Contributed Paper

Use of Linkage Mapping and Centrality Analysis Across Habitat Gradients to Conserve Connectivity of Gray Wolf Populations in Western North America

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Abstract: *Centrality metrics evaluate paths between all possible pairwise combinations of sites on a landscape to rank the contribution of each site to facilitating ecological flows across the network of sites. Computational advances now allow application of centrality metrics to landscapes represented as continuous gradients of habitat quality. This avoids the binary classification of landscapes into patch and matrix required by patch-based graph analyses of connectivity. It also avoids the focus on delineating paths between individual pairs of core areas characteristic of most corridor- or linkage-mapping methods of connectivity analysis. Conservation of regional habitat connectivity has the potential to facilitate recovery of the gray wolf* (Canis lupus), *a species currently recolonizing portions of its historic range in the western United States. We applied 3 contrasting linkage-mapping methods (shortest path, current flow, and minimum-cost–maximum-flow) to spatial data representing wolf habitat to analyze connectivity between wolf populations in central Idaho and Yellowstone National Park (Wyoming). We then applied 3 analogous betweenness centrality metrics to analyze connectivity of wolf habitat throughout the northwestern United States and southwestern Canada to determine where it might be possible to facilitate range expansion and interpopulation dispersal. We developed software to facilitate application of centrality metrics. Shortest-path betweenness centrality identified a minimal network of linkages analogous to those identified by least-cost-path corridor mapping. Current flow and minimum-cost-maximum-flow betweenness centrality identified diffuse networks that included alternative linkages, which will allow greater flexibility in planning. Minimum-cost-maximum-flow betweenness centrality, by integrating both land cost and habitat capacity, allows connectivity to be considered within planning processes that seek to maximize species protection at minimum cost. Centrality analysis is relevant to conservation and landscape genetics at a range of spatial extents, but it may be most broadly applicable within single- and multispecies planning efforts to conserve regional habitat connectivity.*

Keywords: *Canis lupus*, centrality, circuit theory, corridor, graph theory, least cost path, network flow

Utilización del Mapeo de Vínculos y el Análisis de Centralidad en un Gradiente de Hábitats para Conservar la Conectividad de Poblaciones de Lobo Gris en el Occidente de Norte América

Resumen: *Las medidas de centralidad evalúan las vías entre todas las combinaciones pareadas posibles de sitios en un paisaje para clasificar la contribución de cada sitio en la facilitación de los flujos ecológicos en una red de sitios. Los avances de la computación permiten la aplicación de medidas de centralidad en paisajes representados como gradientes continuos de calidad de hábitat. Esto evita la clasificación binaria de paisajes en parches y matriz como lo requiere el análisis de grafos de conectividad basado en parches. Esto también evita el enfoque en la delineación de vías entre pares individuales de áreas núcleo característico*

de la mayoría de los métodos de mapeo de corredores o de vínculos en el análisis de conectividad. La conservación de la conectividad de hábitat regional tiene el potencial de facilitar la recuperación del lobo gris (Canis lupus), *una especie que actualmente esta recolonizando porciones de su rango de distribución histórica en el occidente de Estados Unidos. Aplicamos 3 métodos de mapeo de vínculos contrastantes (vía más corta, flujo de corriente y costo mínimo-flujo máximo) a datos espaciales representando el hábitat de lobos para analizar la conectividad entre poblaciones de lobo en Idaho centra y el Parque Nacional Yellowstone (Wyoming). Posteriormente aplicamos 3 medidas de centralidad análogas para analizar la conectividad de hábitat de lobos en el noroeste de Estados Unidos y el suroeste de Canadá para determinar si sería posible facilitar la expansión del rango y la dispersión interpoblacional. Desarrollamos software para facilitar la aplicación de las medidas de centralidad. La centralidad de la vía más corta identificó una red mínima de vínculos análogos a los identificados por mapeo de corredores con la vía de menor costo. La centralidad de flujo actual y de costo mínimo-flujo máximo identificó redes difusas que incluyeron vínculos alternativos, que permitirán una mayor flexibilidad en la planificación. La centralidad de costo mínimo-flujo máximo, mediante la integración de costo de la tierra y la capacidad del hábitat, permite considerar a la conectividad en los procesos de planificación que buscan maximizar la protección de especies al menor costo. El análisis de centralidad es relevante para la conservación y la genética de paisaje en un rango de extensiones espaciales, pero puede ser ampliamente aplicable en esfuerzos de planificación de la conservación de la conectividad del hábitat de una o múltiples especies.*

Palabras Clave: *Canis lupus*, centralidad, corredor, flujo de redes, teoría de circuitos, teoría de grafos, vía de menor costo

Introduction

Consideration of landscape connectivity in conservation planning has increasingly shifted from a focus on preserving static landscape elements such as corridors to facilitating functional connectivity. Functional connectivity is defined as ecological processes such as demographic and genetic flows that support persistence of peripheral populations and long-term maintenance of a species' evolutionary potential (Taylor et al. 2006; Pressey et al. 2007). Due in part to computational limitations, most current reserve-design efforts remain focused on landscape pattern (e.g., selection of areas that capture species occurrences) (Cabeza & Moilanen 2001; Pressey et al. 2007). However, effective conservation of connectivity requires evaluation of how landscape composition and structure influence ecological and evolutionary processes at multiple levels of biological organization (Rayfield et al. 2011).

