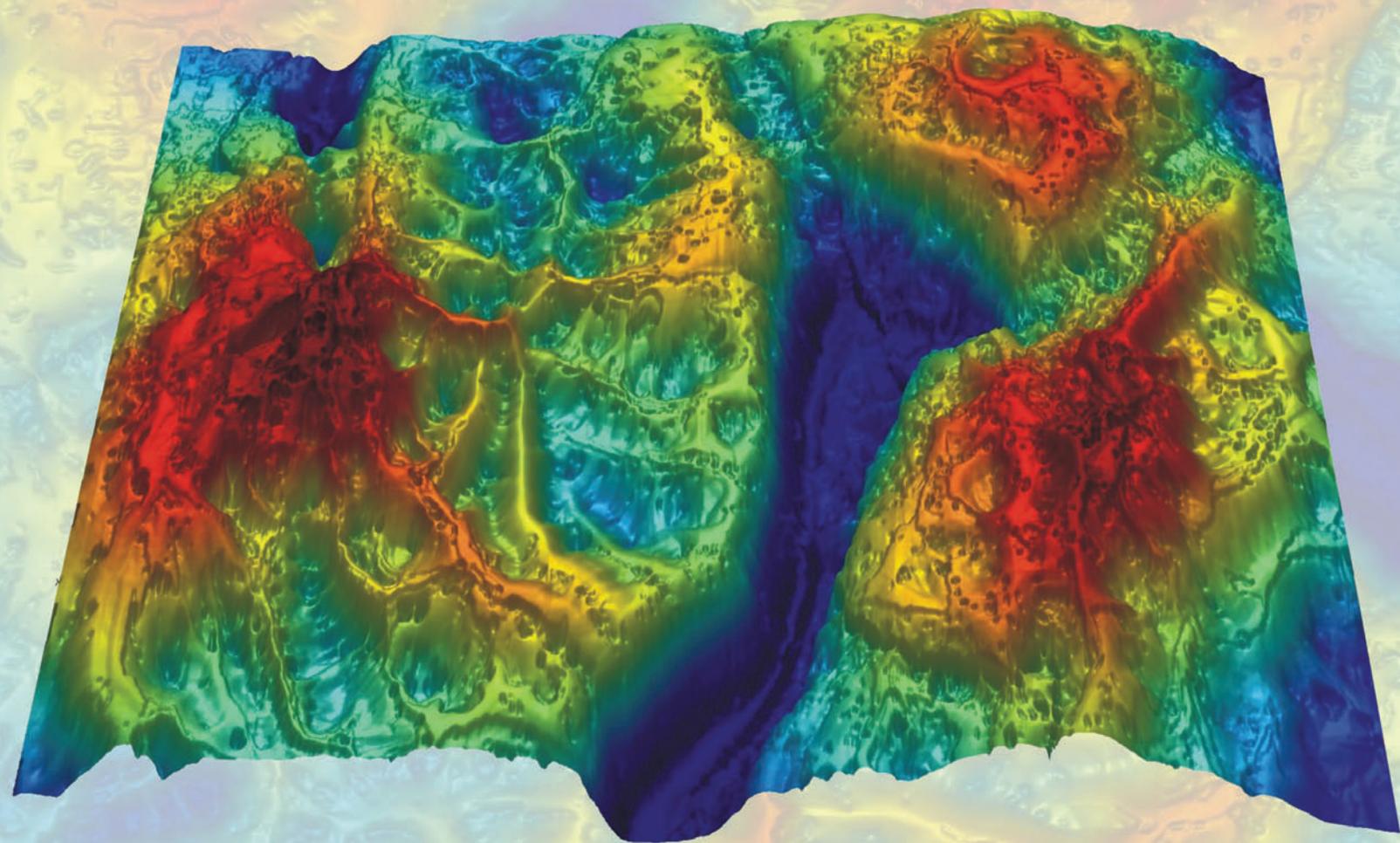


Ecological Associations, Dispersal Ability, and Landscape Connectivity in the Northern Rocky Mountains

Samuel A. Cushman and Erin L. Landguth



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ABSTRACT

Population connectivity is a function of the dispersal ability of the species, influences of different landscape elements on its movement behavior, density and distribution of the population, and structure of the landscape. Often, researchers have not carefully considered each of these factors when evaluating connectivity and making conservation recommendations. We present a general method for efficient evaluation of functional connectivity for large numbers of native species across vast geographical areas. Connectivity was evaluated for 36 groups of species with different ecological associations; within each of these groups, three dispersal abilities were evaluated across the United States northern Rocky Mountains. We quantified the extent and fragmentation of predicted connected habitat for each of these 108 species and identify those for which the current landscape has the lowest area and the highest fragmentation of habitat. We then conducted a multivariate ordination and use landscape trajectory analysis to assess multivariate differences in the extent and fragmentation of connected habitat across taxa. We mapped habitat connectivity for each of the 108 species, quantified the extent and pattern of connected habitat for each species, identified which species have the most limited extent and most highly fragmented pattern of connected habitat, identified any groups of species with similar patterns of connected habitat across dispersal abilities, and quantified the sensitivity to landscape pattern of connected habitat to dispersal ability and different ecological associations. We found large differences among groups of species in terms of the extent and connectivity of habitat, and the sensitivity of connectivity to dispersal ability. Species with limited dispersal ability associated with low-elevation forest have the most limited and fragmented distribution of connected habitat. Species associated with high-elevation forest also appear highly vulnerable to habitat loss and fragmentation based on limited extents and connectivity of habitat.

Keywords: landscape connectivity, dispersal ability, resistant kernel, multi-taxa, Rocky Mountains

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Introduction

Habitat loss has consistently negative effects on biodiversity (Fahrig 2003), including reductions in species richness (Findaly and Houlahan 1997; Gurd and others 2001; Schmiegelow and Monkkonen 2002; Steffan-Dewenter and others 2002), population declines, and changes in distribution (Gibbs 1998; Sanchez-Zapata and Calvo 1999; Best and others 2001; Bascompte and others 2002; Donovan and Flather 2002). Habitat loss and fragmentation change the distribution of resources and can affect individual behavior and spatial activity patterns, changing the ability of the organism to acquire the resources needed to survive and reproduce (Mangel and Clark 1986; Wiens and others 1993). Reduction in movement among habitat patches can have dire consequences for individuals and populations. Increased population isolation increases extinction risk by reducing demographic and genetic input from immigrants and reducing the chance of recolonization after extinction (Lande 1988; Schoener and Spiller 1992; Sjogren-Gulve 1994). Subdivision and isolation of populations can lead to reduced dispersal success and patch colonization rates, which may reduce the persistence of the local populations and increase probability of regional extinction for the entire metapopulation (e.g., Lande 1987; With and King 1999).

One of the ultimate consequences of habitat loss and fragmentation is the disruption of movement patterns and the resulting isolation of individuals and local populations. The degree to which habitat loss or fragmentation is biologically relevant will vary among species depending on how each perceives and interacts with landscape patterns (Dale and others 1994; With and Crist 1995; Pearson and others 1996; With and others 1997). Less vagile species with restrictive habitat requirements and limited gap-crossing ability will likely be most sensitive to isolation effects (e.g., Marsh and Trenham 2001; Rothermel and Semlitsch 2002). In addition, the composition and structure of the intervening landscape mosaic may determine the permeability of the landscape to movements. Each habitat may differ in its “viscosity” or resistance to movement—facilitating movement through certain elements of the landscape and impeding it in others (e.g., Cushman 2006).

The functional connectivity of a landscape is a composite result of the simultaneous effects of several important processes. These include the dispersal ability of the species, the influences of different landscape elements on its movement behavior, the density and distribution of the population, and the structure of the landscape. Often, researchers do not carefully consider each of these factors when evaluating connectivity and making conservation recommendations (Cushman 2006), which may lead to erroneous conclusions. The goal of this paper is to present a general method for efficient evaluation of functional connectivity for large numbers of native species across vast geographical areas. The specific illustration focuses on functional landscape connectivity across the United States

northern Rocky Mountains for a broad range of organisms expressing different sensitivity to landscape structure and different dispersal abilities. Specifically, we evaluate connectivity for 36 groups of species (totaling 108 species) with different ecological associations; within each of these groups, we evaluate three dispersal abilities.

We quantify the extent and fragmentation of predicted connected habitat for each of these 108 species and identify those for which the current landscape has the lowest area and the highest fragmentation of habitat. We then conduct a multivariate ordination and use landscape trajectory analysis to assess multivariate differences in the extent and fragmentation of connected habitat across taxa. The specific objectives are to: (1) map habitat connectivity for each of the 108 species, (2) quantify the extent and pattern of connected habitat for each species, (3) identify which species have the most limited extent and most highly fragmented pattern of connected habitat, (4) identify any groups of species with similar patterns of connected habitat across dispersal abilities, and (5) quantify the sensitivity to landscape pattern of connected habitat to dispersal ability and different ecological associations.

Methods

Study Area

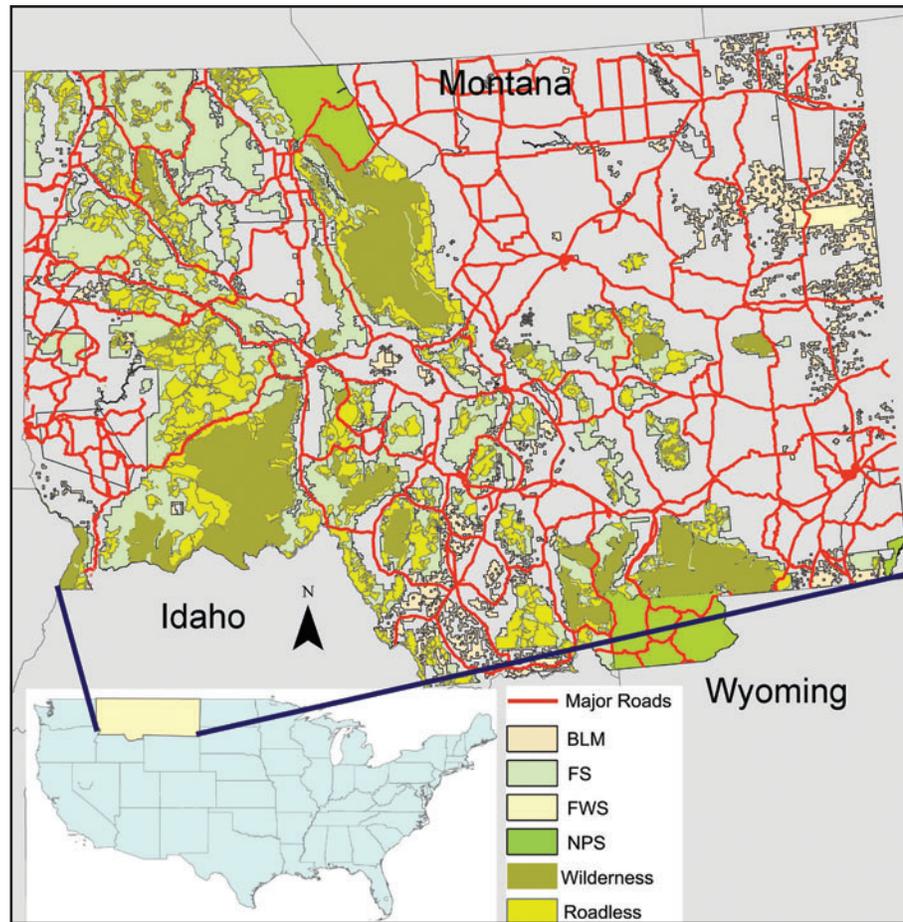
The study area includes Montana and northern Idaho in the United States Rocky Mountains (Figure 1) and contains large areas of Federally managed forest land, including extensive Wilderness and roadless areas and private land, mainly in the large valleys between major mountain ranges. The human population in this study area is rapidly growing (up to 44% increases since 1980 in some counties; 2000 U.S. Census data), causing extensive changes in land-use practices on the landscape, and necessitating the evaluation of wildlife corridors. In addition, an extensive network of highways bisects the study area, potentially impeding species’ movement.

