Grizzly Bear Habitat Selection and Predicted Movement Corridors in Western Montana

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EXECUTIVE SUMMARY

Over the past two centuries, persecution and habitat loss caused grizzly bears (*Ursus arctos*) to decline from a population of approximately 50,000 individuals to only 4 fragmented populations within the continental United States. In recent decades, these populations have increased and expanded in size and range due to collaborative conservation efforts and protections under the Endangered Species Act. Today, population estimates exceed 1000 animals each in the Northern Continental Divide Ecosystem (NCDE) and Greater Yellowstone Ecosystem (GYE). The Selkirk Ecosystem (SE) has approximately 50 grizzly bears, and augmentations into the Cabinet-Yaak Ecosystem (CYE) helped boost the population to an estimated 50 – 60 animals. To date, the Bitterroot (BE) and North Cascades Ecosystems (NCE) lack any known permanent residents.

Eventual connectivity between populations is a conservation goal, as is establishment of populations in currently unoccupied recovery areas. An understanding of habitat selection by grizzly bears within existing populations is crucial for predicting potential linkage zones and suitable habitat. A second urgent conservation challenge is identification of areas where grizzly bears are likely to disperse among recovery ecosystems, and proactive efforts to reduce human-grizzly bear conflicts. Our overall objective in this study was therefore to model grizzly bear movement, habitat use, and population connectivity to identify specific areas that are important for habitat use and natural connectivity among recovery ecosystems. We developed a multi-phase approach to accomplish these goals.

In phase 1, we aimed to increase understanding of how males and females use habitat within the NCDE. We employed multiple stages to test hypotheses of behavior, use newly gained knowledge to mechanistically simulate individual movements, translate results to predictive habitat maps, and test their predictive power across a large spatiotemporal scale. Mechanistically modeling grizzly bear movements using integrated step selection functions (iSSFs) for GPS-collared grizzly bears (F = 46, M = 19) demonstrated that grizzly bears have highly individualistic spatial behaviors. Some individuals avoided whereas others preferred areas of vegetation green-up, terrain ruggedness, forest edge, riparian areas, building densities, and secure habitat. Such individualism supported the need for an individual-based modeling approach to understand and predict grizzly bear behavior. External validation demonstrated high predictive accuracy with mean Spearman rank scores of >0.90 across seasons and years, and overall scores of 1.0. The top 5 classes of our predictive habitat maps contained 73.5% of female fixes and 83.6% of male fixes, and the top class (comprising 10% of the mapped area) contained 25.6% and 41.7% of female and male fixes, respectively. Results of this phase of our research provide tools for conservation planning and served as the basis for sequential phases of our research.

In phase 2, we tested whether our iSSFs developed for NCDE bears in phase 1 were transferable to the SE, CYE, and GYE. We simulated 100 replicates of 5,000 steps for each iSSF in each ecosystem, summarized relative use into 10 equal-area classes for each sex, and overlaid GPS locations from bears in the SE, CYE, and GYE on resulting maps. Spearman rank correlations between numbers of locations and class rank were ≥0.96 within each study area, indicating models were highly predictive of grizzly bear space use in these nearby populations. Assessment of models using smaller subsets of data in space and time demonstrated generally high predictive accuracy for females. Although generally high

across space and time, predictive accuracy for males was low within some watersheds and in summer within the SE and CYE, potentially due to seasonal effects, vegetation, and food assemblage differences. Altogether, these phase 2 results demonstrated high transferability of our models to landscapes in the Northern Rocky Mountains, suggesting they may be used to evaluate habitat suitability and connectivity throughout the region to benefit conservation planning.

In phase 3, we simulated connectivity corridors for grizzly bears between recovery ecosystems in the Northern Rockies. Building on phases 1 and 2, we modeled movements to identify potential corridors for dispersal, using the iSSFs developed in phase 1. We applied the models in a >300,000 km^2 area including the NCDE, CYE, GYE, and BE. First, we simulated directed movements (randomized shortest paths with 3 levels of exploration) between start and end nodes for routes between 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 iSSF classes (1 = lowest relative predicted use; 10 = highest relative predicted use) and evaluated predictions using 130 outlier grizzly bear locations. Mean iSSF class at outlier locations (≥7.0) and Spearman rank correlations (≥0.88) were highest for undirected simulations and directed simulations with the highest level of exploration. Corridors predicted from these simulations were primarily associated with mountainous areas and secondarily with river and stream courses in open valleys. Our resulting predictive maps will facilitate on-the-ground application of this research for habitat conservation, human-bear conflict mitigation, and transportation planning. Additionally, our overall modeling approach has direct utility for myriad species and conservation applications.

In phase 4, we sought to better understand how females select and use home ranges with respect to landcover type and landscape features. We accordingly created a population-level second order resource selection function (RSF) to understand how females place home ranges in and near the NCDE. We created individual-based third order RSFs to examine how females use space within their home ranges and how space use varies across individuals. We found that females selected areas for home ranges with greater forest, shrub/scrub, wetlands, and barren land than expected based on availability. Within their home ranges, females spent less time in evergreen forest than expected based on availability, but due to the prevalence of this forest type, females were generally more likely to be found there than in other landcover types. The probability of using shrub/scrub cover more than expected increased with age. Many females used areas of their home ranges with greater NDVI values (normalized difference vegetation index, representing food resources). Individual female home range use varied strongly in relation to elevation, ruggedness, distance to forest edge, density of forest edge, density of riparian, and density of roads. This analysis revealed information on home range selection and use by females in our study system. This work represents one phase of a multi-pronged approach to investigating home range use and potential for range expansion. Additional work is ongoing through continued collaboration with the Montana Cooperative Wildlife Research Unit.

This body of research can help meet critical conservation challenges to assist in grizzly bear recovery. Our work can help agencies design conservation strategies to meet recovery goals and manage for the long-term conservation of grizzly bear populations. This research can help identify key habitats, and in turn support habitat conservation programs that focus on easements and acquisitions. Our research can

also help identify sites of potential future conflicts to proactively enact appropriate conservation and mitigation strategies to minimize future human-grizzly bear conflicts. Study results can also help predict sites of potential future safety hazards to help identify appropriate mitigation strategies, e.g., sites where highway crossing structures would improve safety for grizzly bears and people. Altogether, this research can thus help reduce not only conflicts between humans and grizzly bears, but grizzly bear mortalities. Given the slow rate of grizzly bear expansion, each individual venturing beyond existing habitat presents a rare and important opportunity to enhance the prospects that grizzly bears will be successfully conserved into the future, particularly for small populations and currently unoccupied recovery ecosystems.

Contents

INTRODUCTION

Final Report to Montana Fish, Wildlife and Parks, December 2022

Two hundred years ago an estimated 50,000 grizzly bears (*Ursus arctos*) inhabited North America (fws.gov). The arrival of Europeans brought heavy persecution, habitat loss, and rapid decline. By 1975, within the contiguous US only six small populations remained, in just 2% of grizzly bears' former range (USFWS 1993).

Grizzly bears were among the first species protected after enaction of the Endangered Species Act in 1973. Establishment of 6 recovery ecosystems and collaborative efforts among agencies, tribes, landowners, and the public have facilitated slow increases in grizzly bear numbers. Today, population estimates exceed 1000 animals each in the Northern Continental Divide Ecosystem (NCDE) and Greater Yellowstone Ecosystem (GYE). The Selkirk Ecosystem (SE) has approximately 50 grizzly bears, and augmentations into the Cabinet-Yaak Ecosystem (CYE) helped boost the population to an estimated 50 – 60 animals (USFWS 2021). To date, the Bitterroot (BE) and North Cascades Ecosystems (NCE) lack any known permanent residents.

Once-contiguous grizzly bear populations remain largely isolated. Although some ecosystems connect to Canadian populations, grizzly bears in these areas face similar threats of low numbers, habitat loss, and population fragmentation (USFWS 1993). With increasing numbers in the NCDE and GYE, grizzly bears have slowly regained parts of their former range. By 2020, only 57 km separated the two distributions. While the GYE still likely remains isolated, researchers recently identified potential corridors for male-mediated gene flow between the NCDE and GYE (Peck et al. 2017). Although several other ecosystems are in closer proximity to one-another and the NCDE, known natural dispersals among recovery ecosystems remain rare and the likelihood and viability of connectivity remain unknown. Natural connectivity remains the best chance for establishing and recovering healthy populations in the CYE and SE. Natural recolonization is likely required to recover grizzly bears in the BE.

Given the importance of connectivity, an urgent conservation challenge for grizzly bears today is identification of areas where grizzly bears are likely to disperse among recovery ecosystems, and proactive efforts to reduce human-grizzly bear conflicts. Connectivity is likely to first occur through male movements because males disperse farther than females, who often stay in the vicinity of their mothers' home ranges (Blanchard and Knight 1991, McLellan and Hovey 2001, Proctor et al. 2004). Ecosystems will therefore likely become genetically connected first but will remain demographically isolated unless females also become connected through dispersal or range expansion. Demographic connectivity would particularly improve long-term conservation of the CYE and SE populations given their low numbers, and is imperative for recovering grizzly bears in the BE.

Our objective was to model grizzly bear movement, habitat use, and population
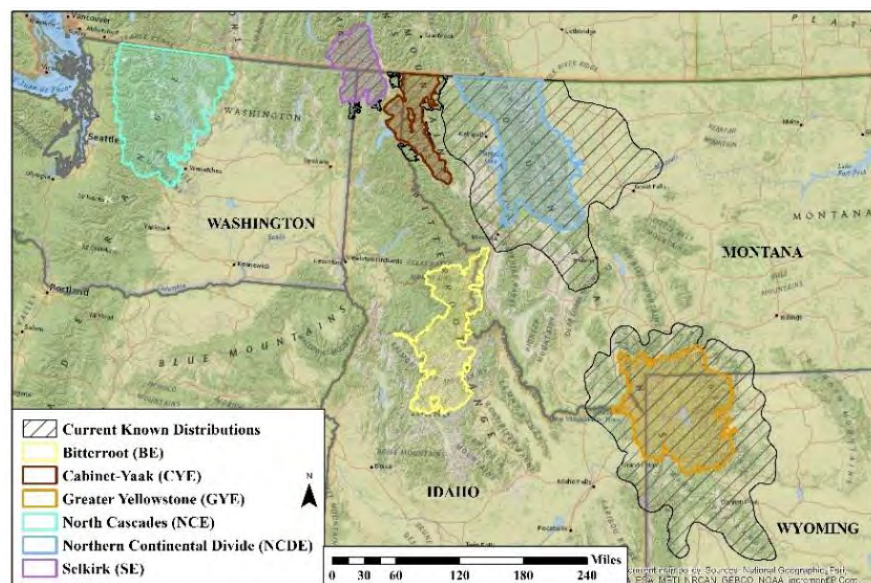
Figure 1. Grizzly bear recovery ecosystems. From usfws.gov.

connectivity to identify specific areas that are important for habitat use and natural connectivity among recovery ecosystems. We used a multi-phase approach to investigate habitat use and potential for connectivity. In phase 1, we developed individual-based integrated step selection functions to model habitat selection within the NCDE, with the goal of better understanding how males and females use habitat within this currently occupied range. In phase 2, we tested whether our models developed for NCDE bears were transferable to the SE, CYE, and GYE. In phase 3, we simulated connectivity corridors between recovery ecosystems in the Northern Rockies. In phase 4, we developed home range models for adult females in the NCDE to further investigate how females select and use home ranges. Each of these phases is presented as separate chapters in this final report to Montana Fish, Wildlife & Parks. Phase 1 was recently published in Biological Conservation, and the official version of the manuscript can be obtained online (doi.org/10.1016/j.biocon.2022.109813). Phases 2 and 3 are currently under peer review. Additional work for phase 4 is ongoing through continued collaboration with the Montana Cooperative Wildlife Research Unit.

