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LETTER

Informing Strategic Efforts to Expand and Connect Protected Areas Using a Model of Ecological Flow, with Application to the Western United States

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Abstract

Under rapid landscape change, there is a significant need to expand and connect protected areas (PAs) to prevent further loss of biodiversity and preserve ecological functions across broad geographies. We used a model of landscape resistance and electronic circuit theory to estimate patterns of ecological flow among existing PAs in the western United States. We applied these results to areas previously identified as having high conservation value to distinguish those best positioned to maintain and enhance ecological connectivity and integrity. We found that current flow centrality was highest and effective resistance lowest in areas that spanned the border between southern Oregon and Idaho, and in northern Arizona and central Utah. Compared to other federal jurisdictions, Bureau of Land Management lands contributed most to ecological connectivity, forming "connective tissue" among existing PAs. Our models and maps can inform new conservation strategies and critical land allocation decisions, within or among jurisdictions.

Introduction

Fundamental principles of systematic conservation planning (e.g., Margules & Pressey 2000) suggest that an ecologically functional system of protected areas (PAs) requires large and intact landscapes, should protect a variety of habitats, and critically, needs to be interconnected (Defries *et al.* 2007; Cumming *et al.* 2015). Globally, well-connected PA networks have the potential to enhance biodiversity within and beyond their boundaries, on land or in the sea (Brudvig *et al.* 2009; Foley *et al.* 2010). Yet, PAs have rarely been selected to conserve biodiversity and maintain ecosystem function (Pressey 1994; Watson *et al.* 2016), nor have they been selected to contribute to a well-connected ecological network. To address this gap, we developed a model of ecological flow among existing PAs to identify areas that are best positioned to maintain and enhance ecological connectivity and integrity across broad landscapes with multiple ownerships and applied it to the western United States.

Vast areas of currently unprotected public lands in the western United States have the potential to enhance the ecological effectiveness of the U.S. PA network. This is particularly true if the ecological significance and context of these lands are used to determine the location of new areas for conservation and protection (Dickson *et al.* 2014, Watson *et al.* 2016). Over 1.4 million km^2 (57%) of land in the 11 conterminous western states is owned by the American public and managed by the federal government. Although a sizable proportion of these lands remain largely undeveloped, the expansion of energy development, mining, timber harvesting, and other extractive land uses threaten to fragment these areas, reducing their ecological function (Hansen & Defries 2007). Furthermore, their degradation could undermine the PA network by reducing existing landscape connectivity and, in turn, lowering the conservation value of adjacent PAs (Berger *et al.* 2014).

Here we apply our model of ecological flow to the western United States to identify areas that can most enhance the ecological value of the U.S. PA network using two complementary estimates of how the areas contribute to ecological connectivity and integrity. These include (1) current flow centrality, which identifies areas important for keeping networks connected for ecological processes such as gene flow (McRae *et al.* 2008) and can be used to predict movement probabilities for animals at local or regional scales (e.g., McClure *et al.* 2016) and (2) effective resistance, which quantifies the isolation of sites or populations (McRae & Beier 2007). We use these estimates to assess and demonstrate the potential contributions of currently unprotected Bureau of Land Management (BLM) roadless lands with high conservation value (Dickson *et al.* 2014) to regional connectivity and PA integrity, where areas with relatively high current flow centrality contribute to maintenance of connectivity across the PA network, and areas of relatively low resistance to nearby PAs have the potential to enhance the integrity of existing PAs.