Here, we describe 3 contrasting methods of connectivity analysis that employ alternative assumptions concerning the relation between habitat and movement and offer complementary information for both corridor design and regional conservation planning. Graph theory provides a common conceptual framework that underlies all 3 methods. In graph theory, a graph (Fig. 1) is a set of nodes in which pairs of nodes may be connected by edges that represent functional connections (e.g., dispersal) between nodes (Urban et al. 2009). Edges may be assigned weights that represent an attribute such as habitat quality. A sequence of nodes connected by edges forms a path. Although they are highly abstracted depictions of landscape pattern, graphs may reveal emergent aspects of landscape structure that are not otherwise discernible.

Graph theory has been widely applied in landscape ecology and conservation planning (Urban et al. 2009). Such applications include analyses that represent continuous habitat gradients as a binary patch-matrix structure, with patches (nodes) linked by edges whose attributes (e.g., weight) are defined on the basis of geographic distance or attributes of the intervening matrix (Bodin et al. 2006; Urban et al. 2009). This patch-based approach contrasts with methods used within geographic information systems (GIS) to delineate corridors between pairs of habitat patches in raster grids (Beier et al. 2008). Although seldom transparent to the user, graph algorithms also underlie these latter methods, which analyze continuous habitat gradients by representing each raster cell (pixel) as a node in a regular lattice (an arrangement of points in a regular pattern). Edges in such graphs connect only a node and its immediately adjacent neighbors. We term these types of graphs *landscape lattices* (Supporting Information) in contrast to graphs that delineate discrete patches within a landscape matrix (Supporting Information).

Corridor-delineation methods available in GIS software analyze raster data by representing cost (e.g., energetic cost or mortality risk) of movement through different habitat types as distance (points in less permeable habitat are conceived as farther apart). Such methods then use computationally efficient algorithms to identify the route between 2 predetermined endpoints that has the shortest total distance (least total cost) (Supporting Information; Newman 2010). We use the term *shortest path* (Supporting Information) in place of *least-cost path* to avoid confusing the cost of moving between patches with monetary cost (e.g., of land purchase) (Newman 2010). Recent applications of shortest-path methods have
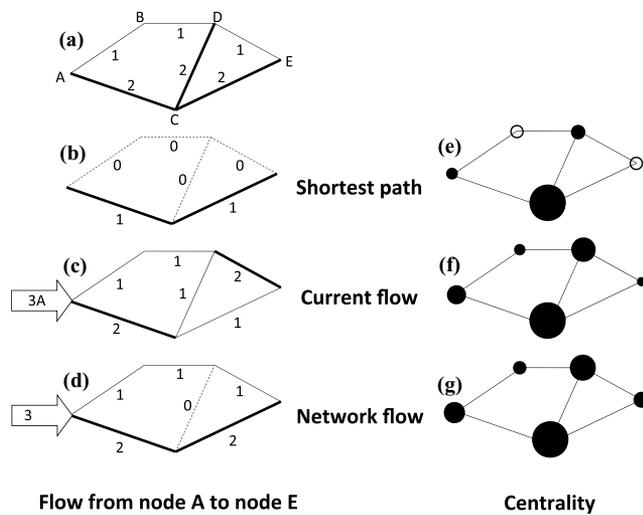
Figure 1. *A simple graph with 5 nodes and 6 edges demonstrates contrasts between graph analyses with shortest- or least-cost-path, current-flow, and maximum-flow methods. (a) Edge values shown may be derived from models of habitat quality. Edge values are proportional to conductance (current flow) and flow capacity (minimum-cost-maximum-flow) and inversely proportional to distance (shortest path). (b–d) Pairwise flow between nodes A and E, with line widths proportional to flow ([b] shortest-path analysis; [c] current-flow analysis with a 3-ampere source at A; [d] maximum-flow analysis with a 3-unit flow source at A and a 3-unit flow sink at E). (e–g) Centrality analysis of flow between all node pairs in the graph, with node sizes proportional to centrality values (open circles indicate zero values; [e] shortest-path betweenness centrality; [f] current-flow betweenness centrality; and [g] maximum-flow betweenness centrality).*

broadened their focus from identifying a single path or corridor to identifying a set of near-optimal paths that may be termed a habitat linkage or landscape linkage (Chetkiewicz et al. 2006; Beier et al. 2008).

