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Modeling an aspirational connected network of protected areas across North America

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Abstract. Connecting protected areas remains an important global conservation strategy in the face of ongoing and future threats to biodiversity. Amid our growing understanding of how species' distributions will respond to climate change, conservation scientists need to plan for connectivity conservation across entire continents. We modeled multiscale connectivity priorities based on the least human-modified lands between large protected areas of North America using least-cost and circuit theory approaches. We first identified priority corridors between large protected areas, then characterized the network's structure to unveil priority linkages most important for maintaining network- and regional-level connectivity. Agreement between least-cost corridors and current flow varied throughout North America, reflecting permeable landscape conditions and "pinch points" where potential ecological flows may concentrate between protected areas. Priority network-level linkages derived from each approach were similar throughout the continental network (e.g., Rocky Mountains and Canadian boreal), but critical linkages that bridged regional protected-area networks varied. We emphasize the importance of planning for connectivity at continental scales and demonstrate the utility of multiple methods when mapping connectivity priorities across large spatial extents with wide gradients in landscape conditions.

Key words: centrality; corridors; graph theory; minimum spanning tree; network analysis.

Introduction

Protected areas safeguard intact habitats that sustain ecological functions (Gaston et al. 2008). Climate change, habitat loss, and fragmentation of landscapes continue to affect global patterns of biodiversity adversely (Fahrig 2003, Parmesan and Yohe 2003, Di Marco et al. 2018). In response, the Convention on Biological Diversity (CBD) recommends creating well-connected, ecologically representative networks of protected areas to mitigate threats to biodiversity (CBD 2014). Because well-connected networks may prevent ecosystems and populations from becoming isolated, maintaining or restoring connectivity among protected areas remains a global conservation priority (Dinerstein et al. 2019).

Socio-political boundaries can adversely affect biodiversity conservation planning because of scale mismatches between ecological processes and governance (Dallimer and Strange 2015). There may be unique opportunities for successful transboundary conservation among the United States, Canada, and Mexico given their relatively high degree of collaboration and institutional capacities (Mason et al. 2020). Some highly mobile and migratory species in North America occupy home ranges or seasonal habitats that span international borders (e.g., Aubry et al. 2007, Thogmartin et al. 2017). Over longer time frames, expected movements between current and future species distributions (Lawler et al. 2013) and climate analogue locations (Carroll et al. 2018) further emphasize the need to plan for connectivity across North America.

Functional connectivity analyses can identify locations that facilitate movement of individual species or gene flow based on habitat requirements, dispersal, behavioral avoidance, or risk of mortality (Taylor et al. 2006). In contrast, many structural connectivity models are "species-agnostic" and offer conservation planners insight into locations where relatively natural conditions

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could facilitate movement of species (Marrec et al. 2020). Models that use "naturalness" or "landscape integrity" as a proxy for species-based connectivity models can identify similar connectivity networks as models that incorporate species-specific movement patterns and traits (Krosby et al. 2015). Therefore, finding the least human-modified lands linking protected areas is a reasonable "coarse filter" approach (sensu Tingley et al. 2014) for identifying priorities to establish a connected network (Belote et al. 2016, Dickson et al. 2017).

Structural connectivity models often map priorities for linking core areas using algorithms derived from least-cost or circuit theory. Each approach uses the same mathematical structures from graph theory to model relationships between objects (Urban and Keitt 2001). When using least-cost methods, the distance between node pairs (e.g., core habitat or protected areas) in a graph reflects the shortest topological path. In contrast, circuit theory models the "resistance distance" between node pairs in a graph like current flows through resistors of an electrical circuit. Unlike least-cost methods, the resistance distance between a source and destination encapsulates multiple pathways beyond the least-cost path (McRae et al. 2008). From an ecological perspective, a fundamental distinction between the two is their assumptions regarding potential movement (Zeller et al. 2018). Least-cost methods assume organisms have perfect information of landscape resistance to movement, and therefore traverse "optimal" routes to minimize cost-weighted distance between a source and destination. Conversely, circuit theory assumes organisms have zero information of landscape resistance beyond their immediate surroundings, akin to a "random walker" (McRae et al. 2008). Their differences have been evaluated from functional connectivity perspectives (e.g., McRae and Beier 2007, Schwartz et al. 2009), but we lack an understanding of their respective utility—and consequences—for identifying connectivity priorities across large spatial extents with wide gradients in resistance.

