



Predicted connectivity pathways between grizzly bear ecosystems in Western Montana

Sarah N. Sells^{a,*}, Cecily M. Costello^b, Paul M. Lukacs^c, Lori L. Roberts^b, Milan A. Vinks^b

^a US Geological Survey, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812, United States of America

^b Montana Fish, Wildlife and Parks, 490 N Meridian Rd, Kalispell, MT 59901, United States of America

^c Wildlife Biology Program, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT 59812, United States of America

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ABSTRACT

Habitat and corridor mapping are key components of many conservation programs. Grizzly bear populations in the continental US are fragmented and connectivity among federal recovery areas is a conservation goal. Building on recent work, we modeled movements to predict areas of connectivity, using integrated step selection functions (iSSFs) developed from GPS-collared grizzly bears ($F = 46$, $M = 19$) in the Northern Continental Divide Ecosystem (NCDE). We applied iSSFs in a $>300,000$ km² area including the NCDE, Cabinet–Yaak (CYE), Bitterroot (BE), and Greater Yellowstone (GYE) Ecosystems. First, we simulated directed movements (randomized shortest paths with 3 levels of exploration) between start and end nodes across populations. Second, we simulated undirected movements from start nodes in the NCDE, CYE, or GYE (no predetermined end nodes). We summarized and binned results as classes 1 (lowest relative predicted use) – 10 (highest relative predicted use) and evaluated predictions using 127 outlier grizzly bear locations. Connectivity pathways were primarily associated with mountainous areas and secondarily with river and stream courses in open valleys. Values at outlier locations indicated good model fit and mean classes at outlier locations (≥ 7.4) and Spearman rank correlations (≥ 0.87) were highest for undirected simulations and directed simulations with the highest level of exploration. Our resulting predictive maps can facilitate on-the-ground application of this research for prioritizing habitat conservation, human–bear conflict mitigation, and transportation planning. Additionally, our overall modeling approach has utility for myriad species and conservation applications.

1. Introduction

Connectivity among wildlife populations is of pressing concern given ongoing and accelerating habitat loss to human development, which fragments remaining habitats and isolates populations (Crooks et al., 2017, 2011; Fahrig et al., 2021). Connected landscapes are those that facilitate movements of animals between patches (Fahrig et al., 2021; Taylor et al., 1993). Loss of connectivity among populations may reduce their genetic variation and ability to respond to and recover from environmental perturbations. Theory and empirical precedent have shown that island populations face greater risks of extinction, especially when small (MacArthur and Wilson, 1967). Isolation of populations may accordingly accelerate irreversible losses of species.

Today, grizzly bears (*Ursus arctos*) represent an example of a species threatened by habitat loss and population fragmentation. Worldwide, brown bear populations have become extirpated or fragmented,

particularly on the southern edge of their distribution (McLellan et al., 2017). In the conterminous United States, an estimated 50,000 grizzly bears were likely present 200 years ago (USFWS, 2022). The arrival of Europeans brought heavy persecution, habitat loss, and rapid decline. By 1975, when grizzly bears were listed as a threatened species under the Endangered Species Act, only six remnant populations were thought to remain in the conterminous US. These were found in large tracts of mostly public land, such as National Parks and National Forests, representing just 2 % of the species' former range (USFWS, 1993). Later evidence indicated that two of these populations had also become extirpated.

Establishment of recovery zones within each grizzly bear ecosystem (Fig. 1; USFWS, 1993) and collaborative efforts among state and federal agencies, tribes, landowners, and the public have facilitated slow increases in grizzly bear numbers and range extent. As of 2021, population estimates exceeded 1000 animals each in the Northern Continental

* Corresponding author.

E-mail address: sarah.sells@umontana.edu (S.N. Sells).

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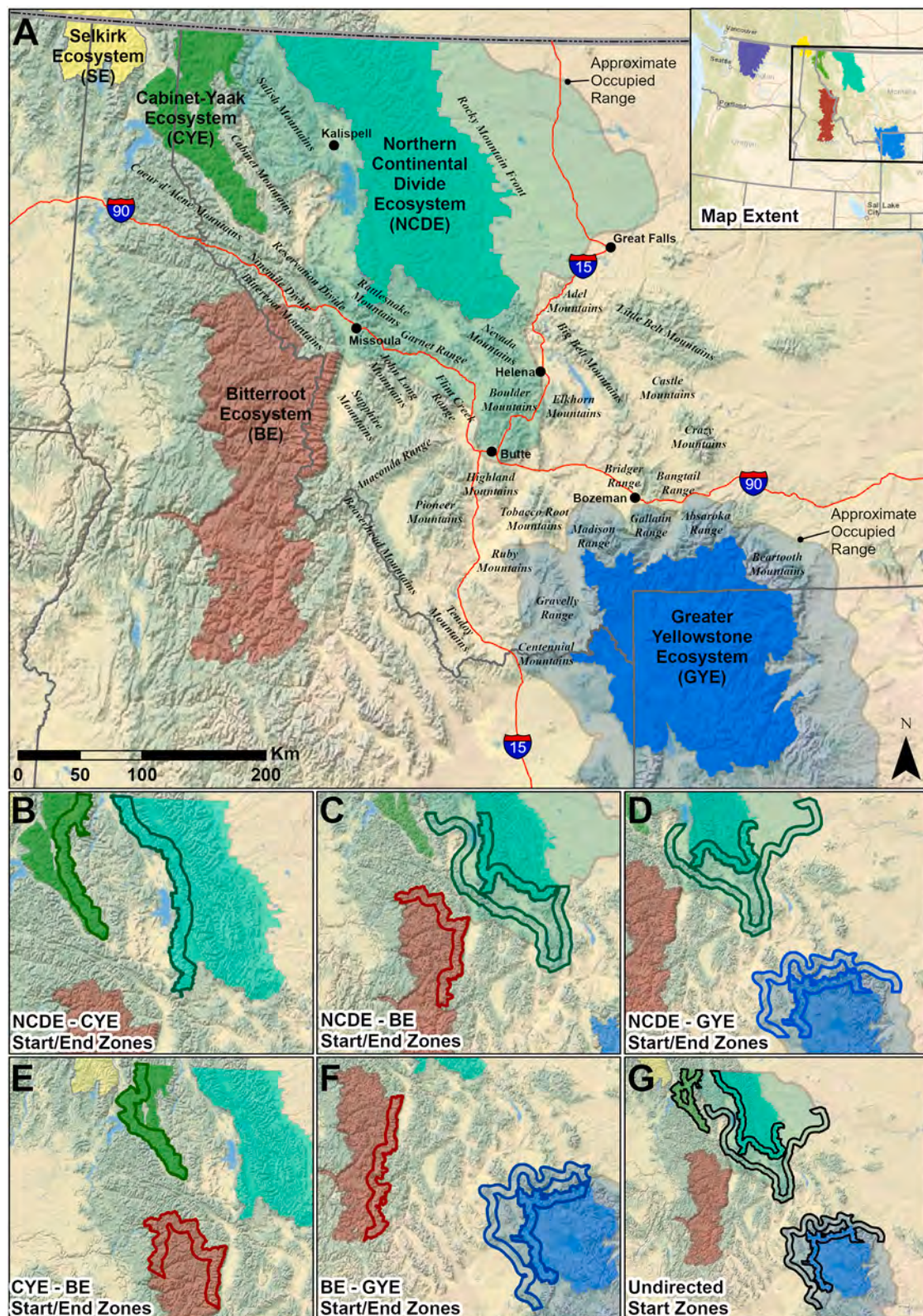


Fig. 1. The study area (A) encompassed the NCDE, CYE, BE, and GYE grizzly bear recovery zones and the current estimated occupied range of populations in and near the NCDE and GYE. The BE recovery zone boundary was a combination of the recovery zone boundaries identified in alternatives 1 (reintroduction) and 2 (natural recolonization) of the reintroduction plan for the BE (USFWS, 2000). Mountain ranges noted in the main text are labeled for reference. (The 6th recovery zone, the NCE, is visible to the west in the extent map in purple.) Each directed simulation iteration drew random start and end nodes from within start and end zones (bold polygons) as shown for the NCDE to the nearby recovery zones (B, C, D) and from the CYE and GYE to the BE (E, F). Each undirected simulation iteration drew a random start node from within the NCDE, CYE, or GYE start zones (G). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Divide Ecosystem (NCDE; Costello and Roberts, 2017; Mace et al., 2012) and Greater Yellowstone Ecosystem (GYE; Van Manen et al., 2021). The Selkirk Ecosystem (SE) had >83 grizzly bears (Proctor et al., 2012) with >44 in the US portion (Kasworm et al., 2021b), and the Cabinet-Yaak Ecosystem (CYE) had ~60 animals (Kasworm et al., 2021a; Kendall et al., 2016). The Bitterroot (BE) and North Cascades (NCE) Ecosystems lacked any known permanent residents.