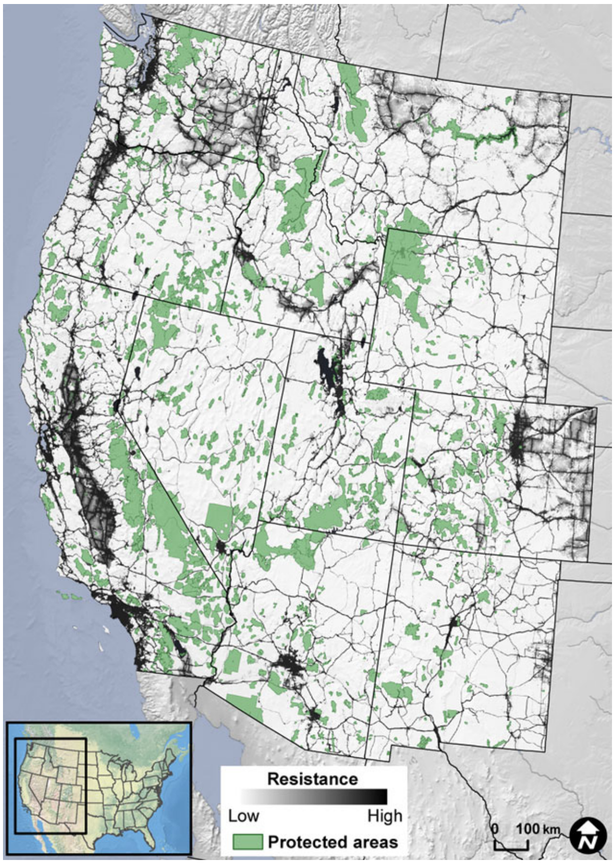

Figure 1 Distribution of protected areas and landscape resistance values across 11 states in the western United States. Protected areas are defined as those in IUCN categories I-IV and $\geq$ 20.2 km^2 in size.

Methods

Our study area included the eleven western states in the contiguous United States: Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming (Figure 1). We defined the network of existing PAs within this extent using land management designations from the U.S. PA Database v1.3 (USGS 2012). We considered only those PAs that were designated within IUCN categories I-IV and that were $\geq$20.2 km^2 in size, as this is the federally mandated minimum size for wilderness areas in the United States (Wilderness Act 1964). We combined PA polygons when they were immediately adjacent and used geometric centroids (i.e., single pixels, constrained to polygon interiors) to represent each unique polygon in the connectivity analyses ($n = 1{,}043$ centroids).

As a first step to modeling landscape connectivity, we created a resistance surface (R) that combined data on human modification and slope using the equation $R = (H + 1)^{10} + s/4$, where H is the human modification score and s is percent slope (see also SI Methods). After Theobald (2013), we quantified the degree of human modification (H) of the western landscape circa 2010, with scores ranging from 0.00 (unmodified) to 1.00 (completely converted) using multiple data layers including land cover, transportation, housing density, and oil and gas well density. To account for possible movement processes that avoided relatively large elevation changes or steep terrain (e.g., crossing over mountain ranges or through deep valleys), we added to H a penalty for areas with steep slopes, following Theobald *et al.* (2012). Finally, we used the National Hydrography Dataset Plus (USGS 2008) and assigned all rivers with annual mean flow >1,000 cubic feet per second a resistance of 1,000 to reflect their role as barriers to movement for many terrestrial organisms. Overall, this resulted in resistances value R ranging from 1.00 for unmodified lands to approximately 1024.00 for completely developed lands. We evaluated the sensitivity of our centrality results to different modeling choices for resistance surface parameterizations (SI Methods).

Next, we treated the PA centroids as focal nodes to be connected and calculated cumulative current flow among centroids using Circuitscape v4.0.5 (McRae *et al.* 2013), which implements a model of potential

