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Contributed Paper

Trade-offs and efficiencies in optimal budget-constrained multispecies corridor networks

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Abstract: *Conservation biologists recognize that a system of isolated protected areas will be necessary but insufficient to meet biodiversity objectives. Current approaches to connecting core conservation areas through corridors consider optimal corridor placement based on a single optimization goal: commonly, maximizing the movement for a target species across a network of protected areas. We show that designing corridors for single species based on purely ecological criteria leads to extremely expensive linkages that are suboptimal for multispecies connectivity objectives. Similarly, acquiring the least-expensive linkages leads to ecologically poor solutions. We developed algorithms for optimizing corridors for multispecies use given a specific budget. We applied our approach in western Montana to demonstrate how the solutions may be used to evaluate trade-offs in connectivity for 2 species with different habitat requirements, different core areas, and different conservation values under different budgets. We evaluated corridors that were optimal for each species individually and for both species jointly. Incorporating a budget constraint and jointly optimizing for both species resulted in corridors that were close to the individual species movement-potential optima but with substantial cost savings. Our approach produced corridors that were within 14% and 11% of the best possible corridor connectivity for grizzly bears* (Ursus arctos) *and wolverines* (Gulo gulo), *respectively, and saved 75% of the cost. Similarly, joint optimization under a combined budget resulted in improved connectivity for both species relative to splitting the budget in 2 to optimize for each species individually. Our results demonstrate economies of scale and complementarities conservation planners can achieve by optimizing corridor designs for financial costs and for multiple species connectivity jointly. We believe that our approach will facilitate corridor conservation by reducing acquisition costs and by allowing derived corridors to more closely reflect conservation priorities.*

Keywords: Connectivity, conservation planning, cost-effective conservation, economics, optimization, protected areas, threatened species, wildlife corridor

Compensaciones y Eficiencias en las Redes Óptimas de Corredores de Especies Múltiples Restringidas por el Presupuesto

Resumen: *Los biólogos de la conservación reconocen que un sistema de áreas protegidas aisladas será necesario pero insuficiente para alcanzar los objetivos de la biodiversidad. Las estrategias actuales para conectar las áreas núcleos de conservación por medio de corredores consideran la ubicación óptima de estos*

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con base en un solo objetivo de optimización: maximizar, comúnmente, el movimiento de una especie blanco a lo largo de una red de áreas protegidas. Mostramos que diseñar los corredores para una especie única con base solamente en un criterio ecológico lleva a enlazamientos extremadamente caros que son sub-óptimos para los objetivos de conectividad de especies múltiples. De manera similar, adquirir los enlazamientos menos caros lleva a soluciones ecológicamente pobres. Desarrollamos algoritmos para optimizar los corredores para el uso de especies múltiples dado un presupuesto específico. Aplicamos nuestra estrategia en el oeste de Montana para demostrar cómo las soluciones pueden utilizarse para evaluar las compensaciones en la conectividad de dos especies con requerimientos de hábitat diferentes, áreas nucleares diferentes y valores de conservación diferentes bajo presupuestos diferentes. Evaluamos los corredores que fueron óptimos para cada especie individualmente y para ambas especies en conjunto. Incorporar una restricción de presupuesto y optimizar en conjunto para ambas especies resultó en corredores que estuvieron próximos al potencial óptimo de movimiento de las especies individuales pero con ahorros sustanciales de gastos. Nuestra estrategia produjo corredores que estuvieron dentro del 14 % y el 11 % de la mejor conectividad posible entre corredores para los osos pardos (Ursus arctos) *y los glotones* (Gulo gulo)*, respectivamente, y ahorro el 75 % del costo. De igual manera, la optimización conjunta bajo un presupuesto combinado resultó en una conectividad mejorada para ambas especies en relación a la división del presupuesto en dos para optimizar para cada especie individualmente. Nuestros resultados demuestran la economía de escala y las complementariedades que los planeadores de la conservación pueden obtener al optimizar los diseños del corredor para financiar los costos y para los objetivos de conectividad de especies múltiples en conjunto. Creemos que nuestra estrategia puede facilitar la conservación de corredores al reducir los costos de adquisición y al permitir que los corredores derivados reflejen más cercanamente las prioridades de conservación.*

Palabras Clave: áreas protegidas, conectividad, conservacián rentable, corredor de vida silvestre, economía, especies amenazadas, optimización, planificación de la conservación

Introduction

Under the pressures of rapid human development and climate change, wildlife habitat has been diminished and fragmented, which at times compromises the ability of many species to persist (Hanski & Ovaskainen 2000; Fahrig 2003; Haddad et al. 2015). Faced with these trends, conservation biologists have pushed for the creation of systems of protected areas (Hole et al. 2009). This has resulted in extensive research and development of methods that inform reserve design (Sarkar et al. 2006; Moilanen et al. 2009).

Biologists and ecologists recognize that a simple system of protected areas, serving as isolated safe-haven islands for biodiversity, will not be sufficient for the long-term maintenance of biodiversity. Thus, preserving and restoring habitat connectivity is as a key conservation priority for government agencies and conservation organizations (Crooks & Sanjayan 2006; Beier et al. 2011; Haddad et al. 2015) and is increasingly considered in conservation methodologies (Beier et al. 2008; Lentini et al. 2013). Specifically, the protection of wildlife corridors can maintain migration and prevent populations from the negative genetic and demographic impacts of becoming isolated (Haddad et al. 2003). Protecting wildlife corridors can also help counteract habitat fragmentation and link isolated reserves in a connected system.

