



Examining local and regional ecological connectivity throughout North America

R. Travis Belote · Kevin Barnett ·
Katherine Zeller · Angela Brennan · Josh Gage

Received: 19 May 2022 / Accepted: 17 September 2022 / Published online: 28 September 2022
© The Author(s) 2022

Abstract

Context Conservation scientists recommend maintaining and restoring ecological connectivity to sustain biodiversity in the face of land-use and climate change. Alternative connectivity assessments conducted at multiple spatial scales are needed to understand consequences of varying assumptions and for use in multi-scale conservation planning.

Objectives We compared mapped output from different model scenarios conducted to identify areas important for ecological connectivity across North

America. We asked how areas important for connectivity vary with spatial scale and assumptions regarding the way in which human modification affects landscape resistance.

Methods We conducted a factorial experiment using omnidirectional connectivity analyses across North America where we crossed “treatments” represented by four moving window sizes and three resistance surfaces. The three resistance surfaces represent a gradient in species’ sensitivity to human modification.

Results Maps of connectivity importance varied among scenarios. The effects of moving window size were more conspicuous than effects of different resistance surfaces. Outputs from small moving windows revealed mottled patterns of connectivity importance, while outputs from larger moving windows revealed broad swaths of connectivity importance across mountainous and boreal areas of North America. Patterns of connectivity importance tended to be more channelized from resistance surfaces produced to represent more human-sensitive species and more diffuse from resistance surfaces produced to represent more human-tolerant species.

Conclusions Our scenarios and output represent alternative hypotheses and predictions about how multiple species may move in response to varying degrees of human modification. Our output can be compared to species-specific models to investigate which of our scenarios best matches observed movements of organisms. Our output can also be used as coarse-filter and multi-scale connectivity assessments

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10980-022-01530-9>.

R. T. Belote (✉) · K. Barnett
The Wilderness Society, Bozeman, MT 59715, USA
e-mail: travis_belote@twc.org

K. Zeller
USDA Forest Service, Rocky Mountain Research Station,
Aldo Leopold Wilderness Research Institute, Missoula,
MT 59801, USA

A. Brennan
Interdisciplinary Biodiversity Solutions Program,
University of British Columbia, Vancouver, Canada

A. Brennan
Institute for Resources, Environment and Sustainability,
University of British Columbia, Vancouver, Canada

J. Gage
Gage Cartographics, Bozeman, MT 59715, USA

for conservation plans. Notably, our outputs highlight the importance of small and isolated fragments of relatively natural land while simultaneously identifying broad regions important for maintaining connectivity across natural areas of North America.

Keywords Circuit theory · Conservation planning · Human modification · Omniscape

Introduction

Human modification of natural landscapes results in loss and fragmentation of habitat and disruption of ecological processes (Haddad et al. 2015; Venter et al. 2016). Humans modify ecosystems by converting land to agricultural, residential, or commercial uses, building roads, railways, transmission lines, or by otherwise altering natural lands (Kennedy et al. 2019; Theobald et al. 2020). In response to habitat loss and fragmentation, conservation scientists have repeatedly recommended that we (1) stop eliminating habitat (Fahrig 1997; Wilcove et al. 1998) and (2) ensure that habitat fragments remain connected (Hilty et al. 2006; Beier 2012). How to maintain or restore connectivity between core habitats, population sources, and protected areas remains a critical conservation challenge, especially in the face of climate change (McGuire et al. 2016; Littlefield et al. 2017; Parks et al. 2020).

Various methods for identifying priority locations for maintaining or restoring connectivity between core areas have been developed in the last few decades (Rudnick et al. 2012; Correa Ayram et al. 2016). Least-cost paths, least-cost corridors, resistant kernels, and methods applying circuit theory are among the most popular (Compton et al. 2007; Carroll et al. 2011; Dickson et al. 2019; Phillips et al. 2021). Each of these methods require (1) gridded data of pixels estimating landscape resistance to movement and (2) locations of core areas or source points to connect (e.g., habitat patches, population sources, or protected areas). Developing resistance surfaces that best predict movement of species is an active area of research (Zeller et al. 2012, 2018; Keeley et al. 2016; Carroll et al. 2020). Other research seeks to develop resistance surfaces that are “species-agnostic” so that they represent assumptions of how multiple species move in response to landscape conditions (Krosby et al.

2015). Species-agnostic connectivity assessments range from mapping corridors between protected areas (e.g., Barnett and Belote 2021) to identifying potential flows of ecological processes and movements of myriad species (Littlefield et al. 2017; Carroll et al. 2018).

Maps of landscape resistance are often based on assumptions that certain landscape features, like areas of high human modification or unsuitable habitat, will be avoided by individuals, require a high physiological cost to traverse, or constitute high mortality risk (Compton et al. 2007; Cushman and Landguth 2012; Tucker et al. 2018). Resistance surfaces are created using a combination of geospatial layers representing human modification, topography, and vegetation (Zeller et al. 2012). For species-agnostic approaches, maps of human modification often serve as the basis of resistance under the assumption that maintaining connectivity through the most “natural” lands will provide the best opportunities for successful movement for the greatest number of species (Lawler et al. 2013; Belote et al. 2016; Parks et al. 2020; Barnett and Belote 2021). The precise relationship between human modification and landscape resistance to movement is usually poorly quantified (Tucker et al. 2018; Brennan et al. 2022). Identifying connectivity priorities for “human-tolerant” species compared to “human-sensitive” species can be done using different transformations of human modification data to create maps of landscape resistance (Keeley et al. 2016; Belote et al. 2016; Belote and Wilson 2020).

While developing resistance surfaces that accurately predict wildlife movement and ecological flows is important, connectivity models have been shown to be sensitive to the number and locations of areas to connect (Koen et al. 2014; Belote et al. 2016). Therefore, the decision of where to place source locations or core areas is not trivial. When known, locations of source populations can be used as core areas in a connectivity model (Peck et al. 2017). In other cases, researchers have distributed source points or core areas in connectivity models based on estimated population densities or habitat suitability (Cushman and Landguth 2012; Keeley et al. 2016; McClure et al. 2016; Carroll et al. 2020). In species-agnostic cases, researchers have modeled connectivity among protected areas (Belote et al. 2016; Ward et al. 2020; Barnett and Belote 2021). Given model sensitivity to the number and location of core areas, and

because sources and/or destinations may be unknown, researchers have developed ‘coreless’ connectivity model approaches (McRae et al. 2016; Pelletier et al. 2017; Koen et al. 2019). These models use either resistant kernels to estimate a density of movement (Compton et al. 2007) or ‘wall-to-wall’ or ‘omnidirectional’ current flows using circuit theory (McRae et al. 2016; Koen et al. 2019; Phillips et al. 2021).