Resistance Hypotheses

Our analysis is based on quantification of landscape connectivity across a broad range of landscape resistance hypotheses. These resistance hypotheses express different patterns of movement cost across the study area as functions of landscape conditions, such as elevation, vegetation cover, land use, and roads. Each resistance hypothesis is in the form of a landscape resistance map (Spear and others 2005; Vignieri 2005; Cushman and others 2006).

We defined 36 resistance surfaces for analysis from the pool of 108 models evaluated in Cushman and others (2006). The selected landscape resistance models represented combinations of the effects of three landscape features of resistance to movement: elevation, forest cover, and roads

Figure 1. Study area orientation map showing major roads and major land ownerships. BLM: Bureau of Land Management; FS: U.S. Forest Service; FWS: U.S. Fish and Wildlife Service; NPS: National Park Service.



(Cushman and others 2006). Resistance of these features was modeled across four levels for elevation and three levels for roads and forest (Table 1). The four levels for *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 1 at 500 (EL), 1000 (EM), and 1500 (EH) m elevation above sea level, respectively, 500 m standard deviation, and maximum resistance of 10. Similarly, three levels of *forest* were modeled. 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 minimum 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 bear strongly favors movement through forest. In the forest low (FL) level, non-forest classes have lower landscape resistance (Table 2). Finally, three levels for *roads* (R) were used: 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

Table 1. Description of factors and levels combined to create 36 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
Roads	High resistance	RH	High resistance due to roads
	Low resistance	RL	Low resistance due to roads
	Null	RN	No relationship with roads
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

Table 2. Cover classes and resistance values used in landcover resistance modeling.

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

relatively weak effect of roads on resistance (RL; Cushman and others 2006). Isolation by Euclidean distance was included as a 36th model, represented by a raster layer with uniform resistance of 1 cost unit. The landscape resistance models corresponding to each feature and level were combined into the 36 landscape resistance models by addition as in Cushman and others (2006). To improve computational efficiency, the 36 resistance models were resampled to 270 m pixel size by bilinear interpolation. Cushman and Landguth (2010) showed that coarsening the pixels size in floating point resistance grids has little effect on the strength of landscape genetic relationships, which suggests that connectivity models are quite robust to coarsening of pixel grain.

Resistant Kernel Modeling

Pixel-level resistance to movement does not provide sufficient information to evaluate the strength and location of barriers and corridors. Cushman and others (2008) argued that while resistance maps are point specific, connectivity is route specific. The resistance model is the foundation for connectivity analyses, but it is explicit consideration of connectivity across the resistance surface that provides the key information for conservation and management. Specifically, functional landscape connectivity is a product of multiple factors acting simultaneously, including the dispersal ability of the species, its response to landscape conditions (the resistance map), and its distribution and density in the landscape. We utilize a resistant kernel connectivity modeling approach (Compton and others 2007) to explicitly incorporate these factors into our analysis.

Resistant kernel connectivity modeling has a number of advantages as a robust approach to assessing functional landscape connectivity for multiple wildlife species. First, unlike most corridor prediction approaches, it is spatially

synoptic and provides prediction and mapping of expected migration rates for every pixel in the study area extent rather than only for a few selected “linkage zones” (Compton and others 2007). Second, scale dependency of dispersal ability can be directly included to assess how species of different vagilities will be affected by landscape change and fragmentation under a range of scenarios (e.g., Cushman and others 2010a). Third, it is computationally efficient, enabling simulation and mapping across the entire vast geographical extents for a large combination of species (e.g., Cushman and others 2010b, 2011).

The resistant kernel approach to connectivity modeling is based on least-cost dispersal from a defined set of sources cumulatively across a resistant landscape. The sources in our case are all pixels in the study area with resistance of 1 (lowest resistance and highest quality dispersal habitat) in each of the 36 resistance models. The resistance surface is in the form of the cost of crossing each pixel. These costs are used as weights in the dispersal function such that the expected density in a pixel is down-weighted by the cumulative cost from the source, following the least-cost route (Compton and others 2007).

The initial expected density was set to 1 in each source cell. Using the model, we calculated the expected relative density of each species or species group in each pixel around the source given the dispersal ability of the species, the nature of the dispersal function, and the resistance of the landscape (Compton and others 2007; Cushman and others 2010a). We wrote an ESRI ArcGrid (ESRI 2007) script to calculate the resistant kernel (Rk) density. The script uses the ArcGrid COSTDISTANCE function to produce a map of the movement cost from each source up to a specified dispersal threshold. These COSTDISTANCE grids are inverted and scaled such that the maximum value for each individual kernel is 1. Once the expected density around each source

cell is calculated, the kernels surrounding all sources are summed to give the total expected density at each pixel. The results of the model are surfaces of expected density of dispersing organisms at any location in the landscape. To bracket the range of dispersal abilities of most animal species in the study area, we ran the models for each of the 35 resistance maps across four 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.

Analysis of Extent and Pattern of Connected Habitat

The resistant kernel modeling produces spatial predictions of the areas on the landscape that are connected by dispersal given the resistance model, distribution, and density of the population and the dispersal ability of the species. Our objectives were to quantify the differences in the extent and pattern of connected habitat across resistance models and dispersal abilities. To accomplish this, we calculated a suite of fragmentation metrics with FRAGSTATS (McGarigal and others 2002) metrics on each of the 108 maps of predicted connected habitat. We selected eight landscape metrics (Table 3) that reflect several universally important gradients of landscape structure (Cushman and others 2008). Specifically, these metrics were chosen to robustly reflect two major gradients of landscape structure that are particularly important in driving population response to landscape structure (Cushman and others 2010b). These two gradients are (1) a gradient from high extent of connected habitat to low extent of connected habitat; and (2) a gradient from low edge density, small number of isolated patches, and high habitat aggregation to highly fragmented conditions characterized by high density of isolated habitat patches of small size and high total edge density.

Landscape Trajectory Analysis

Multivariate ordination has frequently been used to efficiently summarize differences in landscape structure

among many landscapes, as measured by many landscape metrics (e.g., Riitters and others 1995; Cushman and others 2008). In our case, we have a single study area landscape but 108 different maps of functional connectivity based on different ecological associations and dispersal abilities. In addition, we were interested in quantifying the differential effects of resistance map (ecological association) from dispersal ability. This was done by conducting landscape trajectory analysis within the ordination framework (Cushman and Wallin 2000; Cushman and McGarigal 2006). Landscape trajectory analysis is a method to quantify multivariate change in landscape structure across a landscape, usually measured at multiple times (e.g., Cushman and Wallin 2000; Cushman and McGarigal 2006; Nonaka and Spies 2006). In such an application, the displacement of a landscape in the multivariate ordination space between dates indicates the amount of change in landscape structure over time (Cushman and McGarigal 2006). Comparison between initial and final locations in ordination space quantifies the total degree of landscape change. Displacement along each ordination axis provides quantification of landscape change along independent gradients of landscape structure. The degree of divergence of different landscapes in the ordination over time quantifies the degree to which the landscapes become more different in terms of landscape structure.

In this analysis, instead of quantifying landscape trajectories through time, we quantified trajectories in the extent and pattern of connected habitat across the three levels of dispersal abilities. We used principal components analysis on the correlation matrix of all 108 connectivity maps. We plotted 36 trajectories, consisting of the three different dispersal abilities (5000 m, 10,000 m, and 20,000 m) for each of the resistance maps. We then clustered trajectories based on proximity in the ordination space (McGarigal and others 2000), enabling us to identify the resistance maps that are most similar in terms of the extent and pattern of connected habitat across dispersal abilities. Next, we quantified the displacement of each trajectory relative to the first two ordination axes to measure the amount of change in landscape structure as a function of dispersal ability. Then, we quantified the divergence of all pairs of trajectories (resistance

Table 3. Landscape metrics calculated for each of the 108 connectivity maps produced by resistant kernel modeling.

Metric name	Acronym	Description
Percentage of Landscape	PLAND	Percentage of the landscape occupied by connected habitat
Number of Patches	NP	Number of isolated habitat patches
Correlation Length	GYRATE_AM	Correlation length of connected habitat
Area-weighted Mean Patch Size	AREA_AM	Area weighted mean patch size of connected habitat
Landscape Shape Index	LSI	Aggregation of connected habitat patches
Total Edge	TE	Total length of edge between connected habitat patches and non-habitat
Largest Patch Index	LPI	Largest patch of connected habitat percentage of the landscape
Clumpy	CLUMPY	Composition adjusted aggregation of habitat

maps) across dispersal abilities to identify which converge to similar final landscape structures and which retain different landscape patterns across all dispersal abilities.

Results

Landscape Connectivity Across Resistance Models and Dispersal Abilities

To visualize changes in landscape structure across the different resistance models, we produced three-dimensional colored cubes for each landscape metric (Figures 2, 3, and S1-S4). The cubes are organized as in Cushman and others (2006) and reflect a factorial of the three landscape elements (*elevation, roads, and forest*) that constitute the 36 resistance models. For example, Figure 2a shows differences in percentage of the landscape covered by connected habitat across the 36 models at a 5000 m dispersal ability. Figures 2b and 2c show changes in the percentage of the landscape in connected habitat at 10,000 m and 20,000 m dispersal abilities.