This body of research can help meet critical conservation challenges to assist in grizzly bear recovery. Our work can help agencies design conservation strategies to meet recovery goals and manage for the long-term conservation of grizzly bear populations. This research can help identify key habitats, and in turn support habitat conservation programs that focus on easements and acquisitions. Our research can also help identify sites of potential future conflicts to proactively enact appropriate conservation and mitigation strategies to minimize future human-grizzly bear conflicts. Study results can also help predict sites of potential future safety hazards to help identify appropriate mitigation strategies, e.g., sites where highway crossing structures would improve safety for grizzly bears and people. Altogether, this research can thus help reduce not only conflicts between humans and grizzly bears, but grizzly bear mortalities. Given the slow rate of grizzly bear expansion, each individual venturing beyond existing habitat presents a rare and important opportunity to enhance the prospects that grizzly bears will be successfully conserved into the future, particularly for small populations and currently unoccupied recovery ecosystems.

Acknowledgements

PREDICTED MALE AND FEMALE MOVEMENT CORRIDORS BETWEEN GRIZZLY BEAR ECOSYSTEMS IN WESTERN MONTANA

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RH: Predicted movement corridors for grizzly bears

Abstract Habitat mapping and corridor modeling are key components of many conservation programs. For example, 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 identify potential corridors for dispersal, 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 km^2 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 for routes between 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 iSSF classes (1 = lowest relative predicted use; 10 = highest relative predicted use) and evaluated predictions using 130 outlier grizzly bear locations. Mean iSSF class at outlier locations (≥7.0) and Spearman rank correlations (≥0.88) were highest for undirected simulations and directed simulations with the highest level of exploration. Corridors predicted from these simulations were primarily associated with mountainous areas and secondarily with river and stream courses in open valleys. Our resulting predictive maps will facilitate on-the-ground application of this research for habitat conservation, human-bear conflict mitigation, and transportation planning. Additionally, our overall modeling approach has direct 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). 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 (www.fws.gov/species/grizzly-bear-ursus-arctos-horribilis; 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 (RZs, 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 1,000 animals each in the Northern Continental Divide Ecosystem (NCDE) (Costello and Roberts, 2020; Mace et al., 2012) and Greater Yellowstone Ecosystem (GYE; F. Van Manen, unpublished data). The Selkirk Ecosystem (SE) had >83 grizzly bears (Proctor et al., 2012) with >44 in the US portion (Wayne F Kasworm et al., 2021), and the Cabinet-Yaak Ecosystem (CYE) had ~60 animals (Wayne F. Kasworm et al., 2021; 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, RZs remain largely isolated. 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 distributions, and the NCDE distribution had expanded to connect to a small edge of the BE (Fig. 1). Distances between other populations were also shrinking.

Information is needed to assess potential corridors 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., 2012, 2004). 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 route of population connectivity among the existing grizzly bear 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. Occupation of intervening landscapes by recolonizing resident females may be necessary to facilitate natural connectivity.

Focusing on the four recovery areas in Montana (where most of the connectivity landscape occurs), our present objective was to identify areas between grizzly bear ecosystems with habitat conditions suitable for dispersal movements by female and male bears. This study builds on a larger study initiated by Sells et al. (2022) and demonstrates a multi-phase modeling approach with application to myriad other species and conservation decisions (Fig. 2). This general study framework can be easily applied to other species to enhance understanding of animal space use, potential corridors, and conservation needs. In the first phase of this work, Sells et al. (2022) modeled habitat use within currently occupied range to better understand how grizzly bears use habitat. Subsequent application of these models to the NCDE demonstrated high predictive power. In a second phase, it was demonstrated that models developed for the NCDE accurately predict habitat use in nearby populations and are therefore transferable and reliable for predicting space use beyond the NCDE (Sells et al. in review[2]). In this present third phase, we

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[2] This manuscript will soon be resubmitted to Conservation Biology for a second round of review.

demonstrate that multiple simulation methods help model predictive corridors and enhance understanding of potential for connectivity and where to focus conservation efforts.

Our present work builds on Peck et al. (2017), who employed step selection functions (SSFs) and randomized shortest paths (RSP) to simulate corridors for male grizzly bear movements between the NCDE and GYE. RSP enables simulating varying degrees of optimal versus exploratory movements (Panzacchi et al., 2016). We employed integrated step selection functions (iSSFs) to model directed movements (i.e., RSPs 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 SSFs 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. Sells et al. (2022)'s 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 (Supplementary Information [SI]). Because Sells et al. (2022)'s iSSFs demonstrated high individual variation in spatial behavior, our corridor simulations were likewise individual-based to account for variations in movement behaviors.

2. Methods

2.1 Study Area

Our >300,000 km^2 study area was centered on the Rocky Mountain region of western Montana, eastern Idaho, and northern Wyoming, including the NCDE, CYE, BE, and GYE RZs (Fig. 1). We defined the BE boundary to be a combination of the RZ 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 was a complex of forested mountain ranges (with ~1900-3900m peaks) and open river valleys (~800-1800m elevation) that transitioned to the Great Plains toward the east. Climate varied with topography and differed across the Continental Divide. A northern Pacific coastal climate with cool summers and mild winters occurred to the west, while a semi-arid continental climate with warm summers and cold winters occurred to the east (weather-atlas.com). Montane conifer (e.g., *Picea*, *Abies*, *Pinus*, *Pseudotsuga* spp.) forests were interspersed with meadows and shrublands at mid elevations and alpine communities at the highest elevations. Shortgrass prairie and sagebrush (*Artemesia* spp.) shrublands were the primary natural communities in the valleys and Great Plains. Forestry, ranching, agriculture, and recreation were major land uses. More than 90% of each of the RZs were publicly owned, but private lands made up roughly 50% of the area between RZs. Major roads passed between RZs, including two interstates (I90 and I15) 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; see also SI). iSSFs were based on location data collected at 3-hour intervals (+/- 45 minutes) from individuals monitored via GPS transmitters (Telonics, Mesa, Arizona, USA) for one or more years from 2003–2020 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. (in review), here we applied each bear's iSSF to the study area (300m 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 SSFs and iSSFs are scale dependent, we thinned steps to reasonably consistent time intervals (Signer et al., 2019, 2017). Second, following Panzacchi et al. (2016), Peck et al. (2017) used the inverse logit transformation to map their SSFs to the landscape for RSP 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 like Peck et al. (2017), 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 corridors 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 RSP 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 RZs 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 NCDE population distribution edge 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 population distribution edge 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 population distribution, and end zones were the northern edges of the GYE and population distribution (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 population distribution, 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 × 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 and used

equal area quantile binning to display results as iSSF classes (1 = low relative predicted use, 10 = highest relative predicted use) (Morris et al., 2016). Resulting maps represented the predicted corridors for each sex. We also summarized Euclidian distances between start and end nodes for each route and sex.

2.4 Undirected Simulations

We next completed simulations of undirected movement following the simulation approach from Sells et al. (2022). For each iteration, we applied the individual bear's conductance surface to the landscape and added the simulated bear to a start point, 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, the bear generated 11 possible steps from its 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 5,000 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 5,700 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 corridors between RZs, we set results to null for areas within each RZ and classified remaining results into 10 quantile iSSF classes (1 = low 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 number of iterations that successfully reached a different RZ from where the simulated bear originated (i.e., number of simulations reaching a different RZ from the origin RZ or distribution area, divided by the number of simulations starting in the origin RZ). Lastly, we measured Euclidian distances between start and end points, and end points and nearest RZ.

2.5 Corridor Evaluation

To evaluate the accuracy of predicted corridors, we plotted locations of 130 verified grizzly bear outlier observations recorded since 2010 (MFWP; unpublished data). Locations were considered outliers if they occurred beyond the extent of the estimated occupied range in that year. For each summarized set of simulations, we measured iSSF classes predicted at outlier locations. We then calculated the percentage of outliers in the top iSSF class, mean iSSF class at outlier locations, and Spearman rank correlations between iSSF classes and numbers of outliers.

As a final step, we mapped primary corridor results for directed and undirected simulations. Using directed results from the lowest θ for each sex (0.0001, i.e., the θ most comparable to undirected simulations), we first filtered values for each sex to iSSF classes 8 – 10. We repeated this for undirected simulations for each sex, and then averaged directed and undirected results. This set any areas not selected as ≥8 iSSF class in both simulations to null, leaving only corridors identified for both simulation methods as the 30% top corridors. We then mapped the final output of the combined analyses.

3. Results

Directed simulations resulted in predicted movement corridors associated primarily with mountainous areas and secondarily with river and stream courses in open valleys (Figs. 2–3; SI). Predicted paths repeatedly converged in these corridors, despite variation in habitat use among individual grizzly bears (Sells et al., 2022), randomly selected start and end points, and different values of θ. Movement corridors were generally similar for females and males. Paths connecting the NCDE and CYE transected much of the Salish and Cabinet Mountains and were generally diffusive networks that interconnected and split regularly. Other paths connecting the NCDE and CYE involved the Reservation Divide and Ninemile Divide Mountains. Paths 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 corridors 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 Mountains, Bridger, and Gallatin Mountains. Paths from the CYE to the BE were again diffusive networks across the Cabinet and Coeur d'Alene Mountains. Two corridors 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 corridors (Figs. 2–3). Of the directed simulations, Spearman rank correlations for male and female maps were highest for θ of 0.0001 (0.92 and 0.88, respectively) as were mean iSSF classes at outlier locations (7.2 and 7.4, respectively; Table 1). Mean Euclidian movement distances ranged from ~130 km for NCDE–CYE to ~320 km for GYE–BE (Table 2).

As expected, undirected movement simulations were concentrated closer to RZs 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 Bridger Mountains. Undirected maps for males and females resulted in high Speakman rank correlations (0.90 and 0.96, respectively) and high mean iSSF classes at outlier locations (7.0 and 7.2, respectively; Table 1). Altogether, 20.8% of male iterations and 15.8% of female iterations reached a RZ differing from where the simulated bear originated (Table 2). Simulated bears starting in the CYE had the greatest chance of reaching other RZs (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). The fewest 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, 1 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 end points to the nearest RZ were 17 and 14 km, respectively (Table 3). Combined results for directed and undirected simulations revealed the primary movement corridors predicted by both methods (Fig. 7).

4. Discussion

This study demonstrates a key component of a novel, multi-phase modeling approach to understand habitat selection and predict movement corridors for a species of conservation concern (Fig. 2). Through individual-based iSSFs and simulations, we developed maps of predicted movement corridors between populations of grizzly bears across a region of >300,000 km^2. Resulting predictions reveal male and female grizzly bear movement corridors within this large landscape that encompasses 4 federally recognized grizzly bear recovery ecosystems. Our finely detailed results can be used for direct application to on-the-ground conservation measures.

Our analyses expanded and improved on previous predictions of male grizzly bear movement corridors between the NCDE and GYE by Peck et al. (2017), not only by involving both sexes and a much larger landscape, but also by improving methodology through our multi-phase approach (Fig. 2). Our predicted movement corridors 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), our methods resulted in areas with heavily predicted corridors, as well as areas with more diffuse networks of paths. Nonetheless, our simulations' predicted movements within mountain ranges and across open valleys between mountains ranges appeared to be more precise. We believe this was owing to two main adjustments in simulation methods compared to (Peck et al., 2017): the correct use of an exponential transformation rather than the inverse logit transformation; and the use of individual models rather than a mean population model. We believe this

improved precision will help in the fine-scale application of this research for on-the-ground conservation actions, such as prioritizing locations for highway crossing structures, conservation easements, or mitigation of human-bear conflicts.