Although approaches to identify wildlife corridors vary, use of Geographic Information Systems (GIS)-based tools predominates (Beier et al. 2011). In the most common approach, researchers develop landscape-resistance surfaces in which each parcel or pixel is associated with a cost value that indicates the resistance to movement, dispersal, or gene flow through particular landscape features for a given species (see Zeller et al. 2012; Wade et al. 2015). Approaches to developing resistance surfaces as a function of environmental characteristics vary widely, ranging from using expert opinion to assign costs, to approximating costs based on genetic distance (Schwartz et al. 2009), to directly estimating costs of movement from mark-recapture or dispersal data (Royle et al. 2013; Graves et al. 2014).

Within these approaches, the effective distance between locations and associated movement costs can be modeled as either a least-cost distance (Singleton et al. 2002) or a resistance distance (McRae et al. 2008). All models are based on the assumption that a path of higher total resistance cost corresponds to a more difficult or less likely route for the animals to take (Cushman et al. 2009; Rayfield et al. 2010; Parks et al. 2013). In all cases, the resulting resistance surface underlies all approaches for corridor design (Spear et al. 2010), which include evaluation of network properties (Garroway et al. 2011), algorithms that delineate the least-cost paths or corridors (Adriaensen et al. 2003), simulations of animal movements that identify most likely paths, and algorithms evaluating connectivity-restoration opportunities (Dilkina et al. 2011; Torrubia et al. 2014).

Resistance surfaces also form the basis for determining pinch points, or areas where many likely dispersal paths overlap (McRae et al. 2008). Recent studies have also examined corridors across multiple species, highlighting areas of overlap that may be of higher conservation priority (Cushman et al. 2013; Krosby et al. 2015). Most studies both for single and multiple species focus on identifying the species-optimal corridors from a biological perspective, but, except for simple post hoc financial feasibility analysis, they do not explicitly include land purchases and economic costs. Ideally, one would use a single optimization algorithm that jointly considers both ecological and economic criteria.

Several recent studies show that to design conservation strategies that are efficient and practical, it is crucial to incorporate economic, ecological, and biodiversity considerations from the outset of the planning process (Stewart & Possingham 2005; Naidoo et al. 2006; Torrubia et al. 2014). In the United States in 2011, the President's Council of Advisors on Science and Technology recommended that "federal agencies that implement biodiversity and ecosystem conservation programs should prioritize expenditures based on their cost-effectiveness" (PCAST 2011). For reserves, optimal design, given constraints, has been formally addressed; multiple computational models and tools allow conservation planners to systematically study the trade-off between economic costs and ecological benefits of reserves (Sarkar et al. 2006; Moilanen et al. 2009), and reserve design software is relatively mature (Moilanen et al. 2009). However, similar decision-making support for wildlife corridor design is largely lacking, although not due to lack of interest or need (Beier et al. 2008). Computationally, design of wildlife corridors is intrinsically a more difficult optimization problem. Although reserve site selection can be mathematically formulated as optimization over sets, the corridor design problem requires spatially explicit reasoning and network design constraints that enforce path connectivity.

We devised an optimization framework for a budget-constrained corridor design (BCD) problem that simultaneously incorporates spatially explicit models of species-specific resistances and spatially heterogeneous economic costs of conservation actions. The methods we developed support joint optimization across species and allow weighting of species so that multispecies optimization reflects both social and biological priorities. We applied our method in a case study of corridor design for wolverines (*Gulo gulo*) and grizzly bears (*Ursus arctos*) in western Montana.

Methods

We developed a numerical method that selects parcels to preserve landscape connectivity given a set of land parcels, the financial cost of parcel acquisition, species-specific resistance costs associated with crossing each parcel or pixel on the landscape, and pairs of core areas (e.g., natural reserves or biologically significant areas). A corridor design consists of a set of pixels (or parcels) to be protected through acquisition that, together with existing protected land, form a conservation network that includes at least 1 path that connects each pair of core areas. To avoid confusion between the 2 types of cost for a given corridor design, we hereafter refer to the movement or resistance cost as *cumulative resistance* and financial cost as *expenditure*. The expenditure required for a corridor design is the sum of the acquisition costs for parcels that comprise the corridor design. Given a proposed corridor design, the cumulative distance between a core-area pair is measured as the sum of resistances along the least-resistance path connecting the pair that falls entirely within the corresponding conservation network. This captures our assumption that unconserved parcels are at risk of land-use changes that result in the parcels becoming uninhabitable or unpassable for the species of interest (Gude et al. 2006) and that purchasing parcels conserves them from that risk. The cumulative resistance of a corridor design is the sum of effective distances for all specified core-area pairs.

Ideally, one wants to spend limited financial resources efficiently to obtain the conservation network with the highest overall connectivity (lowest cumulative resistance). In the BCD, we incorporated both optimization criteria explicitly: expenditure (i.e., a budget constraint that puts a cap on the maximum-allowed expenditure for an acceptable design) and connectivity or cumulative resistance (i.e., the optimization objective that minimizes the sum of the effective distances for the specified core-area pairs). The problem we studied is close in spirit to the corridor design problem considered in Dilkina and Gomes (2010), Conrad et al. (2012), and Jafari and Hearne (2013), where the goal was to maximize the suitability of all protected areas for a single species while meeting a budget constraint and ensuring mutual connectivity between all core areas. In contrast, here the connectivity provided by a corridor design is measured for each core-area pair separately and summed over all specified pairs. Our connectivity objective more closely addresses the widely accepted least-cost model for measuring the ecological benefit of a corridor design rather than other optimization models for conservation planning that consider connectivity (e.g., Onal & Wang 2008; Cerdeira et al. 2010; Jafari & Hearne 2013).