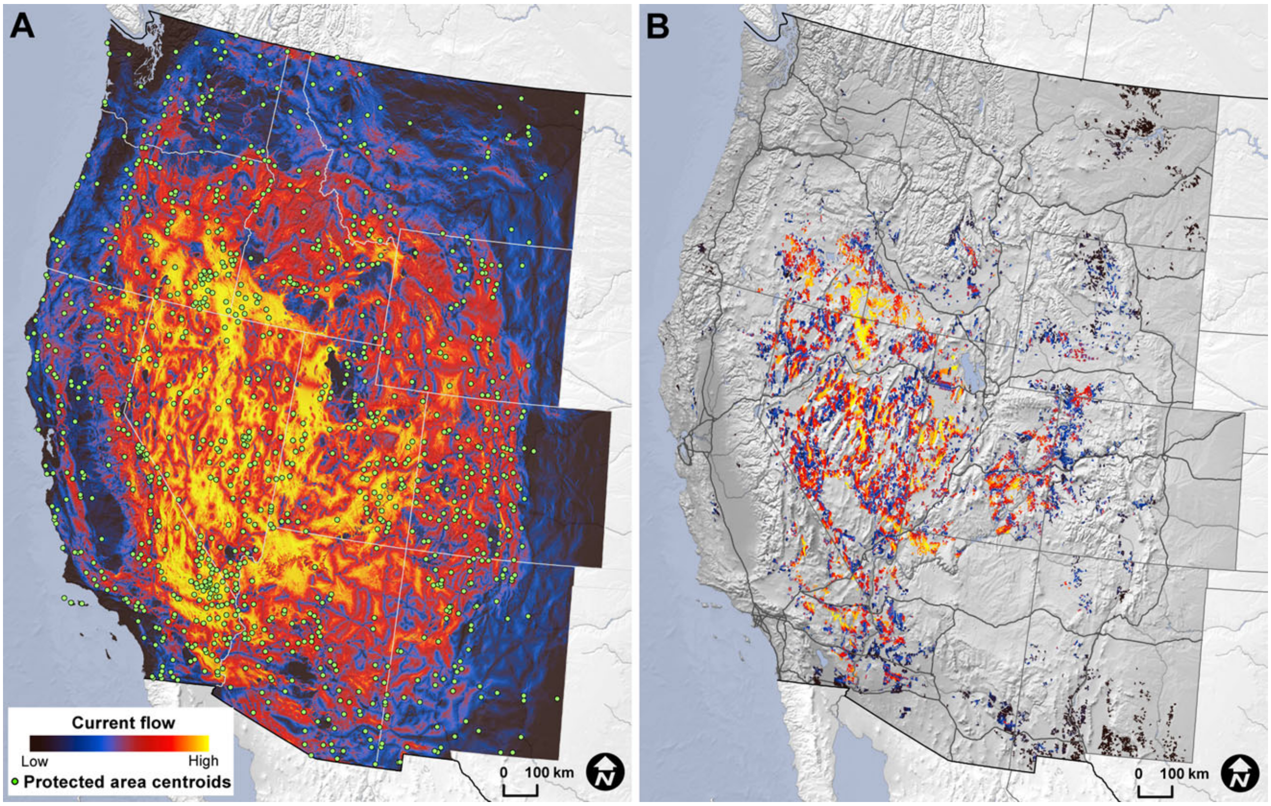

Figure 2 Current flow across the 11 western states (A) and within unprotected, roadless BLM lands (B). Protected area centroids were calculated as the geometric center of individual or immediately adjacent protected areas. Major interstate highways also are shown.

connectivity based on electrical circuit theory (McRae *et al.* 2008). Similarly to Theobald *et al.* (2012), our novel use of PA centroids (i.e., single pixels and not polygons) allowed us to more realistically estimate flow within each PA boundary as a continuous process, rather than treat each PA as a homogeneous patch with zero resistance, which is typical for connectivity studies. This approach also permitted a comprehensive comparison of current flow values among jurisdictions, including those that encompassed the PAs we analyzed. In addition, the use of centroids resulted in a substantial decrease in computation time. We used Circuitscape's all-to-one mode iterated across all centroids, connecting each to ground while injecting 1 Amp of current into the remaining centroids and allowing current to flow across the study area to the grounded centroid (McRae *et al.* 2013). Current densities were added across all iterations to produce a map of current flow centrality values for each intervening grid cell (pixel). This provided a measure of betweenness centrality (Newman 2005), which reflects the importance of each grid cell for maintaining connectivity among all centroid pairs. Current flow centrality includes contributions from all paths between nodes, not just the shortest or least-cost paths, while still giving more weight to low-resistance paths (Newman 2005).

