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Evaluating the sufficiency of protected lands for maintaining wildlife population connectivity in the U.S. northern Rocky Mountains

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ABSTRACT

Aim The goal of this study was to evaluate the sufficiency of the network of protected lands in the U.S. northern Rocky Mountains in providing protection for habitat connectivity for 105 hypothetical organisms. A large proportion of the landscape falls into one of several categories of protected lands. However, protected lands in the region are primarily higher elevation forest and mountain habitats. Little is known about how the network of protected lands may maintain connectivity for a broad spectrum of species expressing different habitat requirements and dispersal abilities.

Location The study was conducted across the states of Montana and northern Idaho, USA, comprising an area of 30.2 million hectares.

Methods We used resistant kernel modelling to map the extent of the study area predicted to be connected by dispersal for each of 35 species groups with different ecological associations. We evaluated the effect of vagility on protected area sufficiency by varying dispersal ability across three levels for each species group. We evaluated the degree of vulnerability of each of the 105 hypothetical species (35 species groups × 3 dispersal abilities) in terms of the extent of the total study area predicted to be connected by dispersal. We defined nine categories of risk as the combination of species vulnerability because of the extent of connected habitat and the degree to which that habitat was protected.

Results We found high variation in the vulnerability of species because of the extent of connected habitat, and the extent to which connected habitat overlapped protected lands. Species associated with high elevations and species associated with lower elevations were predicted to have limited extent of connected habitat. Species associated with high elevations were predicted to have the vast majority of their connected habitat protected by federal Forest Service and National Park Service lands. In contrast, species associated with lower elevations were poorly protected by the existing network of protected lands.

Main conclusions Low elevation and non-forest habitats are at highest risk of human-induced habitat loss and fragmentation in the study area. Conservation efforts in the region may be most effective if they focus on expanding the network of lower elevation protected lands in such a way that maximizes connectivity across the landscape.

Keywords
Connectivity, dispersal threshold, gap analysis, protected lands.

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INTRODUCTION

Many researchers have attempted to assess the sufficiency of protected areas in supporting viable populations of native species. Early efforts focused on the relationships between the extent of a protected area the number of species expected to be found there (MacArthur & Wilson, 1967; Diamond, 1975). All other things being equal, species richness will be higher and extinction rates lower in large protected areas (MacArthur & Wilson, 1967). However, all other things are rarely equal, and area alone has been shown to be an insufficient indicator of the effectiveness of reserve networks (Patterson & Atmar, 1986). For example, the effectiveness of protected lands in providing for viable populations of native species may be highly influenced by the degree to which dispersal is enabled among patches of occupied habitat (Wilcox & Murphy, 1985; Hanski & Ovaskainen, 2002). A full assessment of the effectiveness of any network of reserves requires both consideration of the extent of protected habitat as well as the impacts of habitat fragmentation on population connectivity (Fahrig 2003). More recently, much attention has focused on assessing the functional connectivity of reserve networks, under the assumption that single isolated reserves will be unable to provide long-term viability because of demographic stochasticity, genetic drift and environmental fluctuations (Briers, 2002; Cabeza, 2003).

Effective broad-spectrum biodiversity conservation also requires that conservation strategies simultaneously meet the needs of multiple species (Nicholson & Possingham, 2006; Regan *et al.*, 2007). A well-connected reserve system covering a broad range of environments is often proposed as an efficient structure for maintaining most species (Noss 1983; Hunter *et al.* 1988). The assumption that protecting a particular set of habitats will effectively conserve any particular species has rarely been evaluated, however. Cushman *et al.* (2008) found that coarsely defined habitat characteristics were poor predictors of species occurrence across broad landscapes, suggesting that coarse-filter approaches to species conservation should be carefully evaluated based on how they address the ecological needs of the individual species. Other researchers have proposed using large and wide-ranging species as umbrellas for habitat and connectivity protection plans (Noss *et al.*, 1996; Carroll *et al.*, 2001). However, these species are generally highly mobile habitat generalists and thus likely will be inadequate umbrellas for other species (Beier *et al.* 2009; Minor and Lookingbill 2010). In addition, Cushman *et al.* (2010a,b) argue that it may often be ineffective to use the ecological associations required by one species as an indicator of habitat quality or ecosystem health from the perspective of another. Thus, the performance of any conservation reserve network in providing habitat for a large suite of species should be evaluated by formally considering how the network meets the needs of each species individually.

The U.S. northern Rocky Mountains contain one of the most extensive networks of protected lands in the world (Noss *et al.*, 1996; Chambers *et al.*, 2010). The U.S. Federal Government manages approximately half of the landbase, with a high proportion of that given strict protection as designated roadless or congressionally withdrawn Wilderness areas (National Atlas of the United States 2006). These protected lands provide for the habitat and population connectivity needs of many native plant and animal species (Hansen *et al.*, 2005). However, protected lands in the region are primarily higher elevation forest and mountain habitats (Hansen *et al.*, 2002). Little is known about how well the existing network of protected lands maintains connectivity for a diverse set of taxa that express a range of habitat requirements and dispersal abilities.

Recent patterns of land use change have led to concentrated development in lower elevation valley bottom locations (Brown *et al.*, 2005; Compas, 2007; Gude *et al.*, 2007; Jarvis, 2008). Increasing housing density (Hansen *et al.*, 2005) and expansion of the road and highway network (Forman & Alexander, 1998) may increase the isolation of blocks of higher elevation protected habitat and may directly threaten taxa associated with lower elevation habitats. As a result, the current pattern of development in the northern Rocky Mountains may result in reduced connectivity among core protected areas and high fragmentation of habitat of species associated with low elevation habitats. For these species, the matrix of unprotected lands may be essential for their continued viability (Scott *et al.*, 2001).