Actual dispersal movements are highly individualized, poorly understood, and difficult to simulate. While neither our directed nor undirected simulations were entirely realistic in terms of direction or total length of movement, we believe both approaches have merit, individually and in combination, given that the habitat selection underlying the movements was based on actual GPS-collared grizzly bears with high transferability (Sells et al., 2022). For example, although they unrealistically forced simulated bears to move between ecosystems, the directed paths appeared to be a valuable tool for identifying the most likely paths across open habitats between isolated mountain ranges. In contrast, while often failing to link ecosystems, undirected paths were probably more realistic predictions of current or imminent grizzly bear movement patterns. Indeed, outlier observations were most highly correlated with undirected simulations or with the more exploratory directed simulations ($\theta = 0.0001$). Directed simulations with higher θ (i.e., approaching least-cost paths) were less correlated with outlier locations. This suggests that least-cost analyses, especially over long distances, may be less appropriate than methods that explicitly incorporate exploratory movements. While the more diffusive maps of $\theta = 0.0001$ provided more diffusive corridors than those approaching least-cost paths, targeting conservation at these areas would help buffer against the inherent uncertainty with forecasting movement corridors, and provide more route options to dispersing individuals.

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, whether directed or undirected, were larger than typical 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). On average, undirected paths were shorter, but still lengthy, and relatively few successfully connected ecosystems. However, long-distance dispersal events of this magnitude have been reported. In fragmented, but expanding brown bear populations in Europe, researchers have observed inversely density-dependent dispersal, resulting in long-distance dispersal near the periphery by both males and females (Jerina and Adamič, 2008; Karamanlidis et al., 2021; Kojola and Laitala, 2000; Swenson et al., 1998). Studies 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 Adamič, 2008; Karamanlidis et al., 2021; Proctor et al., 2004; Shirane et al., 2019; Støen et al., 2006). Recent observations in our region have been similar to these previous observations. In the NCDE, females appear to be equally represented among individuals captured near the periphery (C. Costello, unpublished data), such as in the Salish range and in the prairie habitats on the East Front, where occupied range has expanded eastward by about 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 (C. Costello, unpublished data). 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, 2020; Wayne F. Kasworm et al., 2021). Additionally, several translocated bears, including a female, have reached the BE in recent years from the CYE and NCDE (Wayne F. Kasworm et al., 2021). 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 movement corridors – may indeed provide the opportunity for population connectivity through dispersal movements.

Predicted corridors between the two closest ecosystems, the NCDE and CYE, were generally similar comparing directed and undirected simulations, and the combined top predictions spanned much of the intervening landscape, especially to the north. Combined predictions also revealed simulated movements throughout the Reservation Divide, Ninemile Divide, Rattlesnake, and Garnet Ranges between the CYE,

NCDE, and BE. Unlike most other mountains ranges in our study area, the ranges between the NCDE and CYE (Salish, Cabinet, Reservation Divide, and Rattlesnake Mountains) were dominated by private land, therefore it is possible the rate of successful exchange of individuals is compromised by the human landscape between these ecosystems. While our simulations suggested that the higher road and building densities associated with these private lands would not hinder grizzly bears from selecting these ranges for dispersal movements, previous studies suggest that the human access may result in lower grizzly bear survival (Boulanger et al., 2014; Lamb et al., 2017; Schwartz et al., 2010) and, thus, lower immigration rates than predicted by habitat selection alone. Indeed, the Flathead and Mission Valleys hold sizable human populations and experience higher than average levels of human-caused mortalities, such as conflict removals and vehicle strikes (Costello and Roberts, 2020). Elsewhere, where public lands dominate most mountain ranges, we should similarly expect lower survival rates in the more human-populated valleys between stepping-stone mountains ranges, perhaps compromising connectivity.

Although undirected paths were closer to RZs and relatively sparse midway between the NCDE and GYE, combined predictions identified two primary NCDE–GYE corridors following the Garnet, Nevada, Boulder, Tobacco Root, Madison, and Gravelly Ranges and following the Big Belt Mountains, Bridger, Bangtail, and Gallatin Ranges. These two routes were also identified by Peck et al. (2017)'s study and additional outlier locations along those corridors have since occurred.

Notably, simulated bears avoided the larger urban areas of Kalispell (population ~24,000), Missoula (~76,000), Butte (~34,000), Helena (~33,000), Great Falls (~59,000), and Bozeman (~48,000; datacommons.org; Figs. 3–4; SI). Corridors were also largely devoid in the increasingly urbanized Bitterroot Valley south of Missoula. However, corridors occurred near each of these communities, indicating the growing potential for human-bear conflicts, particularly for homes in exurban and rural areas adjacent to nearby towns. As human populations and the associated developments continue to grow around these urban areas, the efficacy of our predicted grizzly bear corridors will likely be reduced.

The numerous potential crossing sites along major roads (Figs. 3–7; SI) may benefit from proactive mitigation in the form of crossing structures and fencing to prevent mortalities of bears and collision risk for humans. Grizzly bear movements have been shown to be strongly affected by major roads (Proctor et al., 2012; Roever et al., 2010; Waller and Servheen, 2005). Previous work demonstrated that grizzly bears along Glacier National Park's southern boundary were more likely to cross US2 at night when traffic volumes were lowest, and that subadults appeared more willing to cross than adults (Waller and Servheen, 2005). Similarly, (Proctor et al., 2012) found that greater traffic volume and human settlements infringed on grizzly bear movements. However, grizzly bears may be attracted to areas near roads, putting them at increased risk of mortality from collisions (Roever et al., 2010). Negative behavioral responses to roads, development, and risks of mortality are likely to only increase in future years as Montana's human populations and visitation rates continue to increase. Installation of crossing structures within predicted corridors along 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 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 to grizzly bears. 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 near RZs 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 be more effective 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 corridors (Sage et al., 2022) may also help facilitate connectivity between populations by preventing future human developments that inhibit grizzly bear movements and inevitably increase human-bear conflicts (Graves et al., 2019).

4.1 Considerations and Assumptions

Predicted corridors carry important assumptions. 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 (SI) explained movement decisions across western Montana. We considered a wide range of potential covariates for which there were sufficient data. Work by Sells et al. (2022) demonstrated the high predictive power of the iSSFs for habitat use in and around the NCDE. Recently, validation efforts demonstrated that undirected simulations using the NCDE iSSFs in the SE, CYE, and GYE yielded strong predictive accuracy to these external populations, particularly for SE/CYE females and both sexes in the GYE (Sells et al. in review). 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). 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 our conclusion.

Our simulations also assume that our set of individuals in each sex was representative of bears most likely to use dispersal corridors. 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 be exploring their surroundings to select a home range into early adulthood (C. Costello, unpublished data). 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 corridors (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.

Percentiles of simulation iterations that reached RZs different from where the simulated bear originated (Table 2) were calculated to evaluate the potential for connectivity; they should not be interpreted as probability of dispersal between RZs. Our simulations did not incorporate risk of mortality, which would be undoubtedly high in numerous areas between RZs. Simulations also did not incorporate direct effects of roads, although secure habitat was a measure of security from roads on public, 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.) 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 corridors, 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, meaning that dispersal events spanning more than a single active season would require suitable denning habitat en route. Future efforts to simulate denning habitat along corridors may be helpful.

Predictions assumed 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 also 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 both assumptions by adding propensity to explore during movements rather than follow optimal paths. Undirected simulations likewise alleviated these assumptions by having simulated bears assess only the next step in the nearby vicinity. Our decision to filter steps to 3-hour intervals should also help alleviate the second assumption; because average step length is shorter at closer time intervals, conditions at step endpoints should be more detectable than had we used longer time intervals.

Our results should not be interpreted to represent areas suitable for establishing home ranges, as further studies are needed to help identify areas likely to support home ranges and population expansion. However, our results provide potential clues to areas of potential home ranges and range expansion. We note that narrower directed simulation corridors of greatest predicted use indicated areas lacking good alternative movement corridors, and not necessarily superior habitat for home ranges. Limited options concentrates movements through these areas as bears select for the best of available options. However, areas crossed with wider corridors may offer suitable habitat for home ranges. It is thus possible that bears that find themselves in the areas of diffusive, lower corridor use (lower iSSF classes on maps, Figs. 3–4) or in wider, high-use corridors (higher iSSF classes) may set up home ranges in these areas, whereas bears that wind up in the narrower corridors may move relatively quickly through these areas. Maps from undirected simulations (Figs. 5–6) in contrast revealed areas that may offer suitable home ranges, particularly where there are wide swaths of higher iSSF classes along RZ boundaries.

4.2 Conclusions

The relative accuracy of the predicted corridors will become clearer as more grizzly bear outliers are located over time. However, we expect our results offer the best available predictions given their individual-based nature using iSSFs, which allow for mechanistic modeling of animal movements (Avgar et al., 2016) and variation in individual behaviors. Furthermore, our results under differing values of θ enabled testing whether known grizzly bear outliers were better represented under simulations of greater exploration (low θ) or greater optimization (high θ). As might be expected for dispersing individuals in relatively unfamiliar terrain, grizzly bear outliers over the past decade were better predicted by more exploratory movements (i.e., low θ and undirected simulations). Based on these findings, our simulation results are expected to be more accurate than least cost path modeling or other approaches that assume optimal movements.

Our results can be used by agencies and organizations to inform their conservation planning and prioritization processes. Results of this work are available to conservationists in the form of GIS layers to assist with grizzly bear conservation. 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 whose protection will achieve larger biodiversity and ecosystem services benefits.

Finally, our overall approach has direct utility to other species and conservation needs. A multi-stage process can be used to first better understand habitat use and test movement models thoroughly within currently occupied range (Fig. 2; Sells et al., 2022). A second phase can assess model accuracy by evaluating the transferability of these models to nearby populations or areas beyond the time and place from which the original data arose (Sells et al., in review). As demonstrated here, a third phase can use both directed and undirected simulations approaches to identify potential movement corridors and assess the likelihood of different resulting maps that assumed animals move in relatively exploratory versus optimal ways. By contrast, in assuming animals move optimally, corridor studies using least cost paths may miss important connectivity habitat and thus misinform conservation efforts. This multi-stage approach makes use of available data to enhance ecological knowledge of animal spatial behavior and

how humans affect wildlife and their habitats, and thus directly improve efficacy of conservation decisions.

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).

Acknowledgements

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Table 1. Evaluation results of grizzly bear movement corridor predictions using verified outlier bear locations obtained during 2010 – 2021. Corridor 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 iSSF 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 iSSF class, mean iSSF class at outlier locations, and Spearman rank correlations between iSSF classes and numbers of outliers.

Sex	Simulation	N outlier locations overlapping	Spearman rank correlation	% of outliers in top class	% of outliers in top 5 classes	Mean class at outliers
Male	Directed, $\theta = 0.01$	80	0.64	15	58	6.3
	Directed, $\theta = 0.001$	92	0.71	21	67	6.6
	Directed, $\theta = 0.0001$	94	0.92	23	71	7.1
	Undirected	99	0.90	15	70	7.0
Female	Directed, $\theta = 0.01$	87	0.70	21	66	6.5
	Directed, $\theta = 0.001$	91	0.67	15	64	6.6
	Directed, $\theta = 0.0001$	92	0.88	23	76	7.4
	Undirected	109	0.96	21	72	7.1

Table 2. Percentages of undirected simulations ending in a Recovery Zone (RZ) different from the origin RZ or distribution area (Fig. 1). Each individual model (46 female, 19 male) was simulated 300 times for a total of 13,800 female and 5,700 male iterations.