Conservation scientists are evaluating connectivity priorities at local (Compton et al. 2007), regional (Leonard et al. 2017; Schloss et al. 2022), continental (Carroll et al. 2018; Barnett and Belote 2021), and global (Ward et al. 2020; Brennan et al. 2022) extents. Providing organisms opportunities to adapt to increasing human pressure and the effects of climate change via long-distance dispersal – over multiple generations and long time periods – is increasingly recognized as an important long-term adaptation strategy in conservation planning (Lawler et al. 2009; Carroll et al. 2018; Parks et al. 2020). At the same time, conservation scientists are recognizing the importance of relatively small, isolated habitat patches (i.e., “fragments”) for maintaining biodiversity, supplying myriad ecosystem services, and functioning as stepping-stones in local habitat networks (Hannah et al. 2014; Belote et al. 2016; Peck et al. 2017; Fahrig 2019; Riva and Fahrig 2022). Broad-scale connectivity models (e.g., those conducted across the continent) may fail to identify the importance of small habitat fragments despite their role for maintaining local connectivity (Koen et al. 2019). Many large landscape connectivity models are coarse in scale and in assumptions of dispersal ability and are therefore limited in their ability to identify the importance of smaller habitat fragments for maintaining local connectivity. Multi-scale connectivity assessments based on alternative assumptions of how human modification may affect movement are needed.

Here, we conducted a factorial experiment to evaluate how spatial scale and resistance surfaces affect the identification of lands important for maintaining connectivity. Specifically, we modeled omnidirectional connectivity at various spatial scales across North America using three alternative maps of landscape resistance representing different sensitivities of species to human modification (McRae et al. 2016). We took advantage of new Omniscape software (Landau et al. 2021; Hall et al. 2021) which allowed us to assess lands important for maintaining connectivity

at multiple spatial scales without deciding which core areas or sources/destinations to include in an analysis. We based our analysis on the premise that lands with minimal human modification will likely facilitate movement of species better than lands with more intense human modification. As in many conservation-planning exercises there is a tradeoff between focusing on species-agnostic, coarse filter versus species-specific, fine filter approaches. Our approach is species agnostic, does not depend on locations of core areas, is focused on multiple spatial scales, and is not constrained to a national border. We asked three primary questions:

- (1) Which areas are important for ecological connectivity across North America?
- (2) Do areas identified as important for connectivity vary among scenarios using different resistance surfaces representing alternative sensitivities of organisms to gradients in human modification?
- (3) How do areas identified as important for connectivity vary among scenarios using moving windows of different sizes, which represent multiple scales of connectivity importance?

Methods

Omniscape overview

We used Omniscape v0.5.8 to run connectivity models in Julia (Landau et al. 2021; Hall et al. 2021) on an Amazon Web Service (AWS) instance (machine type r5a.12xlarge with 48 VCPUs and 384 GB of RAM). We used an estimate of human modification as the basis of landscape resistance (Theobald et al. 2020). Omniscape implements omnidirectional connectivity models using circuit theory (McRae et al. 2007, 2016) and gridded data representing maps of landscape resistance. Omnidirectional connectivity is assessed within moving windows where the center pixels constitute targets and are set to “ground”. Pixels within the moving window serve as sources of current flow injected into the map of landscape resistance (see *Source strength and blocking* below). Like other circuit theory models, movement of electrical current serves as a model metaphor for random-walking organisms moving through a landscape (Dickson et al. 2019).

We produced 12 maps of omnidirectional normalized current flow using three resistance surfaces

crossed with four moving window extents across North America. Omniscape outputs three representations of landscape connectivity: potential current flow, cumulative current flow, and normalized current flow. Potential current flow is assessed based on model runs where current is injected into sources but where resistance of every pixel is constant and set to 1. Cumulative current flow is calculated as the sum of current flow output from overlapping moving windows. Normalized current flow is calculated by dividing current flow by potential current flow (Landau et al. 2021) and is used to highlight areas of concentrated (high values) and impeded (low values) current flow (Brennan et al. 2020; Schloss et al. 2022). We focus attention and interpretation of concentrations of high values which represent channelized flow (i.e., areas of relatively high normalized current density, sensu McRae et al. 2016, Schloss et al. 2022, and Cameron et al. 2022).

Landscape resistance

The 2015 map of human modification is a 1-km resolution (with Lambert azimuthal equal area projection) global composite of variables that represent human impacts to natural ecosystem structure and processes such as roads and transmission lines, modified land cover (e.g., urban areas, agriculture, mines), and density of human population (Theobald et al. 2020). We assume that movement of wildlife species, dispersal of organisms, and flows of other terrestrial processes are least disrupted on lands with lower human modifications. However, the degree of resistance to movement, dispersal, and flow along gradients of human modification are typically unknown. For some species (e.g., human-tolerant species like coyotes, *Canis latrans*), low and moderate levels of human modification may have little effect on movement or flows (Ellington and Gehrt 2019). In these cases, only moderate to high levels of human modification may impede movement. For other species or processes (e.g., human-sensitive species like grizzly bears, *Ursus arctos*), low levels of human modification may have a relatively large effect on movement or flows. And, in other cases, movement may be resisted in a way that is proportional to the degree of human modification. These alternative ways that human modification may influence resistance can be represented spatially through alternative mathematical

transformations of the human modification data. Here, we used three transformations introduced in Keeley et al. (2016), who represented landscape resistance as a function of habitat suitability for species-specific connectivity models. In our cases, we used the map of human modification as the basis of species-agnostic resistance in lieu of species-specific habitat suitability. We used the function:

$$\text{Resistance} = -99 \times \frac{1 - e^{-c \times hm2015}}{1 - e^{-c}} - 1 \quad (1)$$

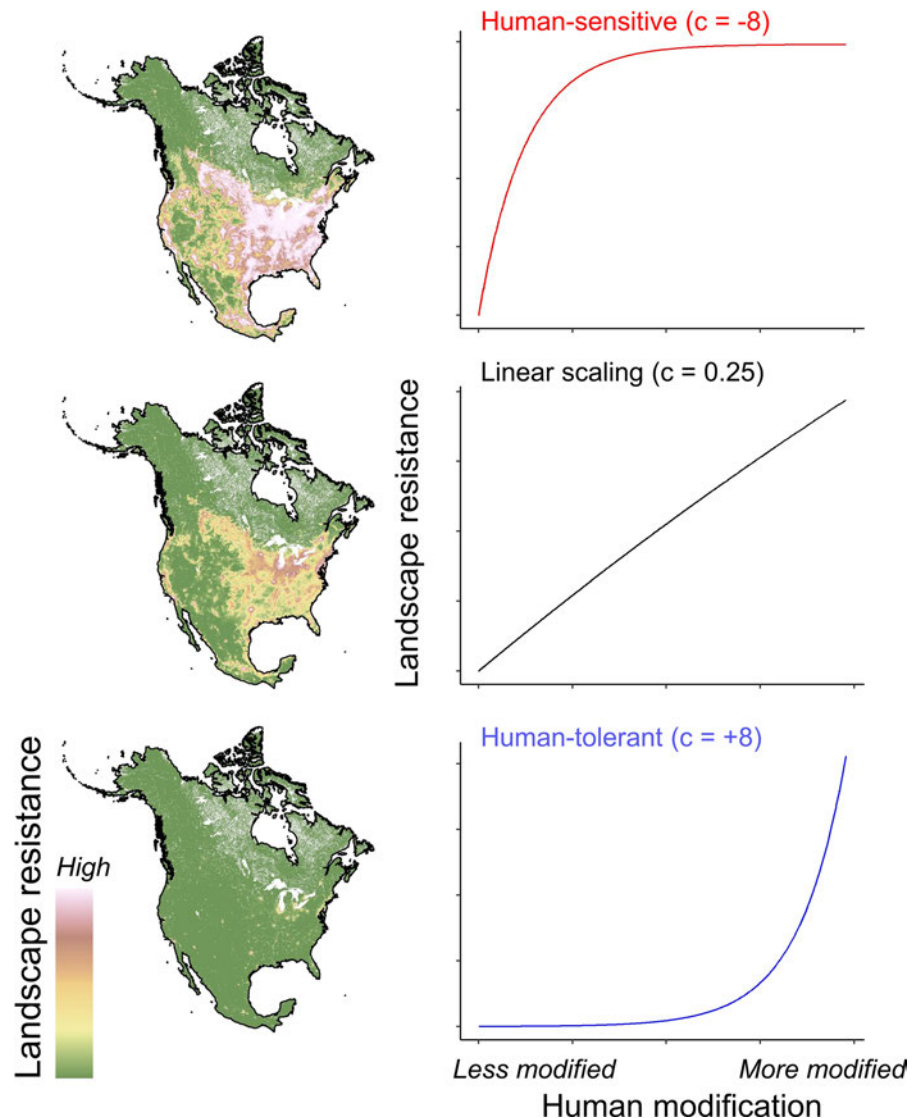
To create three maps of resistance where *hm2015* is the human modification and *c* is equal to -8 , 0.25 , or 8 representing resistance for human-sensitive species or processes, resistance that varies linearly with human modification, and resistance for human-tolerant species or processes, respectively (Fig. 1).