The primary goal of this study is to evaluate the degree to which the network of protected lands in the U.S. northern Rocky Mountains provides population connectivity for a large number of hypothetical species. Our work is designed to accomplish five specific objectives. First, we estimate the extent of the study area predicted to be connected for a large number of hypothetical species to identify those most limited by available dispersal habitat. Second, we quantify the sufficiency of existing protected lands to provide connectivity for each species and identify those species that appear to be well protected and those that are least protected. Third, we quantify the effects of different habitat requirements and dispersal abilities on sufficiency of the existing protected lands network. Fourth, we evaluate conservation risk across a large number of hypothetical species resulting from the combination of extent of connected habitat and the degree of protection of that habitat. Finally, we provide specific conservation recommendations to mitigate protection gaps for the most vulnerable species.

METHODS

Study area

The study area includes 30.2 million hectares of Montana and northern Idaho in the United States Rocky Mountains (Fig. 1). Federally owned lands comprise 44% of the study area, of which 3.5 million hectares are designated roadless, and 2.8 million hectares are designated Wilderness areas. The human population in the study area is growing more rapidly than many areas of the USA (Mackun & Wilson, 2011), with

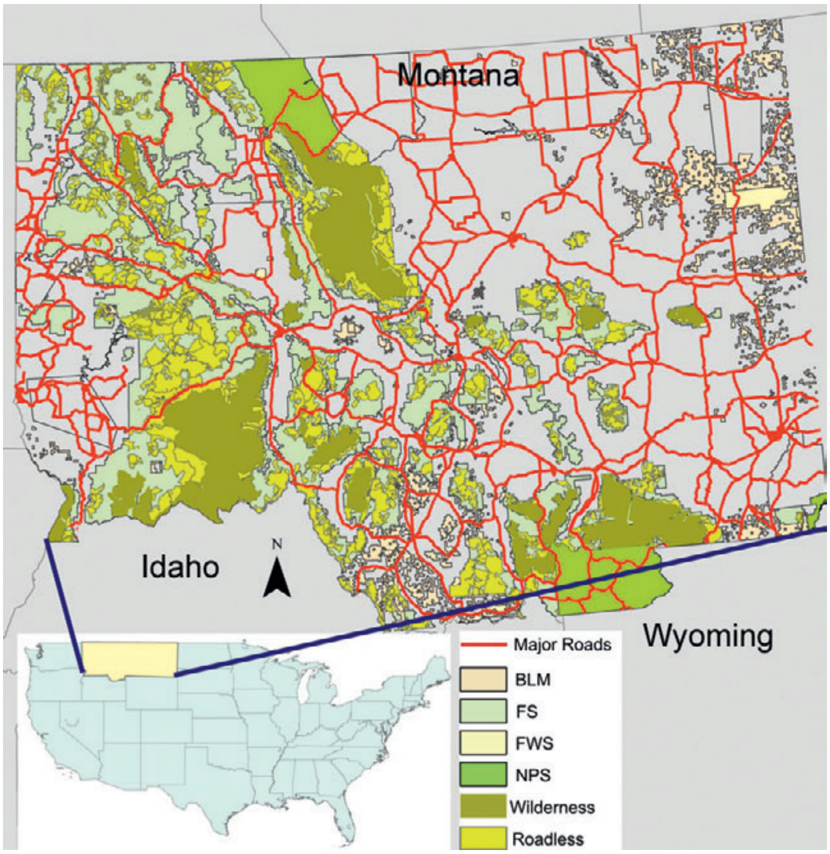

Figure 1 Study area orientation map. The study area consists of the state of Montana and the northern third of Idaho. Land management designations, including Wilderness, national park, designated roadless and other federal lands are indicated in different colours. Federal and state highways are shown in red. BLM, Bureau of Land Management; FS, U.S. Forest Service; FWS, U.S. Fish and Wildlife Service; NPS, National Park Service.

ongoing development concentrated in low elevation valley locations (Gude *et al.*, 2006; Jarvis, 2008). In addition, there are over 16,000 km of state, federal and interstate highways bisecting the study area, which likely have large impacts on regional population connectivity for many species (Forman & Alexander, 1998).

Our analysis focuses on quantifying the intersection of connected habitat with three levels of protected lands. The first level of land protection includes all federally owned lands, which provide protection from residential and urban development, but variable protection from resource extraction activities. The second level of protected lands includes designated roadless, Wilderness and National Parks. This provides a considerably higher level of protection, with most resource extraction activities prohibited. However, designated roadless areas, while currently protected, have relatively weak statutory protection. Thus, the third level of protection consists of the lands with the strongest statutory protection, including congressionally designated Wilderness areas and National Parks.

Resistance surfaces

Quantitative analysis of population connectivity often uses landscape-resistance models to reflect constraints on organism movement as functions of multiple variables (Cushman *et al.*, 2006; Spear *et al.*, 2010). The pixel values in the resistance surface represent the unit cost of crossing each pixel (Fig. 2). These resistance models are essential foundations for applied analyses of population connectivity and permit spatially explicit identification of corridors and barriers. We defined 35 resistance surfaces for analysis from the pool of models evaluated in Cushman *et al.* (2006; Fig. 2). The selected landscape-resistance models represent combinations of the effects of three landscape features on resistance to movement: elevation, roads and forest cover (Cushman *et al.*, 2006). Resistance of these features was modelled across four levels for elevation and three levels for roads and forest (Table 1). The four levels for the feature elevation (E) consisted of a null model (En), in which there was no penalty for elevation in the resistance surface, and three inverse-Gaussian resistance models, with minimum resistance of one at 500 (El), 1000 (Em) and 1500 m (Eh) elevation above sea level respectively, 500 m standard deviation, and maximum resistance of 10 (e.g. maximum resistance 10 times minimum resistance; Cushman *et al.*, 2006). Similarly, three levels of the forest cover feature were modelled. The first level was the null model (Fn) in which forest cover had no effect in the resistance surface. The remaining two levels were models in which we posited that landscape resistance is least in closed canopy forest and linearly increases in non-forest cover types. In the forest high (Fh) level, we stipulated high relative resistance for crossing non-forest cover types, representing a condition where an individual species strongly favours movement through forest, while in