		% successful	
Origin	Destination	Females	Males
CYE	BE	7.1	9.2
CYE	NCDE	16.3	19.9
CYE	NCE	0.00	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

Table 3. Summary of Euclidian distances, between start and end points or between end points and nearest Recovery Zone (RZ), for directed and 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 end point	94	1	528
		End point and nearest RZ	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 end point	82	0	469
		End point and nearest RZ	30	0	318

Figure. 1. The study area (A) encompassed the NCDE Recovery Zone (RZ) and the current approximate distribution of grizzly bears in and near the NCDE, plus the RZs of the CYE, BE, and GYE. The BE RZ boundary was a combination of the RZ boundaries identified in alternatives 1 (reintroduction) and 2 (natural recolonization) of the original reintroduction plan for the BE (USFWS, 2000). Mountain ranges noted in the main text are labeled for reference. 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 RZs (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).

Figure 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. (in review) assessed model transferability by applying our models to nearby populations in the GYE, CYE, and SE. In the present third phase, we applied our models to simulate corridors between populations in Western Montana.

Figure 3. Prediction of female grizzly bear movement corridors in western Montana, summarized and binned 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). iSSF class 1 = lowest relative predicted use, whereas iSSF 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 and resulted in the highest correlation with independent grizzly bear outlier observations (Table 1). Results from other θ values shown in the SI.

Figure 4. Prediction of male grizzly bear movement corridors in western Montana, summarized and binned 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). iSSF class 1 = lowest relative predicted use, whereas iSSF 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 and resulted in the highest correlation with independent grizzly bear outlier observations (Table 1). Results from other θ values are shown in the SI.

Figure 5. Prediction of movement corridors for female grizzly bears in western Montana, summarized and binned from undirected movement simulations using start nodes associated with the NCDE, CYE, and GYE (Fig. 1). iSSF class 1:3 = lowest relative predicted use, whereas iSSF 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 iSSF classes.

Figure 6. Prediction of movement corridors 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). iSSF class 1:3 = lowest relative predicted use, whereas iSSF 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 iSSF classes.

Figure 7. Top predictions for movement corridors of male and female grizzly bears in western Montana combining results from directed and undirected movement simulations (Figs. 3 – 6). iSSF classes for each sex and simulation method were filtered to classes 8 – 10, and then averaged across simulation methods. Areas of purple indicate overlap between sexes.
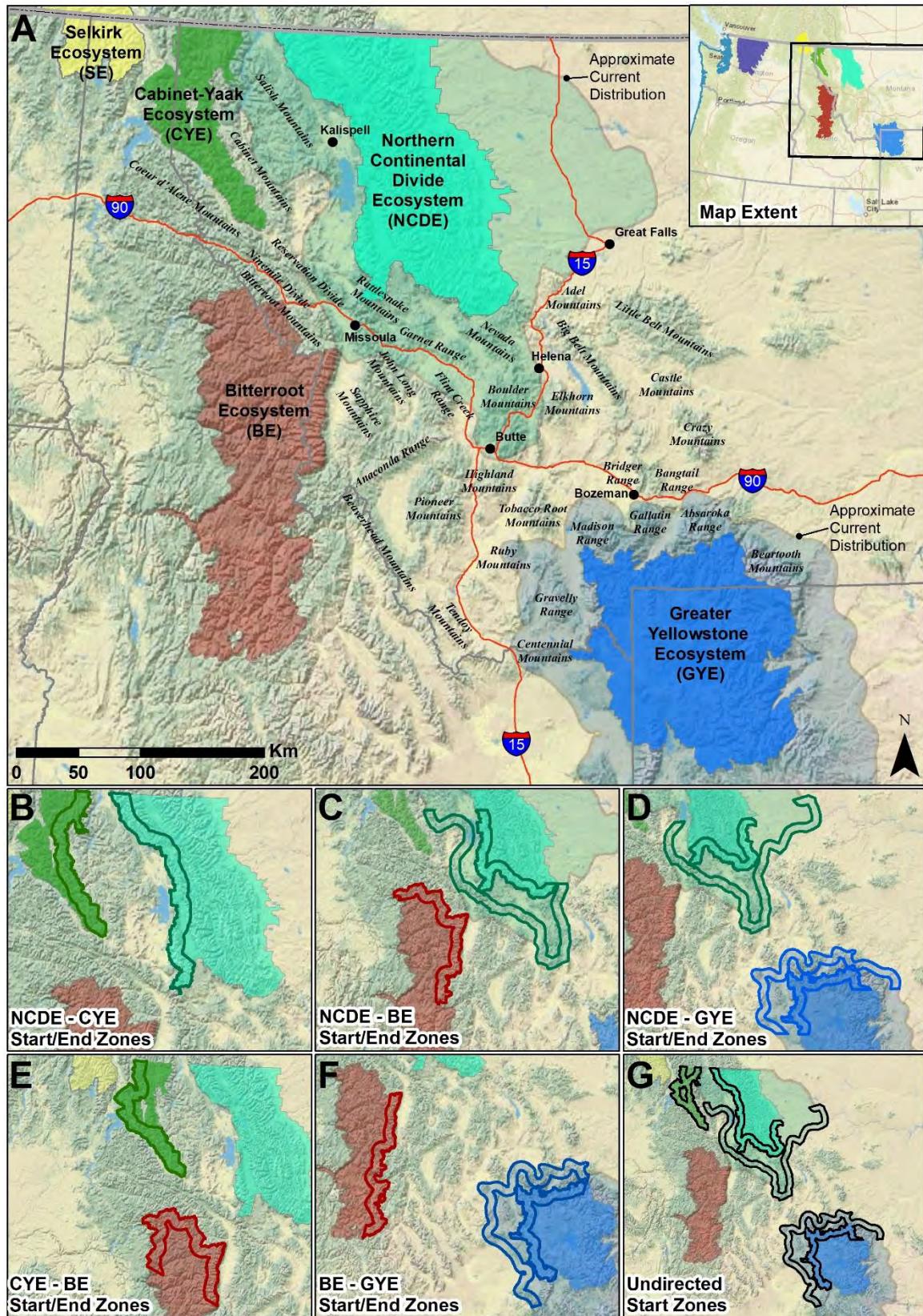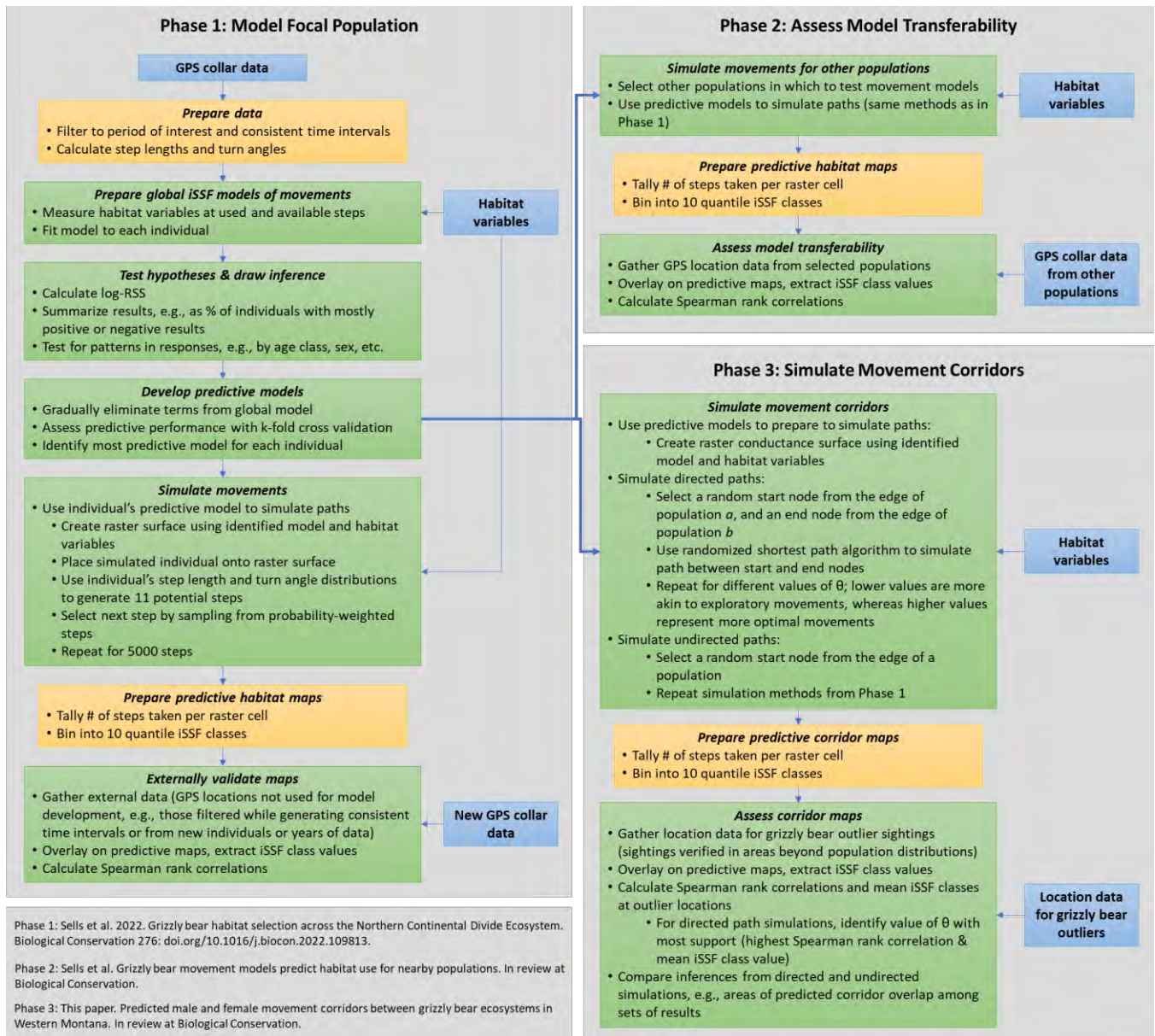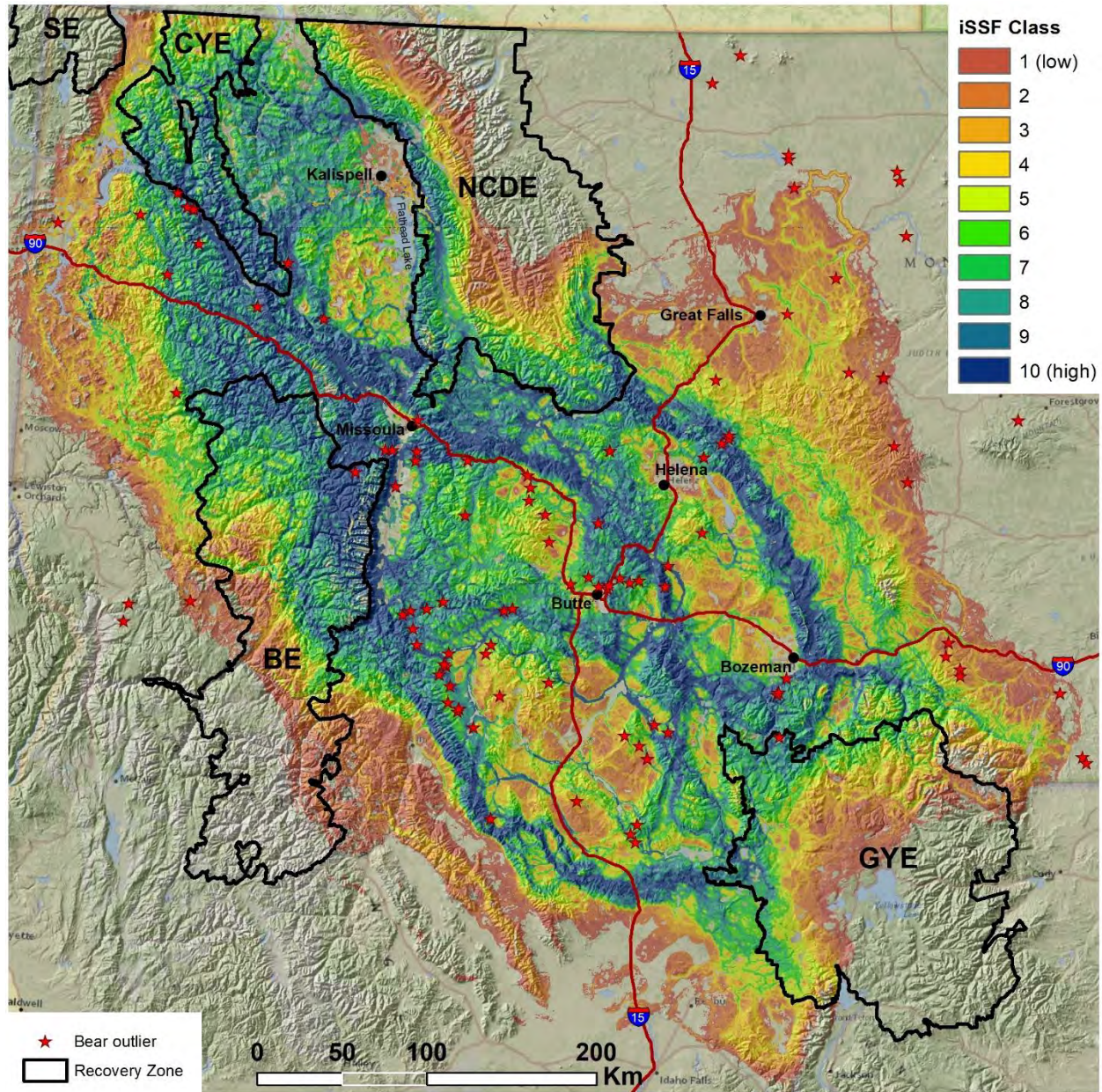
Figure 1.

