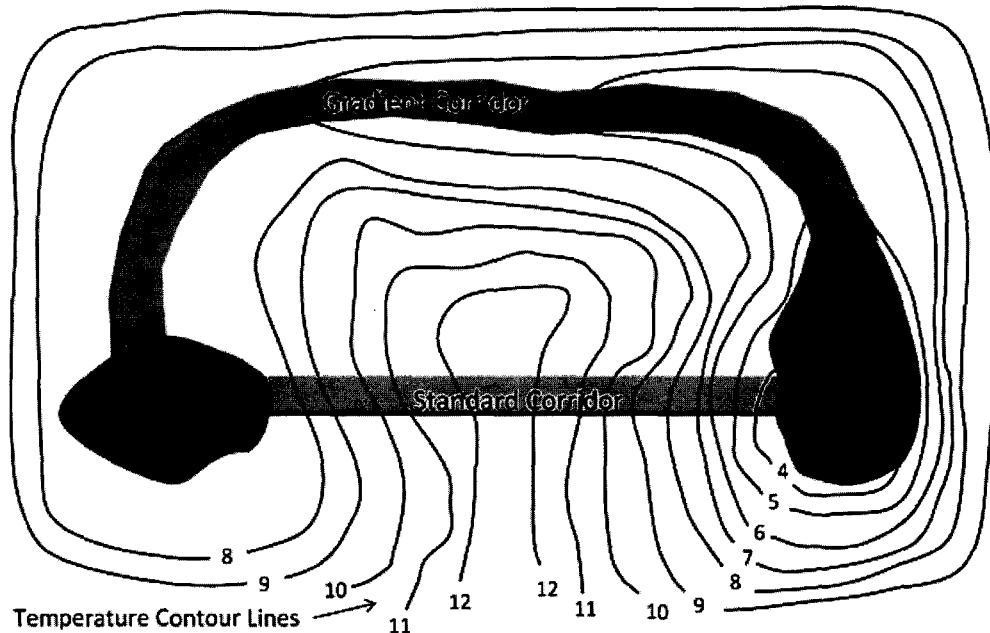


Figure 1. Connection of patches via a standard cost-distance corridor and a climate-gradient corridor. Patches A and B are separated by a temperature gradient (contour lines) (numbers, ranging from 4 to 12, indicate increasing temperature). The standard cost-distance corridor, all else being equal, provides the shortest path between the patches, and the climate-gradient corridor provides the most unidirectional change in the temperature gradient.

Temperature- and Landscape-Integrity Resistance Surfaces

We used mean annual temperature gradients to demonstrate our approach (Fig. 2a). 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 moisture deficit. We used the 30-year mean of mean annual temperatures from 1971 to 2000, which we derived from a 1-km² digital elevation model and the ClimateWNA (western North America) climate data tool (version 4.61) (Wang et al. 2006), which is built from the parameter-elevation regressions on independent slopes model (PRISM) (Daly et al. 2008). This model spatially interpolates weather-station data onto a continuous grid while accounting for elevational, coastal, rain-shadow, and other physiographic influences on temperature and precipitation patterns.

We used landscape integrity (Fig. 2b), an index of naturalness developed by the Washington Wildlife Habitat Connectivity Working Group, as a measure of resistance arising from human land uses to ecological flows (WHCWG 2010). The index is based on methods developed by NatureServe (Comer & Hak 2009) and is similar in construction to other indices including the human-influence index and landscape naturalness (Sanderson et al. 2002; Theobald 2010). The landscape-integrity index ranks 100-m pixels in order of increasing naturalness on a scale from 0.5 to 9.0 and is based on land-cover data, human population density, and proximity of each

pixel to roads (Supporting Information) (WHCWG 2010). To match the spatial resolution of the landscape-integrity data to our climate data, we aggregated the 100-m resolution landscape integrity data to 1-km resolution by taking the mean of the 100-m resistance values in each 1-km cell. Assuming that decreasing naturalness reduces the probability of successful species dispersal, we reversed the integrity index by subtracting each value from 10, which resulted in a movement-resistance index of 1.0–9.5 (9.5, land cover most resistant to movement).

We scaled the resistance index by increasing the maximum resistance (i.e., that corresponding to the most unnatural land cover) to 25, 50, and 100, respectively. We used an exponential transformation to maintain the scaling between the lowest resistance value, 1, and the different maximum resistance values. We mapped test corridors to determine which scaling resulted in corridors that did not cross urban areas, agricultural areas, or areas with a high density of roads (Supporting Information). As a result, we used a maximum resistance of 100 to map the final corridor network.