With increasing numbers, grizzly bears have slowly regained parts of their former range; however, populations remain largely isolated and areas that might facilitate connectivity remain uncertain. The NCDE, CYE, SE, and NCE straddle the international border, but grizzly bears in Canada face similar threats of low numbers, habitat loss, and population fragmentation (Proctor et al., 2012; USFWS, 1993). However, as of 2020, only 57 km separated the NCDE and GYE occupied ranges, and the NCDE range had expanded to slightly overlap a small edge of the BE (Fig. 1). Distances between other populations were also shrinking.

Information is needed to assess potential connectivity pathways that could promote genetic and demographic connectivity among ecosystems. Dispersal of individuals among populations is the primary and preferred means for achieving connectivity among existing populations (Clobert et al., 2012; Crooks and Sanjayan, 2006). Dispersal movements may also facilitate recolonizations of vacant habitats, although establishment of entirely distinct populations through long-distance dispersal may be a slow process (Blundell et al., 2002; Onorato et al., 2004; Valière et al., 2003). Male grizzly bears are more likely to disperse from their natal range and move greater distances than females (Blanchard and Knight, 1991; McLellan and Hovey, 2001; Proctor et al., 2004, 2012). Although females are typically philopatric, long-distance female dispersal sometimes occurs, especially in expanding populations (Jerina and Adamič, 2008; Karamanlidis et al., 2021; Kojola and Laitala, 2000; Swenson et al., 1998). While natal dispersal movements are the most likely means of population connectivity among the existing grizzly bear

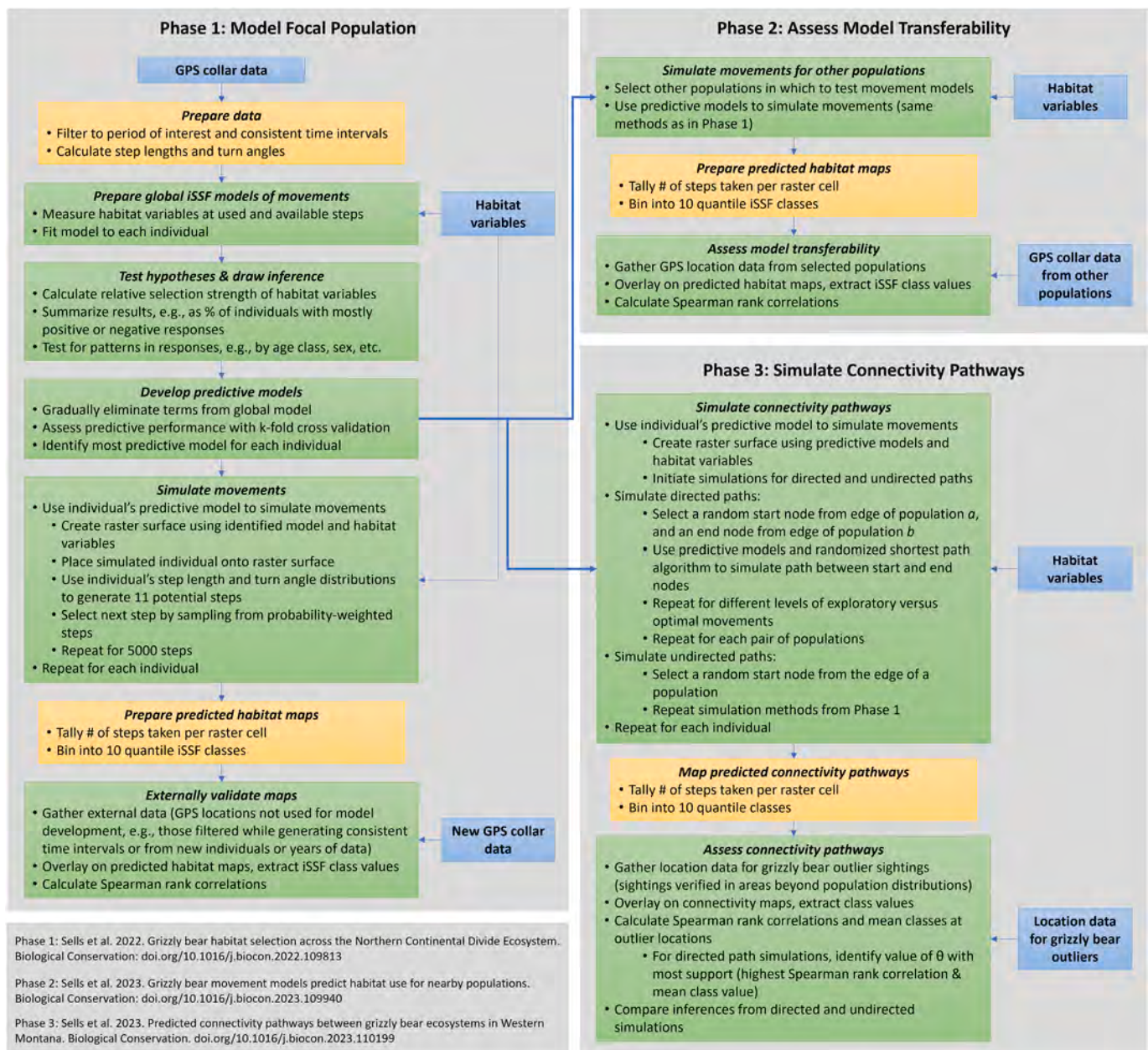


Fig. 2. Our study represented the third phase of a multi-phase study. In the first phase, Sells et al. (2022) focused on developing models for a focal population (the NCDE). In the second phase, Sells et al. (2023) assessed model transferability by applying the models to nearby populations in the GYE, CYE, and SE. In the present third phase, we applied the models to simulate connectivity pathways between populations in western Montana.

populations in the conterminous US, only a few examples of long-distance recolonization of bears or other carnivores have been observed (e.g., [Onorato et al., 2004](#); [Thompson and Jenks, 2010](#)). Whether natural recolonization of currently unoccupied habitat such as the BE is achievable through dispersal alone is unclear. Settlement of intervening landscapes by recolonizing resident females may be necessary to facilitate natural connectivity.

Our present objective was to identify potential connectivity pathways for grizzly bears, i.e., areas predicted to facilitate movements of individuals between populations. This follows the concept of functional connectivity or “the degree to which a landscape facilitates or impedes movements of organisms among resource patches” ([Merriam, 1984](#); [Taylor et al., 1993](#)), which characterizes connectivity by estimating individual movement success in response to landscape structure ([Fahrig et al., 2021](#)). Our study centered on the three occupied (NCDE, CYE, and GYE) and one unoccupied (BE) ecosystems in and adjacent to Montana, as this area contains most of the potential landscape for connectivity within the conterminous US. To achieve our study objective, we built on a larger study initiated in [Sells et al. \(2022\)](#). In this first phase, the authors developed integrated step selection functions within currently occupied range in the NCDE to better understand how grizzly bears use habitat ([Fig. 2](#)). Subsequent application of these models to the NCDE demonstrated high predictive power. In a second phase, [Sells et al. \(2023\)](#) demonstrated that models developed for the NCDE accurately predicted habitat use in nearby populations and were therefore expected to be transferable and reliable for predicting space use beyond the NCDE. In this present third phase, we demonstrate that multiple simulation methods help predict connectivity pathways and where to focus conservation efforts. This general study framework can be easily applied to other species to enhance understanding of animal space use, potential for functional connectivity, and conservation needs.

Our present work expands on [Peck et al. \(2017\)](#), who employed step selection functions and randomized shortest path simulations to predict pathways for male grizzly bear movements between the NCDE and GYE. Randomized shortest paths enable simulating varying degrees of optimal versus exploratory movements between a given start and end node ([Panzacchi et al., 2016](#)). We employed integrated step selection functions (iSSFs) to model directed movements (i.e., randomized shortest paths with start and end nodes) and undirected movements (i.e., from start nodes only with no predetermined end nodes; [Sells et al., 2022](#)). iSSFs extend traditional step selection functions to mechanistically model movement ([Avgar et al., 2016](#); [Signer et al., 2019](#)). We used [Sells et al. \(2022\)](#)'s iSSFs, built using movement data from GPS-collared grizzly bears monitored during 2003–2020 in the NCDE. These iSSFs represented hypotheses that landscape features influencing grizzly bear habitat selection include food availability, terrain ruggedness, forested areas, forest edges, riparian areas, building densities, and distance to secure (unroaded) habitat ([Appendix](#)). Because [Sells et al. \(2022\)](#)'s iSSFs demonstrated high individual variation in spatial behavior, our connectivity simulations were likewise individual-based to account for variations in movement behaviors.