Maps of normalized least-cost corridors or current flow offer conservation planners a way to visualize the relative importance of any given location in facilitating potential movement between core habitats, resource patches, or protected areas. This can help inform landscape conservation planning efforts by, for example, prioritizing land management units that fall within modeled corridors for an elevated protection status (Belote et al. 2016, Dickson et al. 2017). However, these approaches lack the ability to prioritize individual linkages within the protected-area network that may be more important for maintaining network- and regional-level connectivity. Centrality metrics derived from graph theory quantify the importance of individual patches or linkages at maintaining network-level connectivity and provide valuable insight into a network's structure (Rayfield et al. 2011). Additional graph theory concepts can be used to identify regional networks of protected areas that are geographically clustered and highly interconnected. These nested connectivity prioritizations can inform conservation planning initiatives by distinguishing which corridors are likely to contribute efficiently to network- and regional-level connectivity among protected areas.

As conservation scientists strive towards increasing the estate and connectivity of protected areas around the globe (Dinerstein et al. 2019, Ward et al. 2020), we contend that safeguarding the least-human modified landscapes is vital for species and ecological functions to persist under increasing threats from anthropogenic change. The need to maintain, restore, or establish connectivity among protected areas is recognized as an important climate adaptation strategy (Heller and Zavaleta 2009). But what might an aspirational, well-connected network of protected areas across North America look like? How can we distinguish which linkages may be most important for facilitating connectivity among protected areas in the network? And how do conservation practitioners begin to implement an aspirational vision of a continental network of protected areas at tractable management scales? Here we offer a multiscale evaluation of potential connectivity priorities for establishing a continental network of protected areas across North America. We perform this evaluation using two of the most common connectivity modeling approaches—least-cost and circuit theory—and shed light on the conservation implications arising from each method.

Methods

We first mapped the least-human modified corridors that link protected areas in the network using least-cost and circuit theory approaches. We represented movement cost by creating a resistance surface using data on human modification (Theobald et al. 2020). Priority corridors modeled using least-cost or circuit theory methods are those in which cost-weighted distances between protected areas are minimized or current flow is maximized, respectively. We then identified each network's minimum spanning tree (MST), or the set of linkages that connect all protected areas while minimizing total network resistance. These linkages form the "backbone" of the continental network (Theobald et al. 2011). Next, we used the betweenness centrality metric to prioritize individual linkages within each MST. These critical linkages are network-level connectivity priorities because the shortest paths among all protected areas are channeled along these linkages. We then identified regional networks of protected areas and mapped priority linkages that are likely to maintain intra- and interregional connectivity among protected areas. Identifying the most important linkages at these regional levels helps to operationalize a continental network of protected areas into more feasible management scales. Lastly, we demonstrate the utility of an ensemble modeling approach to identify priority corridors by combining maps of least-cost corridors and current flow. See Appendix S1 for detailed descriptions regarding the selection of protected areas, resistance surface development, connectivity model parameters, and functions used in the network analysis.

Results

The least-cost corridor approach identified geographies of the western United States as high priority, including Alaska, the Great Basin, and Rocky Mountains (Fig. 1a). Corridors extended across the midwestern United States to link the network with protected areas located in the Great Lakes region and the Ozark and Ouachita Mountains. Many of the least-cost corridors that connected smaller, highly protected areas of the eastern United States and Canada converged along the Appalachian Mountains stretching from northern Alabama and Georgia through Maine and into New Brunswick. Notably, much of northern Canada extending from the Yukon and Northwest Territories to Quebec was identified as high-priority lands for connectivity conservation using least-cost methods. In addition, large patches of permeable lands between protected areas were found along western Mexico's Sierra Madre Occidental Mountains, the central Mexican plateau, and Baja Peninsula.

Maps of corridor priorities based on circuit theory revealed concentrations of current flow between large protected areas. Current flow tended to be more diffuse compared to least-cost corridors, which in general were more concentrated along least-cost paths or in large areas with very low human modification. Geographic areas with relatively high current flow included regions of western North America and along the Appalachian Mountains, like those identified by the least-cost corridors.

There was agreement among the highest centrality linkages derived from each network's MST, including those in the Canadian Rocky Mountains that extend through Wyoming and into southern Utah, in addition to linkages traversing from west to east through Canada (Fig. 1c, d). There was also agreement between linkages with the lowest centrality values, particularly for linkages located along the network's periphery; agreement for linkages with intermediate centrality values was more equivocal. The spatial structure of MSTs varied slightly throughout the protected-area network.

