Connecting natural landscapes using a landscape permeability model to prioritize conservation activities in the United States

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Abstract

Widespread human modification and conversion of land has led to loss and fragmentation of natural ecosystems, altering ecological processes and causing declines in biodiversity. The potential for ecosystems to adapt to climate change will be contingent on the ability of species to move and ecological processes to operate across broad landscapes. We developed a novel, robust modeling approach to estimate the connectivity of natural landscapes as a gradient of permeability. Our approach yields a map capable of prioritizing places that are important for maintaining and potentially restoring ecological flows across the United States and informing conservation initiatives at regional, national, or continental scales. We found that connectivity routes with very high centrality intersected proposed energy corridors in the western United States at roughly 500 locations and intersected 733 moderate to heavily used highways (10^4–10^6 vehicles per day). Roughly 15% of the most highly connected locations are currently secured by protected lands, whereas 28% of these occur on public lands that permit resource extraction, and the remaining 57% are unprotected. The landscape permeability map can inform land use planning and policy about places potentially important for climate change adaptation.

Introduction

Scientific concern has grown over the loss and fragmentation of natural ecosystems from expanding and intensifying human land use, which has altered ecological processes and caused rapid declines in biodiversity (Foley *et al.* 2005; Butchart *et al.* 2010). Increasingly, conservation scientists believe that maintaining or restoring landscape connectivity is critical to conserving global biodiversity (Bennett 2003; Crooks & Sanjayan 2006; Hilty *et al.* 2006; Worboys *et al.* 2010) and is the most common strategy recommended for ecological adaptation to climate change (Heller & Zavaleta 2009). Land managers and public officials at international, federal, state, and local levels have requested guidance from the scientific community on how to identify and prioritize among places that are important for maintaining or restoring landscape connectivity

and facilitating the adaptation of natural ecosystems to changing climates (Fancy *et al.* 2008; Ackerly *et al.* 2010).

Connectivity is commonly defined as the degree to which a landscape facilitates movement of species, populations, and genes among resource patches, from ecological to evolutionary time scales (Taylor *et al.* 1993). To date, modeling approaches to quantify connectivity have defined resource patches (or cores) and then estimated movement between adjacent patches by a least-cost path (LCP; Walker & Craighead 1997) or least-cost corridor (LCC; Beier *et al.* 2008, 2011; Pullinger & Johnson 2010; Spencer *et al.* 2010). The single-cell width pathway of LCP has been criticized as being biologically unrealistic because it is overly narrow. LCC is slightly more robust because it identifies a broader "swath of land intended to allow passage between two or more patches" (Beier *et al.* 2008), and alternative methods have been developed

such as least-cost distance (LCD) that uses the full surface of values (Singleton *et al.* 2002; Theobald 2006; Pinto & Keitt 2009; WHCWG 2010). In addition, graph-theoretical approaches have been developed (Urban and Keitt 2001; McRae 2006; Urban *et al.* 2009; Dale & Fortin 2010; Saura *et al.* 2011; Rayfield *et al.* 2011; Theobald *et al.* in press), which can identify areas important for movement throughout a network of patches in a landscape, rather than simply the best way to move between a pair of nearby patches.

Although these approaches have been useful for focused conservation applications, it remains challenging to apply them to regional-scale to continental-scale conservation problems. Conceptually, delineating patches can be difficult and problematic (Kupfer *et al.* 2006; Jacquez *et al.* 2008; Kindlmann & Burel 2008) and the definition of nodes has a substantial influence on network properties (Butts 2009). Also, crucial biological information about patch shape and size is lost when a patch is simplified to a central node in a graph representation, and similarly, a single edge between a pair of patches does not adequately capture potential connectivity in real-world landscapes. Rather than a neat arrangement of circular patches, real-world landscapes are often composed of complex, irregular patches of varying size, shape, and arrangement. For example, there might be multiple important places to connect two long, linear patches running parallel along mountain ranges (Theobald 2006) or a single patch containing a nonhabitat island. Moreover, focusing on individual corridors ignores the relative ecological contribution of a particular linkage because of its position within the landscape network and the network's resilience to disruption or removal of a node or linkage (Chetkiewicz *et al.* 2006; Rouget *et al.* 2006; Rayfield *et al.* 2011).

A second conceptual challenge is that most efforts to model landscape connectivity have focused on a limited set of focal species, which may not be effective conservation surrogates for a region's biota (Chetkiewicz *et al.* 2006). Commonly, this approach is based on expert-derived species-habitat relationships, which performs poorly when compared to empirical movement models (Pullinger & Johnson 2010) and is limited to the small percentage of species for which life history information exists and detailed empirical data are available. Also, extreme biogeographic and institutional variability of regional studies often preclude focal-species approach and in practice require a simpler approach based on ecological integrity or "naturalness" (Spencer *et al.* 2010).

Finally, current computational limits for graph theory models are reached roughly between 10^3 and 10^5 nodes, well below the 10^8 nodes needed for a national assessment at relatively fine grain (<1 km²), which preclude

scaling up these methods (Theobald 2006; Urban *et al.* 2009; Saura *et al.* 2011), so that guidance is lacking about connectivity over the broad geographic extents most appropriate for conservation planning and climate adaptation strategies (Soulé & Terborgh 1999; Rouget *et al.* 2006; Beier *et al.* 2008).

We developed a new method to map and prioritize landscape connectivity of natural ecosystems that addresses these challenges in three ways. First, we assumed that "natural" areas—where human modification of land cover and human activities are minimal—are important for connectivity currently and in the foreseeable future because they are more likely to function as movement routes for animals and to allow ecological processes to occur naturally. Second, we considered connectivity to be a function of a continuous gradient of permeability values (Singleton *et al.* 2002; McGarigal *et al.* 2009; Carroll *et al.* in press) rather than attempting to distinguish discrete patches based on subjective thresholds of habitat area, quality, or ownership. To implement the gradient-based approach, we applied percolation theory using LCD methods. Third, we calculated a network centrality metric to quantify the relative importance of each cell to the broader landscape configuration (Borgatti 2005). We calculated the gradient permeability of natural ecosystems to map and prioritize the landscape connectivity of the conterminous United States. As with other approaches, we recognize that our approach assumes a single, static representation of land use and climate change, but we argue that by measuring a primary driver of habitat loss and fragmentation and by basing our model on relatively well mapped land use patterns that we can provide relatively robust information (compared to the uncertainties associated with climate projections and formation of novel communities) that will be useful to land managers who can protect, restore, or mitigate harmful human activities.