2. Methods

2.1. Study area

Our >300,000 km² study area centered on the Rocky Mountain region of western Montana, eastern Idaho, and northern Wyoming, including the NCDE, CYE, BE, and GYE recovery zones ([Fig. 1](#)). We defined the BE boundary to be a combination of the recovery zone boundaries identified in alternatives 1 (reintroduction) and 2 (natural recolonization) of the original reintroduction plan for the BE ([USFWS, 2000](#)). We constrained the study area to the US due to a lack of comparable data for Canada. The historically glaciated landscape is a complex of forested mountain ranges (with ~1900–3900 m peaks) and open river valleys (~800–1800 m elevation) that transition to the Great Plains

toward the east. Climate varies with topography and differs across the Continental Divide. A northern Pacific coastal climate with cool summers and mild winters occurs to the west, while a semi-arid continental climate with warm summers and cold winters occurs to the east ([weather-atlas.com](#)). Montane conifer (e.g., *Picea*, *Abies*, *Pinus*, *Pseudotsuga* spp.) forests are interspersed with meadows and shrublands at mid elevations and alpine communities at the highest elevations. Mixed grass prairie and sagebrush (*Artemisia* spp.) shrublands are the primary natural communities in the valleys and Great Plains. Forestry, ranching, agriculture, and recreation are major land uses. More than 90 % of each recovery zone is publicly owned, but private lands make up roughly 50 % of the area between recovery zones. Major roads pass between recovery zones, including two interstates (I-90 and I-15) and various federal and state routes and highways.

2.2. iSSF overview

[Sells et al. \(2022\)](#) developed 65 predictive iSSFs for 46 female and 19 male grizzly bears in the NCDE ([Fig. 2](#) and [Appendix](#)). iSSFs were based on location data collected at 3-hour intervals (+/- 45 min) from individuals monitored via GPS transmitters (Telonics, Mesa, Arizona, USA) for one or more years from 2003 to 2020 during the primary active season (May–Nov). [Sells et al. \(2022\)](#) first built global iSSFs for each bear in Program R ([R Core Team, 2020](#)) using package amt ([Signer et al., 2019](#)). Global iSSF covariates included the Normalized Difference Vegetation Index (NDVI, as an index to food abundance) during peak green-up (Jun 15 – Jul 15), terrain ruggedness, distance and density of forest edge, density of riparian areas, density of buildings, and distance to secure habitat (i.e., as defined by the US Fish and Wildlife Service, areas on public, state, and tribal lands >500 m from roads). To develop a final predictive iSSF for each NCDE bear, [Sells et al. \(2022\)](#) iteratively eliminated terms from the global iSSF to determine the model formulation that maximized the cross-validation score for that individual. As a result, some bears retained the global iSSF whereas others had reduced iSSFs with fewer variables.

[Sells et al. \(2022\)](#)'s iSSFs for the 65 individuals provided the foundation for our present study ([Fig. 2](#)). As in [Sells et al. \(2022\)](#) and [Sells et al. \(2023\)](#), here we applied each bear's iSSF to the study area (300 m cell resolution), creating a conductance surface to use for that bear in subsequent simulations (described below). We calculated conductance values as $\exp(\beta x_i)$ ([Northrup et al., 2022](#)); β is the coefficient vector of the estimated iSSF and x_i the vector of habitat covariates of cell i . We trimmed extremes using the 0.025 and 0.975 quantile values and normalized remaining values to a 0–1 scale ([Squires et al., 2013](#)).

2.3. Directed simulations

For directed simulations, we expanded on [Peck et al. \(2017\)](#)'s study in important ways. First, their study included widely varying step length intervals; because step selection functions are scale dependent, we thinned steps to reasonably consistent time intervals ([Signer et al., 2017, 2019](#)) of 3 h +/- 45 min. Second, following [Panzacchi et al. \(2016\)](#), [Peck et al. \(2017\)](#) used the inverse logit transformation to map their step selection functions to the landscape for randomized shortest path simulations, whereas we used an exponential transformation as needed for used-available designs to map relative probability of use ([Northrup et al., 2022](#)). Simulations exploring outcomes under both mapping methods demonstrated strong effects of misapplying the inverse logit transformation (these authors, unpublished data), and this may in turn misinform conservation decisions. Third, rather than present raw values for predictions, we summarized predictions within specified areas to aid interpretation of results ([Morris et al., 2016](#)).

For directed simulations, we used each bear's iSSF and conductance surface to simulate movement in Program R ([R Core Team, 2020](#)). We first transformed each conductance surface to a transition matrix of Moore neighborhoods (i.e., a cell's 8 nearest neighbors) with transition

values between neighboring cells i and j calculated based on conductance values of cells i (c_i) and j (c_j): $f(c_i, c_j) = \max(c_i, c_j) - c_i + c_j$ (Panzacchi et al., 2016). Directed simulations employed package *gdistance* (van Etten, 2017) and the randomized shortest path algorithm (Panzacchi et al., 2016), where randomness in movement is defined by θ . Higher values of θ are similar to a least-cost path (i.e., assumes optimal movements) whereas lower values are increasingly similar to a random walk (i.e., akin to exploration). We simulated θ of 0.01, 0.001, and 0.0001 to predict paths representing different levels of optimal movements versus exploratory movements.

Directed simulations entailed 5 overall routes for the NCDE–CYE, NCDE–BE, NCDE–GYE, CYE–BE, and GYE–BE. For each simulation iteration, we paired a random start node with a random end node and predicted paths between nodes. Nodes were drawn from start and end zones designated as 15-km inward buffers from the edges of recovery zones or most recent (2020) estimates of occupied range for the NCDE and GYE (Fig. 1). For NCDE–CYE simulations, the start zone was the western edge of the NCDE and end zone the eastern edge of the CYE (Fig. 1B). (The edge of the NCDE occupied range partially overlaps the CYE, so we excluded this start zone variation for NCDE–CYE simulations.) For NCDE–BE simulations, two sets of start zones were the southern edge of the NCDE and edge of the occupied range north of Interstate 90; the end zone was the northern edge of the BE (Fig. 1C). For NCDE–GYE simulations, two start zones were the southern edges of the NCDE and occupied range, and end zones were the northern edges of the GYE and occupied range (Fig. 1D). For CYE–BE simulations, the start zone was the southwestern edge of the CYE and end zone was the northern edge of the BE (Fig. 1E). For GYE–BE simulations, two start zones were the western edges of the GYE and occupied range, and end zone the eastern edge of the BE (Fig. 1F). For each θ , we identified paths between 12 pairs of randomly selected nodes per bear for each of the 5 routes (to account for computation limitations; for NCDE–BE, NCDE–GYE, and GYE–BE simulations, 50 % of the 12 nodes originated in each variation of start or end zones). This yielded 60 start and end node pairs (12 iterations $\times$ 5 routes) per individual bear iSSF ($n = 46$ female and 19 male iSSFs) per θ (0.01, 0.001, and 0.0001).

For each θ , we combined and summed results by sex to reveal the relative frequency at which grid cells were traversed. We mapped results by first omitting values <0.01 to remove extreme low values. Because we were interested in potential movements between recovery zones, we set results to null for areas within each occupied recovery zone and used equal area quantile binning to display results as classes 1 (lowest relative predicted use) – 10 (highest relative predicted use; Morris et al., 2016). Resulting maps represented the relative predicted connectivity pathways for each sex. We also summarized Euclidian distances between start and end nodes for each route and sex.

2.4. Undirected simulations

We next simulated undirected movement following the approach from Sells et al. (2022, 2023) using each bear's iSSF in turn. For each iteration, we applied the individual bear's conductance surface to the landscape and added the simulated bear to a start node, drawn randomly from any of the start or end zones defined for the directed simulations within the NCDE, CYE, or GYE (i.e., areas currently occupied by grizzly bears in Montana, also including the western edge of the CYE; Fig. 1G). For each sequential step, we generated 11 possible steps from the bear's observed step length and turn angle distributions and sampled which step to go to from the probability-weighted steps (calculated as the iSSF value divided by the sum of the 11 step values). This cycle occurred for 5000 steps, reflecting the approximate steps over three annual active seasons (May through Nov) when sampled at 3-hour intervals. For each individual bear, we iterated this sequence 300 times, totaling 13,800 iterations for females and 5700 iterations for males.

We summarized simulation results as the count of times each grid cell was selected during simulations. Because we were interested in potential

movements between recovery zones, we set results to null for areas within each occupied recovery zone, classified remaining results into 10 quantile classes 1 (lowest relative predicted use) – 10 (highest relative predicted use; Morris et al., 2016) and then collapsed classes 1–3 into a single category because quantile break points were not unique for these lowest classes. We also summarized the percentage of iterations originating from a recovery zone or occupied range where the simulated bear reached a different recovery zone. Lastly, we measured Euclidian distances between start nodes and endpoints, and between endpoints and the nearest recovery zone.

2.5. Connectivity pathway evaluation

To evaluate the accuracy of predicted connectivity pathways, we plotted locations of 127 verified grizzly bear outlier observations recorded since 2010 (Montana Fish, Wildlife and Parks [MFWP]) near the connectivity pathways (Appendix). Outlier locations generally involved isolated observations of presumably unmarked individuals verified with photo documentation of the bear(s) or their tracks. Observations were considered outliers if they occurred >7 km beyond the extent of the occupied range in that year, and likely involved dispersing individuals. If outlier locations corresponded with cells with no predicted pathways, they were assigned a value of 0. Starting with the directed simulation results, we measured classes predicted at outlier locations, Spearman rank correlations between classes and numbers of outliers, the percentage of outliers in the top class, and mean class at outlier locations with class 1–10. We then repeated these measurements using our undirected simulation results.