The figures show two main patterns. First, the percentage of the landscape covered by connected habitat increases substantially with increasing dispersal ability. Second, across dispersal abilities, the species with the largest extent of connected habitat are those that are not sensitive to elevation or forest cover or those that are associated with the lowest elevations with relatively weak preference for forest cover. Conversely, across dispersal abilities, the species with the most limited extent of connected habitat are those associated with the highest elevations or those strongly dependent on forest cover for movement. At the 10,000 m dispersal threshold, on average across the 36 resistance models, 61.5% of the landscape is occupied by connected habitat patches. Eight resistance models show less than 40% of the total study area occupied by connected habitat at 10,000 m dispersal ability (Table 4). Six of the eight are models predicting strong ecological associations with high-elevation forest, with increasing resistance to movement at lower elevations and non-forest cover types. The other two models with less than 40% coverage of connected habitat are for species strongly associated with forest cover at the lowest elevations. In contrast, six resistance models showed extent of connected habitat amounting to over 95% of the study area. These are species not associated with elevation or forest cover, or those associated with low elevations but not limited by the extent of forest cover (Table 4).

A somewhat different pattern was observed for the number of patches of isolated habitat across resistance models and dispersal abilities (Figure 3). Figure 3 shows differences in the number of isolated patches of habitat across the 36 models at a 5000 m, 10,000 m, and 20,000 m dispersal

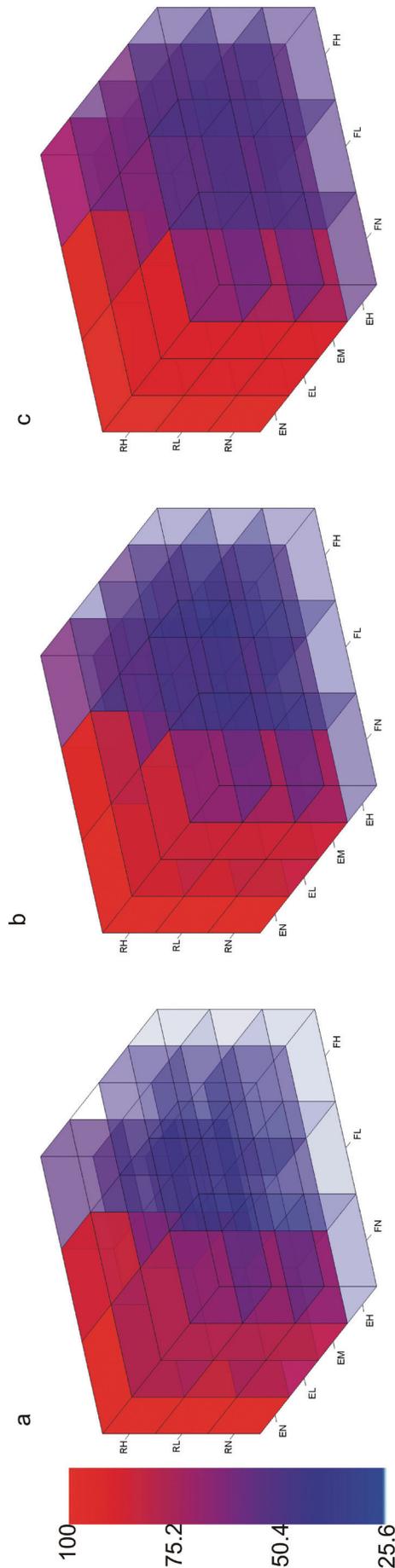


Figure 2. Percentage of the landscape in connected habitat across 36 resistance models, at each of three dispersal abilities. Colored cubes represent a three-way factorial of the three factors (elevation, forest cover, and road resistance). There are 36 combinations across levels of the three factors. Each subcube represents a specific combination. The value of the landscape metric is represented by the color of the cube, scaled linearly from minimum to maximum. The maximum value is red and the minimum is blue. The transparency of the cubes also increases with decreasing relative value of the landscape metrics, such that the lowest value is fully transparent. (a) 5000 m dispersal ability, (b) 10,000 m dispersal ability, and (c) 20,000 m dispersal ability.

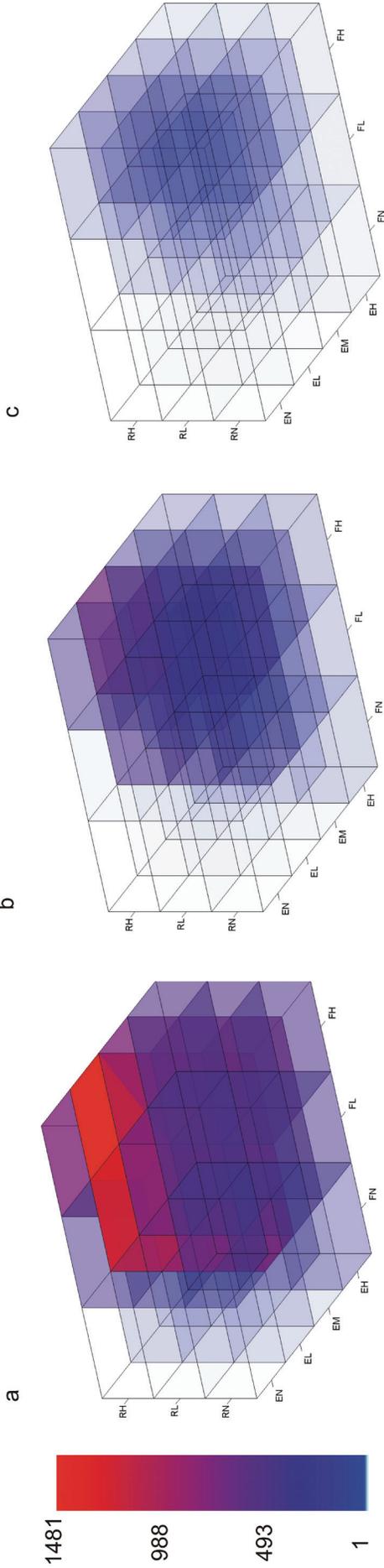


Figure 3. Number of isolated patches of connected habitat across 36 resistance models, at each of three dispersal abilities. Colored cubes represent a three-way factorial of the three factors (elevation, forest cover, and road resistance). There are 36 combinations across levels of the three factors. Each subcube represents a specific combination. The value of the landscape metric is represented by the color of the cube, scaled linearly from minimum to maximum. The maximum value is red and the minimum is blue. The transparency of the cubes also increases with decreasing relative value of the landscape metrics, such that the lowest value is fully transparent. (a) 5000 m dispersal ability, (b) 10,000 m dispersal ability, and (c) 20,000 m dispersal ability.

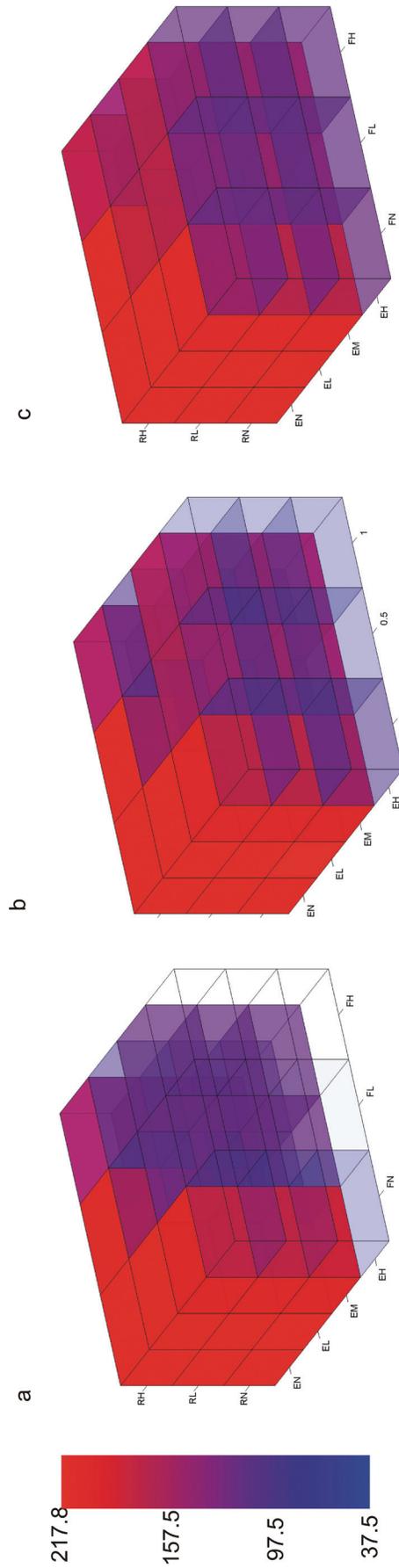


Figure S1. Correlation length of connected habitat across 36 resistance models, at each of three dispersal abilities. Colored cubes represent a three-way factorial of the three factors (elevation, forest cover, and road resistance). There are 36 combinations across levels of the three factors. Each subcube represents a specific combination. The value of the landscape metric is represented by the color of the cube, scaled linearly from minimum to maximum. The maximum value is red and the minimum is blue. The transparency of the cubes also increases with decreasing relative value of the landscape metrics, such that the lowest value is fully transparent. (a) 10,000 m dispersal ability, (b) 20,000 m dispersal ability, and (c) 5000 m dispersal ability.

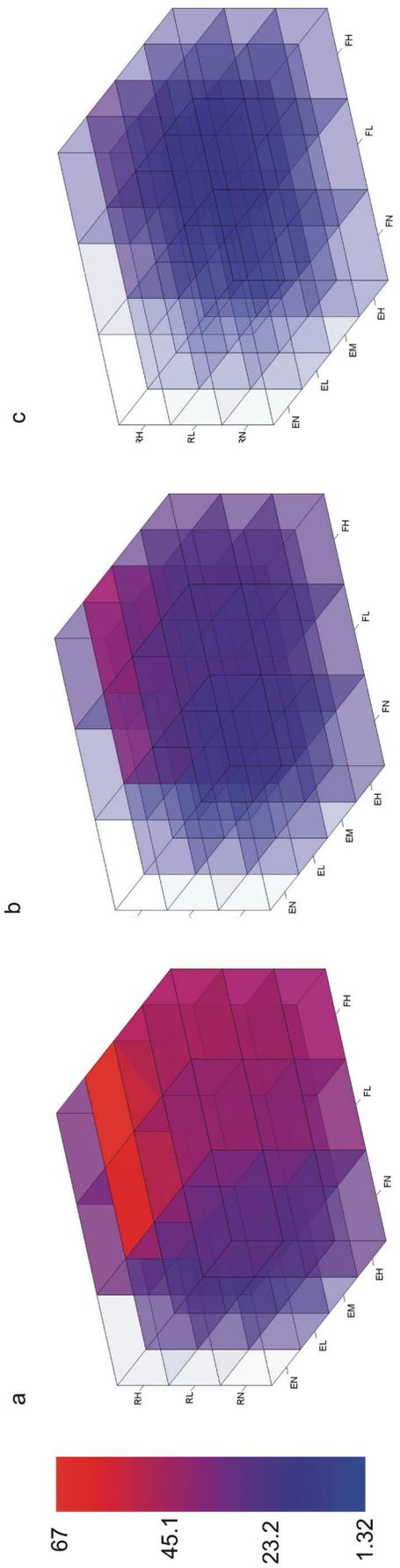


Figure S2. Landscape shape index of connected habitat across 36 resistance models, at each of three dispersal abilities. Colored cubes represent a three-way factorial of the three factors (elevation, forest cover, and road resistance). There are 36 combinations across levels of the three factors. Each subcube represents a specific combination. The value of the landscape metric is represented by the color of the cube, scaled linearly from minimum to maximum. The lowest value is fully transparent. The maximum value is blue. The transparency of the cubes also increases with decreasing relative value of the landscape metrics, such that the lowest value is fully transparent. (a) 5000 m dispersal ability, (b) 10,000 m dispersal ability, and (c) 20,000 m dispersal ability.