Methods

We used four steps to calculate our map of landscape connectivity: (1) compute "naturalness" as a function of land cover types, housing density, presence of roads, and effects of highway traffic, adjusted minimally by canopy cover and slope; (2) estimate resistance values for the least-cost calculation using the inverse of the "naturalness" value; (3) calculate iterations of landscape permeability that originate from random start locations; and (4) calculate a network centrality metric to enable prioritization.

We computed the degree of human modification *H* by estimating the proportion of a 270 m cell that is impacted by five factors, following methods detailed in Theobald

Table 1 The proportion of human-modification for 13 major land cover groups (from USGS Land cover v1 dataset), estimated by calculating the proportion of human-modification by land cover/use types from aerial photography (∼1 m resolution) at 6,000 randomly located "chips" (∼600 m × 600 m) across the conterminous US, following methods described in Leinwand et al. (2010)

	Mean	Low (Mean − 1 SD)	High (Mean + 1 SD)	Percentage of "chips"
Agricultural cropland	0.68	0.51	0.86	16.47%
Agricultural pasture/hay	0.56	0.32	0.80	8.29%
Developed high intensity	0.85	0.68	1.03	0.20%
Developed medium intensity	0.76	0.55	0.97	0.49%
Developed low intensity	0.64	0.39	0.90	1.71%
Developed open space	0.52	0.24	0.80	2.85%
Forest	0.07	−0.08	0.22	25.26%
Shrubland	0.05	−0.08	0.18	19.15%
Grassland	0.17	−0.07	0.42	9.81%
Wetlands	0.11	−0.08	0.30	6.89%
Other disturbed lands	0.24	−0.02	0.51	6.96%
Mine/quarry	0.58	0.42	0.73	0.02%
Sparsely vegetated	0.02	−0.05	0.09	1.90%

(2010; Equation 1):

$$H = \max(c, h, r, t, e) \tag{1}$$

where c is the proportion of land cover modified, h the proportion modified because of residential housing, r the proportion of the physical footprint of roads and railways, t the modification because of highway traffic, and e the proportion modified by extractive resource production (i.e., oil and gas mining).

We developed an empirical estimate of the proportion of land cover modified for each of 13 major land cover types at 30 m resolution (USGS 2010), derived by summarizing detailed estimates from interpretation of high-resolution color aerial photography (ca. 2006) from 6,000 randomly-located samples using methods described in Leinwand *et al.* (2010). We found that "high intensity" developed areas (such as commercial/industrial) had a mean proportion of human modification of 0.85 (SD = ±0.17), cropland had a mean value of 0.68 (SD = ±0.17), and grasslands had a mean value of 0.17 (SD = ±0.25; Table 1).

Although the major aspects of human modification are usefully captured in classified land cover data, information about lower intensity land uses such as low-density residential development (Bierwagen *et al.* 2010) and fine-grained features (<30 m in width) such as roads and trails needs to be incorporated. We included modifications using the detailed land use dataset (Leinwand *et al.* 2010) on the amount of visible land cover modified associated

with housing units and development (*h*; Theobald 2005; Bierwagen *et al.* 2010).

For roads, we estimated the proportion of a 30-m cell impacted by a road *r* as 1.0 for highways, 0.5 for secondary roads, 0.3 for local roads, and 0.1 for dirt and four-wheel drive roads (Theobald 2010) using U.S. Census TIGER 2010 data. To account for likely habitat loss near roads because of use (i.e., human activity), we converted the annual average daily traffic (AADT; number of vehicles) using a quadratic kernel density that assumes the impact *t* declines with distance out to 1 km away from a road (Forman *et al.* 2003; Fahrig & Rytwinski 2009).

To account for impacts associated with widespread resource extraction activities, we used three datasets: oil and gas well density *d* by converting locations of active wells using a kernel density function (1 km radius) and assigned a human-modification factor for wells, *e* of 0.5 for $d > 2.0$ per km^2 and 0.25 for *d* from 0.1 per km^2 to 2.0 per km^2 (Copeland *et al.* 2009); lands that had significant topographic changes associated with mining activities (USGS Topographic Change) were assigned a value of 1.0; and the DMSP "night lights" values for 2009 (Elvidge *et al.* 1999) were converted using the natural log and then normalized.

We estimated movement resistance values *W* using the degree of human modification *H*, as well as canopy cover (*x*) and terrain slope (*s*) (Figure 1):

$$W = H^{(1.0 - s + x)} \tag{2}$$

where *x* is the mean proportion of canopy cover to lower the value of *W* in areas with higher canopy cover, and *s* is the percent slope (expressed as a proportion) to include a minor adjustment for energetic costs to animals associated with moving in areas of steeper slope. To test the sensitivity of our results to the specification of *W*, we compared results to the "best" estimate (*c* = mean) to a low and high estimate (*c* = mean ± standard deviation).

To reduce boundary effects near Canada and Mexico, we included a coarse approximation of human modification based on "night lights" data and land cover that extends 100 km from borders into Canada and Mexico using a global land cover dataset (∼300-m resolution; GlobCover 2010). We reclassified built-up, artificial surfaces, and cultivated areas to 1.0; managed areas, mosaic cropland and mosaic tree to 0.5, water to 0.3, and the remaining classes were considered to be "natural" cover types to 0.0.