Identifying and Linking Patches

We linked 348 patches of land previously identified by the Washington Wildlife Habitat Connectivity Working Group as potential focal points for connectivity planning (Fig. 2c). The group delineated these patches by identifying all contiguous areas >4047 ha (10,000 acres)

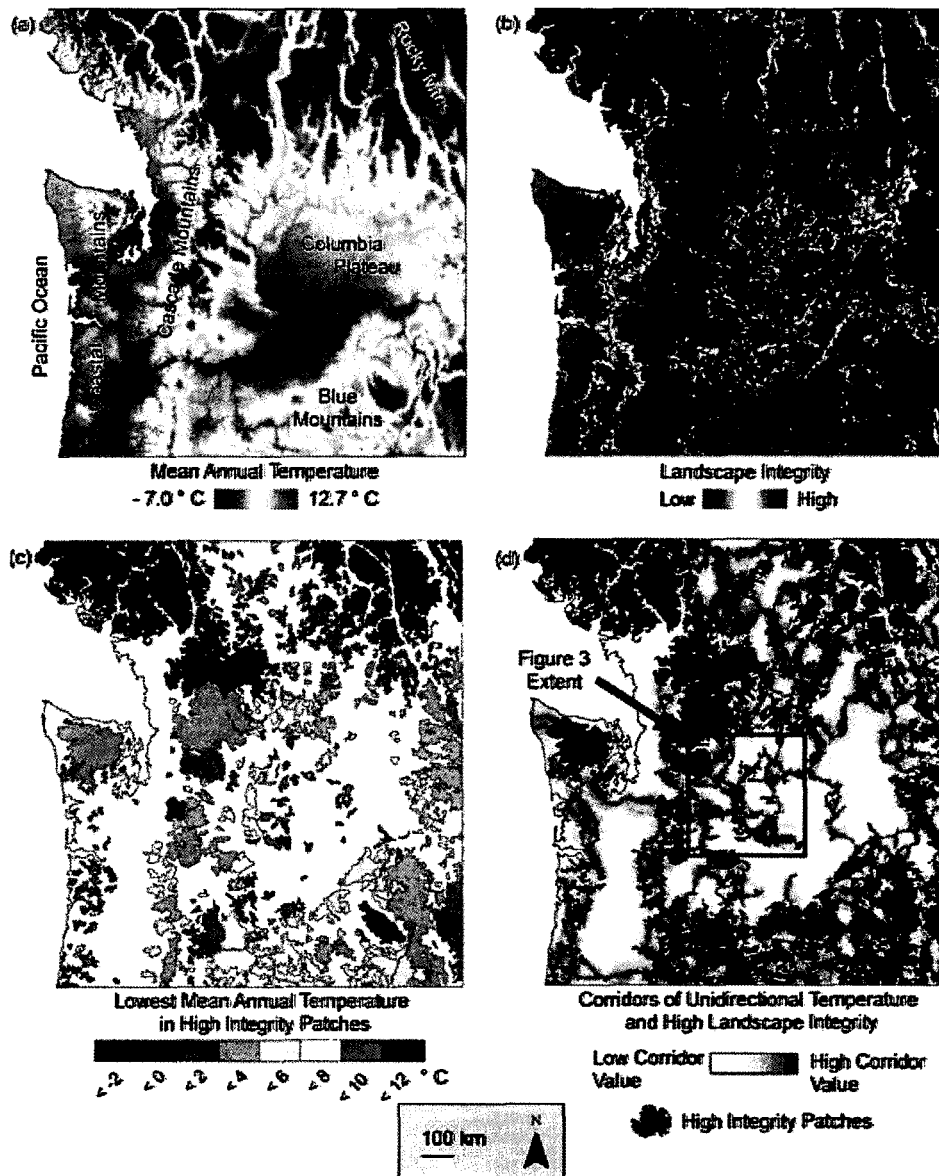


Figure 2. Data used in our climate corridor model included (a) a mean of mean annual temperatures from 1971 to 2000 and (b) a landscape-integrity index (a metric of naturalness that incorporate data on urban areas, distance to roads, agriculture, and other land uses).

High-integrity patches (c) are linked on the basis of differences in temperature within the patches, creating (d) a network of corridors modeled between the patches that contained unidirectional changes in temperature and high landscape integrity.

classified as native cover by the Washington Gap Analysis Project (Cassidy et al. 1997), not crossed by major roads, and with a high landscape-integrity score relative to the surrounding ecoregion (WHCWG 2010). This approach to identifying patches, although based on subjective choices, consistently and transparently identified large areas in which human activities were the least prominent.

We linked all pairs of patches that were ≤ 50 km apart and for which the coldest area within one patch differed in mean annual temperature by at least 1°C from the coldest area of the other (Fig. 2c). The patches varied greatly in size (4,090–1,250,093 ha) and spanned different ranges of temperature (0.1 – 15.1°C), so the coldest temperature in the patch was a more appropriate metric for a linkage rule than the patch's mean temperature. Because global and regional circulation models project the region is warming, the temperature of the coldest area

within a patch indicated the patch's capacity to continue to provide a thermally suitable area for a species. To quantify the temperature of the coldest area within a patch, we subtracted 2 SDs from the mean of the temperatures of all the pixels in the patch and thus reduced the effect of single-pixel temperature outliers.