We compared shortest-path analysis with 2 alternate connectivity-analysis methods, current flow and network flow. Current-flow methods examine probabilistic flow across all possible paths, whereas network-flow methods identify optimal flow that could use but may not use all possible paths. Current-flow models use algorithms from electrical-circuit theory to evaluate connectivity (McRae et al. 2008; Supporting Information). These methods treat landscapes as conductive surfaces (i.e., networks of nodes connected by resistors). When current is injected into a source node and allowed to flow across a network until it reaches a target node, the amount of current flowing through each intermediate node reflects the likelihood that a "random walker" leaving the source

node and moving along edges with probabilities proportional to edge weights will pass through the intermediate node on its way to the target node. By modeling the movement of random walkers, current-flow models integrate the contributions of all possible pathways across a landscape or network (Fig. 1c). As in electrical circuits, the addition of new pathways increases connectivity by distributing flow across more routes (McRae et al. 2008).

Network-flow models frame connectivity analysis as an optimization problem rather than as probabilistic movement (Supporting Information; Phillips et al. 2008). Network flow is analogous to the behavior of water in a pipe, in that it has constrained capacity (the amount of flow on an edge cannot exceed its capacity) and flow is conserved (the amount of flow into a node equals the amount of flow out of it, except when the node is a source or sink). There are several types of network-flow analyses. In a maximum-flow analysis, each edge is assigned a flow less than or equal to its capacity, which maximizes total flow between a source and a sink node. Although there may be many alternative sets of paths in a network that allow the maximum flow, computationally efficient maximum-flow algorithms tend to identify maximum flows with low total number of edges (Ahuja et al. 1993). Minimum-cost-maximum-flow algorithms, in contrast, identify which of the alternative maximum-flow sets has minimum total cost (here, monetary cost of land acquisition or management). Minimum-cost-maximum-flow may be more informative than maximum-flow analyses on landscape lattices, particularly when edge capacities are relatively similar, because a large number of equivalent maximum-flow solutions exist on such lattices.

Centrality and Regional Connectivity Analysis

Shortest path, current flow, and network flow have largely been applied to evaluate options for linking predetermined endpoints rather than analyzing habitat connectivity across the landscape (but see Phillips et al. 2008). However, a group of analogous graph-theory metrics are based on the concept of centrality (Supporting Information). These metrics consider paths between all possible pairs of nodes in order to evaluate the role of each node in mediating ecological flows (Bunn et al. 2000; Borgatti 2005). The loss of a node that lies on a large proportion of the paths in the network would disproportionately lengthen distances or transit times between nodes (Brandes 2001). A wide variety of centrality metrics have been proposed (Newman 2010). Many have been applied to analyze patch-based representations of landscapes (Bodin & Norberg 2007; Estrada & Bodin 2008). We did not attempt to comprehensively review centrality metrics; rather, we focused on 3 metrics that are analogous to the 3 major methods of linkage mapping

described above (Chetiewicz et al. 2006; McRae et al. 2008; Phillips et al. 2008).

Centrality calculations increase in computational complexity at a polynomial rate (typically quadratic to cubic) as the number of nodes increases (Ahuja et al. 1993). Although centrality analysis has been applied to patch-based representations of landscapes, networks were typically limited to hundreds of nodes or less (Estrada & Bodin 2008). Computationally efficient algorithms for analysis of large networks, which have recently been developed for purposes such as ranking web pages on the internet, allow analysis of landscape connectivity at a resolution that makes simplifying assumptions less necessary (Hagberg et al. 2008). This facilitates application of centrality metrics to contexts in which a continuous habitat gradient is more ecologically realistic than a binary patch-matrix framework (Chetkiewicz et al. 2006).

Because centrality analysis produces a continuous surface of values, it facilitates integration of the 3 connectivity-analysis methods into commonly used reserve design algorithms along with inputs representing species distribution or other conservation criteria (e.g., Possingham et al. 2000; Moilanen et al. 2009). The methods we developed thus avoid 2 key simplifications of landscape complexity. Because centrality metrics analyze paths between all node pairs, we avoided the a priori identification of endpoints necessary in current methods for delineating habitat linkages. By applying centrality analysis to graphs that represent landscapes as regular lattices, we avoided the binary classification of landscapes into patch and matrix required by patch-based graph analyses.

We used shortest path, current flow, and minimum-cost-maximum-flow (Supporting Information) to delineate habitat linkages between a single source and target patch and contrasted the results. We then developed 3 analogous centrality metrics that analyze connectivity across a landscape without reference to specific source and target patches. We contrasted results from the centrality metrics and assessed their relevance to regional conservation planning in a case study of a gray wolf (*Canis lupus*) metapopulation in the northwestern United States and southwestern Canada.

Methods

Linkage Analysis Methods and Their Analogous Centrality Metrics

Assumptions underlying the 3 methods of habitat-connectivity analysis affect conclusions about the contributions of different edges to connectivity (Fig. 1). In a simple example graph, shortest-path analysis assigns all priority to a single path with the least cumulative distance (Fig. 1b). Current-flow analysis identifies 2 edges

with highest current (used most frequently by random walkers). All other edges have lower but nonzero current levels that indicate the degree to which the other edges provide alternative pathways for random walkers moving from the source node to the target node (Fig. 1c) (Newman 2005; McRae et al. 2008). Maximum-flow analysis between source A and sink E (Fig. 1d) identifies a path with relatively high flow and a path with relatively low flow. Maximum-flow analysis assigns zero flow to edges not on these paths because these edges cannot contribute to increasing the total flow. Because there is only one maximum-flow solution for flow from A to E in Figure 1, minimum-cost-maximum-flow would be identical to maximum-flow.