To estimate permeability across the landscape, we applied gradient-based percolation theory (Sapoval & Rosso 1995) within a Monte Carlo framework to generate *k* iterations of landscape permeability maps using ArcGIS v10 (Esri, Redlands, CA, USA), similar to Cushman *et al.*
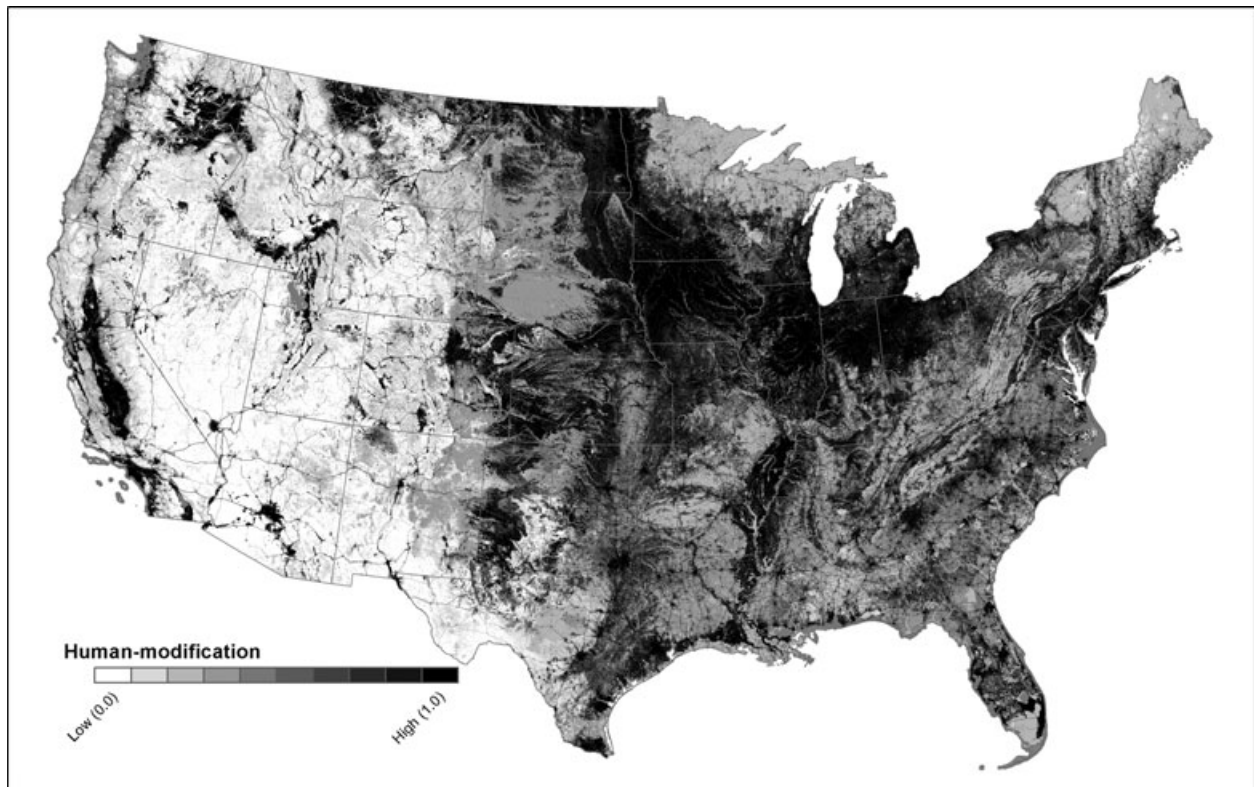
Figure 1 Map of the degree of human modification H for the U.S. circa 2006–2007. Darker areas have higher values of H that contain higher housing density, extensive croplands, more and larger roads, and more extractive resource activities, whereas lighter areas contain higher proportions of natural land cover types and fewer signs of human activities. About 62% of the United States is "natural," conversely about 38% is modified by human activities.

(2008). For each iteration i, we first selected a random start location in the landscape, drawn without replacement, with increasing probability that each cell is "natural," or not human-modified, $N = 1 - H$ (Figure S1). Second, we calculated cost-distance D_i from the start location across the landscape using W as the cost-weights (Figure S2). Locations with lower values of D_i are considered to be more connected to the start location. We identify random locations preferentially in natural cells to be consistent with the assumption of landscape resistance— i.e., starting locations are assigned a cost distance value of 0. Third, we followed the LCP from each cell back to the start location (i.e., using the backlink raster in ArcGIS) to calculate the accumulated proportion of each cell that is natural, N_{ai} (Figure S3). That is, N_{ai} is added to the adjacent cell that it flows into, following the path back to the start cell. Locations with higher N_{ai} values (betweeness) are found in areas with higher landscape permeability, which is directly interpretable as being more connected to a greater amount of land (km^2), weighted by N. Finally, we generated two output maps by calculating the cell-by-cell mean through all k itera-

tions of D_i to generate a map of landscape permeability $\overline{D}$, where locations with a lower average cost-distance are more connected. Similarly, we averaged through all k iterations of N_{ai} to generate a measure of betweeness centrality $\overline{N}_a$.

To understand how and whether variance of permeability declined with increasing number of iterations, we ran 100 iterations (at 810 m for computational reasons) and found that the mean of the cost-distance values (averaged both across a single layer and between layers) stabilized to within ±2% at 70 iterations, but was at 13% and 3% for 30 and 40 iterations, respectively. Therefore, we chose to run our analysis with 40 iterations at the original resolution (270 m). We tested the sensitivity of our results to the uncertainty of our estimates of resistance values by comparing the root mean square difference in the ranks of permeability values produced from mean, mean ± standard deviation of our estimates of c.