We linked patches only if they differed in their coldest temperatures by $\geq 1^\circ\text{C}$ to ensure corridors provided significant temperature transitions. This 1°C threshold may be high, given that observed global warming of 0.76°C during the 20th century has already provoked observable movements of flora and fauna (Parmesan & Yohe 2003; IPCC 2007). We used 50 km as a maximum edge-to-edge Euclidean distance between patches because this distance connected every patch in our region to at least one other that met the temperature difference requirement. We linked each patch to its 3 nearest (in cost-distance units) neighbors with Linkage Mapper 9.3.1 (McRae &

Kavanagh 2011) and produced a network of patches that we incorporated into corridor mapping.

Mapping Corridors

We used cost-distance modeling, a computationally efficient approach used to identify the relative importance of areas between patches for ecological movements (Adriaenssens et al. 2003), to map all corridors. A raster of cost weights, or resistances, associated with movement across a landscape is the primary data input for a cost-distance model (Adriaenssens et al. 2003; Beier et al. 2008). We mapped corridors in a way that avoided developed areas while maintaining unidirectional change in temperature between patches (Fig. 2d) by using cost weights that we based on landscape integrity and temperature gradients. As an intermediate step, we also mapped corridors that ignored land-use patterns and showed only the routes of most unidirectional change in temperature (Supporting Information).

Standard cost-distance corridor models add together costs isotropically, meaning that cost is the same regardless of the direction in which the pixel is crossed. This algorithm is appropriate for cost weights assigned to human land use, such as our reversed landscape-integrity maps. Typically, in cost-distance connectivity models the following equation is used to calculate cost distances from a focal cell to each of its 8 neighbors:

$$\text{Isotropic cost distance} = \left[(\text{cost}_{\text{focal}} + \text{cost}_{\text{neighbor}}) / 2 \right] \times \text{Euclidean distance.} \quad (1)$$

The Euclidean distance is the straight-line distance between cell centers, and the distance between diagonal neighbors is $\sqrt{2}$ times the distance between horizontal or vertical neighbors (Supporting Information).

We used the equation

$$\begin{aligned} \text{Anisotropic cost distance} \\ = (\text{temperature-distance weight} \\ \times |\text{temperature}_{\text{focal}} - \text{temperature}_{\text{neighbor}}|) \\ + \text{Euclidean distance} \end{aligned} \quad (2)$$

to calculate a temperature-only corridor network from the cost of moving between 2 cells on a temperature gradient (Figs. 3a & 3b, Supporting Information). Unlike standard cost-distance corridor models, our approach was built around anisotropic cost calculations instead of isotropic calculations. Anisotropic costs change as the direction in which a gradient is crossed changes (Frank et al. 1993), much in the same way that hiking across the side of a mountain takes less energy than climbing it. By using Eq. (2) to accumulate anisotropic costs from a temperature gradient, we were able to identify routes across a landscape that provide the most unidirectional temperature change available between 2 patches (as in Fig. 1). This equation requires converting an amount

of temperature change into cost-distance units, which we did by specifying a temperature-distance weight. We then multiplied the temperature-distance weight by the absolute value of the difference in the temperatures of the focal cell and the neighboring cell. We added the Euclidean distance traveled so that the corridors followed the most direct route when crossing an area of uniform temperature.

We used the *r.walk* tool in the GRASS GIS package (GRASS 2010) to calculate anisotropic cost distances from the raster of mean annual temperature. We chose the temperature-distance weight of 50 km/1 °C after modeling corridors for 15 40-km-long test corridors. For these test corridors, we modeled temperature-distance weights of 10, 25, 50, 100, and 200 km/1 °C (Supporting Information). We chose 50 km/1 °C because the corridors with this weight maintained a largely unidirectional change in temperature in moving from pixel to pixel and the corridor length remained <3 times the Euclidean distance between the patches.

We used the following equation to calculate the final corridor network (Fig. 2d):

$$\begin{aligned} \text{Combined cost distance} = & \{[(\text{cost}_{\text{focal}} + \text{cost}_{\text{neighbor}}) / 2] \\ & \times \text{Euclidean distance}\} + (\text{temperature-distance weight} \\ & \times |\text{temperature}_{\text{focal}} - \text{temperature}_{\text{neighbor}}|). \end{aligned} \quad (3)$$

Equation (3) combines Eq. (2), the anisotropic costs from moving across a temperature surface, with Equation (1), the isotropic costs of crossing a resistance surface that reflects the impediments to movement from human land use (Supporting Information). We used an additive combination because it is simpler and more intuitive than a multiplicative combination.