We estimated average current flow centrality across the entire extent of each of five federal jurisdictions—BLM, National Park Service (NPS), Department of Defense, US Fish and Wildlife Service, and US Forest Service (USFS)—and for each of 1,678 high conservation value areas by calculating the total current flow across it and dividing by its area. Our database of high conservation value areas (average size = 54.2 km^2, SD = 56.8, range = 20.2–959.5) was drawn from a systematic analysis of seven ecological indicators on contiguous areas of roadless BLM land (the "80/20 scale-dependent core" results and "roadless" definition described in detail by Dickson *et al.* 2014) (see also SI Methods). We considered high conservation value areas with relatively high centrality to be those places more likely to be important for maintaining connectivity among PAs. In doing so, we demonstrate the utility of our connectivity results in identifying areas of high conservation value that also had exceptionally high value for promoting ecological flows.

We also calculated the effective resistance between each high conservation value area and all PAs by setting all PAs to ground and iteratively injecting 1 Amp of current into each high conservation value area. Effective resistance reflects the degree to which a particular node (e.g., a PA) is connected to (or isolated from) others and is affected by proximity but also the resistance and number of connections (or pathways) between nodes (McRae *et al.* 2008). Because effective resistance is most influenced by nearby nodes, and because PA integrity would be most enhanced by nearby PAs, this analysis was restricted to a 250-km radius of each high conservation value area for computational efficiency. We considered high conservation value areas with relatively low effective resistance values to be those places more likely to enhance ecological integrity across the existing PA network.

As a final step, and to identify concentrations of regionally important areas with simultaneously high conservation and ecological connectivity values, we combined our centrality and effective resistance results. To do this, we simply summed each of the 1,678 high conservation value areas according to its ranked values for centrality (from low to high) and effective resistance (high to low).

Results

Patterns of current flow reflected a high overall contribution to ecological connectivity among PAs in the central portion of the western United States (Figure 2A), including large areas of unprotected, roadless BLM land (Dickson *et al.* 2014; Figure 2B). Within this extent, we observed the highest levels of current flow across southeastern Oregon, Nevada, and Utah. In Nevada, the north–south orientation of basin and range landforms appears to facilitate high current flow between the northwestern and southwestern states. Portions of southern Idaho and the desert regions of southern California and western Arizona also exhibit high levels of current flow, which may be driven by close proximity to existing PAs. Overall, we found that BLM lands contribute more to connectivity among PAs (per unit area) than lands managed by the other federal management agencies we analyzed (Table 1).

Among the best (95th percentile) high conservation value areas identified on unprotected roadless BLM lands by Dickson *et al.* (2014), flow centrality was greatest for those spanning southeastern Oregon and southwestern Idaho, central and eastern Nevada, southern Nevada, and northwestern Arizona (Figure 3A). Flow centrality was lowest in southern Arizona and southern New Mexico, where there are relatively few PAs in close proximity, and where there are few large patches of unprotected, roadless BLM land. Effective resistance was lowest in high conservation value areas near or adjacent to PAs in southeastern Oregon and northern Nevada, but also in southeastern Utah and portions of northwestern Arizona and western Colorado (Figure 3B). Notably, areas of low effective resistance also were present in southern Arizona and southern New Mexico.

Table 1 Average current flow (betweenness) centrality for each of five federal jurisdictions in the western United States, ranked according to mean current density

Jurisdiction	Area (km^2)	Mean current density	SD
BLM	706,256	444.4	219.0
NPS	80,624	426.9	241.5
DOD	65,119	423.4	295.5
FWS	29,439	370.1	253.7
USFS	638,200	295.8	134.8

BLM, Bureau of Land Management; NPS, National Park Service; DOD, Department of Defense; FWS, Fish and Wildlife Service; USFS, United States Forest Service.

Based on combined (95th percentile) results for ranked centrality and effective resistance, areas of high conservation value that might simultaneously maintain and enhance connectivity were concentrated in the greater Owyhee Canyonlands of southeastern Oregon and southwestern Idaho, as well as southeastern Utah and the Mojave Desert of southern Nevada and northwestern Arizona (Figure 4). One of the largest (>940 km^2) high conservation value areas identified by Dickson *et al.* (2014) was found in southeastern Utah, overlapping the San Rafael Swell. This area was among over a dozen that neighbored multiple PAs and that would provide high connectivity value across the southwestern region.