Centrality analyses extend these methods from single pairs of source-target nodes to all pairs of nodes in a graph (Newman 2010). The 3 centrality metrics considered here are variants of betweenness centrality (BC), in that they measure to what extent a node contributes to paths or flows between all other nodes (Borgatti & Everett 2006; Newman 2010). Shortest-path BC identifies the one or several shortest (geodesic) paths that connect each pair of nodes on a graph and counts the number of such shortest paths in which a node is included (Borgatti & Everett 2006). Current-flow BC assesses the centrality of a node on the basis of how often, summed over all node pairs, the node is traversed by a random walk between 2 other nodes (Newman 2005). Minimum-cost-maximum-flow BC evaluates a node's contribution to connectivity on the basis of portion of the minimum-cost-maximum-flow that must pass through that node, summed over all node pairs (Freeman et al. 1991).

In Figure 1 shortest-path BC (Fig. 1e; Supporting Information) resembles shortest-path results between a node pair (Fig. 1b) because it assigns high centrality to node C, which lies on the shortest path between many node pairs, and zero centrality to nodes (B, E), which do not lie on the shortest paths between any pair of nodes. Current-flow BC (Fig. 1f; Supporting Information) ranks the importance (for facilitating flow) of nodes similarly as does shortest-path BC, but centrality values are more evenly distributed among nodes and there are no nodes of zero centrality due to the model's random-walk behavior. Maximum-flow BC ranks nodes similarly to current flow BC, but values are distributed more evenly (Fig. 1g). If all edges have equal cost, results of minimum-cost-maximum-flow BC (not shown) resemble maximum-flow BC.

Case Study

The gray wolf was extirpated from the northwestern United States by the 1940s, but it remained extant through much of southwestern Canada (Boyd & Pletscher 1999; Wayne & Hedrick 2011). Natal dispersal of wolves averages 100 km (Boyd & Pletscher 1999). Natural
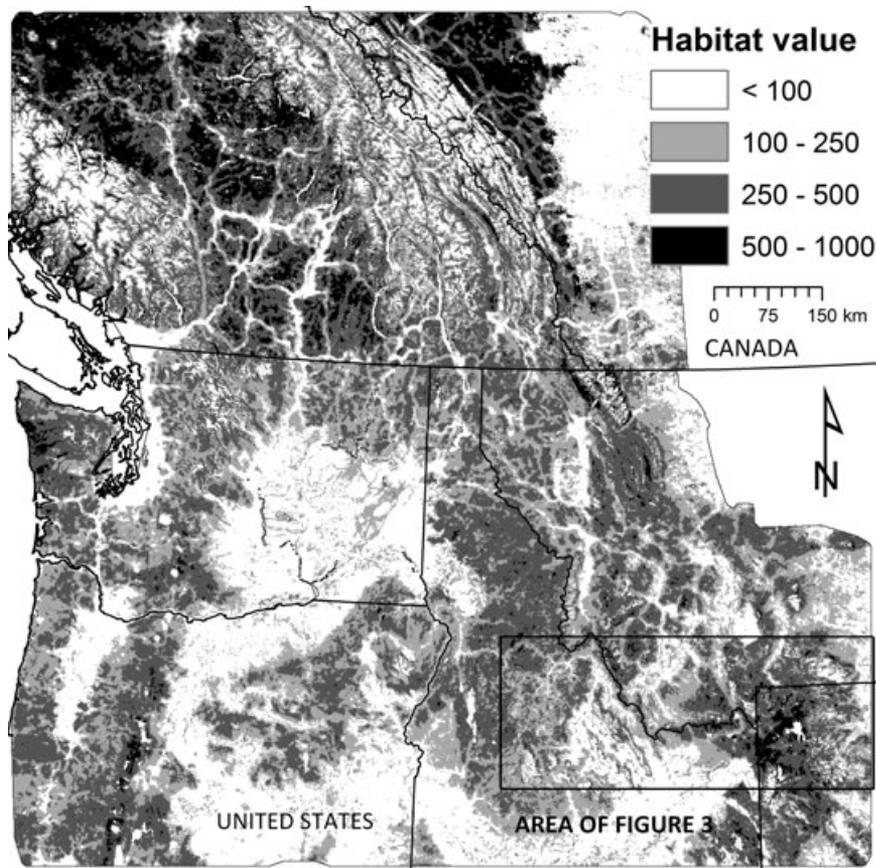
Figure 2. Model of habitat quality for gray wolf in the northwestern United States and southwestern Canada on the basis of land cover, slope, roads, and human population data. Edge weights in the connectivity analyses (Figs. 3–4) are derived from this habitat model.

recolonization via dispersal from Canada reestablished wolves in northwestern Montana in the 1980s and in northern Washington in 2008 (Wayne & Hedrick 2011). Reintroduction of wolves to central Idaho and northwestern Wyoming in 1995–1996 resulted in populations of >1000 in those areas and subsequent dispersal into Oregon, Utah, and Colorado (Wayne and Hedrick 2011). However, ongoing litigation has focused attention on whether habitat connectivity in the U.S. northern Rocky Mountains is sufficient to ensure continued genetic exchange between the region's 3 major wolf populations (Vonholdt et al. 2011; Wayne & Hedrick 2010). Analysis of habitat connectivity for the wolf may identify likely sources of natural dispersal from extant populations into currently unoccupied habitat and evaluate what areas have the greatest probability of facilitating continuing exchange among existing populations.