3. Results

Directed simulations resulted in predicted connectivity pathways associated primarily with mountainous areas and secondarily with river and stream courses in open valleys (Figs. 3–4; Appendix). Predicted paths repeatedly converged in these areas, despite variation in habitat use among individual grizzly bears (Sells et al., 2022), variable start and end nodes, and different values of θ . Pathways were generally similar for females and males. Pathways connecting the NCDE and CYE transected much of the Salish and Cabinet Mountains (Fig. 1) and were generally diffuse networks that interconnected and split regularly. Other pathways connecting the NCDE and CYE involved the Reservation Divide and Ninemile Divide Mountains. Pathways connecting the NCDE and BE were well distributed within the Reservation Divide, Rattlesnake, Garnet, Bitterroot, and Sapphire Mountains, but were relatively sparse in the Missoula and Bitterroot Valleys. Two primary pathways connected the NCDE and GYE, with one west of Helena and Bozeman along the Garnet, Nevada, Boulder, Tobacco Root, Madison, and Gravelly Mountains, and one east of both towns along the Big Belt, Bridger, and Gallatin Mountains. Pathways from the CYE to the BE were again diffuse networks across the Cabinet and Coeur d'Alene Mountains. Two primary pathways connected the GYE and BE: one traversing the Sapphire, Anaconda (a.k.a. Pintler), Highland, Tobacco Root, Gravelly, and Gallatin Mountains; and one along the Beaverhead, Tendoy, and Centennial Mountains. Grizzly bear outliers aligned well with the predicted pathways (Figs. 3–4). Of the directed simulations, Spearman rank correlations for male and female maps were highest for θ of 0.0001 (0.95 and 0.92, respectively) as were mean classes at outlier locations (7.6 and 7.8, respectively; Table 1). Minimum Euclidean movement distances between ecosystem pairs ranged from 26 km for NCDE–CYE to 190 km for GYE–BE. Mean distances ranged from 130 km to 320 km corresponding to the same ecosystem pairs, respectively (Table 2).

As expected, undirected movement simulations were concentrated closer to recovery zones than directed movements (Figs. 5–6). They were well-distributed within the Cabinet, Salish, Reservation Divide, Rattlesnake, Garnet, Nevada, Boulder, northern Big Belt, Centennial, Gravelly, southern Tobacco Root, Madison, Gallatin, Boulder, and southern

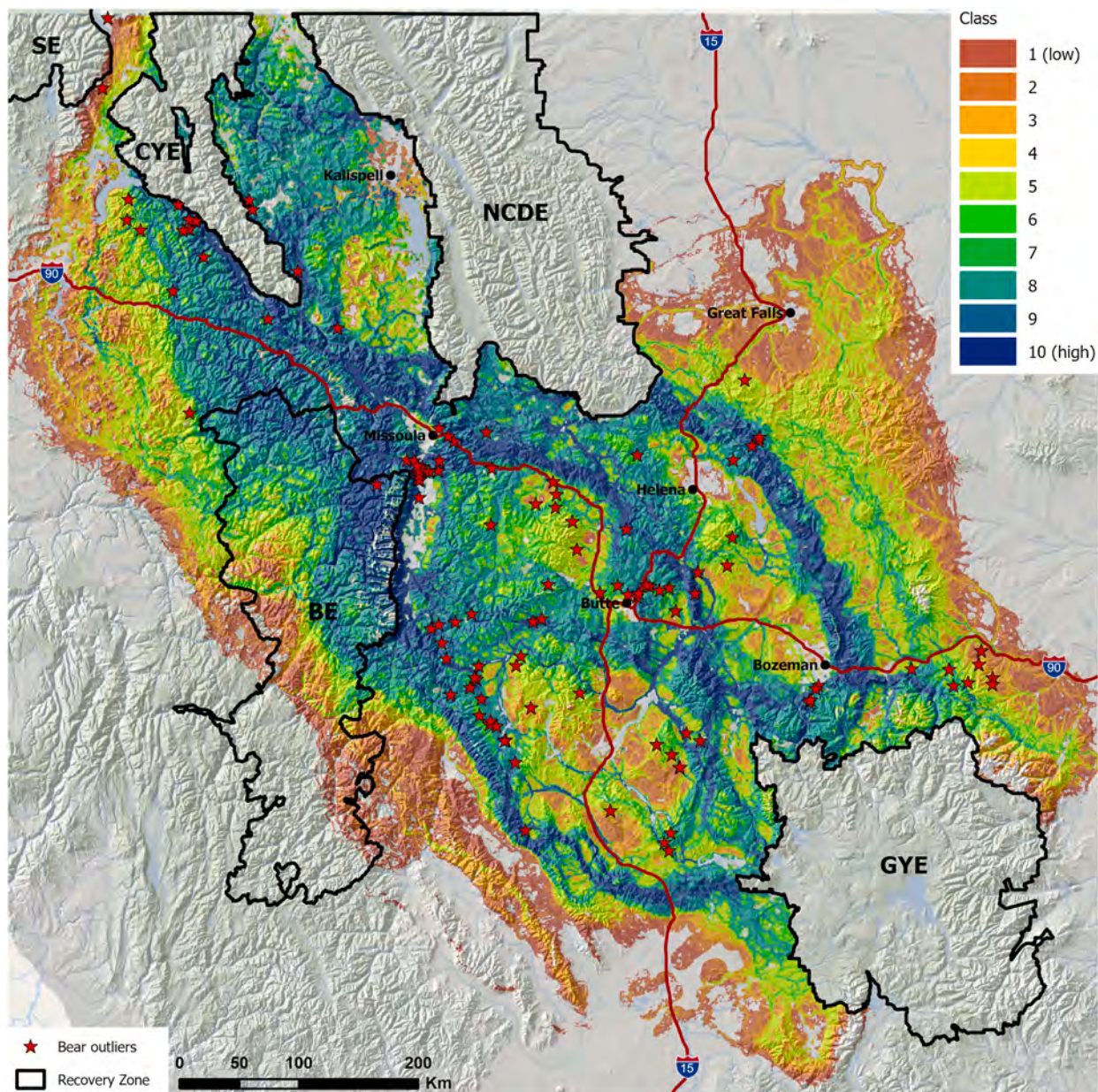


Fig. 3. Prediction of female grizzly bear connectivity pathways in western Montana, summarized from 5 sets of directed (randomized shortest path) movement simulations using start and end nodes associated with routes of NCDE-CYE, NCDE-BE, NCDE-GYE, CYE-BE, and GYE-BE (Fig. 1). Class 1 = lowest relative predicted use, whereas class 10 = highest relative predicted use. Simulations were based on 46 individual iSSFs for NCDE females. These simulations employed the lowest θ value of 0.0001, which resulted in the highest correlation with independent grizzly bear outlier observations (Table 1). Results from other θ values shown in the Appendix.

Bridger Mountains. Overlaying the predicted connectivity pathways for males and females with outlier locations yielded high Spearman rank correlations (0.87 and 0.98, respectively) and mean classes (7.4 and 7.7, respectively; Table 1). Altogether, 20.8 % of male iterations and 15.8 % of female iterations reached a recovery zone differing from where the simulated bear originated (Table 3). Simulated bears starting in the CYE had the greatest chance of reaching other recovery zones (e.g., 31.6 % and 19.9 % of male iterations and 26.5 % and 16.3 % of female iterations starting in the CYE reached the SE and NCDE, respectively). Fewer iterations reached the BE (9.2 % and 11.3 % of male iterations and 7.1 % and 7.2 % of female iterations originating in the CYE or NCDE, respectively). Few connections occurred to or from the GYE; ≤ 0.4 % of the simulations per sex originating from the GYE reached the NCDE or BE, and ≤ 1.0 % originating in the NCDE reached the GYE. Surprisingly, one simulation iteration for males originating in the CYE also reached the

NCE in Washington State. For males and females, mean Euclidian movement distances were 94 km and 82 km, and mean Euclidian distances from endpoints to the nearest recovery zone were 17 and 14 km, respectively (Table 2).