Finally, to examine the potential ecological effects of additional human modifications on landscape connectivity, we computed the spatial intersection of the $\overline{D}$ and $\overline{N}_a$ maps with both (1) designated energy corridors; and
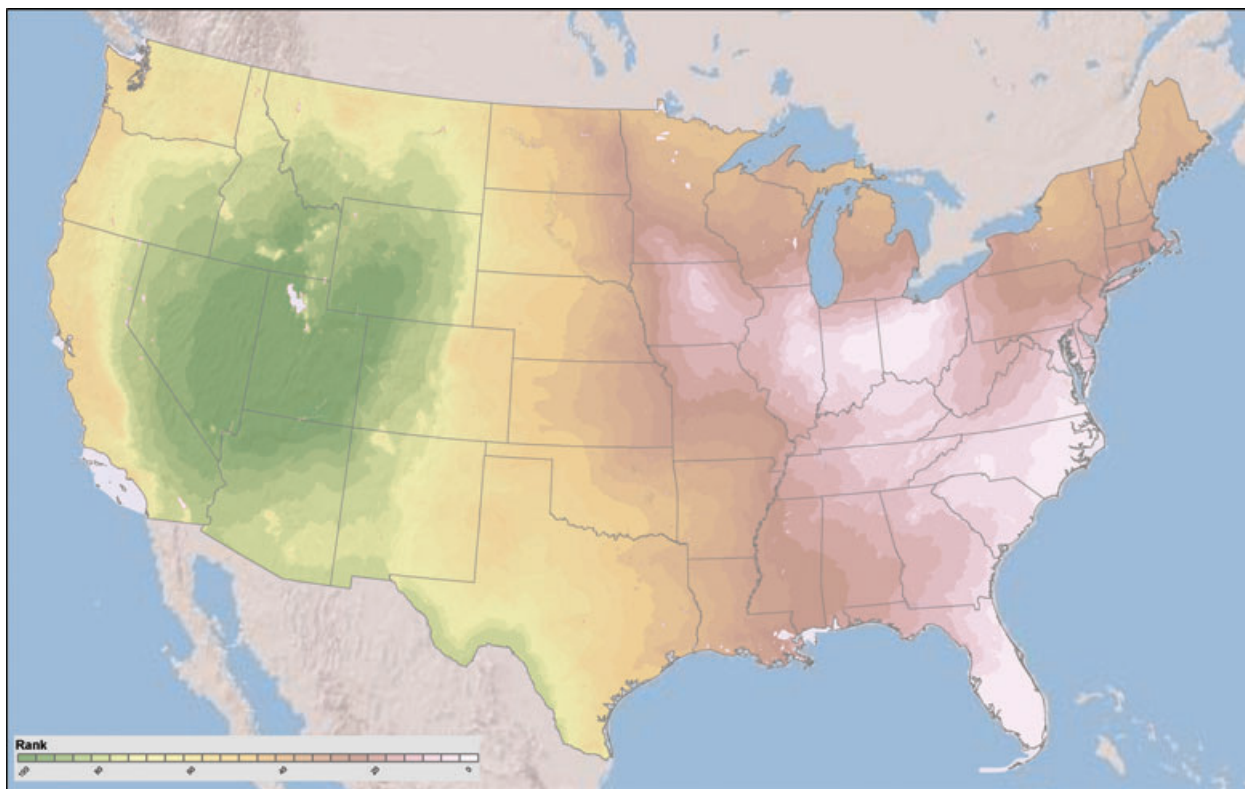
Figure 2 U.S. natural permeability of natural landscapes. This map of connected landscapes shows the natural landscape connectivity as a surface (or gradient) representing each cell's value as a percentile distribution normalized to the United States. Colors represent the amount of connected, natural lands (green = high; yellow = medium; purple/white = low).

(2) highways using four levels of highway traffic volume measured as average annual daily traffic or vehicles (USDOT 2009: low ≤5,000; moderate 5–10,000; high 10–100,000; and extreme >100,000). We also calculated the degree to which highly natural and connected landscapes were protected from conversion to developed land uses (PAD-US v1.1; http://databasin.org/protected-center).

Results

The outputs of our model can be visualized in two main ways: as a landscape permeability surface using $\overline{D}$ that shows the relative proportion of natural, connected locations (Figure 2) or as lines or "routes" of betweeness centrality that emerge indicating high surface permeability connections between areas of high naturalness $\bar{N}_a$ (Figure 3). Note that all cells have a value, but we show only those routes with relatively high connecting values to simplify the visualization of national-extent results.

Generally, the interior portions of the West have many routes with high centrality, showing that these are among the most connected natural landscapes in the United States. In the East, the main route that runs along the Appalachian range is roughly as important as those in the West, but it is a singular route, narrowly confined along the Appalachians and then flowing through central Alabama, Mississippi, and southern Louisiana.

We found 490 intersections between proposed energy corridors and flow routes with high betweeness centrality and 2,047 intersections with medium centrality routes (Figure 4). We also examined where routes intersect major highways nationwide (Figure 5), finding that the medium and high betweeness routes cross 640 minimal ($<10^3$), 2,441 low (10^3–10^4), 723 moderate (10^4–10^5), and 10 high ($>10^5$) use highways (measured by AADT).

As expected, natural connected landscapes and important centrality routes primarily traverse and connect lands that are publicly owned. Roughly 15% of the length of the centrality routes are located on highly protected public lands (GAP status 1 and 2; PAD-US v1.1), another 28% crosses public lands that allow some resource extraction activities (GAP status 3), and 57% cross private lands.
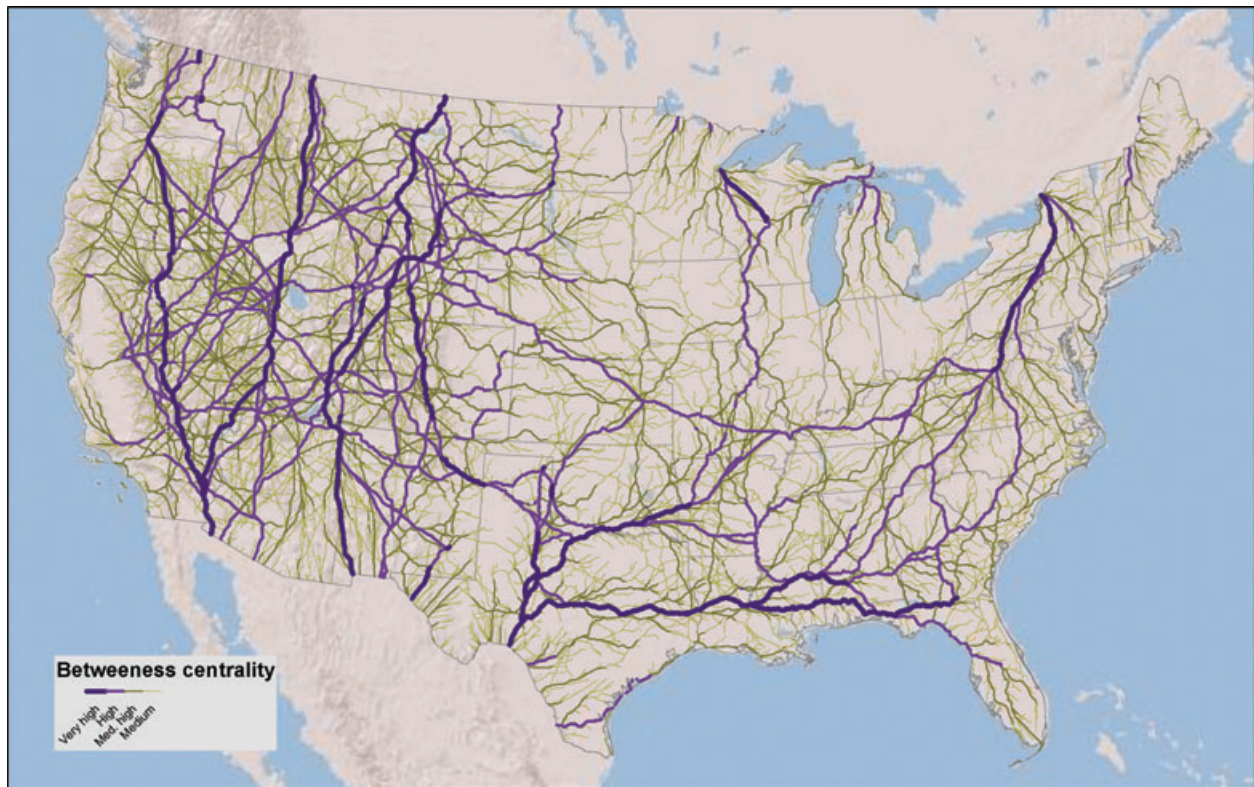
Figure 3 The connectivity of U.S. natural landscapes depicted using flow "routes". This map shows where pathways or "routes" have high amounts of accumulated natural lands flow through an area (i.e., high values of betweenness centrality). Note that to reduce visual complexity on this map, we show only relatively more frequently used routes, but there are numerous flow routes at local scales that potentially are important but not shown. Also, the width of lines are made wider to help portray more important routes of potential movement through natural landscapes.