We calculated combined cost distances from a land-use resistance map with a maximum resistance value of 100 and from a raster of mean annual temperature, for which we used a temperature-distance weight of 50 km/1 °C. As with the temperature-only corridors, we chose this combination of temperature-distance weights and land-use resistances after modeling test corridors (Supporting Information). This combination identified corridors that avoided urban, agricultural, and exurban lands while keeping the spatial temperature change relatively uniform in direction.

Results

The network of corridors we mapped along the Pacific Northwest's major temperature gradients (Fig. 2d) contained routes of unidirectional change in temperature and did not include areas of heavy human land use. The warmest patches in the center of the study area were 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 (Figs. 2c & 2d).

Corridors between warmer patches and cooler patches were oriented in a wide range of directions. This pattern reflected the east-west and north-south orientation of mountain ranges in the region and the large effect of topography relative to latitude on the direction of temperature gradients in our study area. Areas of intensive land use in the western and central portions of the study area had few patches and therefore fewer, longer corridors.

The test corridors we modeled were largely robust to changes in temperature-distance weights. For temperature-only test corridors modeled with Eq. (2), increases in the temperature-distance weight >25 km/ 1°C generally did not result in differences in corridor

shape (Supporting Information). When we modeled test corridors with temperature-distance weights of 25, 50, and 100 km/ 1°C and land-use maximum resistances of 25, 50, and 100, as long as the ratio between maximum land-use resistance and the temperature-distance weight was between 1:1 and 3:1, the corridors were not located in urban and agricultural areas and the direction of the underlying climate gradient did not change (Supporting Information).

The corridors we delineated on the basis of only temperature gradients with Eq. (2) (Figs. 3a & 3b) were narrower and more constrained in mountainous regions than in flatlands due to steeper temperature gradients in the mountains. Because delineation of these corridors was not based on land-use patterns, the corridors often passed