4. Discussion

The goal of this work was to identify important movement routes and habitat linkage areas between grizzly bear ecosystems. By taking a functional approach that used highly transferable movement models based on actual GPS-collared grizzly bears (Sells et al., 2022, 2023), we gained further insight than studies that focus on structural connectivity, or the degree to which patches are connected by similar habitat types (Noss, 1987; Fahrig et al., 2021). Our approach was not intended to predict areas where grizzly bears might settle, although our predictions

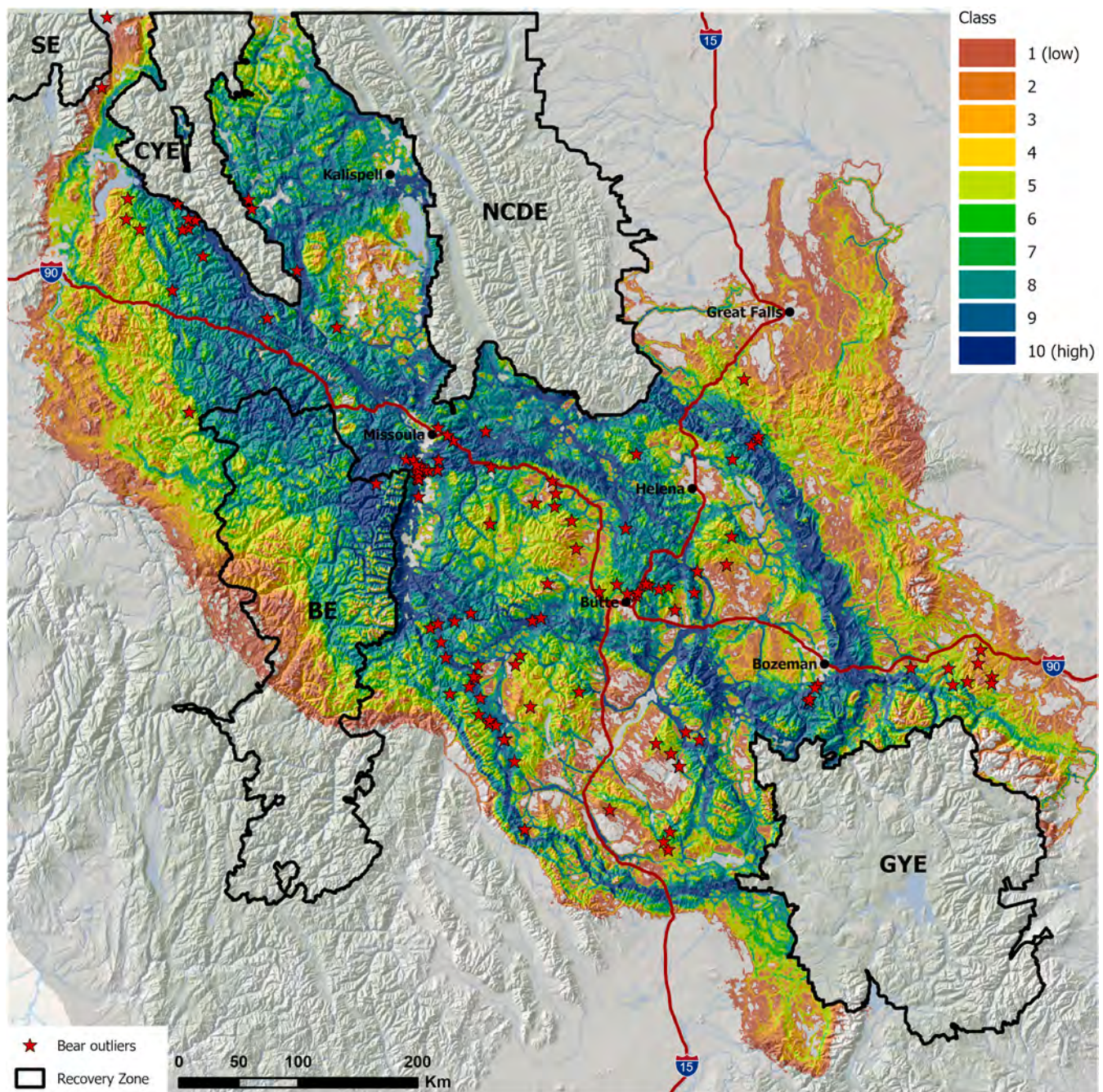


Fig. 4. Prediction of male grizzly bear connectivity pathways in western Montana, summarized from 5 sets of directed (randomized shortest path) movement simulations using start and end nodes associated with routes of NCDE-CYE, NCDE-BE, NCDE-GYE, CYE-BE, and GYE-BE (Fig. 1). Class 1 = lowest relative predicted use, whereas class 10 = highest relative predicted use. Simulations were based on 19 individual iSSFs for NCDE males. These simulations employed the lowest θ value of 0.0001, which resulted in the highest correlation with independent grizzly bear outlier observations (Table 1). Results from other θ values are shown in the Appendix.

likely suggest areas with good potential for occupancy. Instead, our focus was to identify potential dispersal pathways among ecosystems. Actual dispersal movements by grizzly bears are highly individualized and have rarely been documented, making them difficult to simulate. Conceptually, bears likely disperse into unoccupied range in two general ways, either by making long-distance, directional movements away from occupied range or by making shorter-distance meandering movements that encompass occupied range or stretch just beyond it. By predicting movement pathways using both directed and undirected simulations, our study likely accounted for both potential behaviors. Overall, we expect results from both modeling approaches will be useful

when interpreting the potential for habitat to provide connectivity between ecosystems.

Our directed simulations, which forced movements between start and end nodes, were more akin to long-distance, directional dispersal behavior, and answered the basic theoretical question of how bears might move between ecosystems. They allowed us to evaluate the relative value of areas across the entire expanse between ecosystems. The models with lower theta values allowed for more exploratory movements, alleviating some of the assumption of optimality associated with selecting the shortest path (Panzacchi et al., 2016). We believe the forced nature of these simulations were instrumental in helping pinpoint

Table 1

Evaluation of predicted connectivity pathways for grizzly bears using 127 verified outlier bear locations obtained during 2010–2023. Predictions were based on directed and undirected simulations of 46 female and 19 male individual iSSF movement models. For each summarized set of simulations, we measured classes at outlier locations (class 1 = lowest relative predicted use, class 10 = highest relative predicted use). We then calculated the percentage of outliers in the top class, mean class at outlier locations, and Spearman rank correlations between classes and numbers of outliers. If outlier locations corresponded with cells with no predicted pathways, they were assigned a value of 0.

Sex	Simulation	N outlier locations overlapping pathways	Spearman rank correlation	% of outliers in top class	% of outliers in top 5 classes	Mean class at outliers
Male	Directed, $\theta = 0.01$	110	0.75	17	53	6.6
	Directed, $\theta = 0.001$	120	0.79	26	69	7.0
	Directed, $\theta = 0.0001$	121	0.95	28	74	7.6
	Undirected	118	0.87	15	76	7.4
Female	Directed, $\theta = 0.01$	115	0.88	22	65	6.8
	Directed, $\theta = 0.001$	119	0.90	20	66	7.0
	Directed, $\theta = 0.0001$	120	0.92	27	77	7.8
	Undirected	127	0.98	22	83	7.7

Table 2

Summary of Euclidian distances between start and end nodes for directed simulations; and between start node and endpoints, and endpoints and nearest recovery zone, for undirected simulations of grizzly bear movements.

Sex	Simulation type	Distance between	Mean distance (km)	Min distance (km)	Max distance (km)
Male	Directed	NCDE – CYE	130	39	240
		NCDE – BE	166	45	312
		NCDE – GYE	288	66	476
		CYE – BE	191	51	354
		GYE – BE	317	174	428
	Undirected	Start node and endpoint	94	1	528
		Endpoint and nearest recovery zone	32	0	295
Female	Directed	NCDE – CYE	131	26	244
		NCDE – BE	162	31	305
		NCDE – GYE	285	66	481
		CYE – BE	194	56	357
		GYE – BE	320	190	430
	Undirected	Start node and endpoint	82	0	469
		Endpoint and nearest recovery zone	30	0	318

potential routes across open habitats between isolated mountain ranges, but it may have also caused simulated bears to bypass some potentially suitable habitats, especially when ecosystems were far apart. For example, areas within the Flint Creek, Elkhorn, and Ruby Mountains were not highly predicted by directed simulations but contained multiple outlier locations or have even become part of occupied range in recent years; outliers in these areas were more highly predicted by undirected simulations. For directed simulations, outlier observations were most correlated with relatively exploratory movements ($\theta = 0.0001$) compared to simulations with higher θ (i.e., more optimal movements). While the maps of $\theta = 0.0001$ provided more diffuse pathways than those approaching least-cost paths (Appendix), targeting conservation at these areas would help buffer against the inherent uncertainty with forecasting connectivity pathways, and provide more potential pathways to dispersing individuals.

Undirected simulations alleviated the assumptions of predefined end nodes in distant areas and any level of optimal movements to instead allow for entirely exploratory movements that relied only on iSSFs derived from real bears to simulate step-by-step movements. The undirected simulations allowed for any number of potential dispersal behaviors but resulted in predictions concentrated closer to recovery zones or occupied range. This was not unexpected, given that models

informing the simulations, including step length and turn angle distributions, were largely derived from resident bears, rather than bears that were actively dispersing. Still, maximum distances from start to end nodes were as high or higher than directed movements, and mean distances were larger than typical home range diameters for NCDE bears (these authors, unpublished data), indicating some resemblance to dispersal behavior. Many of the outlier locations most distant from recovery zones or occupied range fell into areas predicted by the undirected simulations but in lower quantiles, consistent with an assumption that longer distance dispersal would be more rare than shorter distance dispersal. Many of these same distant outliers, such as those in the Anaconda and Bitterroot Mountains adjacent to the BE, were highly predicted by directed simulations that often forced long movements.