Discussion

Our results offer a preliminary basis for understanding patterns of broad-scale landscape permeability of natural ecosystems and provide the first comprehensive map relevant to regional-scale to continental-scale connectivity conservation initiatives (e.g., in the United States: the Wildlands Networks's *Spine of the Continent* (www.twp.org), Wildlife Conservation Society's *Two Countries One Forest* (www.wcs.org), *Yellowstone to Yukon* (www.y2y.net), the Western Governors' *Association wildlife initiative* (www.westgov.org/wildlife) and *the U.S. Department of Interior lands* (www.fws.gov/science/shc/lcc.html).

Our modeling approach provides a quantitative, nonarbitrary means to assess relative priorities within and among existing connectivity conservation efforts and is intended to complement focal species mapping. However, we emphasize that inefficient conservation actions may result when connectivity analyses are too narrowly focused on individual species or when political consider-

ations restrict the extent of analyses to arbitrary political boundaries that are at a smaller extent than the focal ecological processes. Our results are best used to plan for the connectivity of natural landscapes, particularly in the face of climate change, rather than as a prescription or substitute for identifying existing habitats that support a high diversity of species. Computing the number of intersections of the transportation and natural landscape networks highlights the extent of potential effects of development activities and can help prioritize where natural connectivity and human land use are in conflict.

We found that our estimates of the degree of human modification were relatively insensitive to the variability of land cover values about our mean estimates—the root mean square difference in the ranks of permeability values were 7.20% (SD = 8.17%) and 3.72% (SD = 4.74%) with mean ± 1 SD of c. We chose to combine factors by using the maximum value to eliminate possible issues with interpretation of the modeled results because of colinearity among factors and to avoid logical inconsistencies of an additive model that would
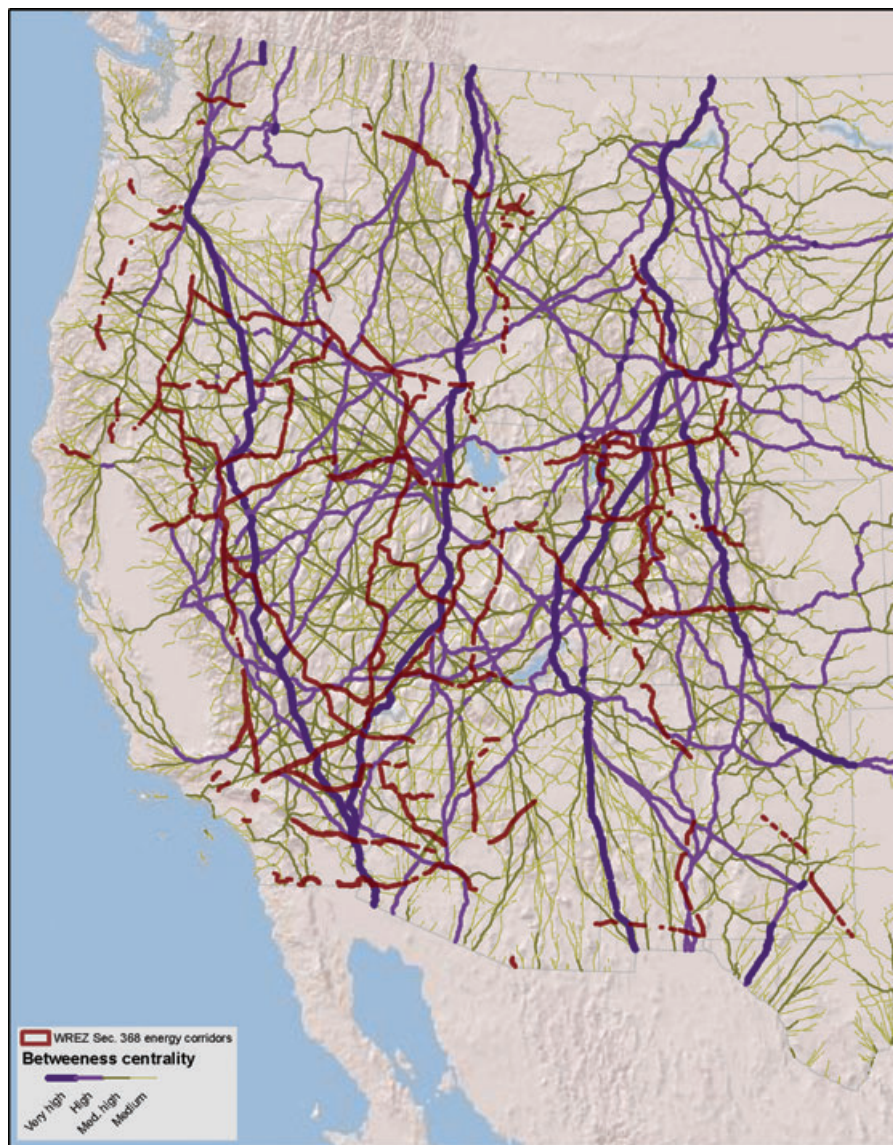
Figure 4 Intersections of natural connectivity flows with proposed energy "corridors". About 500 nationally important routes intersect with the proposed designated west-wide energy corridors (Section 368 of the Energy Policy Act).

potentially result in $H > 1.0$. Consequently, our estimate of human modification is conservative, and future work could explore cumulative, complimentary, or averaging assumptions.