The human modification data assigns natural lakes and rivers no values (i.e., NA), but reservoirs or other impounded waters are assigned values relative to surrounding human modification. In our connectivity models, water assigned as NA functions as complete barriers to movement. While this treatment may represent the way water impedes some movements and spatial processes, we chose to assign all water – irrespective of reservoir or natural lake or river – the maximum value of resistance. We chose to use an eight-neighbor rule which considers corner-adjacent pixels connected in Omniscape. Lacking alternative pathways due to the barrier of water, these corner-adjacent pixels near river oxbows resulted in conspicuously high concentrations of current flow. Assigning the maximum value of resistance to water eliminated these artifacts without changing other nearby patterns of current flow (Supplement 1). We also chose this approach because natural and human-caused water bodies likely do not represent complete barriers of movement for many species. Rather, water may represent areas of high resistance to movement, thus our decision to assign the maximum resistance value to water.

Source strength and blocking

Source strength of pixels constitutes the amount of current injected into a pixel and can represent locations of core habitat or known populations. Because our models are species- and population-agnostic, we

Fig. 1 The way that human modification influences landscape resistance may vary depending on species' sensitivity to gradients in human impacts. We created three maps of resistance based on three alternatives varying the 'c' parameter in Eq. 1. When $c = 0.25$ (black line), resistance scales linearly with human modification. Species movements that are more sensitive to lower levels of human modification were modeled using $c = -8$ (red line), whereas species movement that are more tolerant to lower levels of human modification were modeled using $c = +8$ (blue line)



did not use predetermined locations to represent variability in the sources of dispersing organisms. For our models, we used the inverse of the resistance surface as a source strength layer (McRae et al. 2016; Landau et al. 2021; Schloss et al. 2022). This follows from the assumption that more natural lands with lower human modification will tend to represent greater sources of dispersers. It is important to note that transformations of the human modification data into resistance surfaces likely also influence intensity of movement emanating from a given area. In other words, our “treatments” of resistance surfaces also may influence source strength.

To speed processing, Omniscape allows users to reduce computations by coarsening the source strength layer using a “block size” option (Landau et al. 2021). In preliminary trials, we evaluated processing time and sensitivity of spatial results by varying block sizes and moving windows. Output from model runs using various block sizes were all highly correlated. For all model runs presented here, we chose to use a block size that is 10% of the size of the radius of the moving window. This choice reduced processing time with minimal conspicuous spatial artifacts associated with larger blocking sizes (Supplement 2).

Moving window sizes

We chose to vary the size of the radius of circular moving windows to identify current flow at different spatial scales. Using each of the three resistance surfaces, we ran Omniscape using one of four different moving window sizes with radii of 30-km, 150-km, 300-km, or 700-km (Table 1). The smallest moving window was intended to represent short-range dispersals or connectivity within relatively small areas. The largest moving window was intended to represent the size of broad-scale conservation planning aimed at maintaining connectivity across large regions over potentially many generations of migrating or dispersing organisms. The two medium-sized moving windows were intended to represent intermediate-range (150-km) and long-range (300-km) dispersing individuals or propagules, which have been used in other national connectivity modeling efforts (Belote et al. 2016) corresponding to large-bodied terrestrial vertebrates (Bowman et al. 2002).

Mapping agreement among scenario outputs

After completing the 12 Omniscape model runs (i.e., representing alternative scenarios using three resistance surfaces $\times$ four moving window sizes), we classified values of normalized current flow into percentiles using the *ntile* function in the R package *dplyr* (Wickham et al. 2018) so that each map consisted of integer values ranging from 1 to 100. We then created composite normalized current flow maps by summing all 12 maps together. We also summed the four maps produced from output of different window sizes within each of the three resistance treatments.

We assessed areas of agreement between model runs using different moving window sizes to identify lands important for both local and regional connectivity, local but not regional connectivity, and regional but not local connectivity, etc. Specifically, we classified each of the 12 maps of normalized current flow

into terciles (three classes with equal number of pixels) to create pairwise combinations of connectivity values from output among each moving window size within the three resistance surfaces. For all bivariate maps combining output from the pairwise combinations of output using different moving windows, we calculated the total area (represented as % of North America) within each of the nine bivariate classes. We also calculated the mean and range of area within these bivariate classes among all 18 pairwise combinations (six bivariate maps $\times$ three resistance surfaces) to summarize agreement among outputs using different moving window sizes.

Results

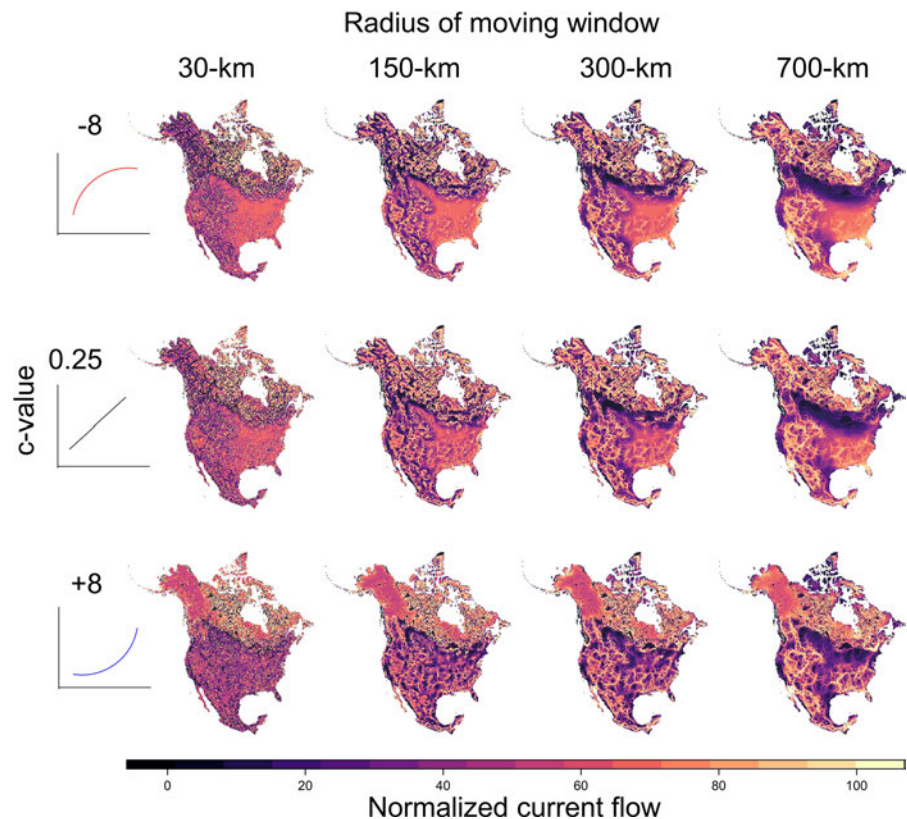
Spatial patterns of normalized current flow varied with moving window size and maps of landscape resistance (Fig. 2). In general, spatial patterns of high normalized current flow from smaller moving window sizes were more mottled than those produced with larger sizes (Fig. 2 and 3). Larger moving windows resulted in more concentrated current flows, especially in the Rocky Mountains, boreal forests, and broader Appalachian region. Omnidirectional connectivity models run with “human-sensitive” landscape resistance ($c = -8$) and linearly transformed resistance ($c = 0.25$) resulted in concentrated current flows in northern latitudes of Alaska and Canada, where models run with “human-tolerant” landscape resistance ($c = 8$) resulted in large areas of moderate current flow in these lands.