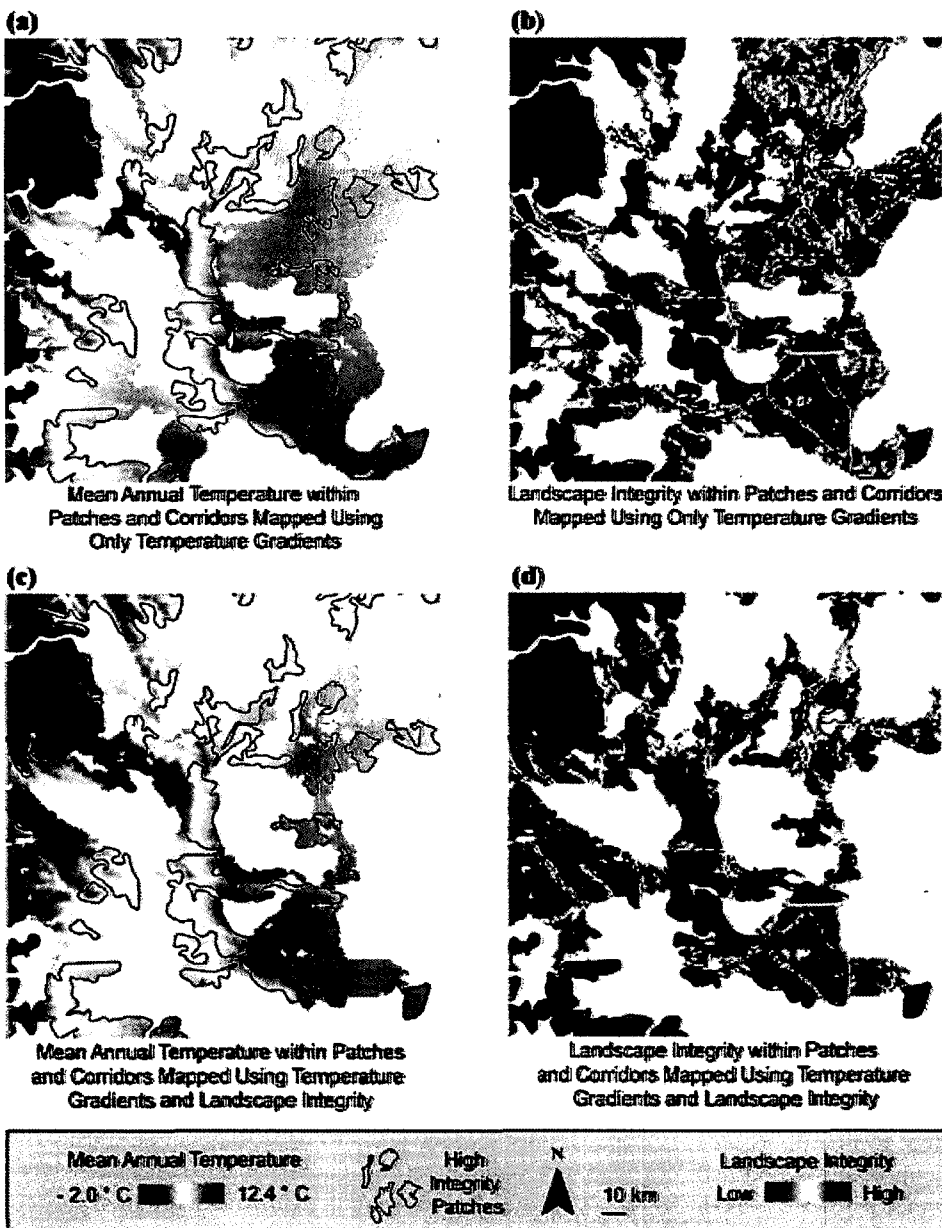


Figure 3. Corridors mapped on the basis of only temperature gradients have (a) unidirectional transitions in temperature between patches (patches are outlined in black) and (b) areas of low landscape-integrity index values (a metric of naturalness calculated from data on urban areas, distance to roads, agriculture, and other land uses). Corridors mapped on the basis of both temperature gradients and landscape integrity have (c) generally unidirectional transitions in temperature and (d) much higher levels of landscape integrity than the temperature-only corridors. The cost-distance threshold used to set the corridor width was 20 cost-distance km for the temperature-only corridors and 100 cost-distance km for the landscape-integrity and temperature corridors.

directly through urban or agricultural regions (Fig. 3b). This pattern suggests that in our study region, species whose movements are restricted by human activities will not be able to move along the most direct temperature gradients as climate changes. In comparison, corridors we delineated on the basis of both temperature and land-use inputs with Eq. (3) did not include areas heavily affected by human modification and generally maintained unidirectional changes in temperature (Figs. 3c & 3d).

Discussion

Our methods delineated corridors specifically relevant for movement in response to changing temperatures. Rather than connecting patches that were similar in current vegetation or that provided current habitat for a set of species, as do standard connectivity models (e.g., Spencer et al. 2010; WHCWG 2010), our model connected areas with temperatures suitable for some species in the present to areas that may have suitable temperatures for those species in the future.

Several approaches have been proposed to increase connectivity as climate changes, but ours is different in its focus on coarse-filter corridors along temperature gradients. In general, coarse-filter approaches in conservation planning are based on community-level, geophysical, or anthropogenic patterns, whereas fine-filter approaches focus on individual species (Hunter et al. 1988). Fine-filter climate-connectivity approaches project the bioclimatic envelopes of small numbers of vertebrate (Vos et al. 2008) and plant species (Williams et al. 2005; Phillips et al. 2008; Rose & Burton 2009) into the future to identify corridors between present and future distributions of species. Bioclimatic-envelope approaches might be useful, especially for species of particular ecological importance. However, the projections of these models have uncertainties associated with greenhouse-gas emission scenarios, global circulation-model projections, downscaling approaches, species-distribution models, and assumptions about species dispersal abilities, particularly at the fine grain used in site-specific conservation planning (Beier & Brost 2010). It is also difficult to combine individual bioclimatic-envelope corridors for all species in a region into a single network because species-specific corridors can differ greatly among species. Modelers struggle with combining corridor networks made for different species even when not considering climate change (Beier et al. 2008; WHCWG 2010).

Comparatively, the simplicity of a coarse-filter approach makes the approach more transparent and more general, but less accurate for individual species. Our approach identifies corridors of natural lands that cross temperature gradients, a concept that is easily understood but does not rely on predictions of specific movements of individual species. Although this simplification does not

eliminate uncertainty, it avoids multiplying uncertainty across component models.

Similar to our approach, several previous connectivity models specific to climate change do not include projections of future climate. In one such approach, bottlenecks to climate-driven movements were identified on the basis of present-day wetland habitats, species-specific habitat needs, and dispersal distances (Vos et al. 2010). Another approach delineated strips 1-km wide of natural land cover between areas of different elevations to provide for movement of ecosystem processes as climate changes (Rouget et al. 2003). A coarse-filter approach connected areas containing similar land facets derived from topographic, soil, and other attributes, via a cost-distance modeling approach (Beier & Brost 2010). This creates connections among areas with similar topographic and geological characteristics for species that may occupy or move through as climate changes (Anderson & Ferree 2010). Although the land-facet approach does not directly incorporate information about climate gradients, it is complementary to our approach because it addresses substrate, local topography, and geology.

The utility of our gradient-based approach to corridor modeling depends on how well our simplifying assumptions about organisms, temperature gradients, and their respective responses to climate change hold under different circumstances. Future refinements of our approach may make it more robust to these assumptions and allow for tailoring to specific locations or groups of organisms. Our first assumption, that species ranges will move to track shifts in suitable temperatures, is supported by paleoecological studies and by observations of species responses to recent climatic changes. Trees, other plant species, insects, and mammals have all tracked climate gradients in response to recent climatic warming (Chen et al. 2009). However, local microclimates provided by riparian areas, canopy cover, or canyons and other topographic features may allow species to remain in or move into an area without tracking coarse-grain climate gradients (Ackerly et al. 2010). In addition, some species may be able to evolve in response to changing conditions and thus may not need to move (Skelly et al. 2007).