Conceptually, our gradient-based approach is similar to the application of graph theory and circuit theory (McRae 2006) that calculate a metric directly on a (regular) graph where each cell is a vertex. These approaches can provide exact calculations of metrics, but on typical 32-bit desktop computers are currently limited in practice to graphs with 10^3–10^5 nodes (Jantz & Goetz 2008; Urban *et al.* 2009; Circuitscape 2011; Connectivity Analysis Toolkit 2011; Saura *et al.* 2011). We were able to successfully compute

our model for the very large networks (10^6–10^9 nodes): our national map contained 2×10^8 cells.

Our approach is similar to traditional connectivity analyses in that it calculates LCD based on a resistance surface, but differs from approaches to model corridors and linkages, including the recently completed statewide assessments for Arizona, California, Montana, and Washington (e.g., Spencer *et al.* 2010; WHCWG 2010). These latter approaches require the boundaries of patches to be specified, model corridors/linkages between adjacent patches only, ignore the amount of resource available (i.e., patch area or quality), and provide little information about the relative importance of a corridor
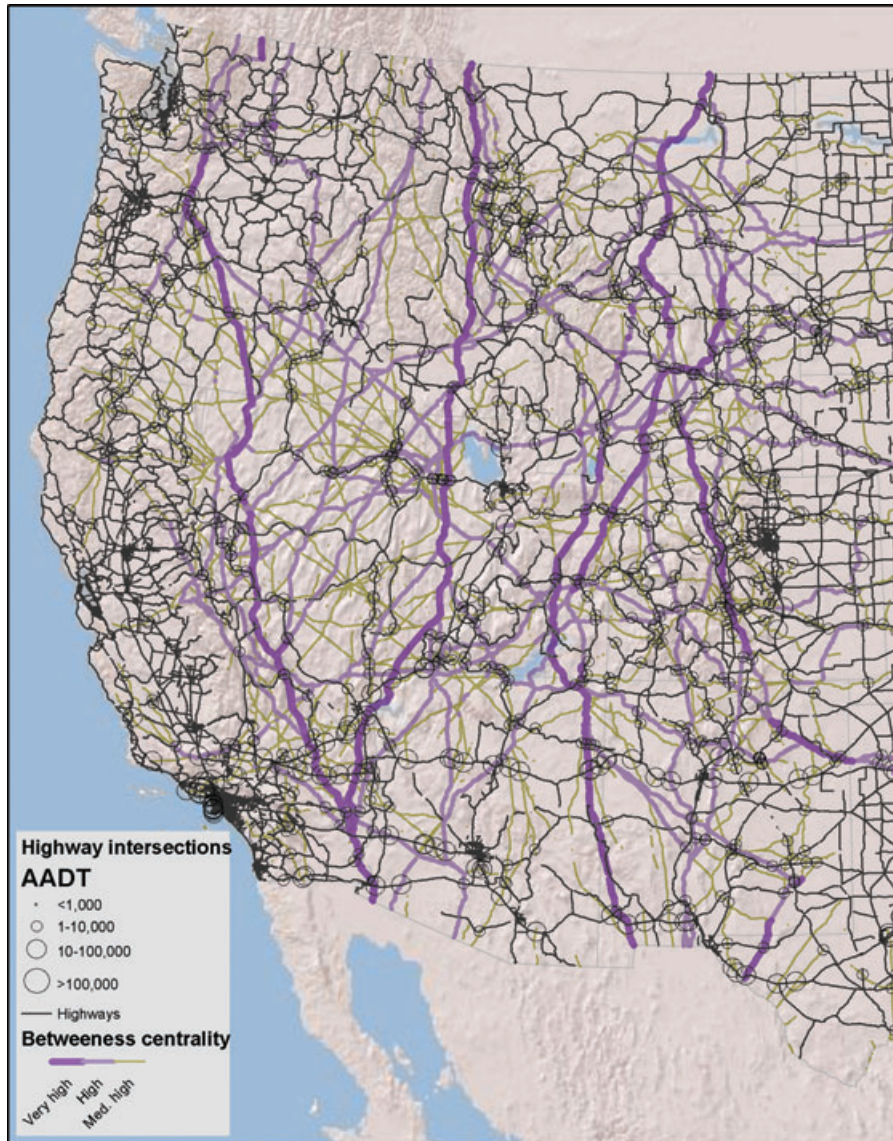
Figure 5 Intersections of natural connectivity routes with major highways in the western United States. Circles represent the locations of highways with accumulated natural flow routes and larger circles signify higher highway traffic volume. Note for clarity, we do not depict all highways or all permeability flow routes.

(or patch) within the broader landscape network. Our approach is conceptually similar to methods that calculate LCD and permeability using multiple pathways (i.e., McRae 2006; Theobald 2006; Pinto and Keitt 2009), but is more easily computed, interpreted, and replicated by conservation practitioners.

In summary, we used the degree of human modification as a practical alternative to parameterize, run, combine, and interpret connectivity models for potentially hundreds to thousands of species. Because we parameterized the model on the basis of an assumption that protecting less-modified lands is important for con-