The problem we addressed is computationally hard and is equivalent to the minimum delay generalized Steiner network problem (LeBras et al. 2013). Following LeBras et al. (2013), we applied a mathematical model based on optimizing a mixed-integer linear program (MILP), which can be solved using standard optimization solvers, providing optimality guarantees. Although actual parcels may be irregular in shape, for simplicity, we represented the landscape as a raster of grid cells or pixels. For each evaluated species, we assumed a resistance surface and core areas were identified. Each core area could span

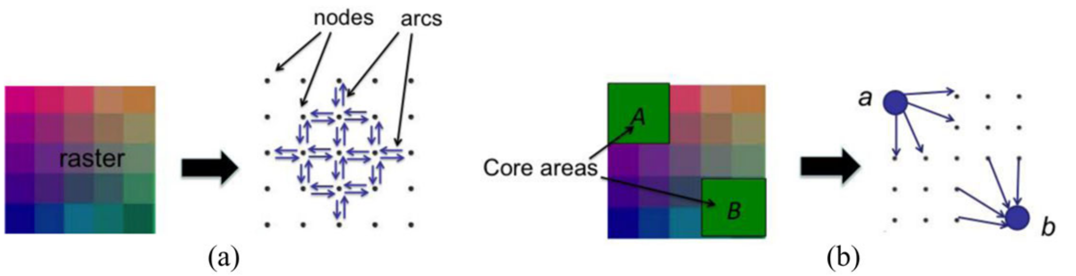

Figure 1. The corridor design problem transformed into an optimization problem on a graph: (a) transformation of a raster surface into a graph of nodes and arcs (directed edges from 1 node to another encoding possibility of movement in the given direction) and (b) transformation of core areas to additional nodes and their connection via directed edges to nodes representing neighboring raster cells.

multiple contiguous raster cells, and we assumed that core areas were already protected.

We abstracted the BCD problem as a graph optimization problem, where each cell in the landscape was a node v in the graph and each pair of adjacent cells was connected by 2 graph edges, 1 in each direction (Fig. 1a). Each graph node v represented a pixel that was included in the decision space, associated with an acquisition cost, $c(v)$, and a resistance value, $r^s(v)$, for each species s. Each core-area pair was also represented as source graph node a and destination graph node b, each of which was then connected with edges to all graph nodes that corresponded to pixels adjacent to the core area (see Fig. 1b). The set $P^s = \{(a1;\ b1);\ (a2;\ b2), \ldots\}$ was the set of core-area pairs for species s. We nominally associated core-area nodes with zero resistance and cost: $r^s(a) = 0$ and $c\,(a) = 0$.

The mathematical optimization model is briefly explained below. A more detailed formulation is in the Supporting Information. For a single species, the overall flow-based MILP encoding of the problem is:

$$R^s\ (B) = \min \sum_{p \in P^s} R^s_p, \tag{1}$$

$$s.t. \sum\nolimits_{v \in V} c(v) * x_v \leq B, \tag{2}$$

$$\prod\nolimits_{sp}\ \forall s \in S,\ \forall p \in P^s, \text{ and} \tag{3}$$

$$x_v \in \{0, 1\} \quad \forall v \in V. \tag{4}$$

The binary protection variable $x_v \in \{0, 1\}$ for each node v corresponds to a raster cell on the landscape, where $x_v = 1$ if cell v is selected for protection and 0 otherwise (Eq. 4). Given a budget limit, B, we are constrained to select a subset of graph nodes, whose total acquisition cost did not exceed the budget (Eq. 2). For a particular core-area pair $p = (a,\ b)$ for species s, $\prod_{sp}$ (Eq. 3) stands for a set of network flow constraints on continuous variables $\mathbf{y^{sp}}$ that enforces that a solution has at least 1 path that connects the pair p for species s given the values assigned to the protection variables $\boldsymbol{x}$. The R^s_p measures the cumulative resistance along the path connecting pair p of species s and is a linear function of the variables $\mathbf{y^{sp}}$. The solution to the optimization problem is the set of nodes, selected for protection, that result in optimal overall connectivity for species s as a sum over the specified core-area pairs, as measured by $R^s(B)$, under budget constraint B.

Multiple Species

The BCD approach allowed us to consider the trade-offs between 2 species at each particular budget level B. The budget B can be anywhere between the minimum expenditure required to connect all core-area pairs and the expenditure of the least-resistance (best ecological connectivity) design. In a 2-species budget-constrained optimization, given a budget limit B, we minimized the weighted sum of the normalized total resistance for each species as follows:

$$\min R^{gw}_{\alpha}\ (B) = \alpha \frac{R^g}{R^g\ (B)} + (1 - \alpha) \frac{R^w}{R^w\ (B)}, \tag{5}$$

where R^g and R^w are the respective resistances for species g and w and α is a weighting parameter valued from 0 to 1. The resistances are normalized by $R^g(B)$ and $R^w(B)$ in order to put the 2 species on a relatively similar scale and to avoid problems when the species-specific resistance models for the 2 species are on largely different numerical scales. The single-species optimal connectivity values, $R^g(B)$ and $R^w(B)$, under budget B, were computed by first solving the 2 corresponding single-species BCDs. By varying α from 0 to 1 in increments, we computed jointly optimal solutions for the same budget but for different species weightings. These solutions were used to determine the Pareto frontier of alternative corridor designs with trade-offs between the connectivity provided for the 2 species. See Supporting Information for the full multispecies optimization model.