In developing a habitat model over this region (the U.S. states of Washington, Oregon, Montana, Idaho, and Wyoming, and the southern portions of the Canadian provinces of Alberta and British Columbia), we were constrained by the limited set of habitat variables for which data are available in all jurisdictions. Although empirical models of wolf habitat have been developed for the U.S. northern Rocky Mountains (Oakleaf et al. 2006), data are not available to allow their extrapolation across the entire region. We sought to demonstrate application of new methods of connectivity analysis rather than developing new habitat models. We therefore used a previously published habitat model (Fig. 2) that predicted wolf habitat quality from data on land cover, primary productivity, slope, road density, and human population density (Carroll et al. 2006). Details of the habitat model are in Supporting Information. We used a metric combining road density and human population density to represent factors negatively associated with wolf survival (Fuller et al. 2003). Because estimates of ungulate abundance are inconsistent across jurisdictional boundaries, we used land cover and tasseled-cap greenness, a satellite-imagery-derived metric, as a surrogate for prey density. Because wolves have reduced hunting success on steep terrain, we incorporated a negative effect of slope (Carroll et al. 2006). Because the above habitat variables may affect selection of dispersal habitat differently than selection of habitat for permanent occupancy, a subsequent refinement of the analysis with a model that is based on dispersal data would improve its accuracy (see Discussion).

Graph Analyses at Multiple Resolutions and Extents

We developed and contrasted analyses of wolf habitat connectivity at 2 spatial extents. First, we applied 3 linkage-mapping methods (shortest path, current flow, and minimum-cost-maximum-flow) at the local extent to

analyze connectivity between 2 areas occupied by source populations of wolves in central Idaho and Yellowstone National Park, Wyoming (Fig. 2). In this analysis, we divided the region into a lattice of hexagons, each with an area of 5 km^2. Each hexagon's centroid became a graph node (total 21,889 nodes) that was connected to the 6 hexagons that were its immediate neighbors. Linkage mapping is a special case of centrality analysis termed subset centrality. In contrast with the application of centrality to analyze all pairs of nodes in a graph, subset centrality considers paths between the nodes of the graph that fall within the source and target patches (Hagberg et al. 2008). To illustrate application of the local minimum-cost-maximum-flow analysis, we simply assigned private lands 2 times the management or acquisition cost of public lands.

We then applied 3 centrality metrics (shortest-path, current flow, and minimum-cost-maximum-flow BC) analogous to the linkage-mapping metrics to assess connectivity across the northwestern United States and southwestern Canada (Fig. 2) with 2 lattices, one of hexagons with areas of 50 km^2 ($n = 23,831$ nodes) and one of hexagons with areas of 100 km^2 ($n = 9601$ nodes). Use of 2 resolutions was necessary because calculation of minimum-cost-maximum-flow BC was computationally infeasible on the higher-resolution graph of 23,831 nodes. For the regional minimum-cost-maximum-flow analysis, we assigned each node a cost of 1. Minimum-cost-maximum-flow analysis with uniform cost values on all nodes results in identification of the maximum-flow solution of minimum total area (minimum number of nodes).

In all analyses, we used either undirected or symmetric directed graphs (Supporting Information) in which the weight of edge i-j (from node i to j) equaled the weight of the edge j-i (Newman 2010). Edge weights were derived from the mean habitat-quality value of the edge's 2 end nodes. We used untransformed habitat-quality values from the conceptual model, which ranged from 1 to 1000, to derive conductance (current flow) and capacity (minimum-cost-maximum-flow) (Supporting Information). We used the reciprocal of the mean habitat-quality value to represent distance in calculating the shortest-path metrics. Each of the 3 methods thus assigned different attributes to the graph edges (distance, conductance, and capacity for shortest-path, current flow, and network flow, respectively) that in effect represent alternative assumptions of how habitat quality affects dispersal (Supporting Information).

Comparison of Graph Metrics

We contrasted results of the different metrics by deriving a Spearman rank correlation matrix of node-centrality values. We hypothesized that metrics might show stronger relations at their extreme rather than mean values. Therefore, we also used quantile–quantile regression to as-

sess whether higher quantiles (e.g., 99th percentiles) of the shortest-path BC metric were significantly correlated with current flow and minimum-cost-maximum-flow BC (Cade & Noon 2003), as might be expected if shortest paths were subsets of the multiple paths identified by the latter 2 methods. To assess the degree to which priority areas for connectivity conservation differed from priority areas for other potential conservation features, we determined the proportion of areas with highest quantile of centrality values that fell within source (lambda, or intrinsic population growth rate > 1) or core (probability of occupancy > 50%) habitat. Population growth rates and occupancy were predicted by a spatially explicit population model that was based on the same habitat model inputs but was limited to the U.S. portion of the analysis region (Carroll et al. 2006).