The composite maps of normalized current flows highlight the patterns of agreement among all models (Fig. 4). The boreal forests and arctic tundra of Canada and Alaska, the Coast Range of British Columbia in Canada, the Rocky Mountains from Canada to Mexico, the Great Basin in the western US, the Sierra Madre to the Yucatan Peninsula in Mexico, and other areas in the eastern US

Table 1 Radius and total area of moving windows used to map omnidirectional connectivity in North America

Radius (km)	Area (km ²)	Justification
30	2,827	Reasonable short dispersal given 1-km resolution
150	70,686	Roughly midpoint between short- and long-distance dispersers
300	282,743	Distance of long-distance dispersers
700	1,539,379	Similar in size to Yellowstone to Yukon for regional conservation connectivity planning

Fig. 2 Maps of normalized current flow from omnidirectional connectivity models using three different resistance surfaces (varying the c value from Eq. 1) and using four different radii of moving windows. Outputs produced where c -values equaled -8 represent conditions for human-sensitive species, while outputs produced with c -value of $+8$ represent conditions of human-tolerant species



all possess conspicuous concentrations of current flow in the composite maps. The lowest normalized current flow in the composite map occurs in areas where relatively high development is adjacent to relatively natural lands (e.g., at the interface of the Great Plains and Rocky Mountains of Canada), not in the lands with the absolute highest resistance.

While spatial patterns varied among outputs produced with different moving window sizes, on average 64% of pixels were classified into the same tercile of normalized current flow across all pairwise combinations of outputs (Table 2). Areas where outputs from smaller moving windows produced high normalized current flow but larger window runs produced low current flow only made up 1.76% (ranging from 0.13 to 5.3%) of the area across all pairwise comparisons. These areas shown in orange in Fig. 5 and Supplement 3 represent places important for local connectivity, even though they may be considered of low importance for regional connectivity planning. These areas are most common in the lands dominated by agriculture in the Midwest and central Canada.

Discussion

Our results highlight important areas for multi-scale, species-agnostic connectivity planning throughout North America while demonstrating the consequences of several key decisions when implementing omnidirectional connectivity models. Both the moving window size and alternative maps of resistance influenced spatial patterns of high normalized current flow. Varying these two factors may represent alternative methods for mapping important connectivity areas based on dispersal distances of species, the extent of connectivity planning, and the sensitivity of species' movements to human-modified lands. Our composite maps highlight areas where all models resulted in high current flow, but differences among models may provide alternative hypotheses on how movement of organisms varies with human impacts to landscapes.

Outputs from models based on the smallest moving window were characterized by a mottled pattern of high current flow without clear swaths occurring throughout North America. Concentrations of

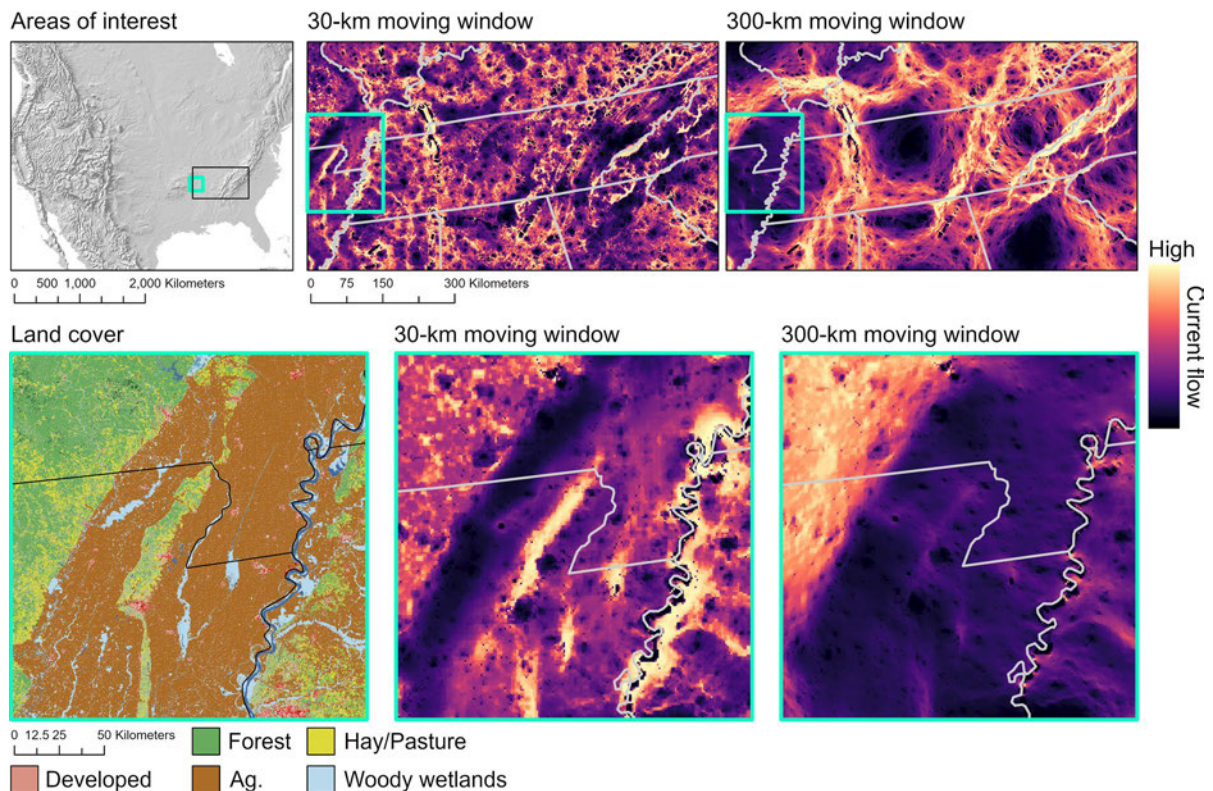


Fig. 3 Zoomed-in maps around the US state of Tennessee and northeastern Arkansas showing normalized current flow based on 30-km and 300-km radii moving windows with a $c=0.25$ transformation. The output from the smaller moving window results in mottled patterns of current flow where smaller patches of relatively natural areas are characterized by high current flow. The larger moving window results in swaths of high current flow connecting larger regions of relatively natu-