Boundary Solutions

The corridor design problem is bounded by 2 solutions. At one end of the spectrum, the least-resistance, or least-cost path, solution represents the best linkages between core areas, ignoring acquisition cost. At the other end, the minimum-expenditure solution corresponds to the least-expensive network that contains a path between each specified pair of core areas with no consideration of resistance. We computed these extreme solutions to provide a frame of reference for the intermediate BCD solutions. Details on how the boundary solutions were computed are in the Supporting Information.

Case Study

We selected 2 species that have broad, overlapping ranges and different habitat requirements to examine the way trade-offs between species influence how a limited conservation budget is allocated. Wolverines and grizzly bears are both top predators in western Montana and have populations concentrated in conserved areas, such as Yellowstone National Park and the Bob Marshall Wilderness Complex. These areas provide large areas of core habitat for breeding. However, due to habitat and territory requirements, core habitat areas are likely too small to preserve genetic diversity within each population, and population sizes in some mountain ranges are so small that demographic rescue is likely required for persistence. Squires et al. (2007) estimated that the population of wolverines across 3 mountain ranges in west-central Montana is 12.8 (95% confidence interval 2.9), and Kendall et al. (2016) estimated the superpopulation of grizzly bears in the 9900-km^2 Cabinet-Yaak recovery zone in northwestern Montana at 48 (95% credible interval 44–62). Thus, maintaining connectivity across western Montana has immediate conservation implications for these species.

Each species has unique habitat requirements that dictate their distribution. Wolverine's primary habitat occurs within areas where snowpack is present through May (Copeland et al. 2010). Grizzly bears use areas where multiple food resources exist in mesic, meadow, and shrub habitats and are at lower densities in developed areas, where the probability of bear-human conflicts and mortality is relatively higher (Graves et al. 2011; Linke et al. 2013). Core habitat areas of wolverines and grizzly bears partially overlap, for example, in conserved areas at high elevation, but they do not fully overlap. Long-distance dispersal has been documented for both species, and wolverines are notorious for large home ranges and exceptional dispersal ability (Moriarty et al. 2009).

The study area included public (National Park Service, U.S. Forest Service, State of Montana, and U.S. Fish and Wildlife Service), tribal, and private lands (held by nongovernmental organizations, timber companies, and private individuals) in western Montana. We limited our analysis to western Montana, where land-acquisition cost data were available and both species are present, and focused our connectivity goals in one of the most critical areas for connectivity in western Montana, between the Northern Continental Divide Ecosystem (NCDE) and the Greater Yellowstone Ecosystem (GYE). Connectivity between grizzly populations in NCDE and GYE is considered critical for maintenance of genetic variability in GYE (Miller & Waits 2003). We calculated both species resistances and acquisition costs on a grid raster of 1000 m resolution in ArcGIS (ESRI 2011).

Acquisition Costs

Acquisition cost data were based on tax records for public and private properties (Montana State Library 2011) and information on conserved lands (Montana State Library 2011), which were assumed free to include in any corridor design. We created a rule set to exclude parcels that would not be considered for purchase, such as bodies of water, urban parcels, and parcels that were <0.081 ha. The completed parcel layer was then converted to a cell-based raster with a resolution of 1000 m in ArcGIS (ESRI 2011), assuming that the expenditure for the cell was the area-weighted sum of all the parcel values within the cell. This rule implicitly assumes that portions of large parcels may be purchased and parcels of <1 km^2 falling in the same pixel may be purchased together.

One factor limiting the extent of our study area was the lack of parcel cost data for the state of Idaho. The Montana cadastral tax data set was unique at this time (NRC 2007). Despite current efforts to improve dissemination of geospatial data (FGDC 2012), for most locations, researchers would be required to build their own data sets. This can be done using county-level tax-assessment information or by estimating hedonic price equations based on recent property sales (e.g., Polasky et al. 2008).

Core Areas and Resistance Surfaces

We considered 2 grizzly core habitat nodes: conserved lands in the NCDE and GYE grizzly recovery areas (Fig. 2a; USFWS 2002). The resistance surface for grizzly bears (Fig. 2b) was estimated based on vegetation, human development, and road density, following the methods of Graves et al. (2013) and data collected by Kendall et al. (2009) (see Supporting Information).