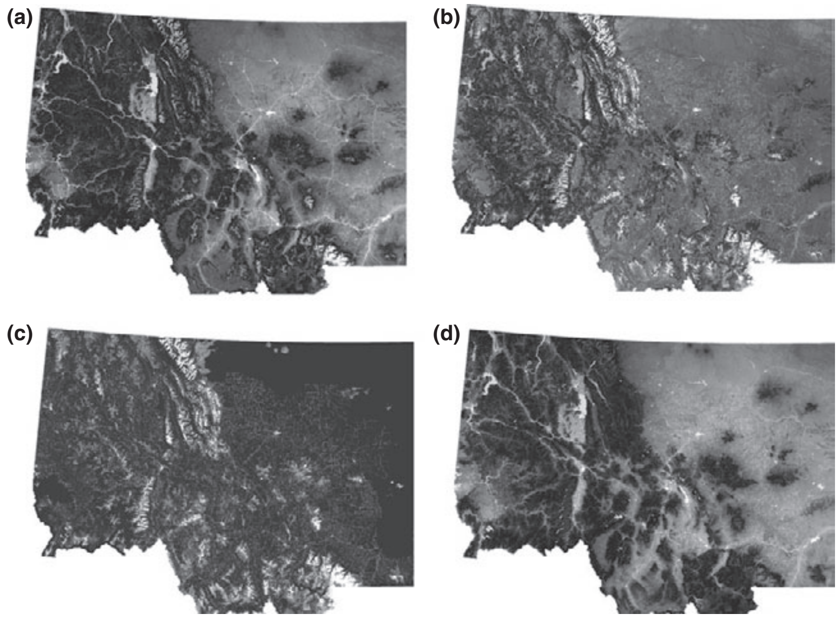

Figure 2 Example of four resistance maps used in the analysis. (a) Model 21, FhEmRh; (b) model 19, FhElRh; (c) model 9, FnElRh; (d) model 17, FhEhRh. Dark areas are low resistance (black = resistance 1), and light areas are high resistance (white = resistance 62).

Table 1 Description of factors and levels combined to create 35 landscape-resistance hypotheses.

Factor	Level	Code	Description
Landcover	High selectivity	Fh	Low-resistance forest; high-resistance non-forest
	Low selectivity	Fl	Low-resistance forest; moderate-resistance non-forest
	Null	Fn	No relationship with landcover classes
Elevation	High elevation	Eh	Minimum resistance at high elevation
	Middle elevation	Em	Minimum resistance at middle elevation
	Low elevation	El	Minimum resistance at low elevation
	Null	En	No relationship with elevation
Roads	High resistance	Rh	High resistance because of roads
	Low resistance	Rl	Low resistance because of roads
	Null	Rn	No relationship with roads

Table 2 Landcover classes and resistance values used to develop resistance surfaces.

Cover class	Resistance in Fl	Resistance in Fh
Urban, water	10	10
Water	10	10
Surface mining	7	10
Shrub flats	7	8
Rock	6	6
Agricultural, snowfields or Ice	5	7
Snowfields or ice	5	6
Mixed barren lands	4	6
Alpine meadow, shrub-dominated riparian, grass-dominated riparian, wetlands, mesic upland shrub, xeric upland shrub subalpine meadow	3	6
Clearcut Conifer, Burned Forest	2	4
Forest-dominated riparian, aspen, ponderosa pine, lodgepole pine, western red cedar, western hemlock, mixed conifer, mixed subalpine forest, mixed whitebark pine	1	1

Fl – Low selectivity for forest; Fh – high selectivity for forest (see Table 1).

the forest low (Fl) level, non-forest classes have lower landscape resistance (Table 2). Finally, three levels for the roads (R) were used, consisting of a null model (Rn) where there was no effect for resistance of roads, a model with relatively strong effect of roads on resistance (Rh), and a model with relatively lower effect of roads on resistance (Rl; Table 1). The landscape-resistance models corresponding to each feature and level were combined into the 35 landscape-resistance models by addition, as in Cushman *et al.* (2006). To improve computational efficiency, the 35 resistance models were resampled from 30 to 270 m pixel size by bilinear interpolation. Cushman & Landguth (2010) showed that connectivity models are robust to grain coarsening. We equate these resistance models to hypothetical species groups to frame our identification of vulnerable species and conservation recommendations.

Resistant Kernel modelling

Pixel-level resistance to movement does not provide sufficient information to evaluate the strength and location of barriers and corridors. The resistance model is the foundation for these analyses, but it is the explicit consideration of connectivity across the resistance surface that provides key information for conservation and management (Cushman *et al.*, 2008). We utilize a resistant kernel approach (Compton *et al.*, 2007) for predicting habitat connectivity for each of our 35 resistance models (i.e. hypothetical species groups). The resistant kernel approach to connectivity modelling is based on least cost dispersal from a defined set of source locations cumulatively across a landscape. The sources in our case are all pixels in the study area with resistance of 1 (lowest resistance and highest quality dispersal habitat) for each of the 35 resistance models. This assumes that dispersing organisms originate from all cells of optimal dispersal habitat, and that no dispersers originate from suboptimal dispersal habitat.