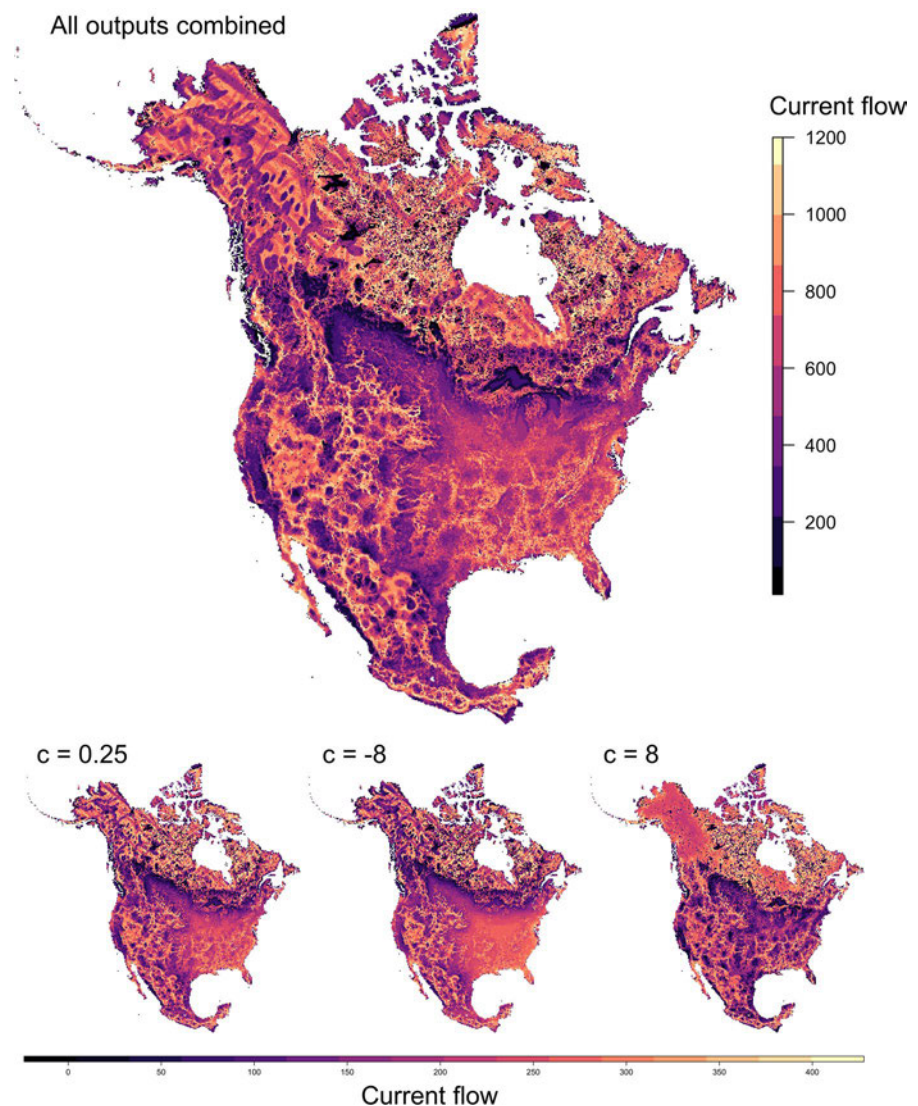
ral lands (e.g., northern Mississippi through the Land Between the Lakes of western Kentucky, the Cumberland Plateau, and the Blue Ridge including Great Smoky Mountains National Park). In northeastern Arkansas small patches of forest and woody wetlands were identified as important for connectivity based on the 30-km moving window but not the 300-km moving window

normalized current flow from the output conducted using the smallest moving window extent could highlight important areas of relatively natural conditions that may support local connectivity. These concentrations of current flow can occur in natural lands embedded within highly developed areas (Fig. 3) and seem to be identified as high normalized current flow when they represent the relatively most natural (i.e., least human modified) lands within a small moving window. Fahrig (2019) suggested that prioritizing large patches of connected habitat over small fragments can undermine local efforts for conserving biodiversity. Conducting a continental assessment of connectivity priorities could easily lead to prioritizing large regions of unfragmented natural areas over small patches of natural lands. We attempted to

overcome this concern by conducting our continental assessment of connectivity using small moving window sizes across the continent and displaying our results as separate maps, as a multi-model composite, and in pairwise bivariate maps. The mottled current flow results from the small moving window may allow local conservation planners to map small fragments of natural areas onto continental connectivity priorities (e.g., Fig. 3).

While proportionally little area was identified as the highest tercile from models produced using smaller moving windows and the lowest tercile from larger moving windows, these lands shown as orange areas in bivariate maps of Fig. 5 constitute areas important for local connectivity that would be “overlooked” from broad-scale models (cf., Koen

Fig. 4 Composite normalized current flow maps that combine all 12 outputs (large map, top) and composite maps combining the four-moving window-size outputs within three resistance factors (bottom maps)



et al. 2019). Even small proportional area represents large total area of land. Consider that one percent of our study area of North America constitutes 213,600 km² which is about the size of the state of Kansas. The bivariate map with the largest proportional area of low broad-scale and high local-scale connectivity priorities was equal to 5.3% of North America, an area nearly three times the size of Montana. Thus, the combined area of small fragments constitutes significant amount of land area.

Researchers and practitioners conducting broad-scale analyses should be aware of the potential to miss locally important areas. This pattern is highlighted in Fig. 3 and shows differences between output from

two moving window sizes in lands identified by high normalized current flow. The smaller moving window (30-km radius) identified patches of forest and woody wetlands in an agriculturally dominated landscape as high connectivity importance, while the larger moving window (300-km) model output identified only the relatively contiguous forests as large swaths of connectivity importance, missing all potential conservation priorities within the agricultural landscape.

In general, as we increased the size of the moving window, clear concentrations of current flow were revealed throughout the broader Rocky Mountain region of Mexico, the US, and Canada. Mountainous areas and some riparian zones of the southeastern US

Table 2 Mean (range) percent area of North America within bivariate classes where terciles of normalized current flow were combined using all pairwise combinations of smaller- and larger-size moving window model runs. The table is arranged the same as the legends in Fig. 5 and shows the mean and range of all bivariate maps. About 64% percent of the total area was classified as the same tercile irrespective of moving window size. However, over 3.5% of North America was classified as the lower third current flow using smaller

moving windows but high tercile of current flow using larger moving windows (blue color in Fig. 5). These are places that are important regionally, but not locally. Alternatively, on average 1.76% was the opposite situation (orange color in Fig. 5; high current flow using smaller moving windows and low current flow using larger sizes). These are places that are important for local connectivity but not identified as important in the regional models. For context, 1% area of our North American study area is 213,600 km²

		Tercile of normalized current flow from smaller moving window		
		Low	Mid	High
Tercile of normalized current flow from larger moving window	High	3.57 (0.66—7.55)	7.26 (4.74—9.81)	22.5 (16—27.9)
	Mid	6.39 (3.92—8.76)	17.9 (12.9—24.2)	9.06 (5.17—12.8)
	Low	23.4 (17—28.8)	8.19 (4.35—11.6)	1.76 (0.13—5.3)