Critical wolverine habitat has been linked to the presence of late-spring snowpack (Aubry et al. 2007; Copeland et al. 2010). We identified 6 wolverine core-habitat nodes (Fig. 2c) in the span between the 2 recovery zones for grizzly bears as contiguous areas with persistent snowpack within conserved lands, such as national parks and forests. To determine the wolverine resistance surface (Fig. 2d), we used the methods of Balkenhol (2009),

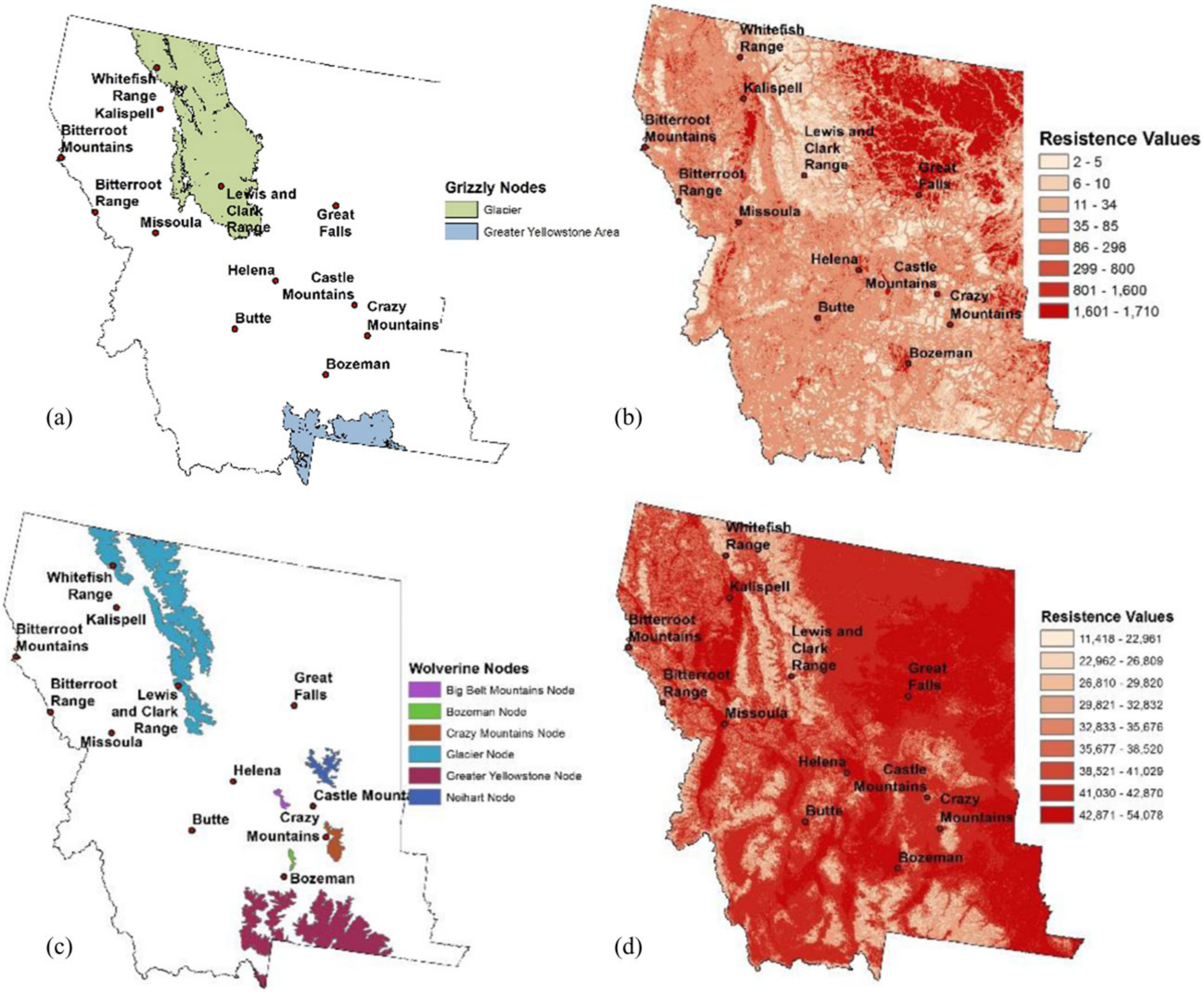

Figure 2. Case study of corridor design for 2 species in the western portion of Montana (U.S.A.): core areas of (a) grizzly bears and (c) wolverines included in the corridor design and resistance values for (b) grizzly bears and (d) wolverines built based on habitat-selection models (the darker the shading, the higher the resistance).

which take into account landscape variables such as snow cover (Schwartz et al. 2009; McKelvey et al. 2011), housing development, and forest edge (see Supporting Information). Resistance surfaces were represented in ArcGIS (ESRI 2011) as cell-based rasters with a resolution of 1000 m.

To decrease computation time and constrain potential corridors to those that were ecologically plausible, we excluded cells that could not be made passable by the species through conservation actions and cells that were very far from any reasonable pathway between a core-area pair (Parks et al. 2013). Adapting the idea of least-resistance path buffer or corridor swath (Beier et al. 2008), for each core-area pair, we eliminated from consideration all cells whose inclusion in paths exceeded 1.5 times the cumulative resistance associated with the least-resistance path for that pair. There remained 42,065 cells of 1 km^2 for which protection decisions were made. The resulting MILP problems were solved using the commercial optimization solver CPLEX version 12 (IBM ILOG CPLEX 2011) on a Linux (version 2.6.18) cluster, where each node had an Intel Xeon Processor X5670 with dual-CPU, hex-core @2.93GHz, 12M Cache, and 48GB RAM. Each corridor optimization took 5–40 h of computer time, depending on the budget level and the species weighting parameter.