servation, it will therefore be most directly useful to identify important areas for species that are sensitive to human disturbance—but our approach could be reformulated to represent different assumptions about sensitivity of species (e.g., that agricultural landscapes are highly permeable). Rather than attempting to delineate patches or natural blocks, we considered connectivity to be a function of a continuous gradient. The centrality metric provides a quantitative measure to understand the broader, landscape-level arrangement of relatively unmodified and connected lands.
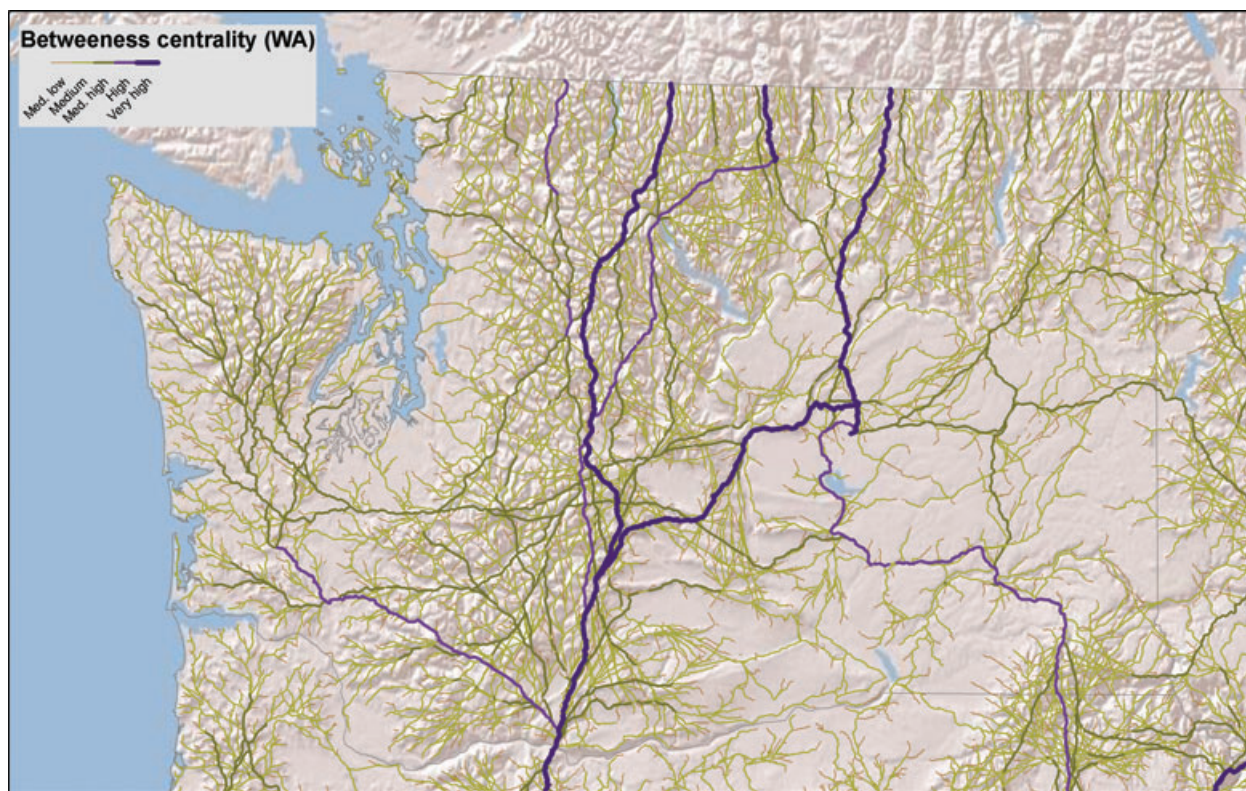
Figure 6 Landscape flow routes, rescaled or "normalized" to show the relative importance within the state of Washington.

Conclusion

Our gradient map of landscape permeability provides the first map capable of informing connectivity conservation initiatives at broad scales by identifying locations and their relative importance for maintaining landscape connectivity, protecting the movement of species, retaining landscape-scale ecological processes, and facilitating adaptation to climate change. Data on land ownership or protected status were not used as input to the model, allowing us to investigate how well land is protected that has natural characteristics. Also, by freeing our analysis from political and ownership boundaries, the results better indicate the value of both public and private lands in contributing to connectivity at a national level. In addition to national priorities, future studies can be refined to provide more regional or state-level priorities (Figure 6).

The potential for ecosystems to adapt to climate change will be largely contingent on the ability of species and ecological processes to move across broad landscapes. Roughly 15% of the locations most important for landscape connectivity for biota and ecological processes (or flow routes) are currently secured by protected lands, whereas 28% of these occur on public lands that permit resource extraction, and the remaining 57% are unprotected. This information can help to identify places where management policies should be reviewed and where future development should be minimized or to anticipate the need for mitigation of negative effects, and can assist the coordination of local and regional conservation efforts so that individual actions can be linked across larger regions to form cohesive connectivity networks.

Acknowledgments

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1: Map of cost weight values used in cost-distance calculations.

Figure S2: Illustration of least-cost distance from the starting location.

Figure S3: Illustration of accumulated natural values along the "back-link" raster or flow routes back to the start location.

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References

Ackerly, D.D., Loarie, S.R., Cornwell, W.K. *et al.* (2010) The geography of climate change: implications for conservation biogeography. *Divers Distrib* **16**, 476–487.

Beier, P., Majka, D.R., Spencer, W.D. (2008) Forks in the road: choices in procedures for designing wildland linkages. *Conserv Biol* **22**(4), 836–851.

Beier, P. W., Spencer, R.F. Baldwin, McRae, B.H. (2011) Toward best practices for developing regional connectivity maps. *Conser Biol* **25**(5), 879–892.

Bennett, A.F. (2003). *Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation.* IUCN, Gland, Switzerland and Cambridge, UK. xiv + 254 pp.

Bierwagen, B., Theobald, D.M., Pyke, C.R. *et al.* (2010) National housing and impervious surface scenarios for integrated climate impact assessments. *PNAS* **107**(49), 20887–20892.

Borgatti, S.P. (2005) Centrality and network flow. *Soc Netw* **27**, 55–71.

Butchart, S.H.M. *et al.* (2010) Global biodiversity: indicators of recent declines. *Science* **328**, 1164–1168.

Butts, C.T. (2009) Revisiting the foundations of network analysis. *Science* **325**, 414–416.

Carroll, C., McRae, B., Brookes, A. In press. Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of gray wolf populations in western North America. *Conserv Biol.*

Chetkiewicz, C.L.B., Clair, C.C. St., Boyce, M.S. (2006) Corridors for conservation: integrating pattern and process. *Annu Rev Ecol Syst* **37**, 317–342.

Circuitscape (2011) *Circuitscape FAQ: how large of a landscape can I analyze with Circuitscape?* Available from: http://www.circuitscape.org/Circuitscape/FAQ.html Accessed 4 September, 2011.

Connectivity Analysis Toolkit (2011) *Online documentation: system requirements.* Available from: http://www.connectivitytools.org, Access 4 September 2011.

Copeland, H.E., Doherty, K.E., Naugle, D.E., Pocewicz, A., Kiesecker, J.M. (2009) Mapping oil and gas development

potential in the US intermountain west and estimating impacts to species. *PLoS ONE* **4**(1), e7400.

Crooks, K.R., Sanjayan, M.A., editors. (2006) *Connectivity conservation*, New York, Cambridge University Press

Cushman, S.A., McKelvey, K.S., Schwartz, M.K. (2008) Use of empirically derived source-destination models to map regional conservation corridors. *Conserv Biol* **23**(2), 368–376.