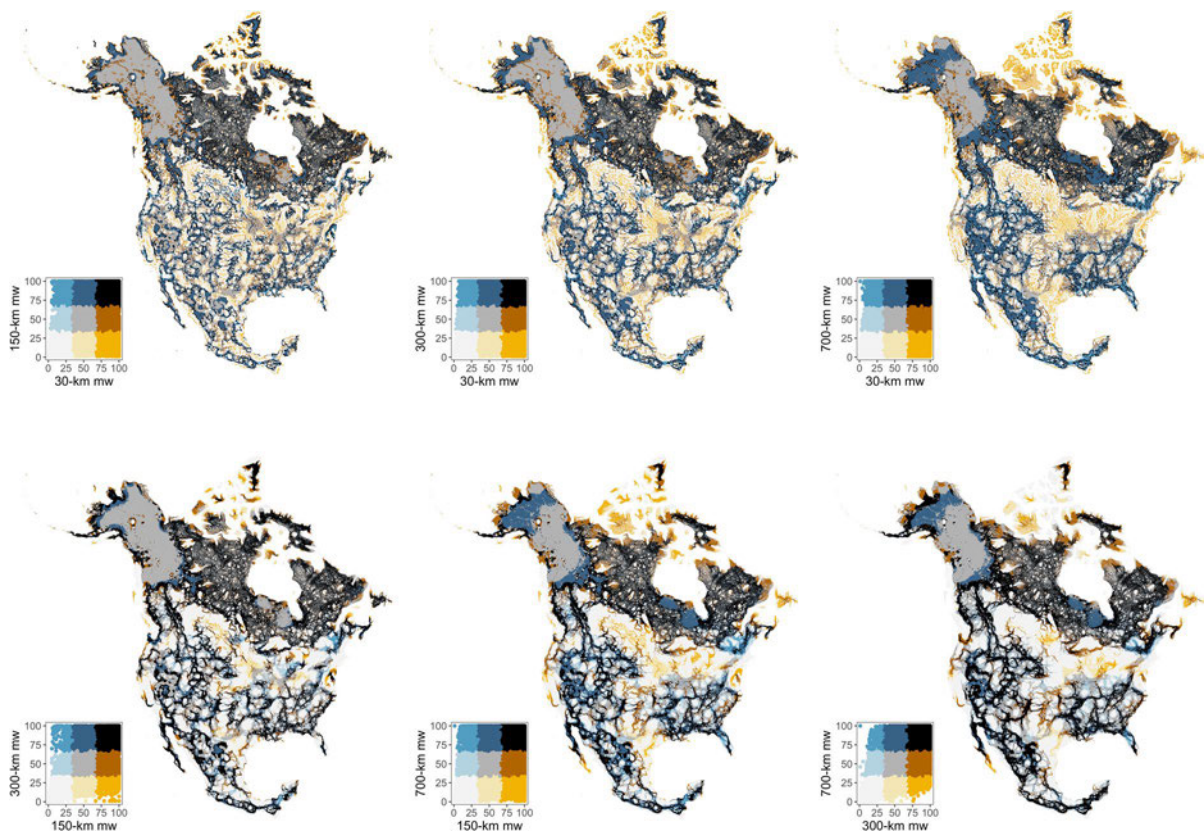


Fig. 5 Bivariate maps showing terciles of normalized current flow for omnidirectional connectivity models using different moving window sizes where resistance was produced from

Eq. 1 with $c=8$ ('human-tolerant' species alternative). Bivariate maps for other resistance surfaces are shown in Supplement 3

were also identified by high concentrations of normalized current flow. Our maps based on outputs using the large moving windows identified broad swaths of current flow that could inform connectivity planning like the vision identified by the Yellowstone-to-Yukon (Y2Y) Initiative. Other programs like Y2Y could be developed throughout the Rocky Mountains of Canada, the US, and Mexico, as well as regional linkages of natural lands in the southeastern US. Many of these regional linkages align with the findings of Barnett and Belote (2020) and Brennan et al. (2022) who modeled connectivity between protected areas across North America using a linear-transformed resistance surface based on human modification. At large spatial extents, connectivity models run with cores (protected areas) and omnidirectional coreless models described here could converge and reveal similar areas to be important for connectivity. Connectivity models conducted at large spatial extents typically rely on data quantifying human modification (Theobald et al. 2020) or human footprint (Venter et al. 2016) as the basis of mapping landscape resistance. The shared assumption among models conducted at large extents that human modification affects landscape resistance likely explains the similarities in patterns.

Interestingly, results varied the most conspicuously among alternative resistance surfaces within northern latitudes on lands with generally low human modification (Alaska and Canada's tundra and boreal forests). In these areas, models run with resistance transformed for "human-sensitive" ($c = -8$) and the linear alternative ($c = 0.25$) revealed maps with concentrations of current flow, while resistance scaled for "human-tolerant" species ($c = 8$) revealed relatively homogenous current flow. These results reflect how gradients in resistance vary at low levels of human modification with the different methods of transformation. In wildlands where little human modification creates variation in landscape resistance, alternative and redundant pathways result in low normalized current flow (i.e., no concentrations of current flow). While Bowman et al. (2020) found that current flow outputs from Circuitscape produced with different ranges of resistance values varied little as long as the rank order of resistance values was maintained, we found that – at least in some areas – patterns of current flow varied among our resistance "treatments".

Patterns of normalized current flow across North America may be used to develop connectivity targets

and objectives. For instance, McRae et al. (2016), Schloss et al. (2021), and Cameron et al. (2022) classified omnidirectional model output using thresholds of normalized current flow to identify areas of impeded, diffuse, intensified, and channelized flow. This classification scheme acknowledges that low normalized current flow can occur in areas of either high resistance or very low resistance and can help tailor connectivity objectives to connectivity outputs (sensu Belote et al. 2020). For instance, wildlands with diffuse flow represent lands where actions that prevent fragmentation of large patches would be implemented, while lands with impeded flow may require restoration of natural habitat to restore connectivity. We used classification thresholds proposed by McRae et al. (2016) and recently adopted by Schloss et al. (2022) and Cameron et al. (2022) with our output with mixed results which depended on the moving window size and resistance used (Supplement 4). In general, the classification thresholds used in earlier efforts seemed most reasonable for our output based on models run with the resistance surfaces developed using the "human-tolerant" (i.e., $c = 8$) transformation. Using these outputs, impeded flows occurred in agriculturally dominated lands, diffuse flows occurred in large areas of minimal human modification, and concentrated flows occurred in lands with a mix of wild and agricultural lands. For most of our output, we recommend interpreting the highest values to be of highest connectivity importance. Except for our output conducted using the human-tolerant resistance ($c = 8$), it is difficult to distinguish between impeded and diffuse flow based on proposed classification thresholds (Supplement 4). We recommend evaluating normalized current flow alongside maps of resistance to aid interpretation of output.