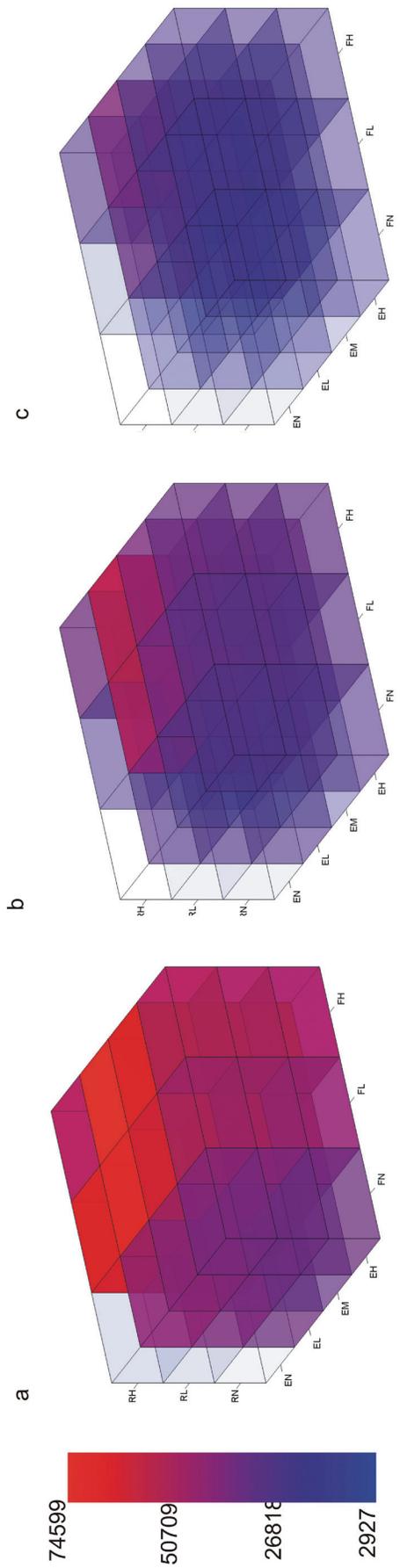


Figure S3. Total length of linear edge of connected habitat across 36 resistance models, at each of three dispersal abilities. Colored cubes represent a three-way factorial of the three factors (elevation, forest cover, and road resistance). There are 36 combinations across levels of the three factors. Each subcube represents a specific combination. The value of the landscape metric is represented by the color of the cube, scaled linearly from minimum to maximum. The lowest value is fully transparent. The maximum value is blue. The transparency of the cubes also increases with decreasing relative value of the landscape metrics, such that the lowest value is fully transparent. (a) 5000 m dispersal ability, (b) 10,000 m dispersal ability, and (c) 20,000 m dispersal ability.

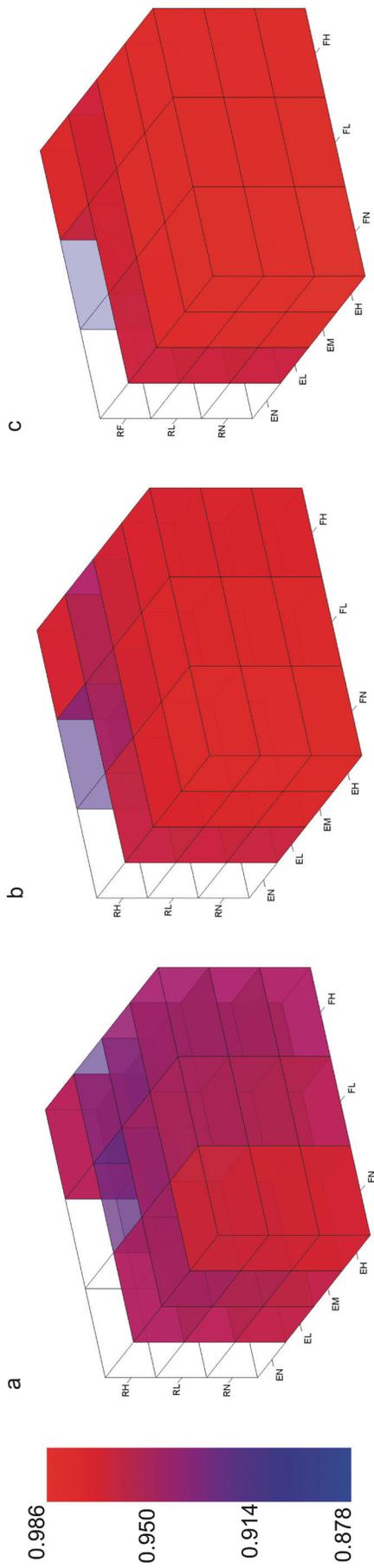


Figure S4. Clumpy index of aggregation of connected habitat across 36 resistance models, at each of three dispersal abilities. Colored cubes represent a three-way factorial of the three factors (elevation, forest cover, and road resistance). There are 36 combinations across levels of the three factors. Each subcube represents a specific combination. The value of the landscape metric is represented by the color of the cube, scaled linearly from minimum to maximum. The maximum value is red and the minimum is blue. The transparency of the cubes also increases with decreasing relative value of the landscape metrics, such that the lowest value is fully transparent. (a) 5000 m dispersal ability, (b) 10,000 m dispersal ability, and (c) 20,000 m dispersal ability.

Table 4. Description of the 36 resistance models used in the analysis, their number, the landscape trajectory numbers associated with that model, the percent of the landscape covered by patches of connected habitat at 10,000 m dispersal ability, the number of isolated habitat patches at 10,000 m dispersal ability, and the clumpy aggregation index at 10,000 m dispersal ability.

Model acronym	Model number	Trajectory numbers (Figure 4)	Model description	Percent	Number of patches	Clumpy
EH	1	1-3	Minimum resistance at high elevations (1500 m)	0.438	103	0.9791
EHFH	2	4-6	Minimum resistance in forest (strong) at high elevations	0.382	148	0.972
EHFL	3	7-9	Minimum resistance in forest (weak) at high elevations	0.393	121	0.9752
EHRH	4	10-12	Minimum resistance at high elevations with high resistance of roads	0.431	102	0.9772
EHRL	5	13-15	Minimum resistance at high elevations with weak resistance of roads	0.432	101	0.9783
EL	6	16-18	Minimum resistance at low elevations (500m)	0.836	11	0.9636
ELFH	7	19-21	Minimum resistance in forest (strong) at low elevations	0.405	627	0.9526
ELFL	8	22-24	Minimum resistance in forest (weak) at low elevations	0.453	405	0.9569
ELRH	9	25-27	Minimum resistance at low elevations with high resistance of roads	0.83	13	0.9626
ELRL	10	28-30	Minimum resistance at low elevations with weak resistance of roads	0.831	13	0.9638
EM	11	31-33	Minimum resistance at middle elevations (1000m)	0.857	20	0.9758
EMFH	12	34-36	Minimum resistance in forest (strong) at middle elevations	0.535	319	0.9697
EMFL	13	37-39	Minimum resistance in forest (weak) at middle elevations	0.566	223	0.9734
EMRH	14	40-42	Minimum resistance at middle elevations with high resistance of roads	0.853	18	0.9718
EMRL	15	43-45	Minimum resistance at middle elevations with weak resistance of roads	0.854	18	0.9744
FH	16	46-48	Minimum resistance in forest (strong)	0.624	350	0.971
FHEHRH	17	49-51	Minimum resistance in forest (strong) at high elevations with high resistance of roads	0.376	154	0.9701
FHEHRL	18	52-54	Minimum resistance in forest (strong) at high elevations with weak resistance of roads	0.377	150	0.9712
FHEL RH	19	55-57	Minimum resistance in forest (strong) at low elevations with high resistance of roads	0.39	657	0.9489
FHEL RL	20	58-60	Minimum resistance in forest (strong) at low elevations with weak resistance of roads	0.393	649	0.951
FHEMRH	21	61-63	Minimum resistance in forest (strong) at middle elevations with high resistance of roads	0.529	322	0.9671
FHEMRL	22	64-66	Minimum resistance in forest (strong) at middle elevations with weak resistance of roads	0.53	318	0.9685
FHRH	23	67-69	Minimum resistance in forest (strong) with high resistance of roads	0.615	360	0.969
FHRL	24	70-72	Minimum resistance in forest (strong) with low resistance of roads	0.617	359	0.9704
FL	25	73-75	Minimum resistance in forest (weak)	0.955	26	0.9169
FLEHRH	26	76-78	Minimum resistance in forest (weak) at high elevations with high resistance of roads	0.386	125	0.9733
FLEHRL	27	79-81	Minimum resistance in forest (weak) at high elevations with weak resistance of roads	0.387	121	0.9744
FLELRH	28	82-84	Minimum resistance in forest (weak) at low elevations with high resistance of roads	0.436	438	0.9531
FLELRL	29	85-87	Minimum resistance in forest (weak) at low elevations with weak resistance of roads	0.438	435	0.9554
FLEMRH	30	88-90	Minimum resistance in forest (weak) at middle elevations with high resistance of roads	0.559	226	0.9706
FLEMRL	31	91-93	Minimum resistance in forest (weak) at middle elevations with weak resistance of roads	0.56	223	0.9721
FLRH	32	94-96	Minimum resistance in forest (weak) with high resistance of roads	0.95	29	0.9087
FLRL	33	97-99	Minimum resistance in forest (weak) with low resistance of roads	0.951	29	0.9146
RH	34	100	High resistance of roads	1	1	0
RL	35	100	Weak resistance of roads	1	1	0
Null	36	100	Uniform resistance	1	1	0

abilities, respectively. Across dispersal abilities, species associated with forest cover at the lowest elevations had the largest number of isolated patches. Conversely, species that were not associated with elevation or forest cover existed in a single or a few large connected patches. At the 10,000 m dispersal threshold, there was an average of 200 isolated patches of connected habitat across the 36 resistance models. Eight resistance models had over 400 patches of isolated habitat and three—FHELRLH, FHELRL, and ELFH—had in excess of 600 isolated habitat patches, reflecting a high degree of habitat fragmentation (Table 4). In contrast, 6 resistance models had fewer than 15 patches of isolated habitat, including species that are not associated with elevation or forest cover (Null, RH, RL, 1 patch) and those that are associated with low elevation but are not limited by the extent of forest cover (EL, 11 patches; ELRH, 13 patches; ELRL, 13 patches).