The least-cost method identified 30 unique regional networks of protected areas, and circuit theory identified 32 (Fig. 1e, f). One regional protected-area network found in northern Quebec was comprised of the set of protected areas using either method. Both approaches identified nine transboundary regional protected-area networks. Three linkages were among the set of linkages that bridged one regional network with another using either method.

Our ensemble map of corridor priority revealed that about 20% of North America was classified in the highest quartile of both least-cost corridor and current flow (Fig. 2). A marked divergence in priority corridors between least-cost and circuit theory methods occurs in the boreal forests of Canada extending north into the taiga and tundra regions of the northern latitudes. Broad least-cost corridors but diffuse current flows cover this large area of low human modification (Appendix S2: Fig. S1).

Discussion

Our analysis offers a multiscale evaluation of potential coarse filter priorities for creating a continental network of protected areas using two alternative connectivity modeling approaches. Expanding the scope of analysis to include connectivity among protected areas in a continental network provides an aspirational and rigorous perspective for international conservation planning. Our explicit recognition of the spatial patterns and condition of permeable lands between protected areas and evaluation of multiple connectivity modeling approaches distinguishes this from the growing body of literature addressing global protected-area connectivity (Santini et al. 2016, Saura et al. 2018, 2019, Ward et al. 2020).

The spatial patterns of corridor priorities varied throughout the continent, reflecting the geographic distribution of large protected areas, the most permeable lands between them, and pinch-points across the continent where ecological flows between protected areas may concentrate (Fig. 1a, b). Lands stretching from Alaska and the Yukon to northern Quebec and Newfoundland were identified as high priorities based on least-cost corridors, but low priorities based on current flow. These regions encompass large patches of low human modification, resulting in broad least-cost corridors but no clearly defined concentrations of current flow. In contrast, for protected areas embedded within a broader region of mixed land use where relatively developed areas occur intermixed with wildlands, least-cost corridors failed to identify alternative potential ecological flows that may exist within the landscape matrix, effectively undervaluing equivalent parallel linkages between protected areas.

Our results demonstrate the implications of focusing on a single connectivity method when regional patterns of landscape resistance vary within a large spatial extent. Circuit theory de-emphasized the intact forest landscapes in the northern latitudes (Fig. 1b), despite these ecosystems comprising highly permeable lands of low human pressure that are crucial for facilitating species' movements (Tucker et al. 2018). However, in other semideveloped regions (e.g., Cumberland Plateau in the eastern United States) circuit theory methods mapped multiple redundant priorities, which—if conserved—