Our models represent alternative hypotheses for how different organisms move through lands of various degrees of human modification, and our outputs may represent different predictions of movement. After comparing connectivity models with movement data of elk (*Cervus canadensis*) and desert bighorn sheep (*Ovis canadensis nelsoni*), Keeley et al. (2016) concluded that a negative exponential function of habitat suitability results in connectivity models most accurately reflecting movement of these species. Results from Carroll et al. (2020) also suggest that wolverine (*Gulo gulo*) movement was best predicted from a resistance surface created from negative

exponential transformation of habitat suitability. These studies suggest that some species may be capable of moving through suboptimal habitat but avoid very poor habitat quality. For their species-specific connectivity models, Keeley et al. (2016) and Carroll et al. (2020) include developed lands and human modification in their creation of habitat suitability and resistance surfaces. Our models are species-agnostic and based on assumptions that organisms will avoid lands with high human modification or will experience higher risks of mortality in lands dominated by human modification. However, our models also may be unrealistic in some areas with very low productivity (i.e., deserts). In these areas, species may experience high cost of movement even when human modification is low but where extreme temperature, low water availability, and low vegetation cover may limit successful dispersal (*sensu* Dobrowski and Parks 2016). Additional research into the relationship between species movement, human modification, and climate could reveal important insights that may inform future work. Our output could be used for comparing species-specific connectivity models or observations of movement to determine which of our model assumptions best align with different species-specific model predictions or observed movements.

Our work here may also be useful to future users of Omniscape. Our preliminary tests helped us decide on a blocking size of 10% that of the moving window and clearly demonstrated that blocking size had little effect on mapped outputs, at least for the scenarios we evaluated. Using AWS, our scenario runs in Omniscape took between ~6.5 to over 56 h with larger moving window scenarios taking longer to run. The largest moving window scenarios (700-km) took – on average – nearly 6 times longer than the smallest moving window scenarios (30-km). To facilitate future work, we share all INI files for our scenarios, including the processing time for all model runs, as supplemental files, and shared all output publicly (see Data Availability).

Our results highlight challenges with interpreting maps of connectivity importance based on circuit theory. Areas of low normalized current flow may be difficult to distinguish from areas of impeded flow. If output maps are used to prioritize conservation actions, areas with relatively low to moderate normalized current flow may be regarded as low importance for connectivity. While the lowest values may

indeed represent areas unimportant for connectivity, other areas with moderately low values may represent some of the most unfragmented lands in a study area. Connectivity objectives in large contiguous areas of low resistance (e.g., diffuse flow) will likely be very different from those of the highest values (concentrated flows classified as “channelized”). Care should be taken in interpreting Omniscape output, especially when considering priorities and conservation actions needed to sustain connectivity (Belote et al. 2020). Here, we found that interpreting the highest normalized current flow (which could be classified as “channelized”) to be the least ambiguous values produced from the models. Therefore, we focused attention on those areas as important for connectivity through our composite and bivariate maps.

While researchers and practitioners should continue to scrutinize the costs and benefits of implementing actions to maintain or restore connectivity (Simberloff et al. 1992), connectivity modeling is increasingly becoming a key component of conservation planning at multiple spatial scales. Sometimes connectivity models are based on observations of individual organisms moving through a landscape or habitat suitability of potential movements. Other times, connectivity modeling is based on identifying landscape features that may provide opportunities for multiple species to move between conservation reserves or habitat patches. These different approaches are sometimes classified as functional versus structural connectivity models (Rudnick et al. 2012). Our work sought to identify lands that may allow organisms to move across landscapes of varying sizes or with varying dispersal distances. Ultimately, these models are based on predictions of how organisms use, avoid, or experience risk depending on the degree of human modification. These predictions vary with assumptions that we hope will be tested and compared with species-specific models and observations.

Author contributions RTB and KB conceived of the study. RTB, KB, KZ, and AB developed and co-wrote the paper. JG performed model runs, analyzed preliminary data, and edited the final drafts.

Funding The Wilderness Society funded the work.

Data availability The datasets generated during and/or analyzed during the current study are available at <https://doi.org/10.5281/zenodo.7058199>. While we focus our assessment on

normalized current flow here, we share current flow and potential flow from our model runs to facilitate additional research and analysis.

Declarations

Competing interests The authors declare no competing interests.

Conflict of interests The authors have no relevant financial or non-financial interests to disclose.”

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Barnett K, Belote RT (2021) Modeling an aspirational connected network of protected areas across North America. *Ecol Appl* 31:e02387. <https://doi.org/10.1002/eap.2387>
- Beier P (2012) Conceptualizing and designing corridors for climate change. *Ecol Restor* 30:312–319. <https://doi.org/10.3368/er.30.4.312>
- Belote RT, Wilson MB (2020) Delineating greater ecosystems around protected areas to guide conservation. *Conserv Sci Pract* 2:196. <https://doi.org/10.1111/csp2.196>
- Belote RT, Dietz MS, McRae BH et al (2016) Identifying corridors among large protected areas in the United States. *PLoS ONE* 11:e0154223. <https://doi.org/10.1371/journal.pone.0154223>
- Belote RT, Beier P, Creech T et al (2020) A framework for developing connectivity targets and indicators to guide global conservation efforts. *Bioscience* 70:122–125. <https://doi.org/10.1093/biosci/biz148>
- Bowman J, Adey E, Angoh SYJ et al (2020) Effects of cost surface uncertainty on current density estimates from circuit theory. *PeerJ* 8:1–18. <https://doi.org/10.7717/peerj.9617>
- Bowman J, Jaeger JAG, Fahrig L (2002) Dispersal distance of mammals is proportional to home range size. *Ecology* 83:2049–2055
- Brennan A, Beytell P, Aschenborn O et al (2020) Characterizing multispecies connectivity across a transfrontier conservation landscape. *J Appl Ecol* 57:1700–1710. <https://doi.org/10.1111/1365-2664.13716>
- Brennan A, Naidoo R, Greenstreet L et al (2022) Functional connectivity of the world's protected areas. *Science* 376:1101–1104. <https://doi.org/10.1126/science.abc18974>
- Cameron DR, Schloss CA, Theobald DM, Morrison SA (2022) A framework to select strategies for conserving and restoring habitat connectivity in complex landscapes. *Conserv Sci Pract* 4:1–16. <https://doi.org/10.1111/csp2.12698>
- Carroll C, Mcrae BH, Brookes A (2011) Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of gray wolf populations in Western North America. *Conserv Biol* 26:78–87. <https://doi.org/10.1111/j.1523-1739.2011.01753.x>
- Carroll C, Parks SA, Dobrowski SZ, Roberts DR (2018) Climatic, topographic, and anthropogenic factors determine connectivity between current and future climate analogs in North America. *Glob Change Biol* 24:5318–5331. <https://doi.org/10.1111/gcb.14373>
- Carroll KA, Hansen AJ, Inman RM et al (2020) Testing landscape resistance layers and modeling connectivity for Wolverines in the western United States. *Glob Ecol Conserv* 23:e01125. <https://doi.org/10.1016/j.gecco.2020.e01125>
- Compton BW, McGarigal K, Cushman SA, Gamble LR (2007) A resistant-kernel model of connectivity for amphibians that breed in vernal pools. *Conserv Biol* 21:788–799. <https://doi.org/10.1111/j.1523-1739.2007.00674.x>
- Correa Ayram CA, Mendoza ME, Etter A, Salicrup DRP (2016) Habitat connectivity in biodiversity conservation: a review of recent studies and applications. *Prog Phys Geogr* 40:7–37. <https://doi.org/10.1177/0309133315598713>
- Cushman SA, Landguth EL (2012) Multi-taxa population connectivity in the Northern Rocky Mountains. *Ecol Model* 231:101–112. <https://doi.org/10.1016/j.ecolmodel.2012.02.011>
- Dickson BG, Albano CM, Anantharaman R et al (2019) Circuit-theory applications to connectivity science and conservation. *Conserv Biol* 33:239–249. <https://doi.org/10.1111/cobi.13230>
- Ellington EH, Gehrt SD (2019) Behavioral responses by an apex predator to urbanization. *Behav Ecol* 30:821–829. <https://doi.org/10.1093/beheco/arz019>
- Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction. *J Wildl Manag* 61:603–610
- Fahrig L (2019) Habitat fragmentation: a long and tangled tale. *Glob Ecol Biogeogr* 28:33–41. <https://doi.org/10.1111/geb.12839>
- Haddad NM, Brudvig LA, Clobert J et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci Adv* 1:e1500052–e1500052. <https://doi.org/10.1126/sciadv.1500052>
- Hall KR, Anantharaman R, Landau VA et al (2021) Circuitscape in julia: empowering dynamic approaches to connectivity assessment. *Land* 10:301. <https://doi.org/10.3390/land10030301>
- Hannah L, Flint L, Syphard AD et al (2014) Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. *Trends Ecol Evol* 29:390–397. <https://doi.org/10.1016/j.tree.2014.04.006>