Principal Components Analysis

The principal components analysis effectively concentrated variance in landscape structure of the 108 connectivity maps across the 8 landscape metrics onto two independent dimensions of landscape structure (Table 5). The first ordination axis accounted for approximately 73% of the variance in landscape structure, and over 88% of the variance in landscape structure was accounted for by the first two ordination axes. The first axis is a gradient from high habitat area and low habitat fragmentation (right, Figure 4) to low area of connected habitat and high fragmentation into small, isolated patches with high edge density (left, Figure 4).

Inspection of the ordination trajectory biplot (Figure 4) shows seven distinct groups of resistance models that are similar with respect to location in the ordination space and trajectory of movement through the space as dispersal ability increases. The first group is in the upper left quadrant and includes trajectory numbers 7-8-9; 79-80-81; 76-77-78; 4-5-6; 52-53-54; and 49-50-51 (Figure 4; Table 4). This group exclusively contains resistance models in which species movement is facilitated at high elevations and resisted at lower elevations. The second trajectory group consists of trajectory numbers 22-23-24; 85-86-87; 82-83-84; 58-59-60; and 55-56-57 (Figure 4; Table 4). This group contains species associated with forest cover at the lowest elevations. The third trajectory group contains trajectory numbers 37-38-39; 91-92-93; 88-89-90; 34-35-36; 64-65-66; and 61-62-63. These species are associated with middle-elevation forests that are sensitive to fragmentation by roads. The fourth trajectory group contains trajectory numbers 46-47-48; 67-68-69; and 70-71-72. These species are those strongly associated with forest cover that avoid moving through non-forest habitats but don't have any association with elevation. The fifth trajectory group contains trajectory numbers 94-95-96; 97-98-99; and 73-74-75. These species are moderately associated with forest cover

Table 5. Results of multi-temporal principal components analysis. Proportion of explained variance and axis loadings for the first three principal components.

	Component		
	1	2	3
Proportional of variance	72.6%	15.4%	8.8%
Cumulative proportion	72.6%	88.0%	97.9%
Loadings			
PLAND	0.402	-0.185	-0.474
NP	-0.314	-0.544	-0.714
LPI	0.390	-0.281	-0.104
TE	-0.342	-0.438	-0.199
LSI	-0.371	-0.386	0.136
AREA_AM	0.389	-0.289	-0.134
GYRATE_AM	0.373	-0.298	-0.283
CLUMPY	-0.205	0.278	-0.912

but are not associated with elevation. The sixth trajectory group includes trajectory numbers 40-42-32; 43-44-45; and 31-32-33. These species are associated with middle-elevation forests but not with forest cover. The seventh trajectory group consists of trajectory numbers 28-29-30; 25-26-27; and 16-17-18 and contains three species associated with low-elevation forests but not with forest cover. The eighth trajectory group consists of three models that were fixed at 100% cover of the study area at all dispersal abilities (Null, RH, and RL) and are given trajectory point 100 in the principal components analysis (PCA) biplot.

There were significant differences between the mean PCA scores on axes 1 and 2 among trajectory groups at each dispersal ability (Table 6), indicating significant separation of the groups in PC space. Across dispersal abilities, over 80% of pairs of groups had significantly different average PC1 scores, and over 60% had significantly different PC2 scores (Table 7). On axis one, only groups 5, 6, and 7 were not significantly different in average PC1 score at any dispersal ability (Table 7). On axis 2, only groups 4 and 6 were not significantly different in average PC2 score at any dispersal ability (Table 7). On axis 1 at the 5000 m dispersal ability, Group 2 had by far the lowest average PC score, indicating that species depending on low-elevation forest and that have limited dispersal ability are probably most limited by the extent and fragmentation of habitat. In contrast, Groups 6 and 7 are approximately tied in average PC1 score at the 5000 m dispersal ability, indicating that species that are associated with low and middle elevations but are not dependent on forest cover have the most extensive and least fragmented distributions of connected habitat (Table 8). At 20,000 m dispersal threshold, there is a change in ranking of groups on PC1, with Group 1 having the lowest extent and highest fragmentation of connected habitat. This indicates that at higher dispersal abilities, species associated with low-elevation forest may be able to

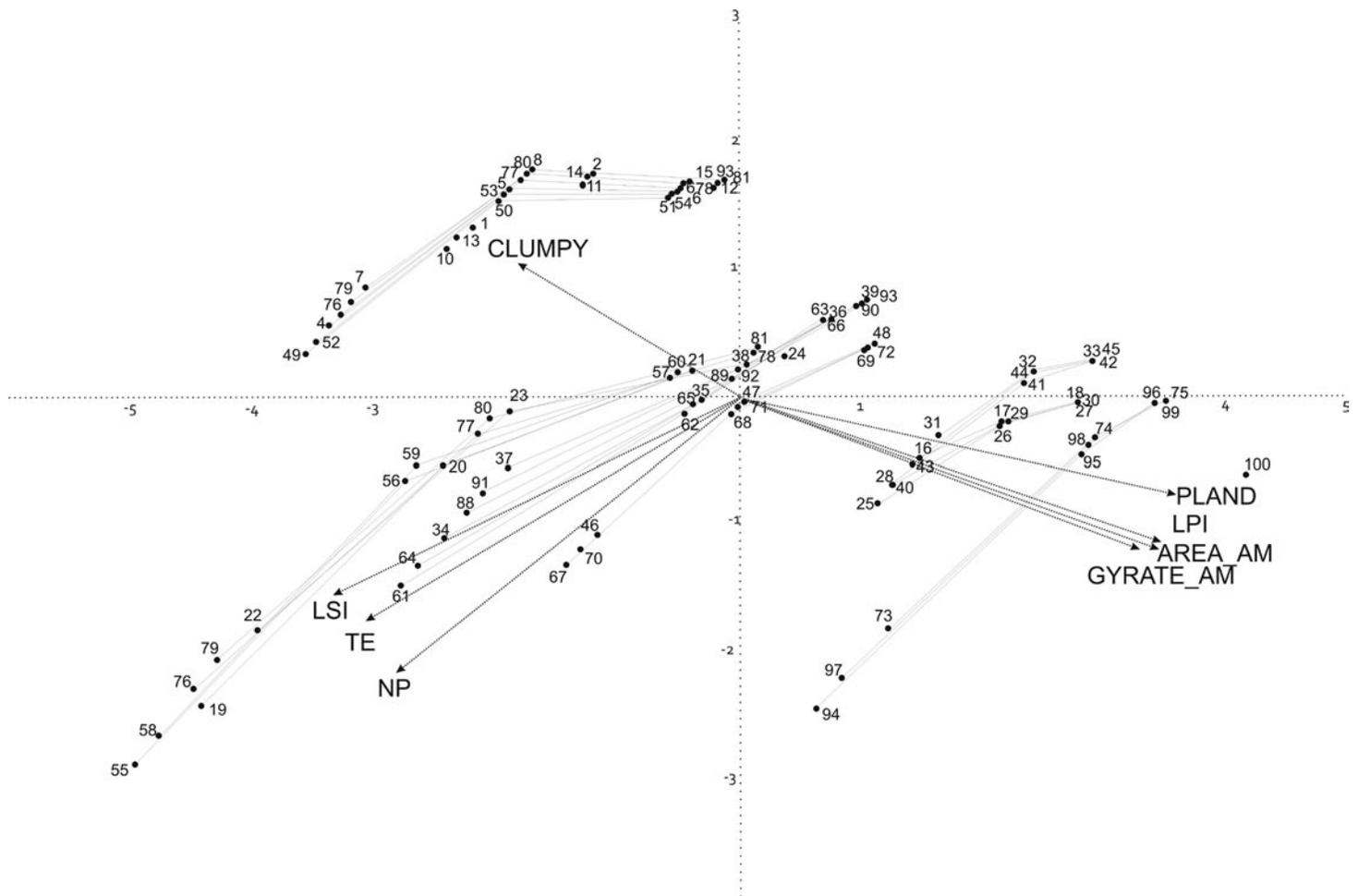


Figure 4. Landscape trajectories PCA biplot. PLAND—percentage of landscape area occupied by connected habitat; LPI—percentage of the landscape occupied by the single largest patch of connected habitat; AREA_AM—area-weighted mean patch size of connected habitat; GYRATE_AM—correlation length of connected habitat; LSI—landscape shape index; TE—total length of connected habitat edge; and NP—number of patches of connected habitat.

Table 6. One-way analysis of variance difference between mean values on PCA axes 1 and 2 among PCA trajectory groups at 5000 m, 10,000 m, and 20,000 m dispersal ability.

PCA axis	Dispersal ability	Degrees of Freedom	Sum of squares	Mean square	F	P
1	5000 m	7	229.1009	32.7287	240.41	<.0001
1	10,000 m	7	170.0089	24.28698	416.34	<.0001
1	20,000 m	7	96.7927	13.82753	316.62	<.0001
2	5000 m	7	45.73135	6.53305	64.07	<.0001
2	10,000 m	7	28.41451	4.059215	235.86	<.0001
2	20,000 m	7	21.78926	3.112751	898.45	<.0001

effectively integrate small and isolated patches, resulting in a large increase in the extent of connected habitat and decreases in fragmentation. Conversely, species in Group 1 associated with high-elevation forests are less able to

integrate isolated patches at higher dispersal abilities, and as a consequence, have the lowest PC1 average score at 20,000 m dispersal ability. Groups 5, 6, and 7 retain the highest PC1 scores at 20,000 m dispersal ability (Table 8).

Table 7. Tukey HSD test of significance of difference of mean value on the first two principal components analysis (PCA) axes between pairs of PC trajectory groups at 5000 m, 10,000 m, and 20,000 m dispersal distance. The mean differences between groups are shown in the right six columns. Pairs that are significantly different are in bold.