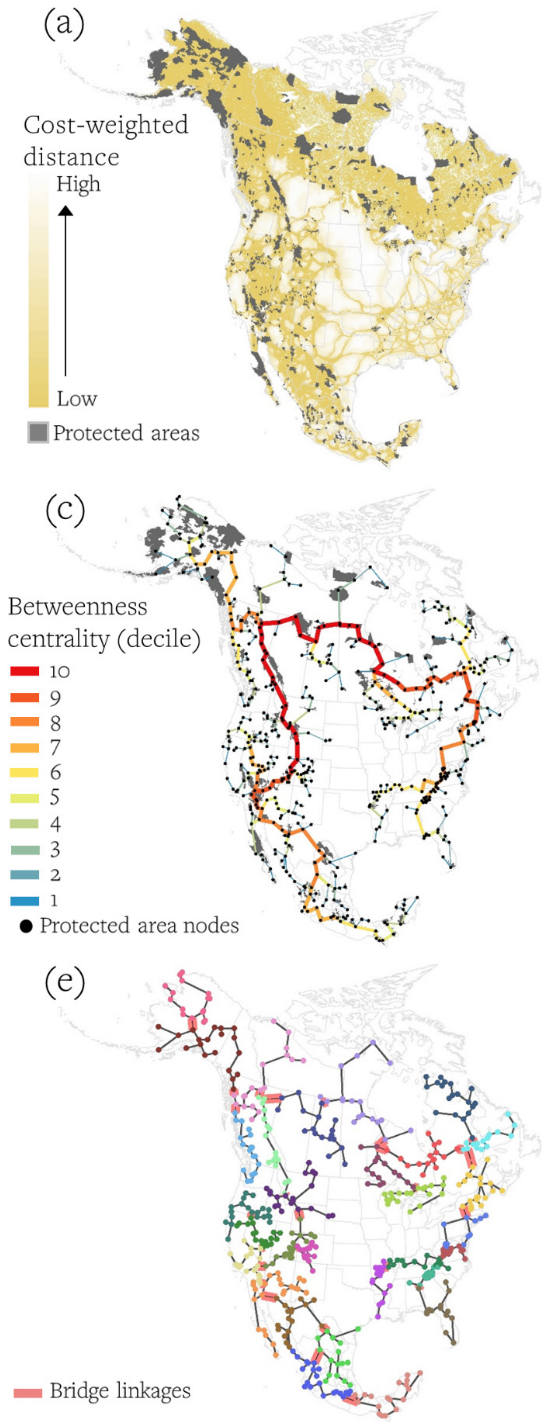

FIG. 1. Maps of corridor priorities based on (a) normalized least-cost corridors and (b) cumulative current flow, derived from least-cost and circuit theory methods, respectively. Minimum spanning tree representations of network connectivity among large protected areas of North America using (c) least-cost and (d) circuit theory methods. Minimum spanning trees represent the set of linkages that fully connect a network and are efficient representations of a network's "backbone." Betweenness centrality, a network-level metric of importance, was calculated for each linkage in the minimum spanning trees, with each linkage subsequently classified into centrality deciles. Maps of regional protected-area networks among the MSTs derived from (e) least-cost and (f) circuit theory methods. Regional protected-area networks are those that are closely interconnected but only loosely connected to other regional networks. The red linkages are those that serve to bridge one regional network with another and may hold significant conservation value. The colored points representing a protected-area polygon are not comparable across panels and only serve to distinguish one regional network from another.

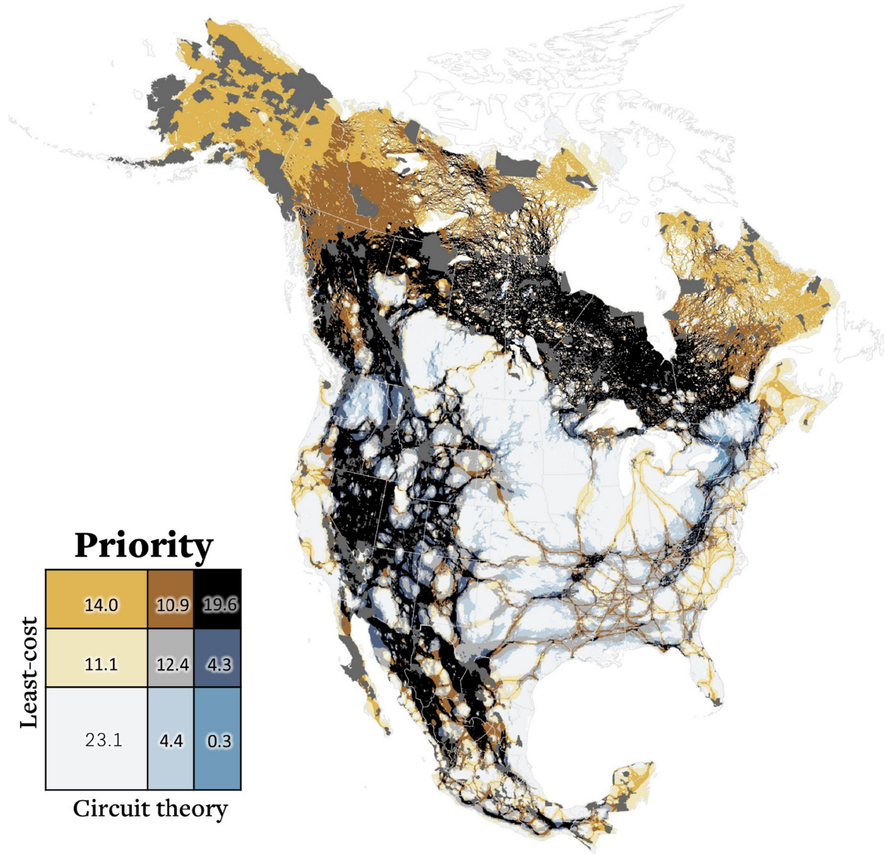

FIG. 2. An ensemble map of bivariate agreement between priority corridors derived from least-cost and circuit theory methods. Each data set was binned into three classes representing low, moderate, and high priority using the median and 75th percentiles of their respective distribution as thresholds. Values embedded in bivariate legend represent the proportion of total area within each bin (e.g., 19.6% of North America was classified into the upper quartile of both least-cost and circuit theory priorities).

would increase the likelihood that protected areas remain connected. The potential for alternative priority corridors revealed by circuit theory methods can be concealed by narrow least-cost corridors (McRae et al. 2008). Within this context of establishing a well-connected continental network of protected areas, circuit theory models of current flow may be most complementary to least-cost approaches in highly modified landscapes. These results affirm recommendations of Belote et al. (2020) that regional context and patterns of landscape condition should inform connectivity conservation planning and highlight the complementary aspects of using both widely used connectivity approaches.