We calculated shortest-path and current-flow BC with the NetworkX library (version 1.3) in Python (version 2.6) (van Rossum & Drake 2006; Hagberg et al. 2008). Network flow metrics were derived with the C++ library LEMON (Library for Efficient Modeling and Optimization in Networks, version 1.2) (EGRES 2010). We used Hexsim software (Schumaker 2011) to import and export files from a GIS. We developed a program, the Connectivity Analysis Toolkit (freely available at www.connectivitytools.org), which has a graphical user interface that allows generation of centrality metrics from habitat data without the need to learn Python or C++ (Carroll 2010).

Results

Computational feasibility varied widely among the different metrics, due to the complexity of the underlying algorithms (Newman 2010) and the specifics of the implementation in the software (Carroll 2010). In the regional-extent analysis, shortest-path BC showed low requirements for both memory and computational time (<1 GB and <1 h on a 3 GHz desktop system), whereas current-flow BC required large amounts of memory (>10 GB) (Carroll 2010). Minimum-cost-maximum-flow BC required low amounts of memory (<1 GB) but very long computational times (>1000 h) for the regional-extent analysis, but it was completed in <3 h for the local-extent analysis, which considered source and target patches encompassing approximately 100 hexagons (Fig. 3c).

Shortest-path analysis identified the single best (least cost) path between each pair of source and target hexagons (Fig. 3a). Current-flow analysis identified areas of high current flow along a more diffuse area surrounding the shortest path, as well as along alternate paths (Fig. 3b). Minimum-cost-maximum-flow analysis identified a set of paths that was diffuse in the western portion of the linkage, but constricted in the eastern portion due to the lower proportion of public lands in that
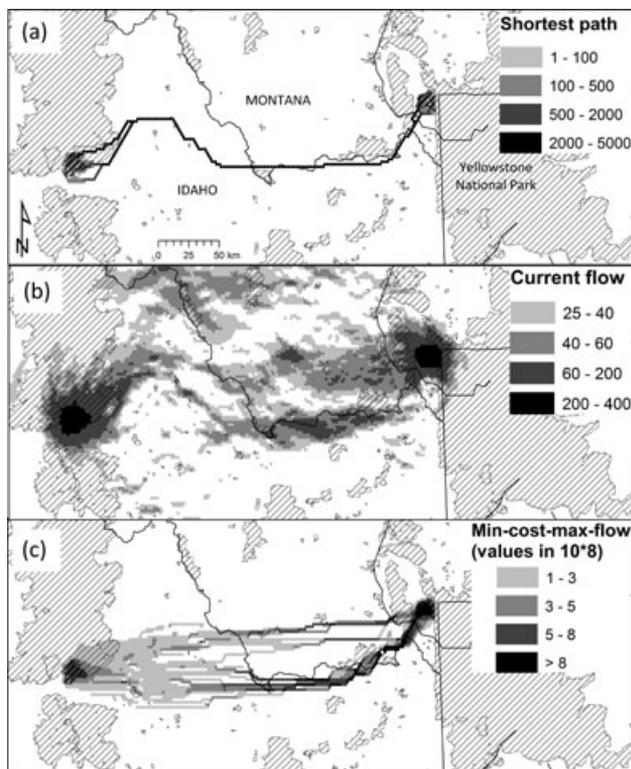
Figure 3. Graph-based analysis of habitat connectivity for gray wolf between central Idaho and Yellowstone National Park. The local-extent analysis compares 3 linkage mapping methods or subset-centrality metrics that are based on (a) shortest- or least-cost path, (b) current flow, and (c) minimum-cost-maximum-flow (min-cost-max-flow). Parks and wilderness areas are crosshatched.

area (Fig. 3c). In the regional-extent analysis, shortest-path BC identified a minimal network connecting the regions of high habitat value (Fig. 4a). Current-flow BC identified areas that encompassed the linkages derived from the shortest-path betweenness analysis, but these areas were more diffusely distributed (Fig. 4b) than were the shortest-path priority areas. Minimum-cost-maximum-flow BC results resembled current-flow results, but were only available at coarser resolution due to their greater computational complexity (Fig. 4c).

At the resolution of 50 km^2 hexagons (n = 23,831), shortest-path and current-flow BC values from the regional analysis were weakly correlated with habitat-quality value (0.55 and 0.58, respectively) and with each other (0.58). At the resolution of 100 km^2 hexagons (n = 9601), correlations were similar (0.59, 0.55, and 0.61, respectively). Additionally, minimum-cost-maximum-flow BC at this resolution was highly correlated with current-flow BC (0.85) but weakly correlated with shortest-path BC (0.45) and habitat-quality value (0.36). Although

shortest-path BC showed low correlation with other centrality metrics in the Spearman correlation tests, quantile–quantile regression results showed a significant relation (p < 0.001) of shortest-path BC with the higher percentiles of both current-flow and minimum-cost-maximum-flow BC (Supporting Information). Source habitat (12.8% of the U.S. portion of the region) held 20.8%, 20.2%, and 21.7%, respectively, of the areas with highest centrality values (top 20%) for the shortest-path, current-flow, and minimum-cost-maximum-flow BC metrics, whereas core or frequently occupied habitat (25.3% of the region) held 36.6%, 35.6%, and 42.9%, respectively, of the areas with highest centrality values for the 3 metrics.