Pair comparison	Axis 1 5000 m	Axis 1 10,000 m	Axis 1 20,000 m	Axis 2 5000 m	Axis 1 10,000 m	Axis 2 20,000 m
1 – 2	1.5033	0.678	-0.24919	3.1938	2.0841	1.38908
1 – 3	-0.6349	-1.4535	-1.24251	1.8485	1.63018	0.98561
1 – 4	-1.6903	-1.6354	-1.45581	2.0274	1.77851	1.26326
1 – 5	-3.8912	-4.5178	-3.82893	2.9882	2.07917	1.70347
1 – 6	-4.4376	-4.0327	-3.28293	1.3266	1.53748	1.37907
1 – 7	-4.2878	-3.827	-3.18984	1.4911	1.90439	1.69534
2 – 1	-1.5033	-0.678	0.24919	-3.1938	-2.0841	-1.38908
2 – 3	-2.1382	-2.1314	-0.99332	-1.3453	-0.45392	-0.40348
2 – 4	-3.1936	-2.3134	-1.20662	-1.1664	-0.30558	-0.12582
2 – 5	-5.3945	-5.1958	-3.57975	-0.2056	-0.00493	0.31439
2 – 6	-5.9409	-4.7107	-3.03375	-1.8672	-0.54662	-0.01001
2 – 7	-5.7911	-4.5049	-2.94065	-1.7027	-0.17971	0.30626
3 – 1	0.6349	1.4535	1.24251	-1.8485	-1.63018	-0.98561
3 – 2	2.1382	2.1314	0.99332	1.3453	0.45392	0.40348
3 – 4	-1.0554	-0.1819	-0.2133	0.1789	0.14833	0.27766
3 – 5	-3.2563	-3.0643	-2.58642	1.1397	0.44899	0.71787
3 – 6	-3.8027	-2.5792	-2.04042	-0.5219	-0.0927	0.39346
3 – 7	-3.6529	-2.3735	-1.94733	-0.3574	0.27421	0.70974
4 – 1	1.6903	1.6354	1.45581	-2.0274	-1.77851	-1.26326
4 – 2	3.1936	2.3134	1.20662	1.1664	0.30558	0.12582
4 – 3	1.0554	0.1819	0.2133	-0.1789	-0.14833	-0.27766
4 – 5	-2.2009	-2.8824	-2.37313	0.9608	0.30066	0.44021
4 – 6	-2.7473	-2.3973	-1.82712	-0.7008	-0.24103	0.1158
4 – 7	-2.5975	-2.1915	-1.73403	-0.5363	0.12588	0.43208
5 – 1	3.8912	4.5178	3.82893	-2.9882	-2.07917	-1.70347
5 – 2	5.3945	5.1958	3.57975	0.2056	0.00493	-0.31439
5 – 3	3.2563	3.0643	2.58642	-1.1397	-0.44899	-0.71787
5 – 4	2.2009	2.8824	2.37313	-0.9608	-0.30066	-0.44021
5 – 6	-0.5464	0.4851	0.546	-1.6616	-0.54169	-0.32441
5 – 7	-0.3966	0.6908	0.63909	-1.4971	-0.17478	-0.00813
6 – 1	4.4376	4.0327	3.28293	-1.3266	-1.53748	-1.37907
6 – 2	5.9409	4.7107	3.03375	1.8672	0.54662	0.01001
6 – 3	3.8027	2.5792	2.04042	0.5219	0.0927	-0.39346
6 – 4	2.7473	2.3973	1.82712	0.7008	0.24103	-0.1158
6 – 5	0.5464	-0.4851	-0.546	1.6616	0.54169	0.32441
6 – 7	0.1498	0.2058	0.09309	0.1645	0.36691	0.31627
7 – 1	4.2878	3.827	3.18984	-1.4911	-1.90439	-1.69534
7 – 2	5.7911	4.5049	2.94065	1.7027	0.17971	-0.30626
7 – 3	3.6529	2.3735	1.94733	0.3574	-0.27421	-0.70974
7 – 4	2.5975	2.1915	1.73403	0.5363	-0.12588	-0.43208
7 – 5	0.3966	-0.6908	-0.63909	1.4971	0.17478	0.00813
7 – 6	-0.1498	-0.2058	-0.09309	-0.1645	-0.36691	-0.31627

Table 8. Mean PC1 and PC2 scores for each group at each of the three dispersal abilities.

Group	Axis	5000 m	10,000 m	20,000 m
1	1	-2.6972	-1.48777	-0.35429
	2	0.737049	1.526015	1.491194
2	1	-4.50015	-2.33104	-0.14447
	2	-2.36197	-0.19959	0.84885
3	1	-2.36197	-0.19959	0.84885
	2	-1.02951	0.065395	0.671277
4	1	-1.30655	-0.01766	1.062149
	2	-1.20842	-0.08294	0.393618
5	1	0.894339	2.864715	3.435274
	2	-2.16921	-0.3836	-0.04659
6	1	1.440701	2.379656	2.889273
	2	-0.50761	0.158093	0.277815
7	1	1.290927	2.173873	2.79618
	2	-0.67215	-0.20881	-0.03846

Landscape Trajectory Analysis

One-way analysis of variance showed highly significant differences in mean displacement in PC space from 5000 m to 20,000 m dispersal ability among PC trajectory groups (Table 9). This indicates that the groups are substantially different in the degree to which landscape structure changes as functions of dispersal ability. Eighty-one percent of group pairs had significantly different axis 1 displacement, and 67% had significantly different axis 2 displacement (Table 9). Only groups 1, 4, and 5 and groups 6 and 7 were not significantly different from each other in the degree to which landscape structure changed from 5000 m to 20,000 m dispersal ability (Table 10).

On both axes, Group 1 had, by far, the largest displacement, showing that species associated with low-elevation forest have the largest change in the extent and fragmentation of connected habitat across the three dispersal abilities (Table 11). In contrast, Groups 6 and 7 had the lowest displacement, indicating that species that are associated with low and middle elevations but are not dependent on forest cover have relatively little change in extent and pattern of connected habitat as dispersal ability increases.

Table 9. One-way analysis of variance of mean displacement between PC trajectory groups from 5000 m to 20,000 m dispersal on each of the first two PCA axes.

Dependent variable	Degrees of freedom	Sum of squares	Mean square	F	P
Disp1	6	27.14947	4.524911	70.76	<.0001
Disp2	6	16.99167	2.831945	34.94	<.0001

Table 10. Tukey HSD test of significance of difference of displacement on the first two PCA axes between pairs of PC trajectory groups. The mean difference between groups are shown in the right two columns. Pairs that are significantly different are in bold.

Group pair	Axis 1 mean difference	Axis 2 mean difference
1 – 2	-1.7524	-1.8047
1 – 3	-0.6076	-0.8629
1 – 4	0.2345	-0.7641
1 – 5	0.0623	-1.2847
1 – 6	1.1547	0.0525
1 – 7	1.098	0.2042
2 – 1	1.7524	1.8047
2 – 3	1.1449	0.9419
2 – 4	1.987	1.0406
2 – 5	1.8147	0.52
2 – 6	2.9071	1.8572
2 – 7	2.8504	2.009
3 – 1	0.6076	0.8629
3 – 2	-1.1449	-0.9419
3 – 4	0.8421	0.0988
3 – 5	0.6699	-0.4218
3 – 6	1.7622	0.9154
3 – 7	1.7056	1.0671
4 – 1	-0.2345	0.7641
4 – 2	-1.987	-1.0406
4 – 3	-0.8421	-0.0988
4 – 5	-0.1722	-0.5206
4 – 6	0.9201	0.8166
4 – 7	0.8634	0.9683
5 – 1	-0.0623	1.2847
5 – 2	-1.8147	-0.52
5 – 3	-0.6699	0.4218
5 – 4	0.1722	0.5206
5 – 6	1.0924	1.3372
5 – 7	1.0357	1.4889
6 – 1	-1.1547	-0.0525
6 – 2	-2.9071	-1.8572
6 – 3	-1.7622	-0.9154
6 – 4	-0.9201	-0.8166
6 – 5	-1.0924	-1.3372
6 – 7	-0.0567	0.1517
7 – 1	-1.098	-0.2042
7 – 2	-2.8504	-2.009
7 – 3	-1.7056	-1.0671
7 – 4	-0.8634	-0.9683
7 – 5	-1.0357	-1.4889
7 – 6	0.0567	-0.1517

Table 11. Average displacement on PC1 and PC2 between 5000 m and 20,000 m dispersal ability for each of the seven trajectory groups.

Group	Axis	Mean displacement
1	1	2.603232
	2	0.837939
2	1	4.355678
	2	2.642651
3	1	3.210817
	2	1.700792
4	1	2.368699
	2	1.602033
5	1	2.540935
	2	2.12262
6	1	1.448572
	2	0.785424
7	1	1.505253
	2	0.63369

The average divergence of the locations of the members of each group in PC space gives an indication of how similar the landscape patterns of connected habitat are across the members of each group at each of the three dispersal abilities (Table 12). Across all dispersal distances, Group 2 had the highest average distance in PC space between pairs of group members, while Group 7 had the lowest. This indicates that species associated with low-elevation forest express a relatively broad range of extent and pattern of connected habitat in response to the effects of factors such as sensitivity to roads and the strength of dependency on forest cover. All seven groups showed very large decreases of within-group divergence as dispersal ability increased. Groups 4, 5, 6, and 7 had a decrease in average pair-wise separation in PC space of over 90%. Groups, 1, 2, and 3 had a decrease in average pair-wise separation of between 60 and 70%, indicating that landscape structure of connected habitat becomes much more similar within groups as dispersal ability increases.

Table 12. Mean within-group divergence among pairs of models within each of the seven trajectory groups across dispersal abilities (5000 m, 10,000 m, and 20,000 m).

Trajectory group	5000 m	10,000 m	20,000 m
1	0.762487	0.385477	0.215961
2	1.292505	0.529829	0.490538
3	0.541026	0.287545	0.197921
4	0.393994	0.099931	0.037889
5	0.427155	0.083046	0.022481
6	0.350103	0.066114	0.023388
7	0.407022	0.159388	0.024642

Quantifying the average divergence between groups across the three dispersal abilities provides a measure of how the differences in landscape structure between groups change as dispersal ability increases (Table 13). As dispersal ability increases, the average landscape structure of connected habitat among groups becomes more similar. Specifically, at the 5000 m dispersal distance, the average distance between group centroids in PC1xPC2 space is 3.30 units. This decreases to 2.71 units at 10,000 m dispersal ability and drops to 2.04 units at 20,000 m dispersal ability. Across dispersal abilities, Groups 1 and 2 are most distant in PC space from Groups 5, 6, and 7 (Table 13). This indicates that there is substantial difference in the extent and pattern of connected habitat for species associated with both forest cover and either high or low elevation and for species associated with elevation but not with forest cover.