The resistance surface values are used as weights in the dispersal function, such that the expected density of dispersing organisms in a pixel is down-weighted by the cumulative cost from the source, following the least cost route (Compton *et al.*, 2007; Cushman *et al.*, 2010a,b). We wrote an ESRI ArcGrid script to calculate the resistant kernel (Rk) density. The analysis begins with the specification of a resistance model describing the cost of movement across each location in the study area (Fig. 3a). The model then selects a single source cell and uses the ArcGrid COSTDISTANCE function to produce a map of the movement cost from that source up to a specified dispersal threshold on the specified resistance map. The cost distance from the source is converted to an estimate of relative density by applying the dispersal function. The dispersal function utilized in our analyses predicts that the relative density of dispersing individuals decreases linearly with cumulative movement cost away from the source, up to the maximum dispersal ability of the species. Expected relative density of dispersing individuals is calculated by inverting the cumulative movement cost grid and scaling such that the maximum value for each individual kernel is one. Thus, a relative density of 1 is given to the source location itself and decreases to 0 at the maximum dispersal cost threshold (Fig. 3b). The model iteratively calculates expected relative density of dispersers from all source cells. Then, the kernels surrounding all sources are then summed to give the total expected relative density at each pixel across the full landscape (Fig. 3c). The results of the model are surfaces of expected density (relative to that of an isolated source cell) of dispersing organisms at any location in the landscape. The analyses in this study are based on the extent of the landscape that is predicted to be connected by the cumulative kernels. To facilitate these analyses, we reclassified the cumulative kernel maps to a value of 1 for all cells with non-zero cumulative kernel value (Fig. 3d). We defined all areas with value 1 in these reclassified maps as connected habitat (CH).

We wished to bracket the range of dispersal abilities of most animal species in the study area. Accordingly, we ran the models for each of the 35 resistance models across three levels of dispersal ability (D), corresponding to maxima of the COSTDISTANCE function of 5000, 10,000 and 20,000 cost units. These reflect dispersal abilities in optimal habitat that range from 5 to 20 km. Optimum habitat would have minimum resistance (a value of 1) and the dispersal kernel in such habitat would be conical in shape with a value of 1 at the source cell, with values decreasing linearly with distance, and reaching a value of 0 at the maximum dispersal distance. In heterogeneous habitat, the dispersal kernel will be reduced in extent as a function of cumulative cost away from the source cell in all directions, as the cumulative maximum cost distance will be reached in different geographical distances in each direction (as seen in Fig. 3b). The combination of 35 resistance models (Table 1) and three dispersal abilities (5000, 10,000, 20,000) define the full set of 105 hypothetical species we simulate in this analysis. Kernel connectivity maps for four of the 105 hypothetical species are shown for illustration in Fig. 4.

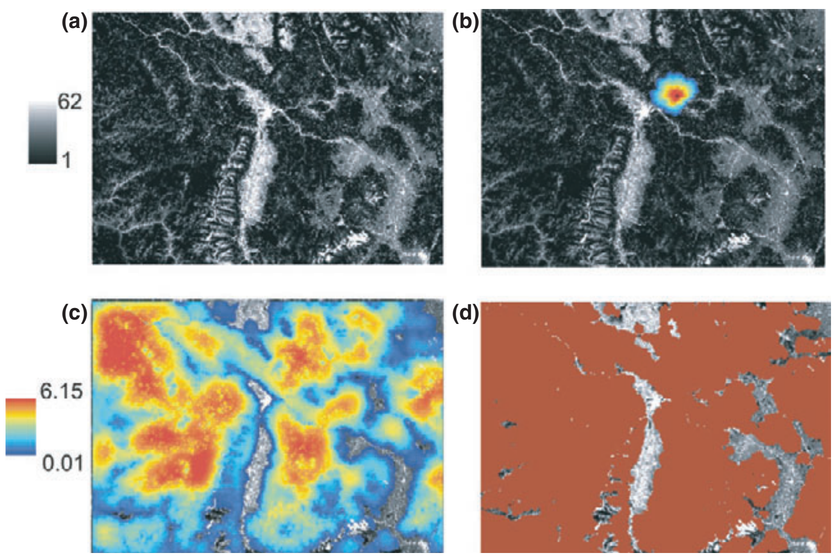

Figure 3 Example of the application of the resistant kernel method to predict extent of connected habitat at the 10-km dispersal threshold. (a) Resistance model 21, FhEmRh, centred over a region near Missoula, MT, (b) a single resistant kernel prediction of disperser density from a single source point near Gold Creek MT, (c) cumulative resistant kernel predicting relative disperser density in all cells, from origin cells of resistance 1, (d) binary representation of connected habitat.

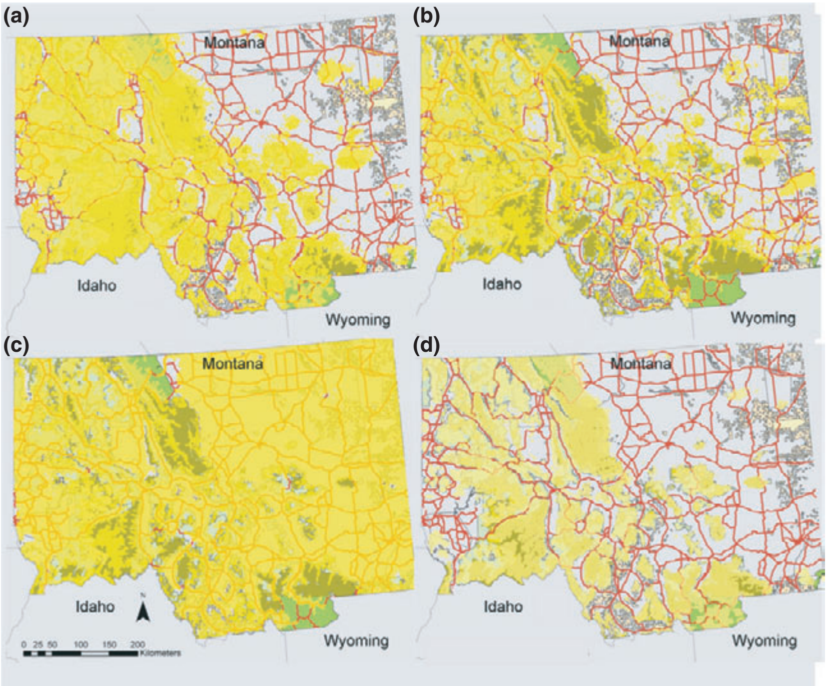

Figure 4 Example of four maps of predicted connected habitat at the 10-km dispersal threshold, overlain on the protected areas and roads map shown in Figure 1. Yellow areas correspond to predicted connected habitat. (a) Model 21, FhEmRh; (b) model 19, FhElRh; (c) model 9, FnElRh; (d) model 17, FhEhRh.