Discussion

Because centrality analysis simultaneously considers the relations between all areas on a landscape, it provides a means to quantitatively incorporate connectivity within the planning process by ranking the contribution of those areas to facilitating ecological flows. Application of centrality metrics to lattices (graphs with nodes arranged in a regular pattern) avoids both the binary classification of landscapes into patch and matrix required by patch-based graph analyses and the focus on paths between a single pair of patches characteristic of corridor-mapping methods. Rather than addressing connectivity by adding linkages to a system of preidentified core areas, it is possible to compare the relative conservation priority of all linkages in a region and incorporate this information within the multicriteria optimization framework of most conservation-planning software (Possingham et al. 2000; Moilanen et al. 2009).

Although centrality metrics from exploratory analyses such as ours may be used to inform regional planning, input data (Carroll et al. 2006) and key assumptions of the methodology should be tested and revised on the basis of observed connectivity data and results from more-detailed population models. Connectivity models are often based on data on species distribution and rarely test the assumption that dispersal habitat resembles habitat that can be occupied. Habitat variables, such as vegetation structure, influence selection of both dispersal and permanently occupied habitat (Chetkiewicz et al. 2006), but short-term dispersal can occur through habitat that lacks resources for long-term occupancy. It is increasingly possible to rigorously build and test connectivity models from observed levels of dispersal and gene flow derived from genetic and telemetry data (Lee-Yaw et al. 2009; Schwartz et al. 2009; Richard & Armstrong 2010). Our goal was not to contrast these 2 approaches, but rather to describe and compare 3 alternative graph-based connectivity methods that are relevant to analysis of either habitat or dispersal data.
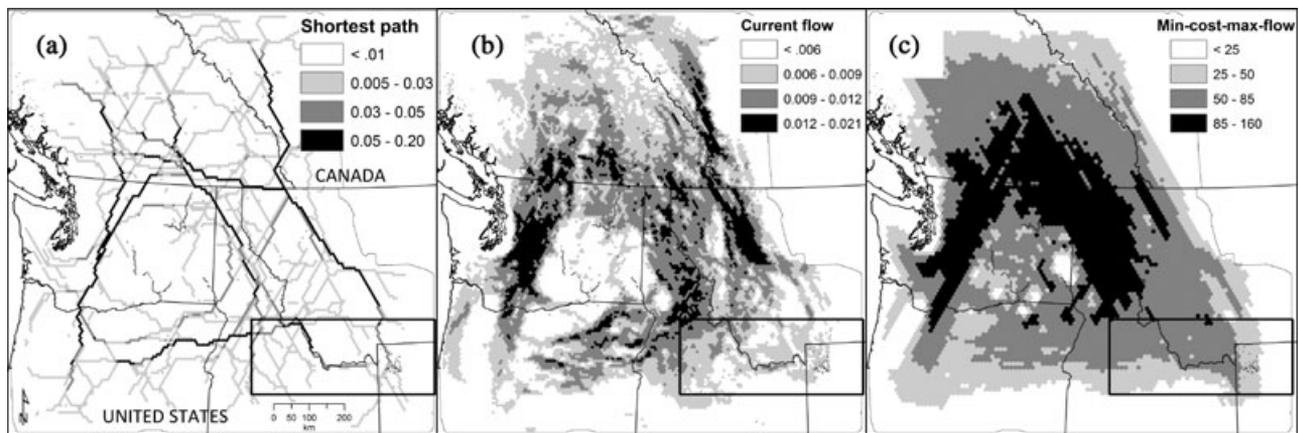
Figure 4. Analysis of habitat connectivity for gray wolf in the northwestern United States and southwestern Canada. The regional-extent connectivity analysis compares results from 3 metrics on the basis of (a) shortest-path, (b) current flow, and (c) minimum-cost-maximum-flow betweenness centrality. The area of the local-extent analysis (Fig. 2) is outlined (rectangle). The units in which the 3 centrality metrics (Figs. 4a–c) are expressed are not directly comparable.

Building and testing connectivity models with empirical dispersal data can help identify the ecologically appropriate spatial resolution and extent for conserving connectivity. Depending on the species of interest, regional habitat linkages may be designed to facilitate individual dispersal events or multigenerational genetic exchange via occupied stepping-stone habitat. Additionally, the degree to which such functional connectivity influences population viability (i.e., how much connectivity is enough to maintain a population) depends on factors such as population size and may be evaluated with more complex population models that simulate both demographic and dispersal processes (Carroll et al. 2006).