By involving a much larger landscape and changing the methodology, our simulations expanded and improved on [Peck et al. \(2017\)](#)'s predictions of male grizzly bear connectivity pathways between the NCDE and GYE. Our pathways of greatest relative predicted use from directed simulations were largely associated with forested mountain ranges, similar to [Peck et al. \(2017\)](#) and other previous connectivity studies ([Bader, 2000](#); [Dilkina et al., 2017](#); [Picton, 1986](#); [Walker and Craighead, 1997](#)). Also, like [Peck et al. \(2017\)](#), some pathways of highest predicted use were notably wide, whereas others were more diffuse networks. However, our directed simulations produced more refined predictions than pathways predicted by [Peck et al. \(2017; Appendix\)](#). We expect this was owing to two main adjustments we made in simulation methods: the correct use of an exponential transformation rather than the inverse logit transformation ([Northrup et al., 2022](#)); and the use of individual models rather than a mean population model. We expect this improved methodology will benefit the fine-scale application of this research for conservation, such as prioritizing locations for highway crossing structures, conservation easements, or mitigation of human-bear conflicts.

The use of both types of simulations also allowed us to interpret our results in the context of observed grizzly bear dispersal behavior. Mean Euclidian movement distances between start nodes and endpoints, whether directed or undirected, were larger than typical female dispersal behavior and at the high end of observed dispersal distances for male grizzly bears ([Blanchard and Knight, 1991](#); [McLellan and Hovey, 2001](#); [Proctor et al., 2004](#)). In fragmented but expanding brown bear populations in Europe, researchers have observed inverse density-dependent dispersal, resulting in long-distance dispersal near the periphery by both males and females ([Jerina and Adamić, 2008](#); [Karamanlidis et al., 2021](#); [Kojola and Laitala, 2000](#); [Swenson et al., 1998](#)). Studies also found that although rates of dispersal were male-biased, peripheral females and males dispersed similar distances from core areas ([Kojola and Laitala, 2000](#); [Swenson et al., 1998](#)). Maximum female dispersal distances of 78–119 km have been reported in North America and Eurasia ([Jerina and Adamić, 2008](#); [Karamanlidis et al., 2021](#);

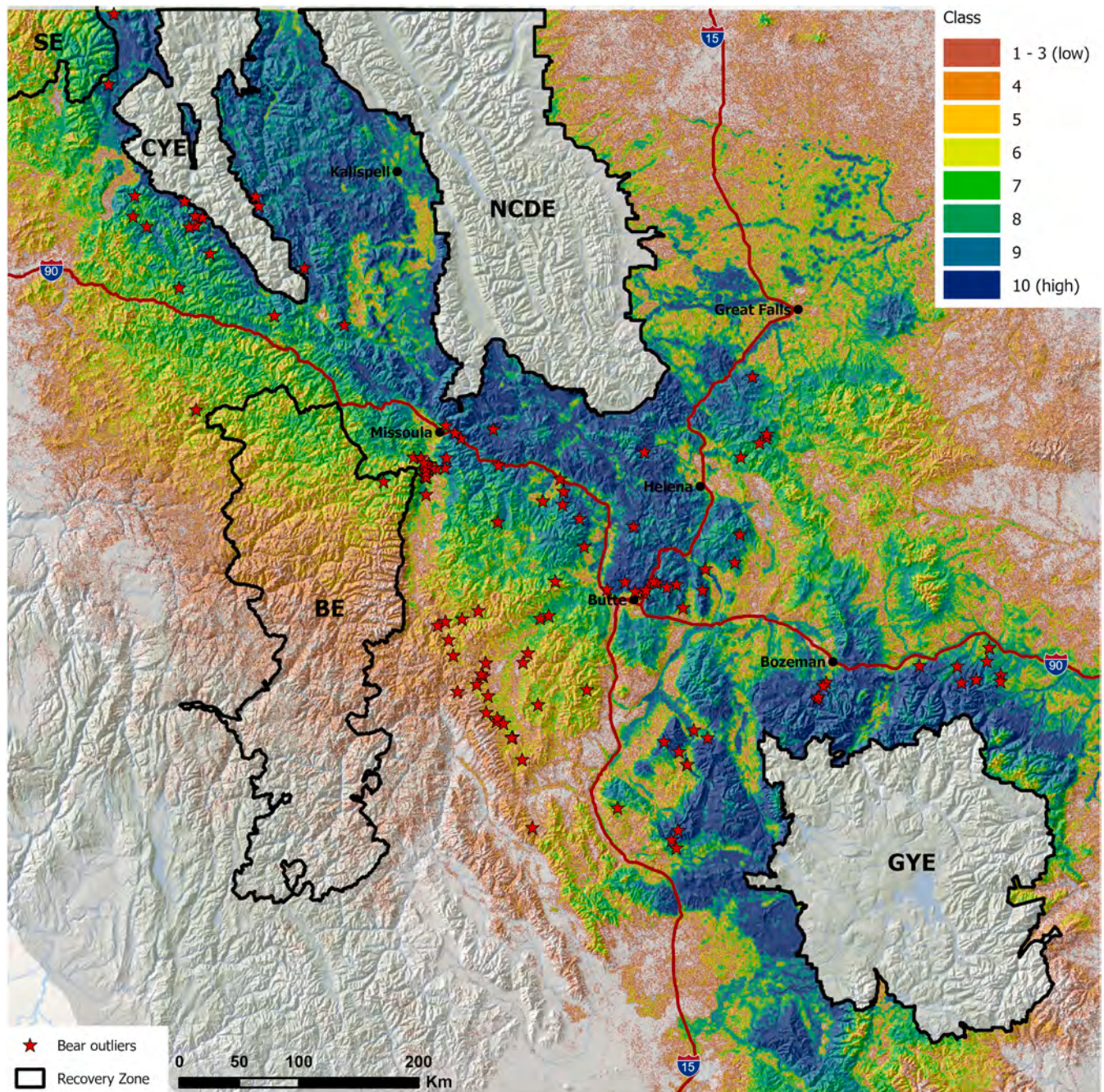


Fig. 5. Prediction of connectivity pathways for female grizzly bears in western Montana, summarized from undirected movement simulations using start nodes associated with the NCDE, CYE, and GYE (Fig. 1). Class 1–3 = lowest relative predicted use, whereas class 10 = highest relative predicted use. Simulations were based on 46 individual iSSFs for NCDE females. Classes 1–3 were collapsed into a single category because quantile break points were not unique for these lowest classes.

Proctor et al., 2004; Shirane et al., 2019; Støen et al., 2006). In the NCDE, females appear to be equally represented among individuals captured near the periphery (Costello and Roberts, 2022), such as in the Salish Mountains and in the prairie habitats to the eastern edge of the NCDE, where occupied range has expanded eastward by ~90 km in the last 10 years. Three outlier bears, genetically identified as male offspring of NCDE bears, were estimated to have dispersed ~128–215 km from their natal range (Costello and Roberts, 2022). An outlier bear genetically identified as originating from the GYE population was estimated to have dispersed ~200 km from his closest relatives. A few cases of natural or post-translocation movements between the NCDE and CYE have also been documented, although no second-generation hybrid offspring have been detected (Costello and Roberts, 2017; Kasworm et al., 2021a).

Several translocated bears, including a female, have also reached the BE in recent years from the CYE and NCDE (Kasworm et al., 2021a). Thus, although long-distance dispersal events may represent relatively rare events, the current conditions in Montana—namely, expanding grizzly bear populations and predicted availability of multiple connectivity pathways—may indeed provide the opportunity for population connectivity through dispersal movements.