The climate-gradient corridor approach can accommodate regional differences in which climatic variables exert the most control on species distribution patterns because mean annual temperature may not be the limiting factor for most species. For example, in boreal systems, the number of growing-degree days or the mean temperature of the coldest month best predict plant distributions, whereas in warmer, arid systems climatic-moisture deficit is more important (Wang & Price 2007). Although we used temperature in our analyses, the climate variable we used to identify corridors can be changed to better reflect the predominant climatic drivers in a specific region. Any climate variable, or a multivariate index of

climate variables, could be substituted for temperature in calculating corridors as long as it can be mapped as a continuous variable. To demonstrate this flexibility, we modeled the same corridor network described above, but we used annual climatic-moisture deficit instead of mean annual temperature (Supporting Information). The moisture-deficit based network was largely similar to the mean annual temperature network, which reflects 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 climate is changing in absolute terms, sets important constraints on the spatial extent and grain sizes with which our approach may be used. We based this assumption on evidence that temperature and moisture gradients across distances from several kilometers and several hundred kilometers are driven largely by topography and other physiographic influences (including elevation, cold-air pooling, rain shadows, proximity to water bodies, and wind patterns) (Daly 2006). Primarily because topography itself is unchanging, we assumed the orientation of these climate gradients will not change substantially at these distances. This same assumption is also present in many downscaled projections of future climate commonly used in climate-envelope models (Ashcroft et al. 2009).

Although this assumption is commonly made, the stability of local and regional climate gradients as climate changes is an area of active research and is not well understood (Pepin et al. 2011). At distances less than several kilometers, results of recent studies suggest temperature gradients may change as climate changes due to local atmospheric decoupling, particularly in climatically complex landscapes (Fridley 2009; Daly et al. 2010). At distances greater than several hundred kilometers, changes in global circulation patterns arising from climate change may make gradients unstable as the climate changes (Daly 2006). It is also possible that land-use changes that modify albedo or aerosol levels could affect local climate gradients or that changes in major climatic patterns or systems (e.g., changes in coastal fog or monsoon patterns) could change the orientation of gradients in some regions. Despite these caveats, as long as the orientations of the gradients along individual corridors remain consistent, we do not expect changes in gradients to result in major changes in the locations of our modeled corridors. Because most conservation corridors are longer than several kilometers but rarely reach several hundred kilometers, these constraints on appropriate extents and grain sizes are less problematic for our approach than might be expected.

Our third assumption, that species will move most easily through areas with climates similar to those they currently inhabit, targets our approach at species limited by climate in their dispersal and colonization ability. This assumption makes the model less relevant for species (or

their habitats) that are primarily constrained by limited dispersal ability or edaphic requirements. These species might be better conserved with other strategies, such as assisted migration. Similarly, our fourth assumption, that targeted species will move most easily through more natural lands, means the model is best suited to species for which human activities generally act as impediments to movement. Our approach is sufficiently flexible that it can be further tailored to address species' specific movement needs or climatic associations. For example, a network for small mammals sensitive to thermal extremes but able to live in agricultural landscapes could be identified by assigning higher movement costs to temperature gradients and lower costs to movement through agricultural lands.

Although the general nature of our approach is useful, it has several limitations. As with most cost-distance modeling in conservation planning (Beier et al. 2008), parameters in the model are inherently subjective. The temperature threshold used to decide whether to link patches and the cost distances applied to land use and differences in temperature depend on the modeler's judgment. We used an iterative process of modeling different potential resistance values. We selected the cost values used in the final model from the cost values that 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. Although subjective, this parameterization approach provided a rigorous, transparent, and repeatable way of assessing the effects of different factors.

Our approach does not highlight all areas that might be useful for promoting species movements in a changing climate. 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 and among wetlands and aquatic systems is not addressed by the climate-gradient approach. These dimensions of connectivity for climate change could be analyzed separately and merged with a climate-gradient-based network.

Next steps in advancing this approach include tailoring the model to specific regions or groups of organisms by incorporating different or multiple climate variables and comparing the corridor network with corridors designed with species-specific climate-envelope and individual-based dispersal models. In addition, emerging climatological research about the regions and distances across which climate gradients remain stable with climate change should be incorporated.

Our approach can be applied as a coarse-filter model or tailored to more specific needs and can incorporate previously identified patches and land-use resistance surfaces. It may thus be most readily implemented by regional

conservation planning efforts that have already used cost-distance connectivity models. In addition, these methods may be useful for major continental connectivity initiatives that include responding to climate change among their primary goals (Vos et al. 2008; Graumlich & Francis 2010). The methods described in this paper have been implemented in the Climate Linkage Mapper (Kavanagh et al. 2012) software tool, a new addition to the Linkage Mapper Toolkit for ArcGIS (McRae & Kavanagh 2011).