Results

The results of our case study illustrate how our solution framework can be used to support decision making and trade-off analysis for corridor conservation. The minimum expenditure necessary to achieve connectivity for both grizzly bears and wolverines was roughly $2.9 million, whereas acquiring the least-resistance

Table 1. Cumulative resistance to species' movement and expenditure or budget necessary to acquire a corridor design for 2 species under different optimization scenarios: minimum expenditure to connect core-area pairs; budget-constrained corridor design with both species weighted equally ($\alpha = 0.5$) for 5 budget levels; and unconstrained least-resistance design.

Optimization scenario	*Cumulative resistance**		*Expenditure or budget (US$)*
	grizzly bear	*wolverine*	
Minimum expenditure	100	100	2,952,577
Budget constrained	87	92	3,000,000
	60	83	3,500,000
	56	73	4,000,000
	49	73	4,500,000
	33	65	8,000,000
Least resistance	29	59	31,832,800

**Shown as percentage of species' cumulative resistance at the minimum-expenditure level.*

corridor design required roughly $31.8 million (Table 1). Because units of resistance associated with the 2 species resistance models were arbitrary, we report scaled resistance for each species as the percentage of the species' cumulative resistance associated with the minimum-expenditure corridor. At the extremes, there were large trade-offs between acquisition costs and resistance. Although the minimum-expenditure corridor design was <10% of the cost associated with the least-resistance corridor design, these economic savings came at a high ecological cost: the grizzly resistance was 248% higher and the wolverine resistance was 69% higher than in the least-resistance corridor design.

Most of the possible improvement in the connectivity of the corridor design was obtained given a relatively small increase in budget. Assuming equal weights for the 2 species ($\alpha = 0.5$), an additional investment of approximately $1.5 million over the minimum-expenditure corridor design, for a total of $4.5 million, achieved 71% and 66% of the possible improvement in resistance for grizzly bears and wolverines, respectively (Table 1 & Fig. 3) and saved over $27 million dollars relative to the least-resistance design. In particular, the possible improvement of cumulative resistance for wolverines was a reduction from 100 at minimum expenditure to 59 at least resistance, for a reduction of 41. The wolverine resistance of 73 under a budget of $4.5 million resulted in an improvement of 27, which is 66% of 41. Increasing the budget further to $8 million resulted in a jointly optimal corridor that was within 14% and 11% of the best possible corridor connectivity for grizzly bears and wolverines, respectively, and saved 75% of the cost (Table 1).

To evaluate trade-offs between grizzly and wolverine connectivity given constant budgets, α varied from 0.0 to 1.0 (Fig. 4). The shape of the trade-off curve, convex to the origin, indicated that the ecological cost, in terms of greater resistance for grizzly bears, of improving connectivity (decreasing resistance) for wolverines increased as connectivity for wolverines improved and vice versa. Because both resistance surfaces and core habitat nodes differed between species, the shape of the optimal corridor network also changed with changing priorities given the same budget (Fig. 5).

To explore possible advantages of optimizing connectivity for both species jointly, we solved 2 separate single-species corridor designs, each allocated a budget of $4 million. The resulting cumulative resistances were 67% and 40% of the minimum-expenditure paths for wolverines and grizzly bears, respectively, at a total expenditure of $8 million. The solution when optimizing for both species jointly with a combined budget of $8 million and $\alpha = 0.5$ (Table 1) was better for both species: the cumulative resistance was 65% and 33% of the minimum-expenditure cumulative resistance for wolverines and grizzly bears, respectively.

Discussion

Practical conservation solutions obtain the best possible design given limited resources. Our results show that designing corridors for single species based on purely ecological criteria can lead to expensive linkages that are suboptimal for multispecies connectivity objectives. Alternatively, acquiring land only for the least-expensive corridor leads to ecologically poor solutions. Instead, by imposing cost constraints on the ecological optimization process, we achieved linkages with much better ecological values given budget constraints marginally above the feasible minimum-expenditure corridor design. Similarly, joint optimization for multiple species led to better connectivity while matching the acquisition costs associated with multiple individual-species corridor designs.

This framework allowed us to examine relative trade-offs between optimizing for 1 species versus another. This can be useful information for policy makers for two reasons. First, societal concerns for species are not equivalent. For example, people rank charismatic megafauna over other species (Kellert 1976) and species that have important ecological function over other species (Montgomery 2002). Although people's opinions may not matter to the species, they drive the allocation of conservation resources. Second, the biological need for connectivity varies among species and populations within the species. For example, wolverines have tiny populations in specific core areas, and therefore are highly dependent on dispersal. Our framework can also easily represent differences in core-area importance by placing different weights not only among species but also among specific core-area pairs. Our method makes trade-offs explicit, thereby allowing policy analysts to

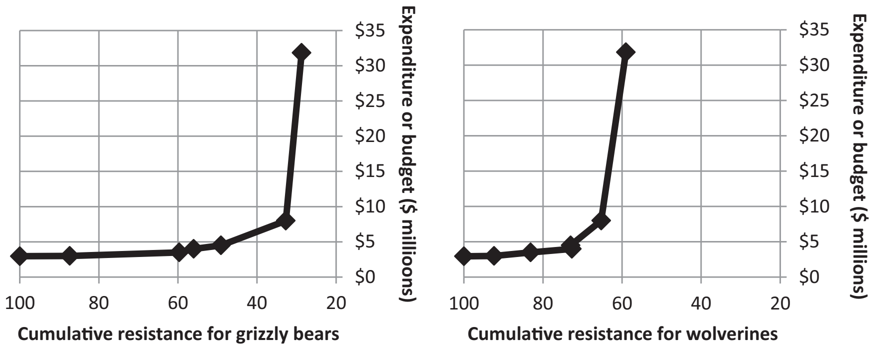

Figure 3. Trade-off curves between expenditure and cumulative resistance for grizzly bears and wolverines in jointly optimized corridor designs ($\alpha = 0.5$). Cumulative resistance is shown as percentage of each species' cumulative resistance at the minimum-expenditure level.