Intersection analysis

We propose that vulnerability of species to habitat loss and fragmentation is primarily a function of the extent of connected habitat (Fahrig 2003). We further propose that the degree of formal protection of habitat for a species can mitigate that vulnerability, reducing risk of population declines or extirpation. We evaluate degree of protection and resulting conservation risk for the 105 hypothetical species through a series of GIS intersection analyses. We computed the spatial intersection of predicted connected habitat (CH) for each of the 105 species with each of the three categories of protected lands (PL) two different ways. First, we computed the intersection as a per cent of the overall landscape area (LA) as (CH∩PL)/LA to gauge the overall commonness or rarity of protected connected habitat within the landscape. We name this intersection 'percent of overall landscape that is connected' and is our index of vulnerability. Second, we computed the intersection as a per cent of connected habitat area as (CH∩PL)/CH to determine the proportion of connected habitat that was protected regardless of how common or rare connected habitat was within the landscape. We name this intersection 'percent of connected habitat that is on federal lands' and is our index of degree of protection. The extent of the spatial intersection was estimated separately for each of the protected land categories. We identified which species had the highest and lowest per cent overlap with the different classes of protected areas.

We defined three levels of vulnerability based on the total proportion of the landscape covered by connected dispersal habitat across species. The levels were as follows: (1) high vulnerability – < 50% of the landscape extent; (2) intermediate – between 50% and 75% of the landscape; (3) low vulnerability – over 75% of the landscape is covered by connected dispersal habitat. We defined three levels of protection of this connected habitat: (1) low protection – < 25% of connected habitat intersected with protected lands; (2) intermediate – between 25% and 75% of connected habitat covered by protected lands; (3) high protection – over 75% of connected habitat protected. We propose that the combination of degree of vulnerability and degree of protection equates to the degree of risk posed by habitat loss and fragmentation. For example, a species with very high extensiveness of connected habitat is at low risk of negative effects of habitat loss and fragmentation, regardless of the degree of protection afforded to its habitat. Similarly, a species with relatively low extensiveness of habitat, but for which nearly all habitat is protected, is also at low risk. In contrast, a species whose habitat is both limited in extensiveness and poorly protected is at high risk to negative effects of habitat loss and fragmentation. We define nine categories of vulnerability and protection, each with an associated level of risk (Table 3).

Table 3 Nine categories of vulnerability and protection, with associated levels of risk to negative effects of habitat loss and fragmentation.

	Protection		
Vulnerability	< 25%	25–75%	> 75%
< 50%	High	Med	Low
50–75%	Med	Med	Low
75–100%	Low	Low	Low

RESULTS

Extent of connected habitat across species

There was high variability in the extent of the study area connected by dispersal across the 35 hypothetical species groups and three dispersal abilities (Fig. 2; Table 4). Across dispersal abilities, models 25, 32, 33, 34 and 35 had the highest predicted extent of connected habitat as a proportion of the study area (all over 85%, Table 4). These models correspond to species that can move equally well at all elevations and are not constrained to move only within forest cover. Conversely, models 2, 7, 8, 17, 18, 19, 20, 26, 28 and 29 had the lowest extensiveness of connected habitat in the study area (all < 30% of the study area at a 5000 m dispersal ability). The five models with the lowest extensiveness of connected habitat (models 7, 19, 20, 28 and 29) are those for organisms that have highest movement ability in lower elevation forest habitat. The next three models with lowest extensiveness of connected habitat reflect those organisms that have their highest density and movement ability in high elevation forest habitat (models 2, 17 and 18).

Table 4 Description of landscape-resistance models used in the analysis and extent of connected habitat under each model at four dispersal thresholds.