Discussion

Around the world, intact but unprotected habitats are rapidly disappearing (e.g., Tilman *et al.* 2001; Butchart *et al.* 2010). These habitats may provide both movement pathways among PAs and sources for colonization of adjacent PAs (Goetz *et al.* 2009) similar to the "spillover" effect documented for marine PAs (Olds *et al.* 2012). Nevertheless, new PAs are rarely established because of their potential to improve connectivity among PAs or enhance the ecological integrity of existing PAs. A flow-based model of ecological connectivity, such as ours, can provide a flexible, yet theoretically grounded and robust method for identifying the location of new PAs wherever data on landscape (or seascape) resistance can be derived. Moreover, complementary estimates of central-

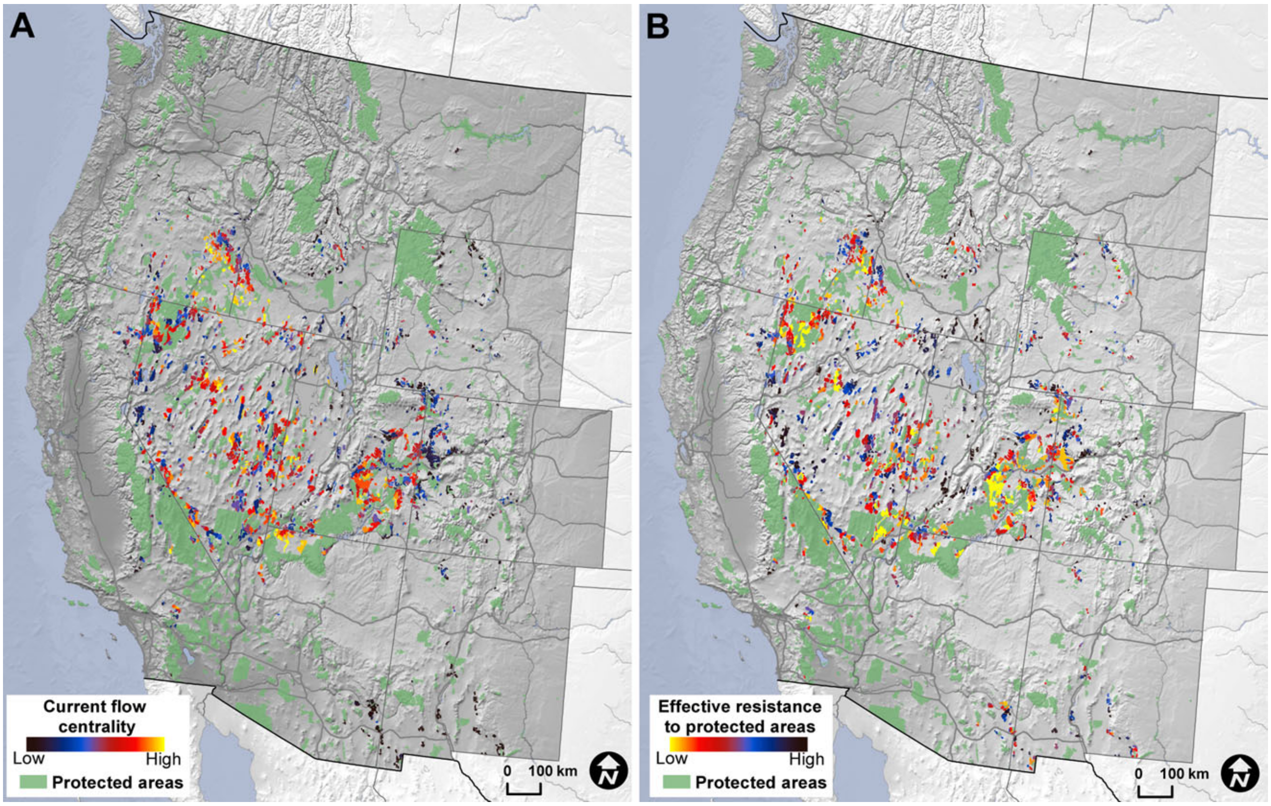

Figure 3 Current flow centrality (A) and effective resistance to protected areas (B) among high conservation value areas identified across unprotected, roadless BLM lands in the western United States. The 95th percentile of values is shown in yellow (scale is reversed for effective resistance). Major interstate highways also are shown.

ity and effective resistance can be combined to understand how new PAs might both facilitate and enhance ecological connectivity over administratively complex landscapes.