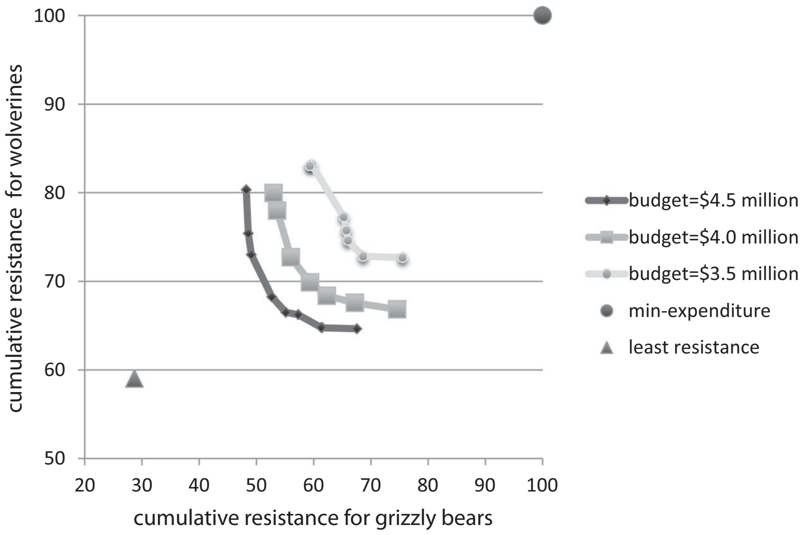

Figure 4. Trade-off curves between the cumulative resistances for wolverines and grizzly bears at different budget levels (each curve is generated by varying the relative prioritization of the 2 species, different curves correspond to different budgets). Minimum-expenditure corridor regardless of habitat quality and least-resistance corridor regardless of cost are extreme solutions and contain no between-species trade-offs; therefore, they are represented as points in the resistance trade-off space.

estimate how 1 species might be affected by prioritizing other species and to constrain the total resistance based on the ecology of the species of interest. Overall, we believe that our optimization framework improves the ability to find pragmatic, transparent solutions to landscape connectivity problems.

The nature of these trade-offs both for single-species and multispecies optimization is profoundly nonlinear. Most of the reduction in corridor resistance can be achieved given small increases in budget; most of the increase in multispecies utility can be achieved by modest consideration of the dispersal needs of additional species. A corridor that is biologically perfect for 1 species may be exceedingly expensive and of little utility to other species. However, more affordable corridors can be built that are both very good for a target species and at least useful for other species.

When considering single-species corridor optimization, it is also important to address dispersal model uncertainty. The model of grizzly bear resistance to gene flow assumes strong habitat and road effects; the wolverine model is more general. Therefore, modeled grizzly bear corridor resistance is much more sensitive to acquisition decisions; relative to wolverines, one can achieve greater optimization at less cost. Still, although dispersal patterns for grizzly bears have been intensively studied, landscape-resistance models for grizzly bears are beset with uncertainties. Given this, it is reasonable to ask whether the opportunity costs and lack of multispecies utility associated with any model-based optimal single-species corridor is commensurate with the knowledge levels that underlie the applied dispersal model. An additional option would therefore be to include a naturalness-based corridor (Krosby et al. 2015).

We could not determine whether the paths in the corridor designs we obtained would be usable by the species or whether the corridors' cumulative resistance would be too high for successful dispersal because little is known about resistance limits on dispersal. Our ecological constraints on admissibility of cells for pair connectivity provided a mechanism for incorporating explicit constraints in the mathematical model to cap the allowed effective resistance of any path when such knowledge becomes available. We made relative comparisons to illustrate how our solution framework can be used to support decision making and trade-off analysis.

The proof of concept we present here suggests several improvements. Although computing times are not exorbitant, they are high relative to unconstrained linkage algorithms for least-resistance paths alone (e.g., Dijkstra's algorithm). However, computing time can be reduced by limiting the solution space prior to solving the