Grizzly bears moving between ecosystems will generally encounter substantial human-altered and human-dominated landscapes, potentially compromising connectivity without proactive conservation measures. Human development is associated with habitat degradation and reduced use by grizzly bears (Whittington et al., 2022) and human access is associated with lower grizzly bear survival (Boulanger et al.,

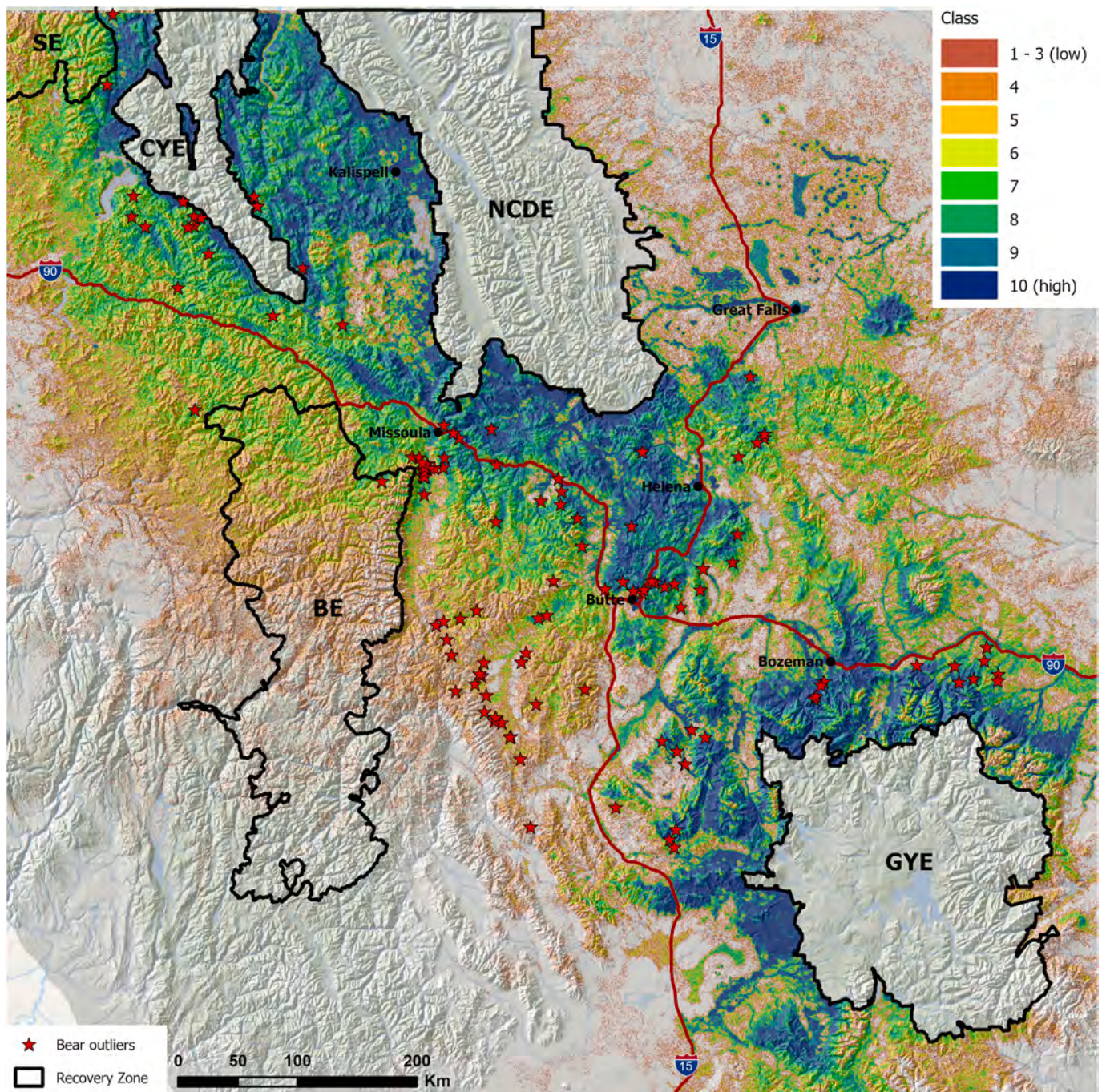


Fig. 6. Prediction of connectivity pathways for male grizzly bears in western Montana, summarized and binned from undirected movement simulations using start nodes associated with the NCDE, CYE, and GYE (Fig. 1). Class 1–3 = lowest relative predicted use, whereas class 10 = highest relative predicted use. Simulations were based on 19 individual iSSFs for NCDE males. Classes 1–3 were collapsed into a single category because quantile break points were not unique for these lowest classes.

2014; Lamb et al., 2017; Schwartz et al., 2010). Grizzly bear movements are also strongly affected by major roads and higher traffic volumes (Proctor et al., 2012; Roever et al., 2010; Waller and Servheen, 2005). However, grizzly bears may be attracted to areas near roads, putting them at increased risk of mortality from collisions (Roever et al., 2010). Accordingly, successful immigration is likely to be reduced in areas of higher human access and roaded areas than predicted by habitat selection alone. For example, because higher proportions of private lands and sizeable human populations exist between the NCDE and CYE, dispersal between grizzly bear populations may be compromised, as evidenced by higher than average levels of human-caused mortalities (e.g., through

conflict removals and vehicle strikes; Costello and Roberts, 2022). Elsewhere, where public lands dominate most mountain ranges, we similarly expect lower survival in human-dominated valleys between mountain ranges. For grizzly bears, risk of mortality and negative behavioral responses to human-altered landscapes are likely to only increase in future years as Montana's human populations and visitation rates continue to increase. Pairing habitat conservation measures along predicted connectivity pathways with installation of crossing structures where pathways cross major roads may facilitate successful connectivity between grizzly bear populations and protect humans, grizzly bears, and other species. Crossing structures are likely to be particularly important

Table 3

Percentages of undirected iterations where simulated grizzly bears reached a recovery zone different from the origin recovery zone or ecosystem (Fig. 1). Simulated bears received only a start node and no predetermined end node, unlike the directed simulations. Each individual model (46 female, 19 male) was simulated 300 times for a total of 13,800 female and 5700 male iterations.

Origin	Destination	% successful	
		Females	Males
CYE	BE	7.1	9.2
CYE	NCDE	16.3	19.9
CYE	NCE	0.0	0.1
CYE	SE	26.5	31.6
GYE	BE	0.2	0.4
GYE	NCDE	0.4	0.4
NCDE	BE	7.2	11.3
NCDE	CYE	10.2	11.9
NCDE	GYE	0.6	1.0

in areas with high and increasing traffic such as areas with growing visitation (e.g., roads to National Parks) and populations (e.g., near major towns in western Montana).

Conservation efforts in the Northern Rockies could be targeted in areas predicted by this study to be important for connectivity among grizzly bear populations. The quickly growing human population in western Montana may hamper habitat use by grizzly bears unless humans can successfully coexist with bears. Proactive efforts may be particularly helpful in areas outside recovery zones that are not currently heavily used by grizzly bears but predicted to be important, such as the edges of the Missoula Valley. Proactive education programs focused on encouraging recreationists to carry bear spray and preventing bears from accessing human foods (e.g., through bear-resistant trash cans, adherence to food storage orders on public lands, and electric fencing of crops, apiaries, and small farm animals) may provide more tangible benefits than efforts focused on changing livestock husbandry practices to reduce depredation by grizzly bears (Costello et al., 2020). However, the efficacy of campaigns to affect each of these human behaviors can be increased by local connections between wildlife professionals and the public and appealing to social behavioral norms rather than individual risk factors (Nesbitt et al., 2021). Conservation easements with willing landowners in vicinities of predicted pathways (Sage et al., 2022) may also help facilitate connectivity between populations by preventing future human developments that inhibit grizzly bear movements and increase human-bear conflicts (Graves et al., 2019).

4.1. Additional considerations

Predicted connectivity pathways carry important considerations. First, our simulations assumed that bears originating in the CYE or GYE move in a similar manner to bears from the NCDE (where iSSFs were derived; Sells et al., 2022) and that the covariates we modeled (Appendix) explained movement decisions across western Montana. We considered a wide range of potential covariates for which there were sufficient data. Our simulations also assumed that any functional responses by individual bears to the covariates encountered do not inhibit application of the iSSFs to other areas. Work by Sells et al. (2022) demonstrated the high predictive power of the iSSFs for habitat use in and around the NCDE. Subsequent validation efforts demonstrated that results from undirected simulations using the NCDE iSSFs in the SE, CYE, and GYE were predictive in these external populations (Sells et al., 2023). Our simulations also assumed that future movements by grizzly bears in western Montana will not strongly differ from movements by bears collared in recent years. Accuracy was high across most recent years that we analyzed (2005–2021; Sells et al., 2022). Accordingly, we expect our study's predictions to remain reliable across these different populations and into future years, but continued validation efforts in

future years could help verify this conclusion.

Our simulations also assume that our set of individuals in each sex was representative of bears most likely to use connectivity pathways. Most dispersal events appear to occur when bears are still maturing as subadults (Schwartz et al., 2003), but some bears in this system appear to explore their surroundings into early adulthood as they select a home range (C. Costello, pers. comm.). Of bears used to develop Sells et al. (2022)'s iSSFs, 39 % of females and 79 % of males were subadults (≤ 5 years in age). Inclusion of the full set of available subadult and adult bears in the present analyses helped maximize sample size. We found that subsetting results to only those for subadult bears revealed minimal effect on predicted pathways (these authors, unpublished data). Additionally, Sells et al. (2022) found no discernable patterns in direction of responses (selection versus avoidance) for subadult versus adult bears to the habitat variables included in the iSSFs. Predictions also assume that steps outside a bear's home range are similarly selected as those within their home range. We selected covariates to be general and thus expect them to affect behavior during both within-home range and exploratory movements, but responses could differ.