Both least-cost and circuit theory–based MSTs unveiled priority linkages (i.e., high betweenness centrality) between large protected areas of North America located throughout the Rocky Mountains of the United States and Canada in addition to the taiga and boreal shields of Canada. This is to be expected, given these regions' vast swaths of lands with low human modification and their relatively central geographic position within the protected-area network. We observed subtle, but important, differences in the overall spatial structure between the network's MST, with instances of a "hub and spoke" pattern when linkages in the protected-area network were weighted by resistance distance versus cost-weighted distance (Fig. 1c, d). If we assume that an MST represents priority linkages across a planners network, these findings suggest our basic understanding of fundamental network properties can be dependent upon the choice of connectivity algorithm. When circuit theory identifies redundant pathways between core areas, these linkages are assigned higher priority in the network relative to least cost, resulting in a redistribution of the MST. How these differences interact with other modeling considerations that we did not address (e.g., scaling of resistance surface, spatial resolution) is an important line of future inquiry.

Understanding the composition and spatial distribution of regional protected-area networks can provide conservation planners with a tractable mechanism to begin implementing an aspirational vision of a well-connected, continental network of protected areas. Identifying regional protected-area networks may serve as an initial step towards developing regional connectivity plans that can inspire conservation investment and actions (Noss et al. 2012). Indeed, our analysis revealed nine transboundary, regional protected-area networks (Fig. 1e, f). The challenges associated with transboundary conservation planning are well documented (Scarlett and McKinney 2016). In response, the U.S. government formalized a system of transboundary landscape conservation planning cooperatives (LCCs) in 2010 to facilitate coordination and collaboration among agencies and stakeholders at regional levels. Although the LCCs have been hailed as a model system for continental-scale conservation planning (Baldwin et al. 2018), failure by the U.S. government to continue financial and administrative support for the program has led to its current state of indefinite hiatus. Reinstating the LCC network may provide a crucial channel by which conservation planners may begin or continue to establish regional networks of protected areas embedded within a continental network.

We recognize our results may be sensitive to myriad factors. We coarsened the human modification data used as the resistance surface from 1-km to 5-km spatial resolution, which may affect the identification of connectivity conservation priorities and properties of the protected-area network (Arponen et al. 2012). Our assumption that resistance to movement scaled linearly with human modification may be a conservative representation of landscape permeability for particular terrestrial species (Keeley et al. 2017), although the evidence remains mixed (Zeller et al. 2018). Placing core nodes at points within protected-area polygons with the least human modification is logical, but connectivity models are known to be sensitive to node placement (Appendix S2: Fig. S2). Our work is temporally static and does not account for future changes in land use and climate that, if included, may shift contemporary conservation priorities (Albert et al. 2017). In addition, the relatively limited pool of protected areas included in this analysis may fail to account for the beneficial stepping-stone effect that smaller protected areas containing relatively unaltered habitats provide. This omission could lead to an overestimation of the movement cost between certain protected areas and a redistribution of network priorities. Our analysis of the network's structure via MSTs and betweenness centrality was admittedly narrow, and we encourage more thorough evaluations in subsequent research, including the roles of different motifs in creating structural resilience. Lastly, it is important to consider how best to integrate this effort with continental-scale connectivity models focused on climate change adaptation and expected climate-driven species movement (Appendix S2: Fig. S3).

Conclusion

Creating, maintaining, or restoring connectivity among protected areas can increase the likelihood of species' survival amid a changing climate and land use patterns (Hilty et al. 2019). We demonstrated how identifying the least human-modified lands connecting protected areas at continental scales can evoke an aspirational vision of conservation (Video S1) but suggest planners judiciously pair connectivity modeling approaches with landscape condition-specific connectivity targets. Our approach may serve as a model for other transboundary-connectivity initiatives around the globe. Ultimately, monitoring of species' movement amid changes in climate and land use are needed to sustain biodiversity.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2387/full

Open Research

Normalized least-cost corridors and current flow data have been archived through Data Basin: https://databasin.org/datasets/fe62805b54b34819af435784cafb876e/