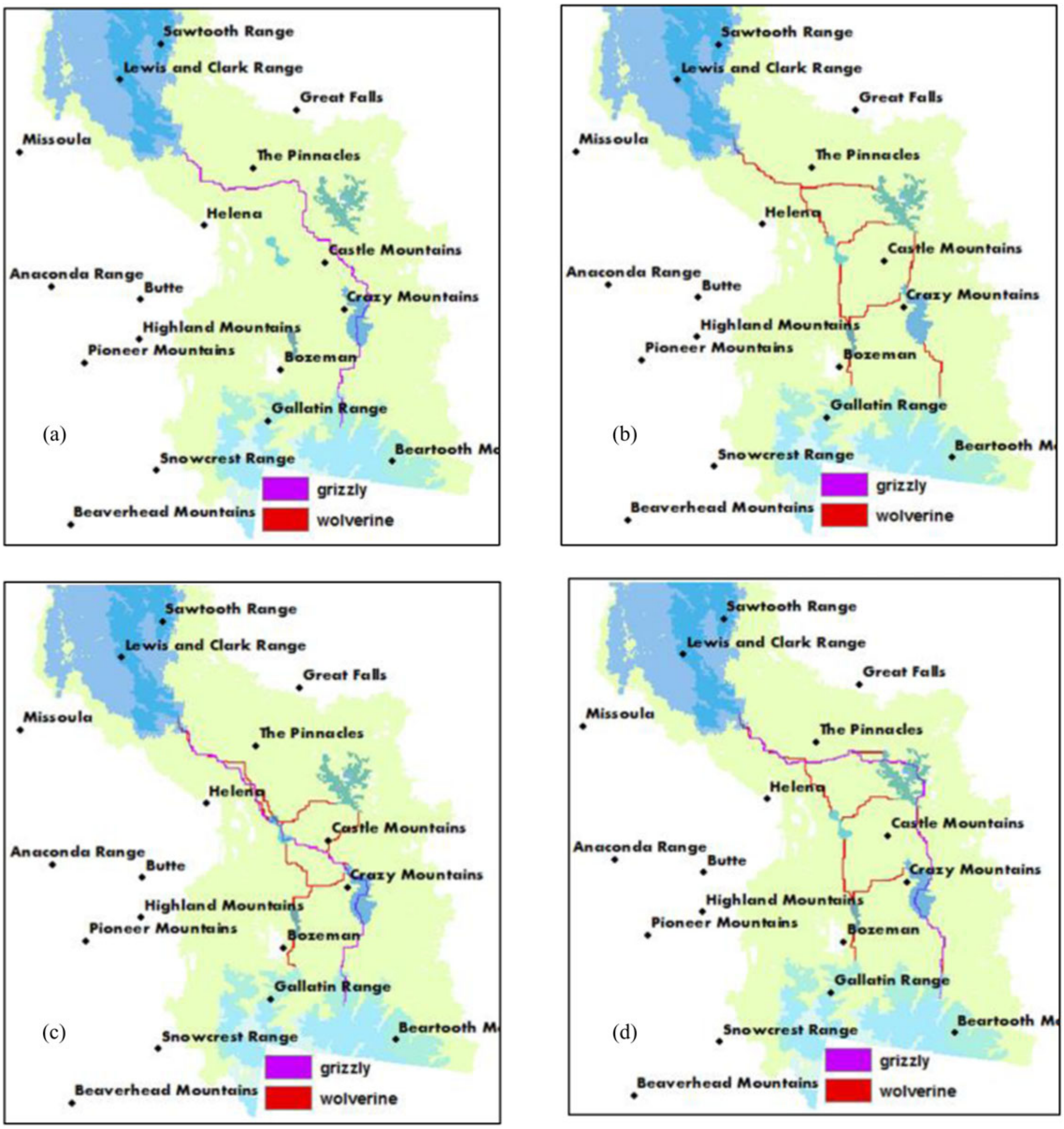

Figure 5. Corridor designs with a budget of US$4 million when optimizing for (a) grizzly bears only, (b) wolverines only, (c) both grizzly bears and wolverines with higher priority for grizzly bears at α = 0.7, and (d) both grizzly bears and wolverines with lower priority for grizzly bears at α = 0.3.

joint optimization problem. For example, we limited the solution space to paths with no more than a 50% increase in effective resistance relative to the least-resistance path for a core-area pair. Further constraints, for example, defining the maximum possible resistance distance for dispersal, could further reduce computing time.

We can conceive of 2 obvious refinements of our current model. First, in the current implementation, for a given core-area pair, the effective connectivity of the pair was measured along a path starting at a border cell of 1 core area and ending at a border cell of the other core area. In other words, we essentially ignored the strategic position of the border cell with respect to the other cells in the core area. To address this, resistance values of the cells internal to a core area could be used to calculate cumulative resistance of moving from points within the core area to different border nodes so that some exit or entry points on the core area border are preferred over others in the solutions. Second, least-resistance path algorithms ignore the context of the path. In the problem presented here, where the acquisition of properties is anticipated, additional uncertainties emerge because of vagaries associated with acquiring properties or easements. Pixels with a high value of ecological connectivity that are adjacent to other high-value pixels could be given lower resistance scores, which would prioritize paths with greater width or redundancy should specific acquisitions fail.

Connectivity modeling that uses least-resistance path or similar algorithms across GIS-based resistance surface has become a popular approach for assessing connectivity at many scales in conservation biology. However, the implementation of this approach across large landscapes has been limited. We believe that formal incorporation of social science and economics in the modeling efforts, as illustrated by our approach, could increase adoption of connectivity planning. Our case study showed the biological and economic advantages of integrating expenditure and multiple-species considerations in connectivity modeling. As this modeling demonstrates, ignoring budget constraints leads to extremely expensive solutions that are only marginally better than much less expensive alternatives. Similarly, ignoring species prioritization, which generally has a large social component, can lead to less efficient and more expensive connectivity solutions.

Management within protected areas may be relatively independent of economic opportunity costs and societal priorities. However, connectivity between protected reserves will mostly occur on private lands and in anthropogenically modified landscapes. Our approach provides a practical, transparent solution to the problem of providing connectivity between reserves that can be used at multiple scales, from evaluating local easement options to developing national strategies.

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Supporting Information

The specifications of the single-species BCD problem and boundary solutions (Appendix S1) and the construction of the grizzly bear and wolverine resistance layers (Appendix S2) are available online. Queries (other than absence of the material) should be directed to the corresponding author.

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