Dale, M.R.T., Fortin, M.J. (2010) From graphs to spatial graphs. *Annu Rev Ecol Syst* **41**, 21–38.

Elvidge, C.D., Baugh, K.E., Dietz, J.B., Bland, T., Sutton, P.C., Kroehl, H.W. (1999) Radiance calibration of DMSP-OLS low-light imaging data of human settlements. *Remote Sens Environ* **68**, 77–88.

Fahrig, L., Rytwinski, T. (2009). Effects of roads on animal abundance: an empirical review and synthesis. *Ecol Soc* **14**(1), 21. [online] Available from: http//www.ecologyandsociety.org/vol14/iss1/art21/

Fancy, S.G., Gross, J.E., Carter, S.L. (2008) Monitoring the condition of natural resources in US National Parks. *Environ Monit Assess* **151**, 161–174.

Foley, J.A., DeFries, R., Asner, G.P., *et al.* (2005) Global consequences of land use. *Science* **309**, 570–574. doi: 10.1126/science.1111772

Forman, R.T.T., Sperling, D., Bissonette, J.A. *et al.* (2003) *Road ecology: science and solutions.* Washington, DC: Island Press.

GlobCover (2010) GlobCover 2009 Product Description Manual. Available from: http://ionia1.esrin.esa.int/

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

Hilty, J.A., Lidicker, W.Z., Merenlender, A.M. (2006). *Corridor ecology: The science and practice of linking landscapes for biodiversity conservation.* Washington, DC: Island Press.

Jacquez, G.M., Fortin, M.J., Goovaerts, P. (2008) Preface to the special issue on spatial statistics for boundar and patch analysis. *Environ Ecol Stat* **15**, 365–267.

Jantz, P., Goetz, S. (2008) Using widely available geospatial datasets to assess the influence of roads and buffers on habitat core areas and connectivity. *Nat Area J* **28**(3), 261–274.

Kindlmann, P., Burel, F. (2008) Connectivity measures: a review. *Landscape Ecol* **23**, 879–890.

Kupfer, J.A., Malanson, G.P., Franklin, S.B. (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecol Biogeogr* **15**, 8–20.

Leinwand, IIF, Theobald, D.M., Mitchell, J., Knight, R.L. (2010) Landscape dynamics at the public-private interface: A case study in Colorado. *Landscape and Urban Plan* **97**(3), 182–193.

McGarigal, K., Tagil, S., Cushman, S.A.. (2009) Surface metrics: an alternative to patch metrics for the quantification of landscape structure. *Landscape Ecol* **24**, 433–450.

McRae, B.H. (2006) Isolation by resistance. *Evolution* **60**(8), 1551–1561.

Pinto, N., Keitt, T.H. (2009) Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach. *Landscape Ecol* **24**(2), 253–266.

Pullinger, M.G., Johnson, C.J. (2010) Maintaining or restoring connectivity of modified landscapes: evaluating the least-cost path model with multiple sources of ecological information. *Landscape Ecol* **25**(10), 1547–1560.

Rayfield, B., Fortin, M-J., Fall, A. (2011) Connectivity for conservation: a framework to classify network measures. *Ecology* **92**(4), 847–858.

Rouget, M., Cowling, R.M., Lombard, A.T., Knight, A.T., Kerley, G.H. (2006) Designing large-scale conservation corridors for pattern and process. *Conserv Biol* **20**, 549–561.

Sapoval, B., Rosso, M. (1995) Gradient percolation and fractal frontiers in image processing. *Fractals* **3**(1), 23–31.

Saura, S, Estreguil, C., Mouton, C., Rodriguez-Freire, M (2011) Network analysis to assess landscape connectivity trends: Application to European forests (1990–2000). *Ecol Indicators* **11**, 407–416.

Singleton, P.H., Gaines, W.L., Lehmkuhl, J.F. (2002) *Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor assessment*. Research Paper N-549. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Soulé, M.E., Terborgh, J. (1999) Conserving nature at regional and continental scales: a scientific program for North America. *BioScience* **49**(10), 809–817.

Spencer, W.D., Beier, P., Penrod, K. *et al.* (2010) *California essential habitat connectivity project: a strategy for conserving a connected California*. Prepared for California Department of Transportation, California Department of Fish and Game, and Federal Highways Administration.

Taylor, P. D., Fahrig, L., Henein, K., Merriam, G. (1993) Connectivity is a vital element of landscape structure. *Oikos* **68**, 571–573.

Theobald, D.M. (2005) Landscape patterns of exurban growth in the USA from 1980 to 2020. *Ecol Soc* **10**(1), 32. [online] Available from: http://www.ecologyandsociety.org/vol10/iss1/art32/.

Theobald, D.M. (2010) Estimating changes in natural landscapes from 1992 to 2030 for the conterminous United States. *Landscape Ecol* **25**(7), 999–1011.

Theobald, D.M. (2006) Exploring the functional connectivity of landscapes using landscape networks. Pages 416–443 in Crooks, K.R. and M.A. Sanjayan, editors. *Connectivity conservation: maintaining connections for nature*. Cambridge University Press.

Theobald, D.M., Crooks K.R., Norman J.B. (2011) Assessing effects of land use on landscape connectivity: loss and fragmentation of western U.S. forests. *Ecol Appl* **21**(7), 2445–2458.

Urban, D.L., Keitt, T.H. (2001) Landscape connectedness: a graph theoretic perspective. *Ecology* **82**, 1205–1218.

Urban, D.L., Minor, E.S., Treml, E.A., Schick, R.S. (2009) Graph models of habitat mosaics. *Ecol Lett* **12**, 260–273.

US Department of Transportation (USDOT). (2009) *National Transportation Atlas Database (NTAD) 2009 CD*. Research and Innovative Technology Administration/Bureau of Transportation Statistics. January 2007.

US Geological Survey (USGS) Gap Analysis Program. (2010) National land cover, version 1.

Walker, R., Craighead, L. (1997). Analysis of wildlife movement corridors in Montana using GIS. *Proceedings of the 1997 ESRI Users conference*, San Diego, CA.

Washington Wildlife Habitat Connectivity Working Group (WHCWG). (2010) *Washington Connected Landscapes Project: Statewide Analysis*. Olympia, WA: Washington Departments of Fish and Wildlife, and Transportation.

Worboys, G.L., Francis, W.L., Lockwood, M. (2010) *Connectviity conservation management: a global guide*. Earthscan, Canberra, Australia, 480 pp.