Figure 2.

Phase 1: Model Focal Population

GPS collar data

Prepare data
- Filter to period of interest and consistent time intervals
- Calculate step lengths and turn angles

Prepare global iSSF models of movements
- Measure habitat variables at used and available steps
- Fit model to each individual

← **Habitat variables**

Test hypotheses & draw inference
- Calculate log-RSS
- Summarize results, e.g., as % of individuals with mostly positive or negative results
- Test for patterns in responses, e.g., by age class, sex, etc.

Develop predictive models
- Gradually eliminate terms from global model
- Assess predictive performance with k-fold cross validation
- Identify most predictive model for each individual

Simulate movements
- Use individual's predictive model to simulate paths:
  - Create raster surface using identified model and habitat variables
  - Place simulated individual onto raster surface
  - Use individual's step length and turn angle distributions to generate 11 potential steps
  - Select next step by sampling from probability-weighted steps
  - Repeat for 5000 steps

Prepare predictive habitat maps
- Tally # of steps taken per raster cell
- Bin into 10 quantile iSSF classes

Externally validate maps
- Gather external data (GPS locations not used for model development, e.g., those filtered while generating consistent time intervals or from new individuals or years of data)
- Overlay on predictive maps, extract iSSF class values
- Calculate Spearman rank correlations

← **New GPS collar data**

Phase 2: Assess Model Transferability

Simulate movements for other populations
- Select other populations in which to test movement models
- Use predictive models to simulate paths (same methods as in Phase 1)

← **Habitat variables**

Prepare predictive habitat maps
- Tally # of steps taken per raster cell
- Bin into 10 quantile iSSF classes

Assess model transferability
- Gather GPS location data from selected populations
- Overlay on predictive maps, extract iSSF class values
- Calculate Spearman rank correlations

← **GPS collar data from other populations**

Phase 3: Simulate Movement Corridors

Simulate movement corridors
- Use predictive models to prepare to simulate paths:
  - Create raster conductance surface using identified model and habitat variables
- Simulate directed paths:
  - Select a random start node from the edge of population *a*, and an end node from the edge of population *b*
  - Use randomized shortest path algorithm to simulate path between start and end nodes
  - Repeat for different values of θ; lower values are more akin to exploratory movements, whereas higher values represent more optimal movements
- Simulate undirected paths:
  - Select a random start node from the edge of a population
  - Repeat simulation methods from Phase 1

← **Habitat variables**

Prepare predictive corridor maps
- Tally # of steps taken per raster cell
- Bin into 10 quantile iSSF classes

Assess corridor maps
- Gather location data for grizzly bear outlier sightings (sightings verified in areas beyond population distributions)
- Overlay on predictive maps, extract iSSF class values
- Calculate Spearman rank correlations and mean iSSF classes at outlier locations
  - For directed path simulations, identify value of θ with most support (highest Spearman rank correlation & mean iSSF class value)
- Compare inferences from directed and undirected simulations, e.g., areas of predicted corridor overlap among sets of results

← **Location data for grizzly bear outliers**

Phase 1: Sells et al. 2022. Grizzly bear habitat selection across the Northern Continental Divide Ecosystem. Biological Conservation 276: doi.org/10.1016/j.biocon.2022.109813.

Phase 2: Sells et al. Grizzly bear movement models predict habitat use for nearby populations. In review at Biological Conservation.

Phase 3: This paper. Predicted male and female movement corridors between grizzly bear ecosystems in Western Montana. In review at Biological Conservation.
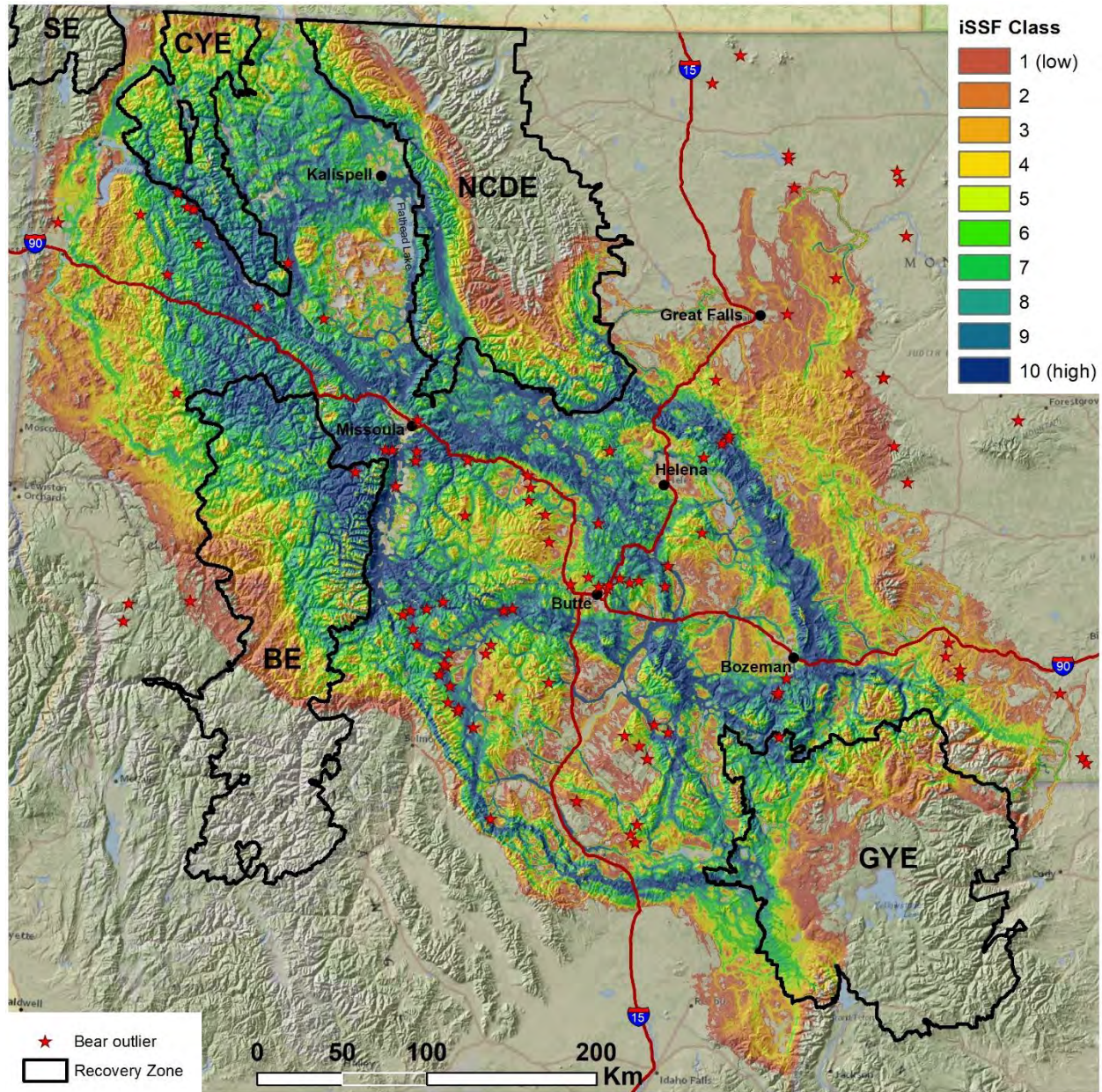
Figure 3.