Whereas shortest-path models implicitly assume dispersers have perfect knowledge of the landscape, current flow assumes dispersers have no knowledge of the path more than one step ahead (Newman 2005). Real-world behavior of dispersers may fall somewhere between these extremes (McRae et al. 2008; Richard & Armstrong 2010). Shortest-path methods have been used to develop empirical multivariate models of habitat connectivity (Schwartz et al. 2009; Richard & Armstrong 2010). Predictions from current flow-based models are also highly correlated with observed genetic distance in several plant and animal populations (McRae et al. 2008; Lee-Yaw et al. 2009). A comprehensive evaluation of the relative accuracy of these 2 methods in a range of species would be informative. However, given that all graph-based methods are simplified representations of complex dispersal behavior, we advocate use of contrasting metrics as complementary sources of information rather than focusing on a single best metric.

We recommend that planning efforts focused on connecting a single pair of core areas (Fig. 3) compare results from the 3 methods to identify primary and alternative linkage options. In our case study, the comparison suggests it would be informative to evaluate 2 alternative or complementary linkage zones (Figs. 3b–c). In minimum-cost-maximum-flow sensitivity analyses, the southern linkage zone for wolves, which is longer than the northern linkage zone but contains less private land, received increasing priority as the difference in cost between public and private land increased (not shown). Unlike shortest-path analyses, which may combine land cost and habitat quality into a single aggregate index, minimum-cost-maximum-flow incorporates the 2 as distinct criteria, facilitating such sensitivity analyses.

Given that it is computationally challenging to derive minimum-cost-maximum-flow BC over regional extents (Fig. 4c), we suggest regional planning efforts compare results from shortest-path and current-flow BC analyses (Figs. 4a–b). Higher-resolution, local extent analysis of individual linkages (Fig. 3) can be placed in context using the priority assigned to the linkage area in regional analyses (Fig. 4). Although resolution of the landscape lattice remains limited by computational feasibility, it may often be possible to approximate resolutions relevant to habitat associations of the species of interest. In some cases, however, a graph derived from a patch-based representation of a landscape may be more informative than a lattice-based graph (e.g., if the coarse resolution of the lattice obscures key habitats such as riparian forest patches within an upland matrix). The software we developed can also be applied to such nonlattice graphs (Carroll 2010).

Our quantile–quantile regression results suggest that areas with high values of shortest-path BC are a subset of areas with high current flow and minimum-cost-maximum-flow BC values. Areas prioritized by shortest-path BC, which were either central to zones of

high-quality habitat or formed shortest paths between them, identify the minimal set of linkages whose loss would greatly reduce regional connectivity (Fig. 4a). In contrast, the zones identified by current-flow BC assist in incorporating redundancy within a linkage network, which may be important for designing networks that are resilient to changing climate and land-use patterns or environmental catastrophes (Fig. 4b) (McRae et al. 2008).

Because nodes near the study-area boundary inherently receive low centrality values (Fig. 4), the analysis area should typically extend beyond the area of interest if data permits. When the scaling of habitat-quality value is not derived from a statistical model that is based on dispersal data, sensitivity analysis with alternate scalings of habitat-quality values (e.g., transforming values by squaring them) can help assess the relative influence on centrality results of a node's habitat-quality value and location in relation to the edge of the analysis area.

Although predictions from network-flow models have not yet been compared with empirical data on dispersal, these algorithms' ability to address flow conservation (Supporting Information) and to consider both cost and capacity suggests they may offer models of connectivity that can be integrated within processes that seek to maximize species protection at minimum cost (Phillips et al. 2008). The minimum-cost-maximum-flow BC metric we used also resembles more complex spatial population models in that it effectively weights the importance of each pairwise relation by the habitat-quality value (and hence ability to produce dispersers) of the source node. Analyses such as ours that prioritize areas with high centrality on the present-day landscape provide a heuristic approach to incorporating connectivity into multicriteria reserve-selection algorithms (Possingham et al. 2000; Moilanen et al. 2009). Full integration of centrality analysis within such algorithms, which requires comparison of the centrality of reserves within many alternate reserve designs, remains computationally challenging.

We focused our case study on informing conservation planning for a single species, the gray wolf. Facilitating dispersal between wolf populations within the western United States and Canada has been proposed as a method to enhance the long-term genetic diversity and viability of the regional wolf metapopulation (Vonholdt et al. 2010). Areas of high centrality were often associated with source or core habitats (Carroll et al. 2006), but they also were found outside those areas. This suggests that conserving connectivity of wolf metapopulations may require different strategies than conserving core populations. Results from our analysis may aid planning to enhance connectivity via habitat protection or reduction of mortality for dispersing wolves within linkage zones. Similar analyses may have broad relevance to conservation planning at a variety of spatial scales appropriate to metapopulations of other species. Centrality analyses may also inform the increasing number of multispecies planning efforts by agencies and nongovernmental organizations that seek to conserve regional habitat connectivity (Western Governors Association 2008).

Acknowledgments

Supporting Information

Glossary of terms (Appendix S1), description of conceptual habitat model for gray wolf (Appendix S2), and quantile–quantile regression plots (Appendix S3) are available online. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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