Our results suggest that intact, unprotected BLM lands disproportionately constitute the "connective tissue" among multiple PAs and jurisdictions. In fact, our cross-jurisdictional comparison revealed that new protections on BLM lands could do more to promote connectivity, on average, than new protections on other federal jurisdictions with many existing PAs. When compared to other federal jurisdictions, BLM lands were often proximate to existing PAs, presented fewer topographic (e.g., steep slopes) and hydrographic barriers to ecological flows, were relatively roadless, and generally encompassed lower levels of human modification (see also Dickson *et al.* 2014). In terms of connectivity, these unique qualities of BLM lands should be considered by efforts to delineate new PAs within this domain to increase the ecological effectiveness of the U.S. PA network as a whole.

Although our approach to modeling ecological connectivity was not conditioned on the movement parameters of a particular focal species or taxonomic group, our results revealed patterns of regional connectivity overlapping with those observed by other studies centered on one or more species of conservation concern (see Krosby *et al.* 2015). For example, the central portion of our study area encompassed much of the highest priority habitat for Greater Sage-Grouse (*Centrocercus urophasianus*), in terms of potential connectivity among populations (Knick *et al.* 2013). Most of this habitat falls within BLM's jurisdiction. The areas of important ecological connectivity we identified on BLM lands also support long-distance migrations by herds of pronghorn antelope (*Antilocapra americana*) moving between Oregon and Nevada (Collins 2016) and through the upper Green River Basin of Wyoming (Seidler *et al.* 2014), as well as mule deer (*Odocoileus hemionus*) in Colorado (Lendrum *et al.* 2013) and Wyoming (Sawyer *et al.* 2012). Remaining, intact expanses of BLM land such as these should be the focus of efforts to maintain, restore, or establish key habitat linkages for wide-ranging species, and could be used to define new PAs that can secure the long term maintenance of connectivity. Concomitantly, thoughtfully

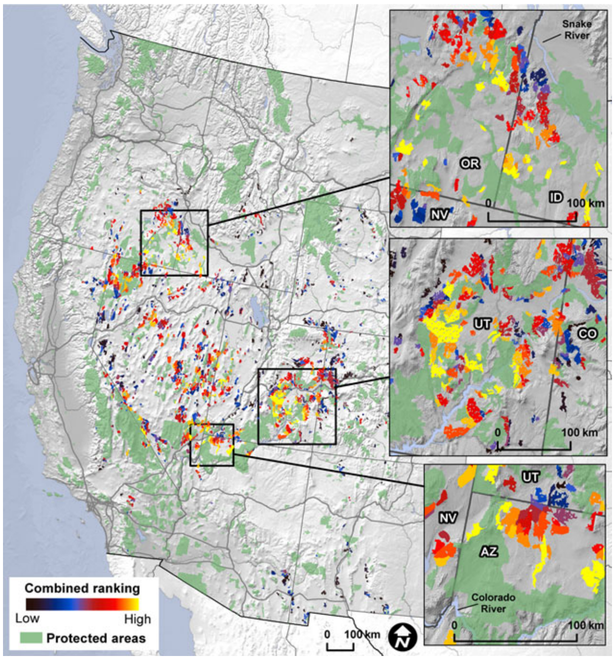

Figure 4 Result of a ranked combination of high conservation value areas with both high current flow centrality and low effective resistance across unprotected, roadless BLM lands in the western United States. The 95th percentile of the ranked combination values is shown in yellow. Insets detail concentrations of highly ranked conservation value areas in the greater Owyhee Canyonlands region (top), central Utah (middle), and northwestern Arizona (bottom). Major interstate highways also are shown.

planned linkages could enhance the movement of other species and ecological flows (Breckheimer *et al.* 2014).