Discussion

Habitat Connectivity, Dispersal Ability, and Ecological Associations

Population connectivity is a function of three factors. First, connectivity is fundamentally mediated by the extent of the distribution and density of the population. A species with a broad distribution across a landscape and with relatively high density will express a very high degree of population connectivity given there are few gaps in distribution to be spanned by dispersal. Conversely, species that have limited distributions or are highly fragmented will probably have much less extensive connected habitat, given that there will be large extents of unoccupied habitat between core population patches. Second, dispersal ability critically determines connectivity. At any pattern of distribution and population density, the degree to which a population is connected across the broad landscape will increase with increasing dispersal ability. Species with very limited dispersal ability will not be able to disperse across even quite small gaps in the distribution, resulting in highly fragmented populations. In contrast, species with very high dispersal ability can cross even broad gaps in distribution, thus spatially integrating the population into a few or a single core patch. Third, connectivity is driven by the resistance of the landscape to dispersal. For example, consider a species that is highly dependent on forest cover at a particular elevation in a complex mountainous landscape such as the northern Rocky Mountains. Resistance to dispersal will be low in forest cover at the optimal elevation but will increase substantially in non-forest areas and at suboptimal elevations. This pattern of strongly heterogeneous resistance gradients across a complex landscape will result in fracture zones and barriers where there are breaks in connectivity because of cumulative movement costs that exceed the dispersal ability of the species. Conversely, a species whose movement costs are independent of forest

Table 13. Average divergence between mean trajectory groups across dispersal abilities (5000 m, 10,000 m, and 20,000 m).

	Trajectory group	1	2	3	4	5	6
5000 m	1						
	2	3.529886					
	3	1.954463	2.526213				
	4	2.639591	3.399948	1.070473			
	5	4.906195	5.398407	3.449992	2.401467		
	6	4.631628	6.227383	3.838317	2.835228	1.749125	
	7	4.539686	6.036204	3.670334	2.652257	1.548702	0.222499
10,000 m	1						
	2	2.191593					
	3	2.184059	2.179247				
	4	2.416133	2.333473	0.234735			
	5	4.973272	5.195756	3.097024	2.898015		
	6	4.315879	4.742303	2.58091	2.409404	0.727126	
	7	4.274607	4.508495	2.38925	2.195146	0.71261	0.420676
20,000 m	1						
	2	1.411255					
	3	1.585954	1.072139				
	4	1.92749	1.213163	0.35013			
	5	4.190771	3.593526	2.684199	2.413609		
	6	3.560826	3.033762	2.078012	1.83079	0.635104	
	7	3.612377	2.956557	2.072636	1.787052	0.639146	0.329691

cover, elevation, or roads would be able to integrate the landscape much more completely through dispersal. For example, many bird species are capable of flying over roads and other terrestrial barriers, and can traverse complex topography with ease.

The ultimate objective of this analysis was to predict the synergistic effects of multiple ecosystem stressors at broad geographical scales on habitat area, fragmentation, and connectivity. We present a general method to estimate habitat area, fragmentation, and corridor connectivity for multiple species across vast geographical areas. The resistant kernel approach to modeling landscape connectivity has a number of major advantages as a robust approach to assessing current and future landscape connectivity for multiple wildlife species under climate change scenarios. First, unlike most corridor prediction efforts, it is spatially synoptic and provides prediction and mapping of expected migration rates for every pixel in the study area extent, rather than only for a few selected “linkage zones” (e.g., Compton and others 2007). Second, it explicitly incorporates the influence of population distribution and density. Third, scale dependency of dispersal ability can be directly included to assess how species of different vagilities will be affected by landscape change and fragmentation under a range of scenarios (e.g., Cushman and others 2010a). Fourth, it ideally quantifies the effect of different patterns of landscape resistance on connectivity, given that the extent and shape of the least-cost dispersal kernels are fundamentally shaped and constrained by the cumulative movement cost across the resistance surface from the dispersal source.

The combination of the method’s sensitivity to distribution, dispersal ability, and differential landscape resistance enabled us to map species-specific, scale-dependent population core areas, fracture zones, and movement corridors across the United States northern Rocky Mountains. We produced 108 different connectivity maps for the combination of 36 resistance surfaces and 3 dispersal abilities. These connectivity surfaces provide spatially explicit prediction of core areas, fracture zones, and corridors for a broad range of native taxa, and could be extremely useful in guiding habitat protection, enhancement, and/or restoration efforts to maximally benefit particular species of concern.

The 108 connectivity maps represent a broad range of native species expressing different ecological associations and different dispersal abilities. Recent empirical research has enabled us to associate several of these hypothetical models with particular native species of conservation concern. For example, Cushman and others (2006) tested the same suite of resistance models in a study of the landscape controls on gene flow of American black bear (*Ursus americanus*). The authors identified the resistance model FHEMRH (model number 21, Table 4) as the most supported explanation of population connectivity for this species. More recently, Short Bull and others (2011) evaluated the same 36 resistance models for black bear population connectivity across a replicate sample of 12 different study areas distributed across the full extent of the U.S. northern Rocky Mountains and affirmed the conclusions of Cushman and others (2006) that black bear gene flow is facilitated by forest cover at middle elevations and is resisted by suboptimal elevations,

non-forest conditions, and roads. The predicted surface of population connectivity for the FHEMRH model at dispersal ability 20,000 m provides a spatially synoptic prediction of population connectivity for black bears across the northern Rocky Mountains. Cushman and others (2008) used a factorial implementation of least-cost paths to predict optimal movement routes of black bear from Yellowstone National Park to Canada based on the FHEMRH resistance layer. That prediction is useful to optimize the location of particular mitigation and restoration projects along the least-cost route of dispersal from Yellowstone to Canada but does not give a spatially complete picture of population core areas, barriers, fracture zones and corridors across the full extent of the northern Rocky Mountains, which is provided by the resistant kernel maps.

Recent work on the landscape genetics of wolverine (*Gulo gulo*; Schwartz and others 2009) identified high-elevation habitats as low resistance to dispersal of this species given its dependence on spring snow for denning and foraging habitat (Aubry and others 2007; Copeland and others 2010). Our EH model (model number 1, Table 4) closely approximates this, and the EH model with a 20,000 m dispersal ability presents a spatially synoptic picture of population core areas, fracture zones, and corridors for this species of conservation concern. Schwartz and others (2009) used a factorial least-cost path approach to produce a network of predicted corridors across the northern Rocky Mountains. However, the factorial least-cost path approach did not include any dispersal thresholds. Thus, the network of predicted corridors includes many paths much greater in length than is reasonable for any terrestrial animal to disperse. The scale dependence of the resistant kernel approach produces predictions of functional landscape connectivity that incorporate the inherent spatial limits of dispersal and provide a more realistic picture of regional connectivity. In addition, the least-cost path approach emphasizes the lowest cost single routes between sources and destinations but ignores the fact that animals rarely utilize optimal dispersal paths and that dispersing animals are naïve to landscape structure, meaning this method may not accurately reflect the probability distribution of a species' likely dispersal movements. The cumulative resistant kernel integrates all paths across the distribution of cumulative dispersal distances up to the dispersal threshold and thus provides a spatially complete and realistic picture of landscape connectivity.

A third species of conservation concern whose population connectivity has recently been studied in the northern Rocky Mountains is the American marten (*Martes americana*; Wasserman and others 2010, in press). Wasserman and others (2010) used landscape genetics to test several hundred alternative resistance models for gene flow of this species and identified elevation as the driver of population connectivity. Specifically, resistance to gene flow was lowest at 1500 m elevation and increased as an inverse Gaussian function at elevations above and below 1500 m. This resistance model is identical to our EH model. Marten and wolverine have the same landscape resistance model, however, they

differ greatly in vagility, such that predictions of population connectivity for marten would not accurately predict that of wolverine. In this case, the FH model at the 10,000 m dispersal threshold most accurately reflects the functional connectivity of American marten populations across the study area. The differences in predicted population connectivity for these two species illustrates the importance of explicit incorporation of dispersal ability. Even though they both have the same resistance model (EH), there are large differences in predicted population connectivity of these species based on dispersal ability. For example, the area of the landscape predicted to be connected by dispersal is 47% greater for the wolverine and the degree of habitat fragmentation is much lower. Specifically, the number of isolated patches of connected habitat is nearly seven-fold higher for marten than for wolverine, reflecting the effects of the wolverine's greater dispersal ability on integrating across gaps that the marten cannot cross.

Importance of Broad-Scope Multi-Taxa Assessment of Landscape Connectivity

Most past evaluations of habitat connectivity and fragmentation in the U.S. northern Rocky Mountains have focused on large carnivores (Weaver and others 1996; Carroll and others 2001; Cushman and others 2008; Schwartz and others 2009). This is in part due to their large home range requirements and potential vulnerability to habitat fragmentation, as well as the fact that many large carnivore species are species of conservation concern. The long-term viability of large carnivores in the Rocky Mountains is believed to strongly depend on regional connectivity of habitat due to the low densities, large home range size, vulnerability to human disturbance, and low fecundity of these species (Noss 1996; Weaver and others 1996; Carroll and others 2001). In addition, a number of researchers have proposed using large carnivores as umbrellas for habitat and connectivity protection plans (Noss 1996; Carroll and others 2001). Although large carnivores are appropriate focal species and flagships (Servheen and others 2001; Singleton and others 2002), other researchers have noted that they are generally highly mobile habitat generalists and thus likely will be inadequate umbrellas for other species (Beier and others 2009; Minor and Lookingbill 2010).

The purpose of this analysis was to produce connectivity mapping for a broad range of native taxa and to not assume that any particular taxa would serve as an umbrella species for many others. We found that several groups of species express similar patterns of landscape connectivity as a result of similar ecological associations. We identified seven species groups that have similar multivariate patterns of landscape structure and change in landscape structure of connected habitat as dispersal ability increases. Specifically, we found that species groups (in parentheses) are associated with (1) high-elevation forest, (2) low-elevation forest,

(3) middle-elevation forest, (4-5) forest cover but not elevation, and (6-7) particular elevations but not forest cover formed highly coherent groups in the principal components analysis of landscape structure trajectories. These groups were significantly different in the extent and pattern of connected habitat at each dispersal ability and the degree to which landscape connectivity changed with increasing dispersal ability. This emphasizes that connectivity predictions for one species or one species group are not likely to accurately reflect functional connectivity for other species with different ecological associations.