Model Number and acronym		Model description	Per cent 5 km	Per cent 10 km	Per cent 20 km
1	FnEhRn	Minimum resistance at high elevations (1500 m)	0.360	0.438	0.526
2	FhEhRn	Minimum resistance in forest (strong) at high elevations	0.298	0.382	0.465
3	FlEhRn	Minimum resistance in forest (weak) at high elevations	0.307	0.393	0.477
4	FnEhRh	Minimum resistance at high elevations with high resistance of roads	0.353	0.431	0.520
5	FnEhRl	Minimum resistance at high elevations with weak resistance of roads	0.354	0.432	0.521
6	FnElRn	Minimum resistance at low elevations (500 m)	0.760	0.836	0.910
7	FhElRn	Minimum resistance at in forest (strong) at low elevations	0.274	0.405	0.568
8	FlElRn	Minimum resistance in forest (weak) at low elevations	0.299	0.453	0.640
9	FnElRh	Minimum resistance at low elevations with high resistance of roads	0.750	0.830	0.907
10	FnElRl	Minimum resistance at low elevations with weak resistance of roads	0.751	0.831	0.907
11	FnEmRn	Minimum resistance at middle elevations (1000 m)	0.798	0.857	0.901
12	FhEmRn	Minimum resistance in forest (strong) at middle elevations	0.449	0.535	0.617
13	FlEmRn	Minimum resistance in forest (weak) at middle elevations	0.470	0.566	0.656
14	FnEmRh	Minimum resistance at middle elevations with high resistance of roads	0.789	0.853	0.900
15	FnEmRl	Minimum resistance at middle elevations with weak resistance of roads	0.791	0.854	0.900
16	FhEnRn	Minimum resistance in forest (strong)	0.541	0.624	0.726
17	FhEhRh	Minimum resistance in forest (strong) at high elevations with high resistance of roads	0.290	0.376	0.458
18	FhEhRl	Minimum resistance in forest (strong) at high elevations with weak resistance of roads	0.291	0.377	0.460
19	FhElRh	Minimum resistance in forest (strong) at low elevations with high resistance of roads	0.256	0.390	0.554
20	FhElRl	Minimum resistance in forest (strong) at low elevations with weak resistance of roads	0.259	0.393	0.556
21	FhEmRh	Minimum resistance in forest (strong) at middle elevations with high resistance of roads	0.437	0.529	0.611
22	FhEmRl	Minimum resistance in forest (strong) at middle elevations with weak resistance of roads	0.439	0.530	0.612
23	FhEnRh	Minimum resistance in forest (strong) with high resistance of roads	0.531	0.615	0.718
24	FhEnRl	Minimum resistance in forest (strong) with low resistance of roads	0.533	0.617	0.719
25	FlEnRn	Minimum resistance in forest (weak)	0.877	0.955	0.989
26	FlEhRh	Minimum resistance in forest (weak) at high elevations with high resistance of roads	0.299	0.386	0.471
27	FlEhRl	Minimum resistance in forest (weak) at high elevations with weak resistance of roads	0.300	0.387	0.472
28	FlElRh	Minimum resistance in forest (weak) at low elevations with high resistance of roads	0.280	0.436	0.626
29	FlElRl	Minimum resistance in forest (weak) at low elevations with weak resistance of roads	0.283	0.438	0.628
30	FlEmRh	Minimum resistance in forest (weak) at middle elevations with high resistance of roads	0.458	0.559	0.650
31	FlEmRl	Minimum resistance in forest (weak) at middle elevations with weak resistance of roads	0.460	0.560	0.651
32	FlEnRh	Minimum resistance in forest (weak) with high resistance of roads	0.861	0.950	0.987
33	FlEnRl	Minimum resistance in forest (weak) with low resistance of roads	0.864	0.951	0.987
34	FnEnRh	High resistance of roads	0.997	1	1
35	FnEnRl	Weak resistance of roads	0.998	1	1

Model description provides information on what landscape variables are included in each model. Per cent 5 km – percentage of the study area occupied by connected dispersal habitat for each resistance model given a 5-km dispersal threshold; Per cent 10 km – percentage of the study area occupied by connected dispersal habitat for each resistance model given a 10-km dispersal threshold; Per cent 20 km – percentage of the study area occupied by connected dispersal habitat for each resistance model given a 20-km dispersal threshold.

Degree of protection by three categories of federal lands

There was high variability in the degree of protection federal lands provided to habitat connectivity depending on the species group, dispersal ability and which category of protected lands was considered (Fig. 5). Models 2, 3, 17, 18, 26 and 27 had the highest proportional overlap with federal ownership (all over 80% at the 10-km dispersal threshold; Fig. 5). All six of these models are for species with their highest density and movement ability within high elevation forest habitat. In contrast, models 6, 8, 9, 10, 11, 14, 15, 25, 28, 29, 32, 33, 34 and 35 had the lowest percentage of connected habitat overlapping federal ownership (all < 50% at the 10-km dispersal threshold; Fig. 5). These are hypothetical species that have their highest density or movement ability at lower elevations.

The average intersection of connected habitat with protected lands at the next higher level of protection, consisting of designated roadless, Wilderness or National Parks, decreased by nearly 50% (31.6% of the study area at 10 km dispersal ability; Fig. 5). Models 2, 3, 17, 18, 26 and 27, corresponding to species associated with high elevation forest, remained among those with the highest overlap with protected areas (all more than 50% at the 10-km dispersal threshold; Fig. 5). Models 6, 8, 9, 10, 28 and 29 were those with the lowest proportional overlap with second-level protected lands (all < 20% at the 10-km dispersal threshold), corresponding to species preferring lower elevations with no or weak association with forest cover.

The average intersection of connected habitat with protected lands at the highest level of protection (Wilderness or National Parks) decreased by an additional 50% (15.5% of the study area extent at the 10-km dispersal threshold; Fig. 5). Models 1, 2, 3, 4, 5, 17, 18, 26 and 27 had the largest proportional intersection with the highest level of protected lands (all between 24% and 26% at the 10-km dispersal threshold). These species are associated with the highest elevations. In contrast, models 6, 7, 8, 9, 10, 19, 20, 28 and 29 all had < 10% of the area of connected habitat intersecting Wilderness or National Parks. These are all species that are strongly associated with lower elevations and not associated, or only weakly associated, with forest cover.

Risk is a combination of vulnerability and protection

There is a strong interaction between dispersal ability and degree of risk. At the 5-km dispersal threshold, 0 species were at high risk and 16 at moderate risk when evaluated based on Category I protected lands; 6 were at high risk and 19 at moderate risk evaluated based on Category II protected lands; and 12 were at high risk and 13 at moderate risk based on Category III protected Lands (Table 5). The number of high risk species declined as dispersal ability increased (Table 5). At the 20-km dispersal threshold, 0 species were at high risk and 18 at moderate risk when evaluated based on Category I protected lands, 0 were at high risk and 24 at moderate risk evaluated based on Category II protected lands, and six were at high risk and 18 at moderate risk based on Category III protected Lands (Table 5).

DISCUSSION

Major implications

There are two major implications of our findings. First, there is a dramatic difference in the sufficiency of the existing network of protected lands depending on the habitat associations of the focal species. Species associated with high elevation habitats, such as American marten (*Martes americana*; Wasserman *et al.*, 2010) and wolverine (*Gulo gulo*; Schwartz *et al.*, 2009), are well protected by existing protected lands. This is encouraging, because a number of recent studies have raised concerns that climate change will reduce the area and further fragment the connectivity of these habitats (Murphy & Weiss, 1992; Schwartz *et al.*, 2009; Shirk *et al.*, 2010; Wasserman *et al.*, 2010). Climate change poses a threat to habitat quality and connectivity of these species, with suitable bioclimatic conditions likely to move up the elevation gradient, which will reduce habitat area and increase fragmentation (e.g. Wasserman *et al.*, 2011).