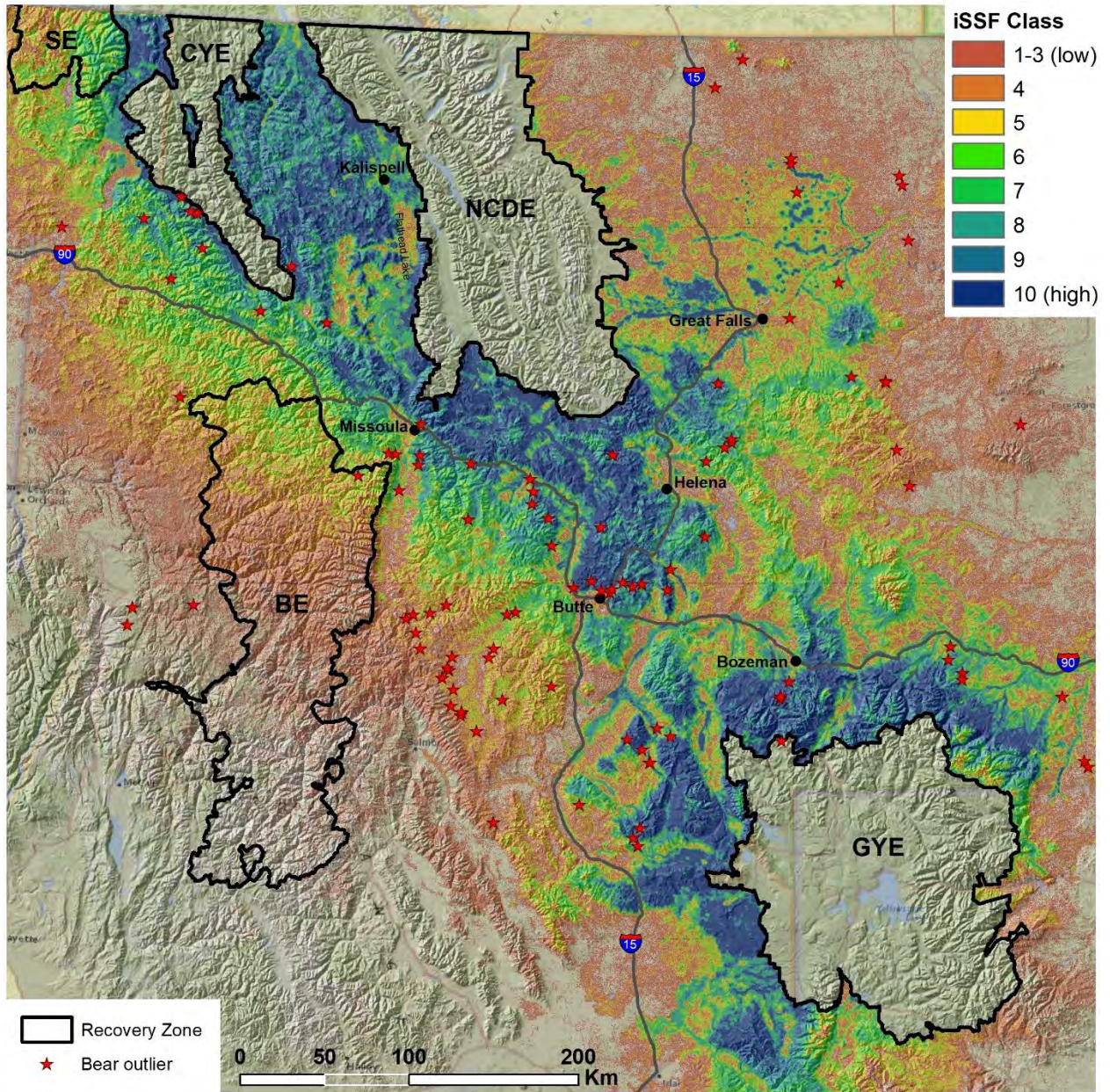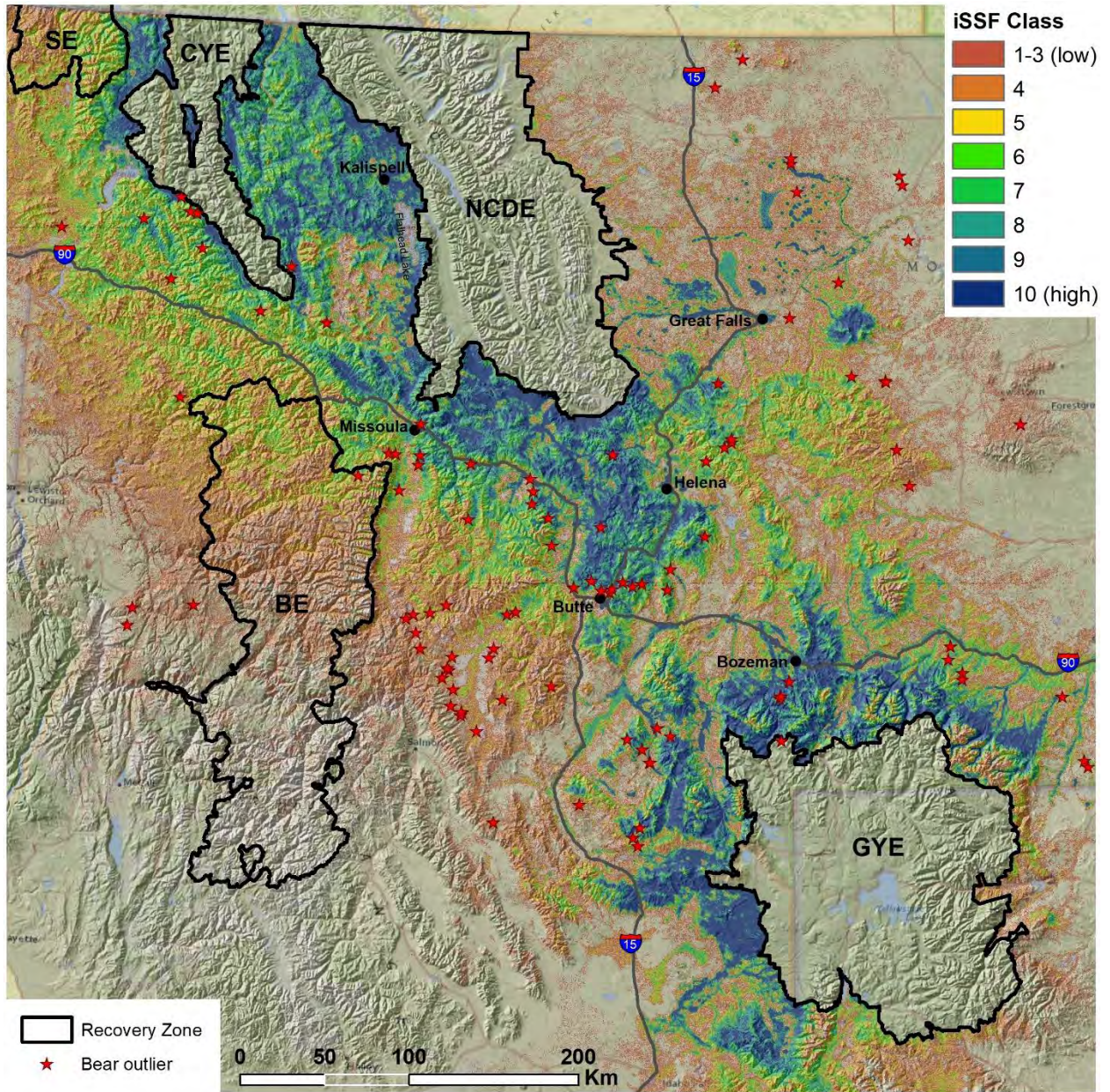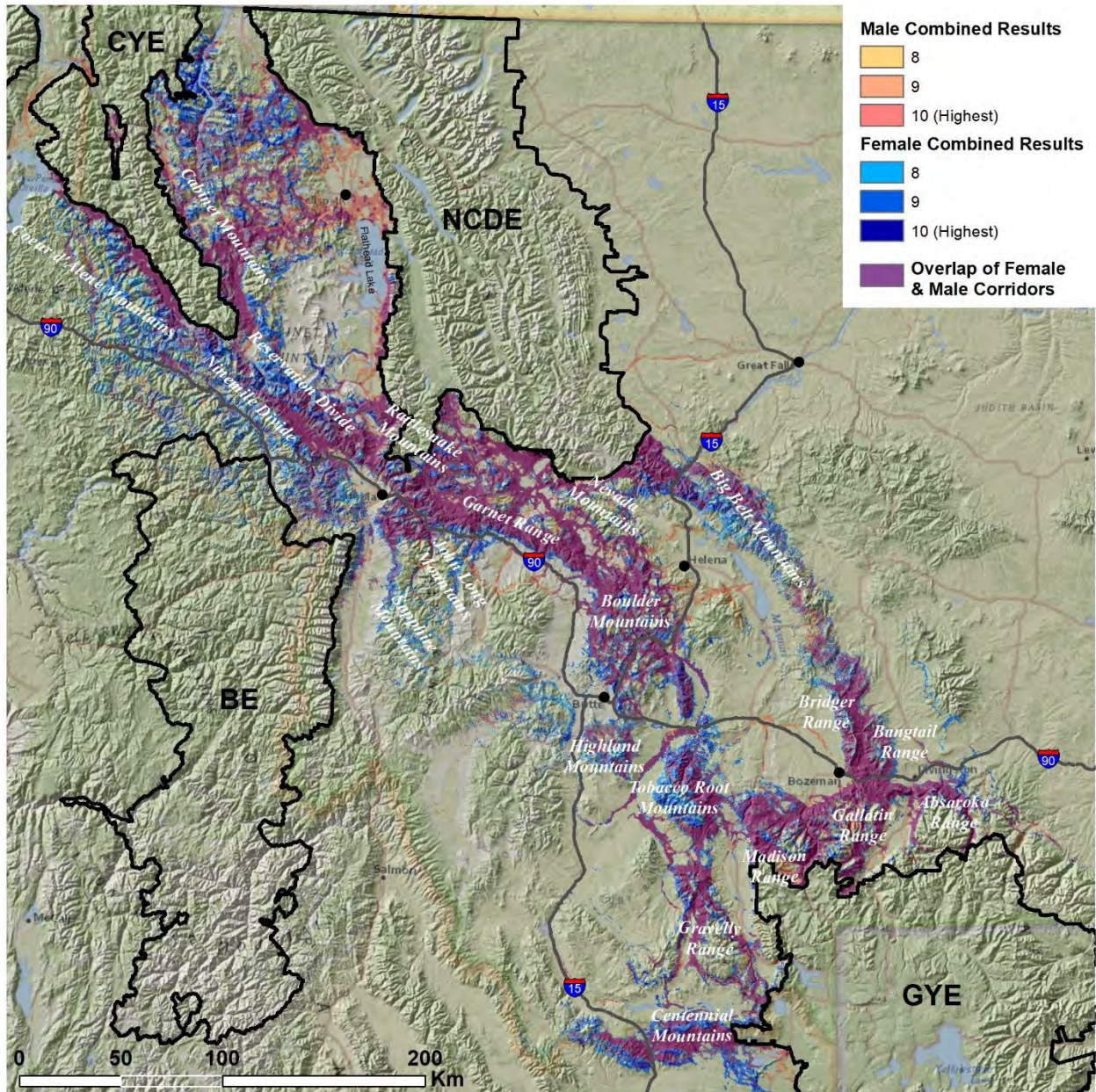**Figure 4.**

Figure 5.

Figure 6.

Figure 7.

Appendix. Predicted Male and Female Movement Corridors Between Grizzly Bear Ecosystems in Western Montana

Our study builds on Sells et al. (2022). The methods used in this earlier study are detailed below.

GPS Data

Sells et al. (Sells et al., 2022) used location data from grizzly bears in the Northern Continental Divide Ecosystem to develop integrated step selection functions (iSSFs) (Avgar et al., 2016; Signer et al., 2019). From 2003 – 2020, grizzly bears were captured using culvert traps or foot-hold snares, collared with Telonics GPS transmitters, and aged from a premolar tooth (Stoneberg and Jonkel, 1966) or based on tooth eruption, wear and coloring.

Sells et al. (Sells et al., 2022) processed grizzly bear GPS data in Program R (R Core Team, 2020) using package amt (Signer et al., 2019). They included data for May – November (to avoid denning months) and omitted dates when bears were trapped, released, or killed. After filtering fixes to 3-hour intervals (+/- 45 minutes) (Avgar et al., 2016), they retained steps of 100 – 15,000 m (omitting stationary and suspect steps), and all bears with ≥100 steps and ≥100 days of steps available. They paired each used step with 10 control steps from the same starting point but with step lengths and turn angles drawn randomly from each individual's gamma and von Mises distributions, respectively, as summarized from their movement data (Signer et al., 2019).

For each bear step (used and control), Sells et al. (Sells et al., 2022) measured the normalized difference vegetation index (NDVI), terrain ruggedness, distance to forest, density of forest edge, density of riparian, density of buildings, and distance to secure habitat (Table A1). They prepared datasets as rasters with 300m resolutions. To index food availability, they used package MODIStsp (Busetto and Ranghetti, 2016) to obtain data during peak green-up (Jun 15 – Jul 15; Peck et al. 2017) each year from 2005 – 2020, which was then averaged at each raster cell. They used package spatialEco (Evans, 2018) to calculate ruggedness as the vector ruggedness measure (Sappington et al., 2007). For distance to forest edge, Sells et al. (Sells et al., 2022) reclassified the 2016 National Land Cover Dataset (mrlc.gov) to forest (deciduous, evergreen, mixed forests, and woody wetlands) and non-forest (remaining classes), identified forest boundaries with package raster (Hijmans, 2022), and measured Euclidean distance. For density of forest edge, they measured forest edge per km^2. For density of riparian, they selected waterbody boundaries, rivers, streams, and artificial paths outside waterbody boundaries in the National Hydrography Datasets (usgs.gov), and measured line density per km^2. They measured ruggedness, density of forest edge, and density of riparian using moving windows with radii of 1100m (females) and 1500m (males) from the cell centroid to represent typical daily movements (Schwartz et al., 2010). For density of buildings, Sells et al. (Sells et al., 2022) calculated centroids of each building footprint in the Microsoft Buildings Footprint dataset (microsoft.com), and measured point density per km^2. For distance to secure habitat, they measured Euclidean distance to polygons identified as grizzly bear secure core (areas >500m from roads on federal, state, and tribal lands; usfws.gov).

iSSFs

Sells et al. (Sells et al., 2022) used iSSFs to develop habitat models for grizzly bears in the NCDE to mechanistically predict space use (Avgar et al., 2016). iSSFs compare covariates associated with animal locations and randomly selected nearby locations using a likelihood equivalent of a Cox proportional hazards model to estimate conditional selection coefficients. The iSSF has exponential form of $w(x) = \exp(x\beta)$, where $w(x)$ is the iSSF score, x is a vector of habitat covariates, and β is the coefficient vector estimated via conditional logistic regression. Higher iSSF scores indicate greater relative probabilities of selection.