Considering that BLM lands are the focus of increased energy production (USDOI 2011), our results are especially timely. For example, utility-scale energy development within this domain is expected to fragment habitats for wildlife, including key migration corridors (e.g., Beckmann *et al.* 2012). Because reliable spatial data and other scientific information on connectivity often are lacking, there remains uncertainty about the impacts of such developments on animal movement and dispersal (Northrup & Wittemyer 2013). As the demands for energy and other land-based resources in the western United States increase (Jones *et al.* 2015), so, too, does the need to balance these demands against the requirements of federal agencies to maintain large, ecologically functioning landscapes (Federal Land Policy and Management Act [Public Law 94–570, 90 Stat. 2743, *43 U.S.C. 1701*], U.S. Forest Service 2012 Planning Rule [77 FR 21162, Section 219.9]). Federal agencies are attempting to address this need through recent environmental initiatives, such as the strategy for improving the mitigation policies and practices of the Department of the Interior (Clement *et al.* 2014) and the National Fish, Wildlife, and Plants Climate Adaptation Strategy (National Fish, Wildlife, and Plants Climate Adaptation Partnership 2012). Our West-wide results, which are the first to identify high-connectivity BLM lands that could serve as critical linkages between existing PAs across all public lands, have the potential to inform these efforts.

Our connectivity results can inform regional-scale planning and legislative or executive actions to expand existing systems of Wilderness Areas, Wilderness Study Areas, National Monuments, National Conservation Areas, and other lands in the National Conservation Lands (NCL) system. This system was established "to conserve, protect, and restore nationally significant landscapes that have outstanding cultural, ecological, and scientific values for the benefit of current and future generations" (Omnibus Public Land Management Act of 2009), and with the intent of maintaining or increasing ecological connectivity across NCL units (Secretarial Order 3308). Our methodology and the "wall-to-wall" nature of our results can help to illuminate the conservation context and significance of BLM and other public lands. These data also can be used to bolster and strategically site new land designations that more effectively protect—and truly network—biodiversity and ecological processes. Administrative designations, such as Areas of Critical Environmental Concern (ACEC) on BLM lands, which can be nominated on the basis of protecting natural processes, have the potential to secure the maintenance of regional connectivity among existing PAs. Although ACECs possess a lower level of protection than NCLs and often encompass small areas, they can provide critical stepping stones for the movement of organisms across western landscapes. For example, the Trapper's Point ACEC in west-central Wyoming was designated primarily to preserve a crucial route for ungulate migration amid oil and gas development (BLM 2008). Similarly, our results are being used to target the location of multiple new ACECs or NCL lands intended to facilitate connectivity in the Greater Yellowstone Ecosystem, in the sagebrush habitats of southwestern Colorado, and across the Owyhee Canyonlands, among other areas of the West. Designation of these areas also would help to mitigate the localized impacts of resource extraction, namely energy or minerals developments, that have the potential to impede ecological flows.

Conclusion

The success of conservation efforts in the United States—and other parts of the world—may hinge in part on the role that underappreciated ecological flows play in overall network effectiveness. Indeed, important land protection decisions are happening across the western United States, but are poorly informed regarding the acknowledged importance of potential ecological connectivity within and across public and private lands. Because BLM lands dominate much of the western United States, relatively roadless and intact landscapes in BLM's domain are likely key to the sustained or enhanced movement of organisms and the flow of fundamental ecological processes among PAs and across jurisdictional boundaries. New protections or special designations for select lands within this domain could help to build a significantly stronger and more ecologically effective network of PAs, one that promotes the environmental conditions that enhance landscape connectivity (Krosby *et al.* 2010) and the capacity for adaptation to future climate change (Dawson *et al.* 2011). Measures (and maps) of potential ecological connectivity, such as ours, should serve as a principal basis for decisions regarding new and critically needed conservation lands. Designations based on potential ecological connectivity would purposefully and strategically strengthen America's PA network.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. Spearman rank correlation values of centrality results for high conservation value areas and the five resistance surfaces

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