- Hilty J Jr, WL, Merenlender A, (2006) Corridor ecology: the science and practice of linking landscapes for biodiversity conservation. Island Press, DC
- Keeley ATH, Beier P, Gagnon JW (2016) Estimating landscape resistance from habitat suitability: effects of data source and nonlinearities. *Landscape Ecol* 31:2151–2162. <https://doi.org/10.1007/s10980-016-0387-5>
- Kennedy CM, Oakleaf JR, Theobald DM et al (2019) Managing the middle: a shift in conservation priorities based on the global human modification gradient. *Glob Change Biol*. <https://doi.org/10.1111/gcb.14549>
- Koen EL, Bowman J, Sadowski C, Walpole AA (2014) Landscape connectivity for wildlife: development and validation of multispecies linkage maps. *Methods Ecol Evol* 5:626–633. <https://doi.org/10.1111/2041-210X.12197>
- Koen EL, Ellington EH, Bowman J (2019) Mapping landscape connectivity for large spatial extents. *Landsc Ecol* 34:2421–2433. <https://doi.org/10.1007/s10980-019-00897-6>
- Krosby M, Breckheimer I, John Pierce D et al (2015) Focal species and landscape “naturalness” corridor models offer complementary approaches for connectivity conservation planning. *Landscape Ecol* 30:2121–2132. <https://doi.org/10.1007/s10980-015-0235-z>
- Landau V, Shah V, Anantharaman R, Hall K (2021) Omniscape.jl: Software to compute omnidirectional landscape connectivity. *J Open Source Softw* 6(57):2829
- Lawler JJ, Shafer SL, White D et al (2009) Projected climate-induced faunal change in the Western Hemisphere. *Ecology* 90:588–597. <https://doi.org/10.1890/08-0823.1>
- Lawler JJ, Ruesch AS, Olden JD, Mcrae BH (2013) Projected climate-driven faunal movement routes. *Ecol Lett* 16:1014–1022. <https://doi.org/10.1111/ele.12132>
- Leonard PB, Baldwin RF, Hanks RD (2017) Landscape-scale conservation design across biotic realms: sequential integration of aquatic and terrestrial landscapes. *Sci Rep* 7:14556. <https://doi.org/10.1038/s41598-017-15304-w>
- Littlefield CE, Mcrae BH, Michalak JL et al (2017) Connecting today’s climates to future climate analogs to facilitate movement of species under climate change. *Conserv Biol* 31:1397–1408. <https://doi.org/10.1111/cobi.12938>
- McClure ML, Hansen AJ, Inman RM (2016) Connecting models to movements: testing connectivity model predictions against empirical migration and dispersal data. *Landscape Ecol* 31:1419–1432. <https://doi.org/10.1007/s10980-016-0347-0>
- McGuire JL, Lawler JJ, McRae BH et al (2016) Achieving climate connectivity in a fragmented landscape. *Proc Natl Acad Sci USA* 113:7195–7200. <https://doi.org/10.1073/pnas.1602817113>
- McRae BH, Dickson BG, Keitt TH, Shah VB (2007) Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89:2712–2724
- McRae B, Popper K, Jones A et al (2016) Conserving Nature’s Stage: Mapping omnidirectional connectivity for resilient terrestrial landscapes in the Pacific Northwest. The Nature Conservancy, Portland
- Parks SA, Carroll C, Dobrowski SZ, Allred BW (2020) Human land uses reduce climate connectivity across North America. *Glob Change Biol* 26:2944–2955. <https://doi.org/10.1111/gcb.15009>
- Peck CP, VanManen FT, Costello CM et al (2017) Potential paths for male-mediated gene flow to and from an isolated grizzly bear population. *Ecosphere* 8:e01969. <https://doi.org/10.1002/ecs2.1969>
- Pelletier D, Lapointe MÉ, Wulder MA et al (2017) Forest connectivity regions of Canada using circuit theory and image analysis. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0169428>
- Phillips P, Clark MM, Baral S et al (2021) Comparison of methods for estimating omnidirectional landscape connectivity. *Landsc Ecol* 36:1647–1661. <https://doi.org/10.1007/s10980-021-01254-2>
- Riva F, Fahrig L (2022) The disproportionately high value of small patches for biodiversity conservation. *Conserv Lett* 15(3):e12881
- Rudnick DA, Ryan SJ, Beier P et al (2012) The Role of Landscape Connectivity in Planning and Implementing Conservation and Restoration Priorities. Ecological Society of America, DC
- Schloss CA, Cameron DR, McRae BH et al (2022) “No-regrets” pathways for navigating climate change: planning for connectivity with land use, topography, and climate. *Ecol Appl* 32:e02468. <https://doi.org/10.1002/eap.2468>
- Simberloff D, Farr JA, Cox J, Mehlman DW (1992) Movement corridors: conservation bargains or poor investments? *Conserv Biol* 6:493–504
- Theobald DM, Kennedy C, Chen B et al (2020) Earth transformed: detailed mapping of global human modification from 1990 to 2017. *Earth System Science Data* 12:1953–1972. <https://doi.org/10.5194/essd-12-1953-2020>
- Tucker MA, Böhning-Gaese K, Fagan WF et al (2018) Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* 469:466–469
- Venter O, Sanderson EW, Magrach A et al (2016) Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat Commun* 7:1–11. <https://doi.org/10.1038/ncomms12558>
- Ward M, Saura S, Williams B et al (2020) Just ten percent of the global terrestrial protected area network is structurally connected via intact land. *Nat Commun* 11:1–10. <https://doi.org/10.1038/s41467-020-18457-x>
- Wickham H, Francois R, Henry L, Muller K (2018) dplyr: A Grammar of Data Manipulation. <https://dplyr.tidyverse.org>, <https://github.com/tidyverse/dplyr>
- Wilcove DS, Rothstein D, Dubow J et al (1998) Quantifying threats to imperiled species in the United States. *Bioscience* 48:607–615. <https://doi.org/10.2307/1313420>
- Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. *Landscape Ecol* 27(6):777–797
- Zeller KA, Jennings MK, Vickers TW et al (2018) Are all data types and connectivity models created equal? validating common connectivity approaches with dispersal data. *Divers Distrib* 24:868–879. <https://doi.org/10.1111/ddi.12742>

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.