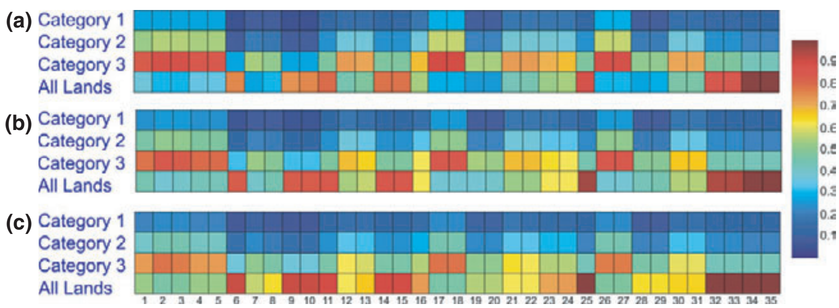

Figure 5 Per cent overlap between connected habitat in each of the 35 resistance models and three classes of land protection (Category I: all federal ownership; Category II: roadless/wilderness/national park; Category III: wilderness or national park), across three dispersal thresholds (a, 5 km; b, 10 km; c, 20 km). The bottom row (percentage of landscape) in each block provides the percentage of the entire study area covered by connected habitat in that resistance model and dispersal threshold. The top three rows provide the percentage of the area covered by connected habitat in each resistance model that overlaps the three levels of protected lands.

Table 5 Risk table for the 105 hypothetical species (35 resistance associations across three dispersal abilities (5000, 10,000, and 20,000 m) Risk can be a considered a function of two factors, vulnerability, in terms of the amount of connected habitat in the landscape, and protection, in terms of the degree to which connected habitat is protected. Cells shaded dark grey are considered high risk because of both low area of connected habitat and a low degree of protection for that habitat. Cells shaded middle grey are considered to be moderately at risk, due to intermediate degrees of habitat extensiveness and protection. Cells shaded light grey are considered to be low risk due to high habitat extensiveness or high degree of protection or both. In each cell combination of Vulnerability and Protection status the number of hypothetical species in each dispersal ability are separated by commas in order from lowest to highest dispersal ability (5000, 10,000, 20,000 m).

	Protection		
Vulnerability	< 25%	25–75%	> 75%
Category I: All federally-owned lands			
< 50%	0, 0, 0	12, 6, 0	9, 9, 6
50–75%	0, 0, 0	4, 9, 18	0, 0, 0
75–100%	0, 0, 0	10, 11, 11	0, 0, 0
Category II: Roadless Areas, Wilderness Areas, and National Park			
< 50%	6, 6, 0	15, 9, 6	0, 0, 0
50–75%	1, 0, 6	3, 9, 12	0, 0, 0
75–100%	10, 11, 11	0, 0, 0	0, 0, 0
Category III: Wilderness Areas, and National Park			
< 50%	12, 9, 6	9, 6, 0	0, 0, 0
50–75%	4, 9, 18	0, 0, 0	0, 0, 0
75–100%	10, 11, 11	0, 0, 0	0, 0, 0

However, these lands seem to be vulnerable to relatively few other anthropogenic threats, given their high degree of strict protection.

Protected lands in the northern Rocky Mountains are concentrated in higher elevation forested mountains. Our analysis shows that species associated with lower elevations and non-forest habitats are poorly protected by the network of federally owned lands. In addition, the vast majority of recent and expected future land use change and habitat loss is concentrated in the lower elevations (see Hansen & Rotella, 2002; Hansen *et al.*, 2002). All major human population centres are concentrated in the lower elevation portions of the study area, and future expansion of residential, urban and industrial land use will be focused in these portions of the study area (but see Huston, 2005). In addition, the transportation network in the study area is concentrated in lower elevations, with most highways and railroads running along the bottom of major valleys between mountain ranges. Thus, current and future human land use impacts on habitat connectivity are concentrated in the lower elevation portions of the study area, making species associated with these conditions particularly vulnerable. Climate change is also likely to reduce the area and increase the fragmentation of low elevation forest habitats, as lower tree line moves upwards in elevation (Grace *et al.*, 2002). Thus, there is a confluence of stressors on species associated with low elevation habitats, which also are least protected by the existing protected lands network.

The second major implication of our findings is that different categories of protected lands provide dramatically different degrees of protection of dispersal habitat. The lowest category of protection (Category I, all federal lands) provides at least moderate protection for all hypothetical species considered in this study and a high degree of protection for species associated with higher elevations. However, roughly half of the species were poorly protected by Category II protected lands (Wilderness, National Parks and Roadless Areas), and no species were well protected by Category II protected lands. This shows that the multiple-use matrix that comprises the majority of federal lands is immensely important to regional population connectivity for most species. Thus, managers must not assume that existing strict protection of Wilderness areas and National Parks will be sufficient. This is particularly true for those species associated with lower elevations. No species were well protected by Category III protected lands, indicating that roadless areas are a critical element in the conservation effectiveness of the strictly protected lands. If roadless lands are released from strict protection and incorporated into the multiple-use matrix, no species would be well protected, and most species would be poorly protected by strictly protected land designations.

Conservation strategies

Our results suggest several conservation strategies to maximize the preservation of habitat connectivity for the largest number of species. First, given the very limited extent of protected lands at lower elevations (Scott *et al.*, 2001), future conservation acquisitions and restoration efforts should focus on lower elevation habitats. Ideally, these additional low elevation reserves would be optimally located to provide ecological representativeness and network connectivity (Briers, 2002; Cabeza, 2003). In addition, the matrix of not formally protected lands at lower elevations will remain critical to providing habitat and connectivity for species associated with those habitats. Proactive efforts should be made to develop best management practices to maintain habitat quality and connectivity. One way to do this effectively would be to designate habitat corridors (Beier & Noss, 2008) to connect newly established low elevation reserves with the major public lands protected areas at higher elevation.