Simulations assumed that bears knew characteristics of steps available to them. This is likely realistic for bears within established home ranges, but somewhat less realistic for bears moving beyond home ranges. We expect the ability to reduce θ for directed simulations helped alleviate this assumption by adding propensity to explore during movements rather than follow optimal paths. Undirected simulations strongly alleviated this assumption by having simulated bears assess only the next step in the nearby vicinity. Furthermore, because Sells et al. (2022)'s iSSFs were built for steps of approximately 3-hour intervals, conditions at step endpoints should be more detectable than had we used longer time intervals.

Our NCDE focal population yielded iSSFs for some grizzly bears that encounter increased levels of human activity such as in the Flathead Valley, which includes the city of Kalispell and several other towns. We thus expect that our iSSFs for NCDE bears enhanced predictive capacity of how bears may use more human populated areas than had we modeled bears from other ecosystems. However, as noted above, bears moving between ecosystems can encounter higher levels of human activities, e.g., near urban centers and major roads; individuals dispersing between ecosystems may have a stronger response to human activity than simulated. Simulations also did not incorporate direct effects of roads, although secure habitat was a measure of security from roads on federal, state, and tribal lands. (During model development, iSSFs with direct data for roads were less predictive than the highly correlated measure of secure habitat; these authors, unpublished data.) Still, evidence of human avoidance in our models is demonstrated, for example, by the outcome that simulated bears largely avoided Kalispell (population $\sim 24,000$), Missoula ($\sim 76,000$), Butte ($\sim 34,000$), Helena ($\sim 33,000$), Great Falls ($\sim 59,000$), and Bozeman ($\sim 48,000$; datacommons.org; Figs. 3–4; Appendix). Pathways were also largely devoid in the increasingly urbanized Bitterroot Valley south of Missoula. Pathways furthermore appeared to be affected by roads by often narrowing into specific crossing locations, reflecting responses to variables in the iSSFs including the human-related variables (building density and distance to secure habitat). In general, when encountering pathways with various levels of human activities, we expect grizzly bears to select paths with lower human exposure. However, because successful habitat use and connectivity depends on human tolerance of grizzly bears, decisions on how to prioritize conservation of areas threatened by human activity will likely be most effective by accounting for social acceptance (Sage et al., 2022) and ways to improve successful coexistence (Nesbitt et al., 2021).

Percentiles of undirected simulation iterations that reached recovery zones which differed from where the simulated bear originated (Table 3) were calculated to evaluate the potential for connectivity; they should not be interpreted as probability of dispersal between recovery zones or probability of time requirements for dispersal between recovery zones.

Our simulations did not incorporate risk of mortality, which as noted above, would be undoubtedly higher in numerous areas between recovery zones.

Our simulations likewise did not include parameters for affinity to known places, meaning they assumed simulated individuals never settled into a home range. As such, were real bears to disperse along the predicted pathways, high quality habitat and local bear densities could entice dispersers to settle into home ranges rather than continue dispersing. Our iSSFs also did not include denning habitat, which would be required for dispersal events spanning more than a single active season. Future efforts to simulate denning habitat along predicted pathways may be helpful. Relatedly, our simulations were not intended to identify areas that are necessarily suitable for establishing home ranges, and further studies are needed to help identify areas likely to support home ranges and population expansion. In particular, directed simulations yielding narrower areas of greatest predicted use indicated fewer alternative movement paths, and not necessarily superior habitat for home ranges; limited options concentrated movements through these areas as bears selected from the best of available options. However, our results from undirected simulations (Figs. 5–6) provide clues to areas of potential settlement, particularly in areas with wide swaths of higher classes along recovery zone boundaries. Future studies could build on this foundation to investigate the potential for home range formation in these areas.

5. Conclusions

Our results can be used by agencies and organizations to inform their conservation planning and prioritization processes. Results of this work are available as GIS layers to assist with grizzly bear conservation (doi.org/10.5066/P91EWUO8). These data can facilitate on-the-ground efforts to establish a functional grizzly bear metapopulation, through habitat conservation, human-bear conflict mitigation, and transportation planning. Additionally, our predictions can be combined with information from other species to help identify areas where conservation efforts can achieve larger biodiversity and ecosystem services benefits.

The relative accuracy of the predicted connectivity pathways will become clearer as more grizzly bear outliers are located over time. However, we expect our results to offer the best available predictions for grizzly bears in the US Northern Rockies because they predict functional connectivity using individual-based movement models. Simulations of individual-based iSSFs allow for mechanistic modeling of animal movements (Avgar et al., 2016) and variation in individual behaviors. Compared to more descriptive approaches, mechanistic approaches are generally expected to be more predictive beyond the spatial and temporal scale of an original study (Aarts et al., 2008; Sells et al., 2018), as evidenced by our earlier work demonstrating that models developed for bears in the NCDE transferred well to the SE, CYE, and GYE (Sells et al., 2023).

Our results contribute evidence that when alternatives exist, caution should be taken in using approaches that predict structural connectivity for dispersing animals, such as least cost paths analyses. Studies that focus on structural connectivity assume that animals are constrained to existing habitat, are repelled by habitat boundaries, and have less success moving outside of typical habitat (Fahrig et al., 2021). Graphs and circuit-based analyses often make the same assumptions. Our directed simulations enabled testing whether known grizzly bear outlier locations between populations were better represented under simulations of greater exploration or greater optimization. As might be expected for dispersing individuals in relatively unfamiliar terrain, outlier locations over the past decade were better predicted by more exploratory movements. Furthermore, by most measures (Table 2), these outliers were overall better predicted by the undirected simulations that assumed an animal moved in an exploratory fashion with no endpoint beyond the immediate next step. While the seemingly refined pathways predicted

by simulations of more optimal movements are alluring because they appear to pinpoint exact locations for conservation efforts (e.g., Appendix), we caution that in assuming animals move optimally, connectivity studies using least cost paths or optimal movements may miss important connectivity habitat and thus misinform conservation efforts. Accordingly, when data and time permit, studies of functional connectivity are likely to be more useful compared to those that rely on structural connectivity (Fahrig et al., 2021).

Our overall approach has utility to other species and conservation needs. A multi-phase process can be used to first better understand habitat use and test movement models within currently occupied range (Fig. 2; Sells et al., 2022). A second phase can assess the transferability of these models to nearby populations or areas beyond the time and place from which the original data arose (Sells et al., 2023). As demonstrated here, a third phase can use both directed and undirected simulations to identify potential connectivity pathways and assess resulting maps that predict how animals would move in relatively exploratory versus optimal ways. This multi-phase approach makes use of available data to enhance knowledge of animal spatial behavior and the associated effects of humans. This knowledge in turn can directly enhance the efficacy of conservation decisions.

Impact statement

Mechanistically modeling grizzly bear movements between populations revealed predicted connectivity pathways, providing tools for conservation planning.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential. Connectivity pathway predictions are available online as raster data at <https://doi.org/10.5066/P91EWUO8>.

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CRediT authorship contribution statement

SS, CC, and PL conceived the ideas and designed methodology; CC, LR, and MV collected the data; SS analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Ethics statement

All grizzly bears were handled following procedures described in the Montana Animal Care and Use Committee protocols for grizzly bears and black bears (Montana Fish Wildlife and Parks, 2004).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2023.110199>.

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Glossary

- BE:** Bitterroot Ecosystem for grizzly bears
- Class:** a factor between 1 – 10 representing relative probability of use based on simulated movements, such that lowest use is class 1 and highest use class 10; frequency of movements were binned into 10 equal-area quantiles to create these classes
- CYE:** Cabinet-Yaak Ecosystem for grizzly bears
- Directed simulations:** simulations of potential connectivity pathways using iSSFs, a pre-defined start and end node, and the randomized shortest path algorithm of [Panzacchi et al. \(2016\)](#)
- Ecosystem:** area surrounding recovery zones in which grizzly bears may be anticipated to occur as part of the same population (www.fws.gov/species/grizzly-bear-ursus-arctos-horribilis)
- GYE:** Greater Yellowstone Ecosystem for grizzly bears
- iSSF:** Integrated Step Selection Function
- Functional connectivity:** extent that a landscape facilitates or impedes movements between populations ([Fahrig et al., 2021](#); [Merriam, 1984](#); [Taylor et al., 1993](#))
- NCDE:** Northern Continental Divide Ecosystem for grizzly bears
- NCE:** North Cascades Ecosystem for grizzly bears
- Recovery zone:** areas for grizzly bear recovery as identified in the 1993 US Fish and Wildlife Service Recovery Plan ([USFWS, 1993](#))
- SE:** Selkirk Ecosystem for grizzly bears
- Structural connectivity:** extent that patches are structurally connected by similar habitat or corridors ([Fahrig et al., 2021](#); [Noss, 1987](#))
- Undirected simulations:** simulations of potential connectivity pathways using iSSFs and only a predefined start node (no end node)