Acknowledgments

We thank E. Fleishman, E. Main, and 4 anonymous reviewers for their constructive comments, and L. Dermer, C. Austin, and C. Hojnowski for commenting on earlier drafts. We thank the Washington Wildlife Habitat Connectivity Working Group for data and input. Funding was provided by the Wilburforce Foundation, the Department of the Interior Great Northern and North Pacific Landscape Conservation Cooperatives, the School of Environment and Forest Sciences at the University of Washington, the ARCS Foundation, and the National Science Foundation Graduate Research Fellowship Program (grant 11-582). Support also came from the Wildlife Conservation Society through its Wildlife Action Opportunities Fund, made possible by the Doris Duke Charitable Foundation.

Supporting Information

Landscape integrity parameterizations and figures with cost-distance test linkages for Eqs. (1), (2), and (3), a climatic moisture-deficit corridor network, and temperature- and landscape-integrity corridor networks (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

- Ackerly, D. D., S. R. Loarie, W. K. Cornwell, S. B. Weiss, H. Hamilton, R. Branciforte, and N. J. B. Kraft. 2010. The geography of climate change: implications for conservation biogeography. *Diversity and Distributions* 16:476–487.
- Adriansen, F., J. P. Chardon, G. De Blust, E. Swinnen, S. Villalba, H. Gulinck, and E. Marthysen. 2005. The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning* 64:233–247.
- Anderson, M. G., and C. E. Fenner. 2010. Conserving the stage: climate change and the geophysical underpinnings of species diversity. *Public Library of Science ONE* 5(7): DOI: 10.1371/journal.pone.0011554.
- Ashcroft, M. B., L. A. Chisholm, and K. O. French. 2009. Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation. *Global Change Biology* 15:656–667.
- Beier, P., and B. Brost. 2010. Use of land facets to plan for climate change: conserving the arenas, not the actors. *Conservation Biology* 24:701–710.
- Beier, P., D. R. Maja, and W. D. Spencer. 2008. Forks in the road: choices in procedures for designing wildlife linkages. *Conservation Biology* 22:836–851.
- Cassidy, K. M., C. E. Grue, M. R. Smith, and K. M. Drommich. 1997. Washington State gap analysis final report. Washington Cooperative Fish and Wildlife Research Unit, University of Washington, Seattle.
- Chen, I. C., H. J. Shin, S. Benedict, J. D. Holloway, V. K. Cheye, H. S. Barlow, J. K. Hill, and C. D. Thomas. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proceedings of the National Academy of Sciences of the United States of America* 106:1479–1483.
- Comer, P. J., and J. Hak. 2009. NatureServe landscape condition model. Technical report for NatureServe Vista decision support software engineering. NatureServe, Boulder, Colorado.
- Crooks, K. R., and M. A. Sanjayan. 2006. Connectivity conservation. Cambridge University Press, Cambridge, United Kingdom.
- Daly, C. 2006. Guidelines for assessing the suitability of spatial climate data sets. *International Journal of Climatology* 26:707–721.
- Daly, C., D. R. Conklin, and M. H. Unsworth. 2010. Local atmospheric decoupling in complex topography alters climate change impacts. *International Journal of Climatology* 30:1857–1864.
- Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis, and P. P. Pastoris. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology* 28:2031–2064.
- Decamps, H. 1993. River margins and environmental change. *Ecological Applications* 3:441–445.
- Frank, A., I. Campari, C. Zhan, S. Memon, and P. Gao. 1993. A directional path distance model for raster distance mapping. Pages 434–443 in S. Hirtle and A. Frank, editors. *Spatial information theory: a theoretical basis for GIS*. Springer, Berlin.
- Fridley, J. D. 2009. Downscaling climate over complex terrain: high finescale (<1000 m) spatial variation of near-ground temperatures in a montane forested landscape (Great Smoky Mountains). *Journal of Applied Meteorology and Climatology* 48:1033–1049.
- GRASS (Geographic Resources Analysis Support System Development Team). 2010. Geographic resources analysis support system (GRASS) software. Version 6.5.svn Open Source Geospatial Foundation, location. Available from <http://grass.osgeo.org> (accessed May 2011).
- Graumlich, L., and W. L. Francis. 2010. Moving toward climate change adaptation: the promise of the Yellowstone to Yukon Conservation Initiative for addressing the region's vulnerabilities. *Yellowstone to Yukon Conservation Initiative*, Commerce, Alberta.
- Hannah, L. 2011. Climate change, connectivity, and conservation success. *Conservation Biology* 25:1139–1142.
- Heller, N. E., and E. S. Zavaleta. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation* 142:14–32.
- Hunter, M. L., G. L. Jacobson, and T. Webb. 1988. Paleocology and the coarse-filter approach to maintaining biological diversity. *Conservation Biology* 2:375–385.
- IPCC (Intergovernmental Panel on Climate Change). 2007. Summary for policymakers. Pages 1–18 in S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. R. Averyt, M. Tignor, and H. L. Miller, editors. *Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom.
- Kavanagh, D. M., T. A. Nuñez, and B. H. McRae. 2012. Climate linkage mapper connectivity analysis software. *Adze Informatics*, Seattle. Available from <http://www.circuitscape.org/linkagemapper> (accessed November 2012).

- Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The velocity of climate change. *Nature* **462**:1052–1054.
- Martinez-Meyer, E., A. Townsend Peterson, and W. W. Hargrove. 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecology and Biogeography* **13**:305–314.
- McRae, B. H., and D. M. Kavanagh. 2011. Linkage mapper connectivity analysis software. The Nature Conservancy, Seattle. Available from <http://www.circuitscape.org/linkagemapper> (accessed November 2012).
- Mote, P. W., and E. P. Salathé. 2009. Future climate in the Pacific Northwest. In *The Washington climate change impacts assessment: evaluating Washington's future in a changing climate*. Climate Impacts Group, University of Washington, Seattle.
- Noss, R. F. 1987. From plant-communities to landscapes in conservation inventories—a look at the Nature Conservancy (USA). *Biological Conservation* **41**:11–37.
- Parnassian, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**:37–42.
- Pepin, N. C., C. Duly, and J. Lundquist. 2011. The influence of surface versus free-air decoupling on temperature trend patterns in the western United States. *Journal of Geophysical Research* **116**(D10): DOI: 10.1029/2010JD014769.
- Phillips, S. J., P. Williams, G. Midgley, and A. Archer. 2008. Optimizing dispersal corridors for the Cape Proteaceae using network flow. *Ecological Applications* **18**:1200–1211.
- Rose, N. A., and P. J. Burton. 2009. Using bioclimatic envelopes to identify temporal corridors in support of conservation planning in a changing climate. *Forest Ecology and Management* **258**:S64–S74.
- Rouget, M., R. M. Cowling, R. I. Pressey, and D. M. Richardson. 2003. Identifying spatial components of ecological and evolutionary processes for regional conservation planning in the Cape Floristic Region, South Africa. *Diversity and Distributions* **9**:191–210.
- Sunderson, E. W., M. Jainch, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002. The human footprint and the last of the wild. *BioScience* **52**:891–904.
- Schlösser, C., T. Nuñez, and J. Lawler. 2012. Dispersal will limit the ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences* **109**:8606–8611.
- Skelly, D. K., L. N. Joseph, H. P. Possingham, L. K. Freidenburg, T. J. Faurugia, M. T. Kimmison, and A. P. Hendry. 2007. Evolutionary responses to climate change. *Conservation Biology* **21**:1353–1355.
- Spencer, W. D., P. Beier, K. Pemrod, K. Winters, C. Paulman, H. Rustigian-Romoso, J. Strickholt, M. Parisi, and A. Pentler. 2010. California essential habitat connectivity project: a strategy for conserving a connected California. California Department of Fish and Game, Sacramento. Available from <http://www.dfg.ca.gov/habcom/connectivity> (accessed June 2012).
- Theobald, D. M. 2010. Estimating natural landscape changes from 1992 to 2050 in the conterminous US. *Landscape Ecology* **25**:999–1011.
- Tischendorf, L., and L. Fahrig. 2000. On the usage and measurement of landscape connectivity. *Oikos* **90**:7–19.
- Vos, C. C., P. Berry, P. Opdam, H. Baveco, B. Nijhof, J. O'Hanley, C. Bell, and H. Kuipers. 2008. Adapting landscapes to climate change: examples of climate-proof ecosystem networks and priority adaptation zones. *Journal of Applied Ecology* **45**:1722–1731.
- Vos, C. C., D. C. J. van der Horst, and M. Vonk. 2010. Spatial planning of a climate adaptation zone for wetland ecosystems. *Landscape Ecology* **25**:1465–1477.
- Wang, A., and D. T. Price. 2007. Estimating global distribution of boreal, temperate, and tropical tree plant functional types using clustering techniques. *Journal of Geophysical Research-Biogeosciences* **112**(G1): DOI:10.1029/2006JG000252.
- Wang, T., A. Hamann, D. L. Spillhouse, and S. N. Aitken. 2006. Development of scale-free climate data for western Canada for use in resource management. *International Journal of Climatology* **26**:383–397.
- WHCWG (Washington Wildlife Habitat Connectivity Working Group). 2010. Washington Connected Landscapes Project: statewide analysis. Washington Department of Fish and Wildlife, Olympia. Available from <http://waconnected.org/statewide-analysis> (accessed May 2011).
- Williams, P., L. Hammah, S. Andelman, G. Midgley, M. Araujo, G. Hughes, L. Mamm, E. Martinez-Meyer, and R. Pearson. 2005. Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology* **19**:1063–1074.