Sells et al. (Sells et al., 2022) used Program R (R Core Team, 2020) and package amt (Signer et al., 2019) to prepare a predictive iSSF for each bear for use in simulating habitat selection. They internally evaluated predictive capacity of a global candidate model for each bear (all habitat covariates as quadratic terms) using 100 iterations of 25% testing data and 75% training data via k-fold cross-validation (Boyce et al., 2002). They then gradually eliminated or re-added terms to determine which model formulation (global or reduced) maximized cross-validation scores for each bear.

After identifying the top model for each individual bear, Sells et al. (Sells et al., 2022) used the models as detailed in the main text to run simulations.

Table A1. Hypotheses, predictions, and variables for grizzly bear habitat selection, tested by Sells et al. (Sells et al., 2022). These variables constitute the predictive movement models for the present study.

Variable	Predicted relationship[1]	Alternative prediction	Sells et al. (in review) Result
Normalized difference vegetation index (NDVI)	Positive (to increase access to foods)	Uncertain or negative relationship (if access to high local food availability)	Extensive variability among individuals (i.e., support for both predictions). Females particularly select for NDVI.
Terrain ruggedness	Negative to intermediate (to balance energy expenditures versus security from humans and dominant bears)	Positive (to obtain seasonal resources or maximize security)	Extensive variability among individuals. Males were more likely to avoid areas of higher ruggedness.
Distance to forest edge	Negative to intermediate (to balance security versus access to food	Strongly negative (for security from humans or dominant bears)	Extensive variability among individuals. Females were more likely to avoid large distances from forest.
Density of forest edge	Positive (to increase access to foods)	Negative (for security from humans or dominant bears)	Extensive variability among individuals. Females in particular used areas of greater densities of forest edges.
Density of riparian	Positive (to increase access to food, thermal cover, and water)	Uncertain or negative relationship (to avoid dominant bears or if access to high local riparian densities)	Extensive variability among individuals. Males particularly selected for riparian.
Density of buildings	Negative (to decrease exposure to human risk)	Positive (to access anthropogenic food resources)	Variability among individuals. Both sexes generally avoided buildings.
Distance to secure (unroaded) habitat	Negative (to increase security from human risk)	Uncertain or positive effect (if access to high local levels of secure habitat, or if conditioned to human presence)	Variability among individuals. At least some bears avoided areas further from secure habitat.

Citations: (Carnahan et al., 2021; Schwartz et al., 2003; USFWS, 2021)