Species-Specific Connectivity

Our analysis identified several important patterns of functional landscape connectivity in relation to resistance model and dispersal ability. Across dispersal abilities, species strongly associated with forest cover and high-elevation or low-elevation habitats had the lowest extent and highest fragmentation of connected habitat. The vast majority of protected lands in the study area (Federal ownership, Figure 1) are at middle to higher elevations. The lower-elevation areas of the study area are mostly in private ownership and are experiencing rapid development. An extensive network of highways bisects the study area, with the majority of major highways located in lower elevation valleys. In addition, climate change will likely lead to an upward migration of lower tree lines in the northern Rocky Mountains (J. Littell, pers. comm.), further reducing the extent and increasing the fragmentation of lower elevation forest habitat. As a result of the combination of these factors, species with limited dispersal ability associated with lower elevation forest will probably be most vulnerable to habitat loss and fragmentation in the northern Rocky Mountains.

In contrast, among species with greater dispersal ability (20,000 m), the most limited extent of connected habitat across dispersal thresholds was for species associated with high forest cover at the highest elevations (FHEHRH). These species are likely less vulnerable to human development than those that rely on lower elevation habitats, given that much of the landscape these species occupy is protected by public ownership. However, there are numerous bottlenecks in the distribution of high-elevation habitat, and these usually coincide with mountain passes in which major highways have been built (e.g., Cushman and others 2008; Schwartz and others 2009; Shirk and others 2010). Thus, landscape connectivity of these species may also be highly impacted by transportation infrastructure. As climate warms, the ecological conditions these species depend on will shift upslope and become more limited in area and more fragmented.

Dispersal Ability and Habitat Connectivity

Our analysis showed important differences among species groups in terms of the sensitivity of landscape connectivity

to dispersal ability. Species groups that are predicted to have high extent and low fragmentation of connected habitat showed relatively little change in connectivity with increasing dispersal ability. For example, groups 4, 5, 6, and 7, which are associated with forest cover but not elevation (4-5) or elevation and not forest cover (6-7) are predicted to have relatively high connectivity even at low dispersal abilities. As a result, as dispersal ability increases, there is relatively little change in connectivity for these species.

In contrast, species groups 1 and 2, which are associated with high- and low-elevation forest habitats, respectively, have much higher sensitivity to change in dispersal ability. As dispersal ability increases, these species groups experience large increases in the extent of connected habitat and decreases in fragmentation. There is a large and important difference between these two groups. Models for group 2, the low-elevation forest associated species, predict a much greater increase in connectivity with increasing dispersal ability than for group 1. At low dispersal abilities, the low-elevation forest species have substantially lower area and higher fragmentation of connected habitat than any other group. However, at high dispersal abilities, it is the high-elevation forest species that are most limited by habitat extent and fragmentation. This follows from the differences in the patterns of landscape resistance in the two models. For low-elevation forest species, there is a large number of scattered and isolated patches of low resistance habitat, corresponding to low-elevation forest areas. At low dispersal abilities, these are mostly isolated as fragments. However, as dispersal ability increases, dispersing organisms are able to move between the fragments, resulting in coalescence of these isolated patches into large and contiguous blocks of habitat that are connected by dispersal. Conversely, the high-elevation species are associated with relatively large but highly disjunct patches of low resistance habitat, corresponding to mountain peaks and ranges. As dispersal ability increases, individuals are increasingly able to move among neighboring mountains, but the average distance between such low resistance patches is much higher than for low-elevation forest and there is much less coalescence into large contiguous connected patches.

As dispersal ability increases, there is a marked convergence of habitat connectivity within species groups. At low dispersal abilities, the extent and fragmentation of habitat for species with similar ecological associations is modest but increases dramatically with increasing dispersal ability, such that by 20,000 m dispersal ability there is near complete overlap in the extent and pattern of connected habitat for species within each of the seven trajectory groups we identified. This suggests that multiple-taxa conservation efforts aimed at promoting population connectivity are likely to be more effective for highly mobile species than for species with limited dispersal ability. There is an analogous convergence of the extent and pattern of connected habitat among groups as well. The average separation of the seven species groups in the principal component space becomes significantly smaller as dispersal ability increases. This reflects that

as dispersal ability increases, the extent of connected habitat for each species increases, and thus, the degree of overlap among species and species groups also tends to increase.

Scope and Limitations

Uncertainty in Landscape Resistance

Most of the published studies using landscape resistance maps have utilized expert opinion to estimate resistance to movement due to landscape features given the lack of detailed information on animal movement or gene flow (e.g., Compton and others 2007). This is not surprising given the difficulty in gathering sufficient sample sizes of reliable data on relationships between animal movement and multiple landscape features at broad spatial scales (McGarigal and Cushman 2002; Cushman 2006). However, basing analyses on unvalidated expert opinions is not desirable (Seoane and others 2005) and has been a major weakness in past efforts. Landscapes are perceived by particular species in ways that may not correspond to our assumptions concerning connectivity and habitat quality (With and others 1997; Shirk and others 2010; Wasserman and others 2010).

We sought to mitigate this uncertainty by evaluating potential landscape resistance parameterizations that represent a broad range of species' sensitivities to land use, forest cover, elevation, and roads. We repeated all analyses on 36 different resistance maps that reflect different relative resistance of roads, human development, agriculture, and forest cover. The purpose was to explicitly evaluate the sensitivity of connectivity predictions to differences in ecological associations. We were also able to quantify uncertainty due to variability in functional landscape resistance among species and species groups.

Uncertainty in Dispersal Ability

What constitutes functional connectivity is highly dependent on the dispersal behavior of the particular species in question. For example, patches that are connected for one species may be isolated for another. Thus, habitat connectivity is affected by population distribution and habitat continuity, but the magnitude and nature of the effect depends on the dispersal ability of the particular species. The cumulative cost distances organisms are able to traverse, and the probability distributions of movements as function of cost distances between sources and potential destinations vary greatly among species. Generally, larger organisms can travel longer distances. Therefore, a 100 m wide agricultural field may be a complete barrier to dispersal for small organisms such as invertebrates (e.g., Usher and others 1993) or amphibians (Rothermel and Semlitsch 2002; Marsh and others 2004), yet may be quite permeable for larger and more vagile organisms such as birds. We sought to explicitly quantify this uncertainty by evaluating a range

of potential dispersal abilities. Our goal was to evaluate a low end, middle, and high end estimate of dispersal ability to quantify the effects of differential mobility on predictions of the extent and connectivity of habitat in the northern Rocky Mountains. Our results indicate that predictions of the extent and pattern of core areas, and the degree to which they are linked by dispersal is extremely sensitive to dispersal ability.

Uncertainty in Species Distributions

The methods we employ are based on predicting population cores, fractures, and corridors based on quantitative modeling of dispersal from a collection of source locations in the landscape. These sources reflect expected locations occupied by the species. Therefore, the analysis is highly dependent on accurate information on species distribution and density. Analysis based on incorrect species distribution information may be highly misleading. To mitigate uncertainty in the distribution of the focal species, we conducted a habitat-based species group analysis. Specifically, we modeled dispersal from all cells in the landscape that were predicted to have low resistance (and thus high suitability) for each of the 36 resistance maps. This analysis reflects connectivity of habitat but not any actual population, as we did not incorporate actual distribution and density information from real species. Given our goal of evaluating a broad range of ecological associations and dispersal abilities, it would have been impossible to obtain sufficiently accurate distribution and density information for real species reflecting each of our 108 combinations of resistance model and dispersal ability.

Uncertainty in Critical Fragmentation Thresholds

A critical threshold is an abrupt, nonlinear change that occurs in an organism response (e.g., dispersal success, productivity, and patch occupancy across a small range of habitat loss and/or fragmentation (With and King 1999). Both empirical data (Koopowitz and others 1994; Carlson and Stenberg 1995; Doncaster and others 1996; Jansson and Angelstam 1999) and theoretical models predict critical thresholds of habitat where ecological relationships change abruptly (O'Neil and others 1988; Turner and Gardner 1991; With and Crist 1995; Bascompte and Sole 1996; Flather and Bevers 2002). For example, neutral landscape models, derived from percolation theory as applied in the field of landscape ecology (Gardner and others 1987, 1989; Gardner and O'Neill 1991; Pearson and Gardner 1997; With 1997; With and King 1999), have been used to characterize habitat loss and fragmentation as a threshold phenomenon (With and King 1999). Above the so-called percolation threshold, habitat loss results in a simple additive loss of habitat. At the threshold, a qualitative change in landscape structure occurs. A small additional loss of habitat at this point produces a physically disconnected landscape in which the organism's

habitat no longer maintains continuity across the landscape. Further habitat loss merely leads to greater discontinuity. The existence, nature, and severity of critical thresholds in the population response to fragmentation among wildlife species inhabiting the northern Rocky Mountains is largely unknown. Our analysis quantifies location, size, and connectivity of core patches, fracture zones, and corridors for a large range of ecological associations and dispersal abilities. The principal components analysis shows differences in connectivity among several species groups and the relative effects of changes in dispersal ability. However, full interpretation of the biological implications of these patterns would require knowledge of how incremental change in core areas, fracture zones, and corridors would affect demographic and genetic processes affecting viability. This would likely require modeling over a much larger number of increments in dispersal ability and a much finer gradation of resistance models—an area that deserves additional investment and research.

Conclusion

Population connectivity is a product of the dispersal ability of the species, the influences of different landscape elements on its movement behavior, the density and distribution of the population, and the structure of the landscape. Failure to explicitly consider each of these factors, however, may lead to incorrect conclusions. In this paper, we evaluated population connectivity across the United States northern Rocky Mountains for a broad range of organisms expressing different sensitivity to landscape structure and different dispersal abilities. Human land use and climate change alter the composition and configuration of landscapes, but the impact of these changes on loss and fragmentation of suitable habitat for a particular organism depends on the scale and nature of those changes in relation to how that organism perceives and interacts with landscape patterns (With and Crist 1995; Pearson and others 1996; With 1997; With and others 1997). For example, changes in the size and isolation of mature forest patches at a particular scale may have little or no detectable impact on species that perceive and respond to landscape patterns at a different scale, select habitat on the basis of other environmental variables (e.g., shrub cover and litter depth), or utilize a broad range of habitats (i.e., generalist or multi-habitat species). Our spatially synoptic predictions of population connectivity for all 108 species may be highly useful to guide species specific and multi-species conservation efforts. We found large differences among groups of species in terms of the extent and connectivity of habitat and the sensitivity of connectivity to dispersal ability. We found that species with limited dispersal ability and associated with low-elevation forest have the most limited and fragmented distribution of connected habitat. Species associated with high-elevation forest also appear highly vulnerable to habitat loss and fragmentation based on limited extent and connectivity of habitat.

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