Several researchers have proposed basing landscape conservation strategies in the Northern Rocky mountains on large carnivore focal species (Noss *et al.*, 1996; Weaver *et al.*, 1996; Carroll *et al.*, 2001). Noss *et al.* (1996) advocated a regional reserve network composed of wilderness core areas, multiple-use buffer zones and optimized corridors linking the core protected areas. Our analysis suggests that the general framework of core protected areas linked by semi-protected corridors is perhaps the best approach to achieve multi-taxa connectivity in the northern Rocky Mountains, but that existing protected public lands are insufficient and additional core areas at lower elevations will be needed. In addition, our analysis suggests that focusing on large carnivores, most of which depend on large, higher elevation core protected areas, may not give sufficient attention to habitats and species at lower elevation and in areas with higher human footprint. Several of the carnivore species of conservation concern in the northern Rocky Mountains, notably Grizzly bear (*Ursus arctos*), are seasonally dependent on low elevation habitats that are poorly protected by existing public lands and reserves.

Recent research has developed robust, empirically based connectivity maps for several large carnivore species in the northern Rocky Mountains. Cushman *et al.* (2006) developed a landscape-resistance map for black bear using molecular genetic data, and Cushman *et al.* (2008) applied factorial least cost path modelling to predict movement corridors across the northern Rocky Mountains. Schwartz *et al.* (2009) used a similar approach to map landscape resistance and movement corridors for wolverine. Wasserman *et al.* (2010, 2011) used an improved method of landscape genetic modelling to predict landscape resistance and movement corridors for American marten under current and future climate scenarios. These recent empirical studies enable an evaluation of the 'umbrella' focal species approach proposed by Noss *et al.* (1996). Specifically, the landscape-resistance models produced by the empirical studies above are included in our 105 hypothetical species. The Cushman *et al.* (2006) bear model is our model 21 (FhEmRh). The Schwartz *et al.* (2009) wolverine model and the Wasserman *et al.* (2010) marten models are the same, model 1 (FnEhRn). Our analysis shows that habitat connectivity for these species is well protected by existing protected areas, and, conversely, that habitat connectivity for a large number of other species associated with lower elevations is not. This suggests that focus on large carnivores and high elevation, low human footprint ecosystems may be a poor strategy in the effort to conserve biodiversity in the northern Rocky Mountains.

Carroll *et al.* (2001) used multivariate habitat modelling to predict habitat suitability for multiple carnivore species and evaluate spatial intersection among quality habitat locations. They concluded that core habitat for many species of carnivore could be conserved simultaneously in large, high elevation core areas, but did not address connectivity among them and the important role of low elevation core habitats and corridors. Connectivity for species associated with high elevation habitats is also critically dependent on protection of lower elevation areas. For example, Cushman *et al.* (2008) predicted keystone movement corridors for American black bear between Yellowstone National Park and the Canadian Border. They found over 20 locations where these corridors were potentially broken or threatened by human land use. Nearly all of these locations were in low elevation valleys. Similarly, Schwartz *et al.* (2009) found that wolverine population connectivity in the Northern Rockies is driven by the extent and linkage of high elevation habitats that hold snow cover late into the spring. They modelled movement corridors across the northern Rockies and found that the most important unprotected movement corridors linking the regional population were located in low elevation valleys between high mountain ranges. Thus, strategic protection of undeveloped low elevation areas will provide critical protection of habitat for species associated with low elevations, and efficient protection of population connectivity for species associated with high elevation mountains.

Scope and limitations

Our analysis makes several assumptions that should be considered in interpreting the results. First, we model habitat connectivity for 105 hypothetical organisms with different ecological associations and dispersal abilities. It is unknown the degree to which these hypothetical species reflect the landscape-resistance properties of the full range of real native species in the system. However, the limited empirical research that has been performed to develop robust connectivity maps for native species has matched models we use in our set (e.g. Cushman *et al.*, 2006; Schwartz *et al.*, 2009; Shirk *et al.*, 2010; Wasserman *et al.*, 2010). In addition, land cover, elevation and roads are major attributes of the landscape that are likely to have dominant effects on movement and dispersal of most native animals. Proposing a large combination of resistance models based on these variables, and evaluating them across a range of dispersal abilities, we feel likely produces a set of hypothetical species that reflect the range of response of most native species.

Our analysis is based on modelling habitat connectivity for each hypothetical species. In doing this, we assumed that dispersing organisms originated from each location in the landscape with optimal dispersal habitat conditions and that no dispersers originated from locations with suboptimal conditions. Given that we are modelling connectivity for a large range of hypothetical organisms, real distribution and abundance data are not available. Thus, using habitat quality as a surrogate for distribution is necessary and appropriate. However, it should be kept in mind that real populations are often distributed idiosyncratically with respect to patterns of habitat quality because of a range of historical population factors (Van Horne, 1983; Pulliam, 1988). Thus, our results indicate habitat connectivity for species associated with each resistance model. This is quite different than population connectivity *per se*, which is highly constrained by the actual distribution and density of the species in question (e.g. Cushman *et al.*, 2011). To apply these methods to predict actual population connectivity for real species would require (1) empirical validation that the resistance model is correct (such as Cushman *et al.*, 2006; Schwartz *et al.* 2009; Wasserman *et al.*, 2010), and (2) reliable and spatially complete information on the distribution and density of the species across the study area. Our results, however, by evaluating habitat connectivity for a broad range of hypothetical species, and the sufficiency of public lands in protecting habitat connectivity, give useful information on which species in which parts of the ecosystem are likely to be most in need of protection and provide a framework for developing optimal conservation strategies for those species.

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