Results: Additional Maps
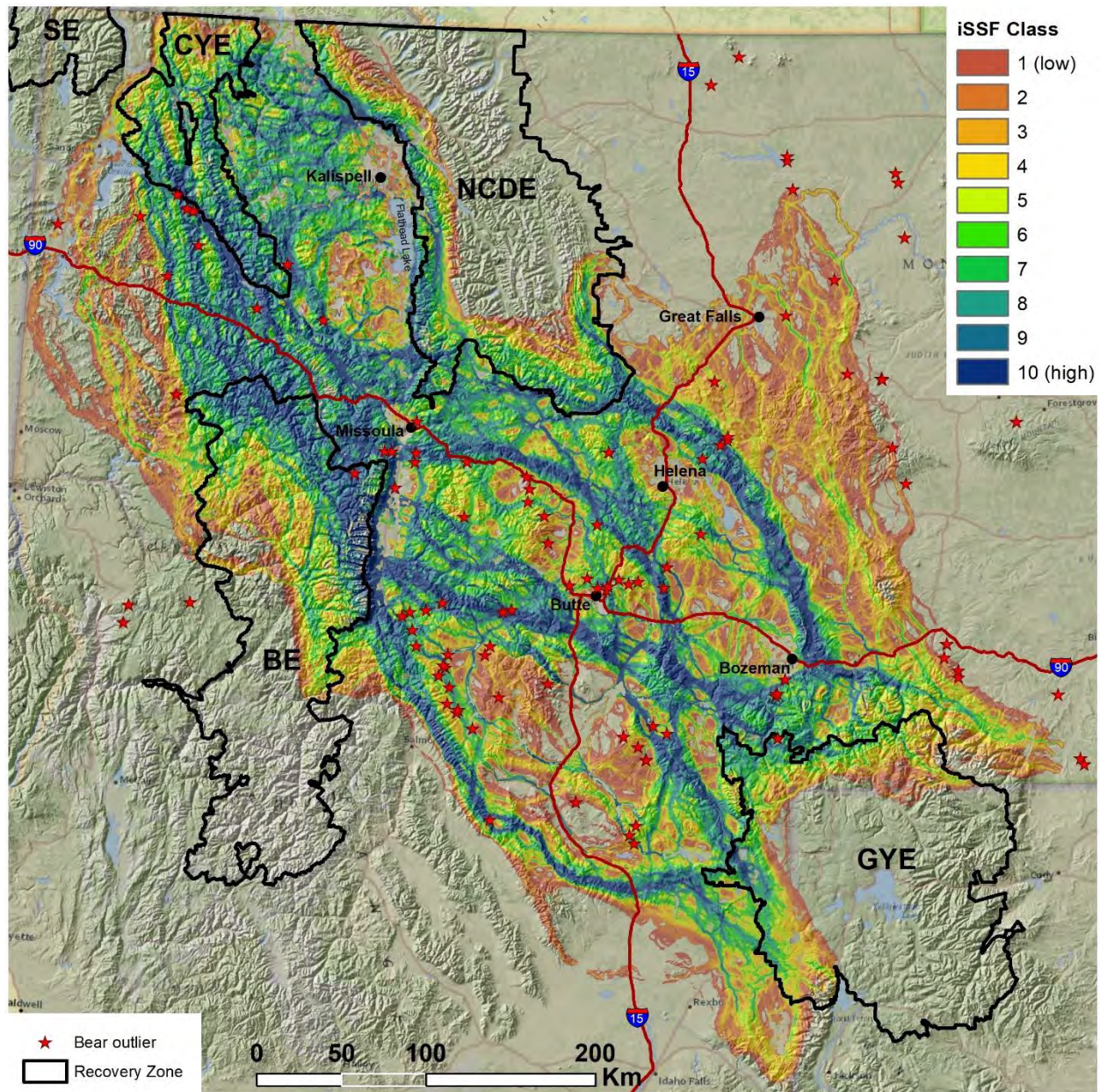
A1. Prediction of female grizzly bear movement corridors in western Montana, summarized and binned from 5 sets of directed (Randomized Shortest Path) movement simulations using start and end nodes associated with routes of NCDE-CYE, NCDE-BE, NCDE-GYE, CYE-BE, and GYE-BE (Fig. 1). Simulations were based on 46 individual iSSF models for NCDE females. Here, θ is 0.01 (the highest value simulated). Higher values of θ represent relatively optimal movements whereas lower values of θ represent more exploratory movements. Results are binned into 10 equal-area quantiles.
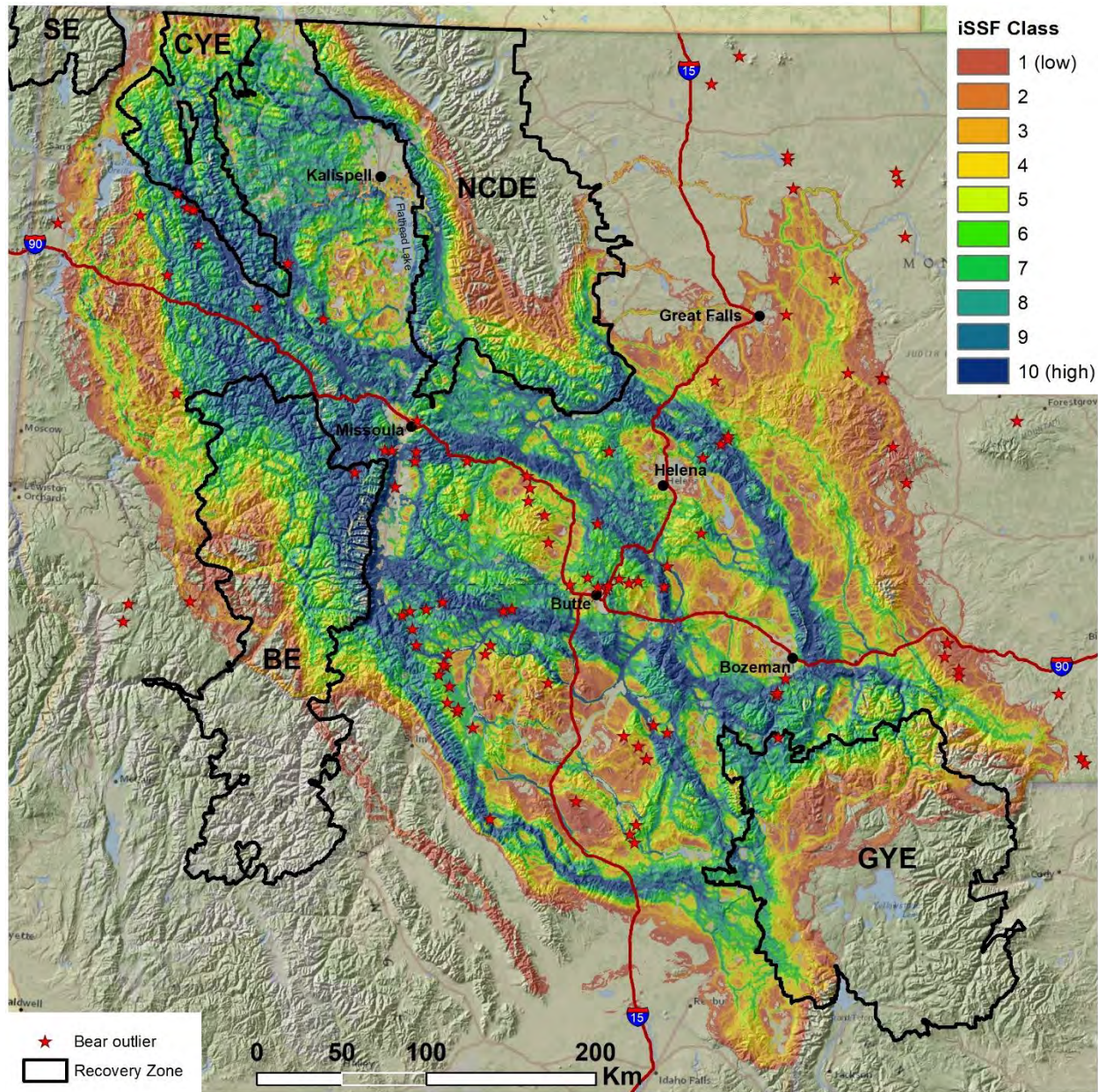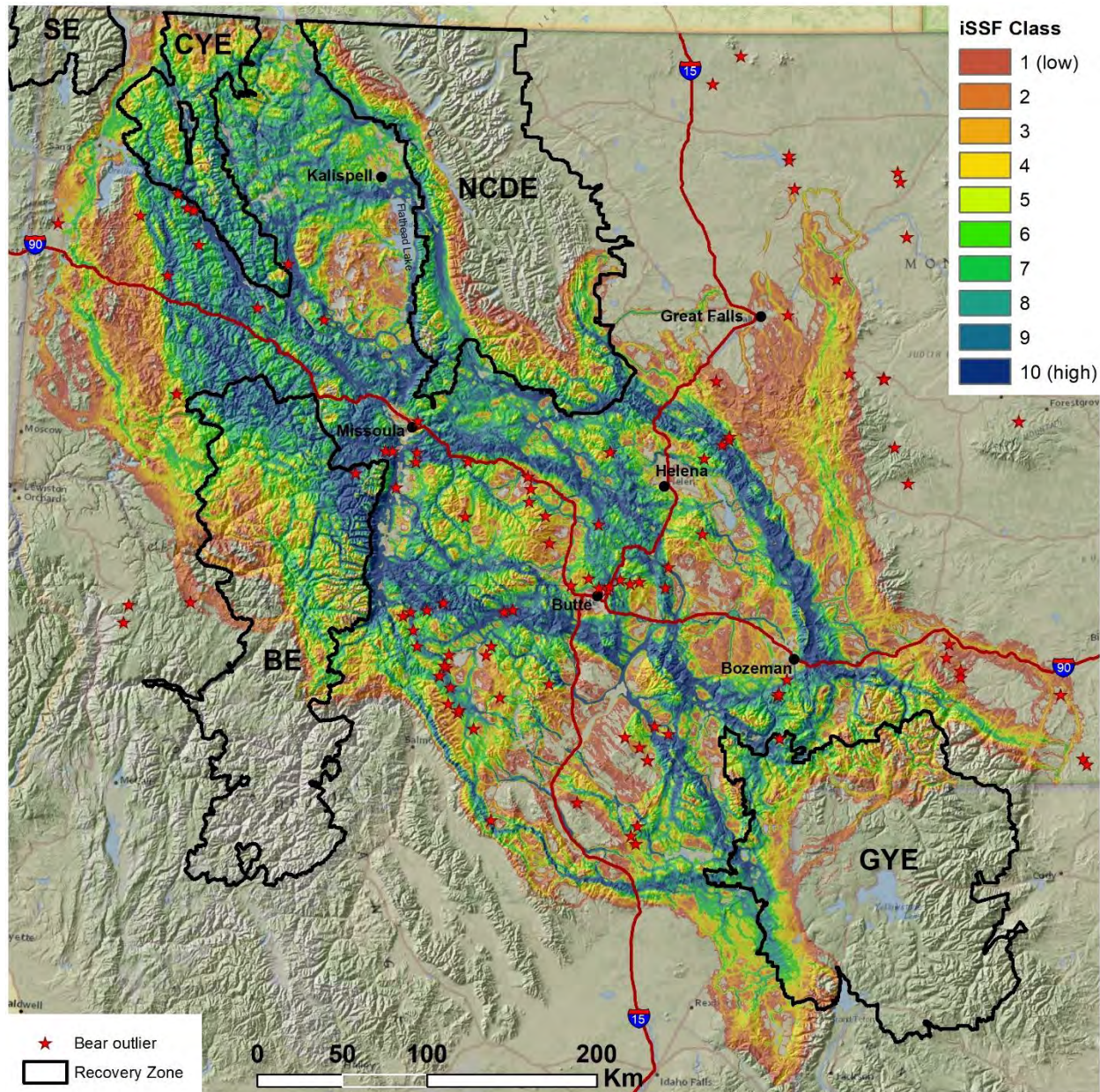
A2. Predicted movement corridors for female grizzly bears from the NCDE to nearby Recovery Zones in western Montana, for θ of 0.001 (the mid value simulated, representing more exploratory behavior).
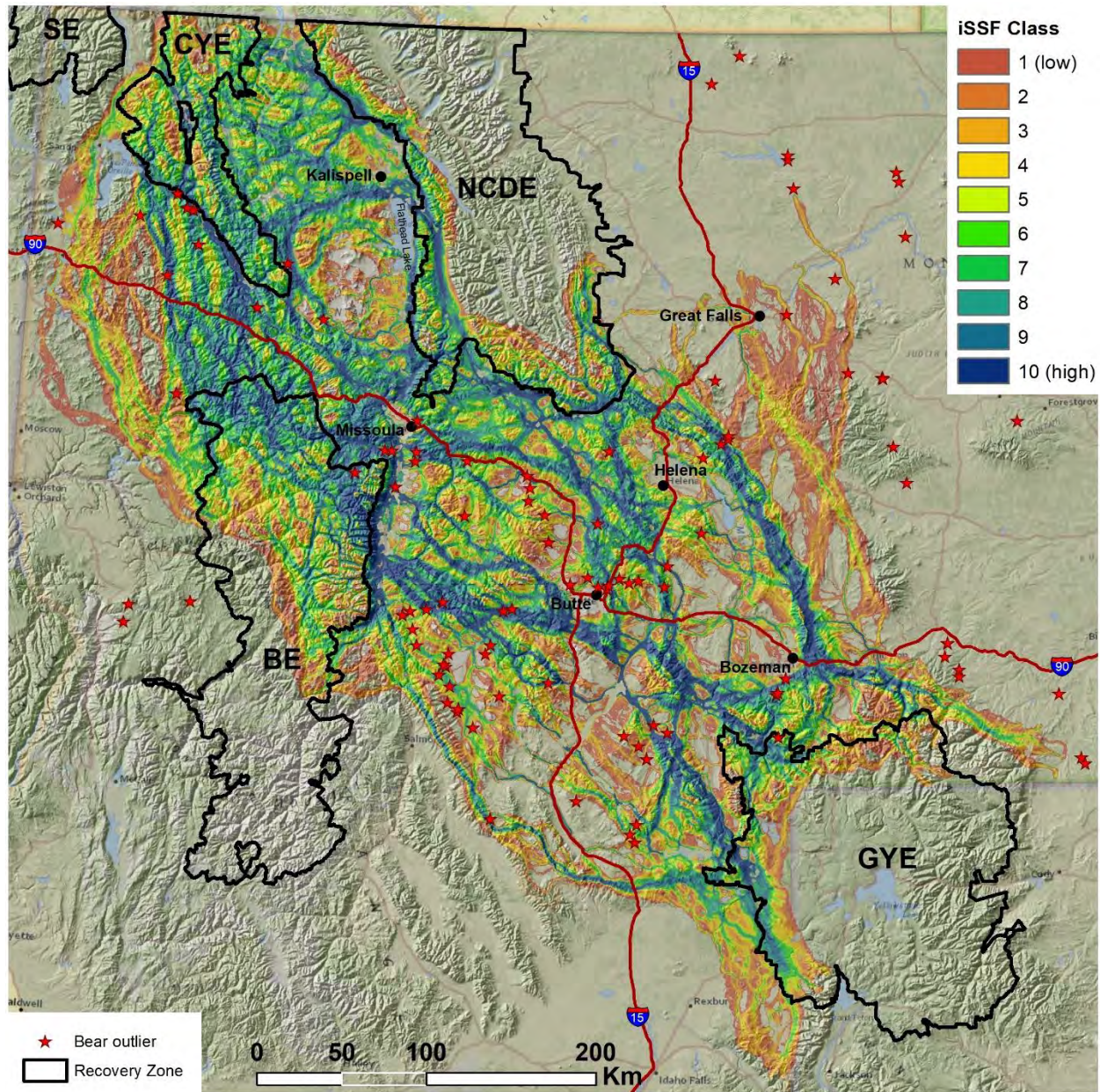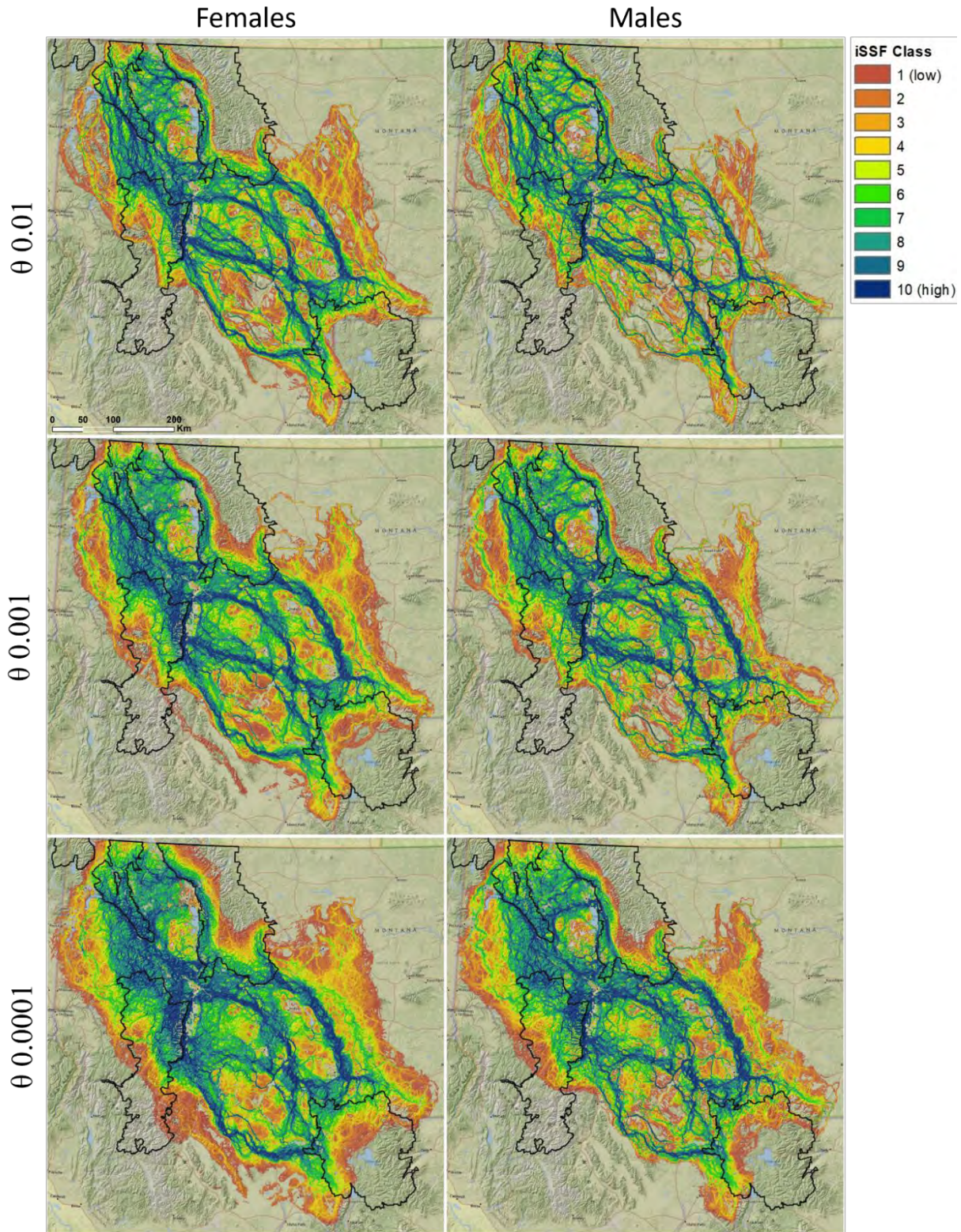
A3. Larger view of predicted movement corridors for male grizzly bears from the NCDE to nearby Recovery Zones in western Montana, for θ of 0.01 (the highest value simulated, representing more optimal movements).

A4. Larger view of predicted movement corridors for male grizzly bears from the NCDE to nearby Recovery Zones in western Montana, for θ of 0.001 (the mid value simulated, representing more exploratory behavior).

A5. Side by side comparison of predicted movement corridors for grizzly bears from the NCDE to nearby RZs in western Montana based on iSSFs and directed simulations using RSP. Higher values of θ represent relatively optimal movements whereas lower values of θ represent more exploratory movements. Results are binned into 10 equal-area quantiles.

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