



## Does hunting-mortality risk affect landscape connectivity? Insights from brown bear movement ecology

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### ABSTRACT

Landscape connectivity supports key ecological processes of animal populations by enabling movement and ensuring gene flow. Habitat corridors are crucial for facilitating connectivity but may expose transient individuals to high mortality risk in human-modified landscapes. Historically, intense hunting led to fragmentation of Scandinavian and Karelian brown bear *Ursus arctos* populations in Fennoscandia. Currently, the Finnish-Russian Karelian population is managed through legal hunting and shows limited gene flow toward the Scandinavian peninsula (Sweden and Norway). Using a two-dimensional modelling framework and long-term datasets, here we assessed landscape connectivity in the Karelian population range and whether hunting-related mortality risk affects intra-population connectivity toward Scandinavia. First, we used GPS data (2002–2014) from 37 bears to perform a step-selection analysis, derive a resistance surface, and model connectivity by circuit theory across Finland and Russian Karelia. Next, we used Finnish bear harvest data (1174 locations, 2002–2014) and resource selection functions to model hunting-mortality risk across Finland, which we integrated with previously identified corridors. Connectivity was highest in forests along central-eastern Finland, southern Finnish-Russian border, and southern Russian Karelia, while it was limited in the northern Finnish reindeer husbandry region, probably due to higher cover of shrubland/open areas. Hunting-mortality risk was highest throughout central-eastern Finland. About 44% of Finland's corridor area fell within high-risk zones, which may potentially constrain connectivity to Scandinavia by acting as functional barriers. To enhance connectivity with Scandinavia, conservation actions in Finland should minimise forest fragmentation and decrease hunting pressure, e.g., within corridors and by protecting females with offspring and solitary subadults.

### 1. Introduction

Landscape connectivity, originally defined as the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al., 1993), is a vital component of the spatio-temporal dynamics of animal populations. Connectivity across the landscape may fulfil several ecological processes, including regular/seasonal movements for foraging, mating and migration, colonisation of the unoccupied habitat through dispersal from natal ranges, and gene flow among otherwise isolated populations (e.g., Benz et al., 2016; Elliot et al., 2014; Frankham, 2006; Gantchoff et al., 2021; Proctor et al., 2012; Viau et al.,

2024). A stable connection among populations, through successful movements of individuals, may be essential to maintain genetic variability and mitigate the potentially deleterious effects of inbreeding depression and genetic drift, hence enabling species to adapt to changing environmental conditions (Crooks and Sanjayan, 2006; Frankham, 2006; Pearman et al., 2024; Schloss et al., 2012). Preserving landscape connectivity is especially critical in human-modified landscapes, where most species occur as partially isolated populations fragmented by habitats of limited or inadequate suitability and/or by high levels of human-caused mortality (Hanski, 1999).

Despite the evident benefits for connectivity, conservationists have

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also argued that habitat corridors may have undesirable consequences (Beier and Noss, 1998; Crooks and Sanjayan, 2006). In particular, edge effects might increase the exposure of transient individuals travelling within corridors to risk derived from competitors, predators, and human activities, eventually creating death traps (i.e., “mortality sinks”) (Crooks and Sanjayan, 2006; Hobbs, 1992; Simberloff et al., 1992). For instance: (a) caribou *Rangifer tarandus* were at higher risk of predation by wolves *Canis lupus* when they occupied habitat near linear corridors (James and Stuart-Smith, 2000); and (b) roadkill risk for mammalian carnivores, such as the stone marten *Martes foina*, the Eurasian badger *Meles meles*, and the golden jackal *Canis aureus*, was shown to be higher in high-connectivity areas (Fabrizio et al., 2019; Frangini et al., 2022; Grilo et al., 2011).

Functional connectivity is an emergent property of species-landscape relations, resulting from the interaction between animal movement behaviour and the physical structure of the landscape (Taylor et al., 2006). Large carnivores are species particularly susceptible to the loss of inter-population connectivity resulting from habitat fragmentation and anthropogenic disturbance, due to their high energetic requirements, large home ranges, slow life histories, and low population densities (Crooks, 2002; Ripple et al., 2014; Woodroffe, 2000). For these reasons, conserving connectivity for large carnivores is challenging and would need large-scale planning and management interventions, often encompassing transboundary geographical areas (Chapron et al., 2014; Maiorano et al., 2019; Penteriani et al., 2018; Recio et al., 2021). However, although human-caused mortality is a key factor limiting large carnivore populations (Benson et al., 2023; Lamb et al., 2020; Woodroffe and Ginsberg, 1998), few studies have contributed an integrated assessment of landscape connectivity and the effects of spatially heterogeneous mortality risk (e.g., Maiorano et al., 2019), and none have considered hunting as a source of mortality (but see Ghoddousi et al., 2021). This may be partially due to the difficulty of collecting mortality data over large spatial scales (Bruskotter et al., 2025), which has led to the inclusion of only-simulated mortality risk in spatially explicit models (Ash et al., 2020; Kaszta et al., 2020, 2019).

In the 1800s and early 1900s, large carnivores in Europe experienced intense human persecution and substantial range contractions, surviving as small, isolated, and fragmented populations (Ripple et al., 2014; Woodroffe, 2000). The once-continuous Fennoscandian brown bear *Ursus arctos* population was heavily reduced by hunting in Scandinavia (i.e., Sweden and Norway) and Finland, gradually splitting into the Scandinavian and Karelian populations (Kojola et al., 2020, 2003; Swenson et al., 1995). Following the implementation of conservation-minded legislation and management practices in the second half of the 20th century, however, both bear populations have increased in number and expanded during recent decades (Chapron et al., 2014; Swenson et al., 2023). In Finland, up to the late 1960s, the brown bear range was restricted to the northern and easternmost parts of the country. Since then, however, the species initiated a gradual expansion to the west and south, and over the last 50 years, bear numbers increased by a factor of ten, due to improved protection and continuous dispersal from core areas in the Russian Karelia region (Kojola et al., 2006, 2003). Nowadays, both Karelian and Scandinavian populations are managed through legal hunting (Penteriani et al., 2018), with Finland and Sweden controlling their bear numbers by annual harvest (Kojola et al., 2020; Milleret et al., 2024).

During the recovery process, several studies have investigated the genetic diversity and population structure of brown bears in Scandinavia, Finland, and northwestern Russia (e.g., Hagen et al., 2015; Kopatz et al., 2021, 2014, 2012; Schregel et al., 2015, 2012). The latest genetic study across the entire Fennoscandia revealed the restoration of once-lost connectivity between the Scandinavian and Karelian populations (Kopatz et al., 2021). However, this study showed that gene flow between Karelia and Scandinavia was asymmetrical, with a low immigration rate of individuals from the Karelian population into Scandinavia, which may not ensure the long-term maintenance of

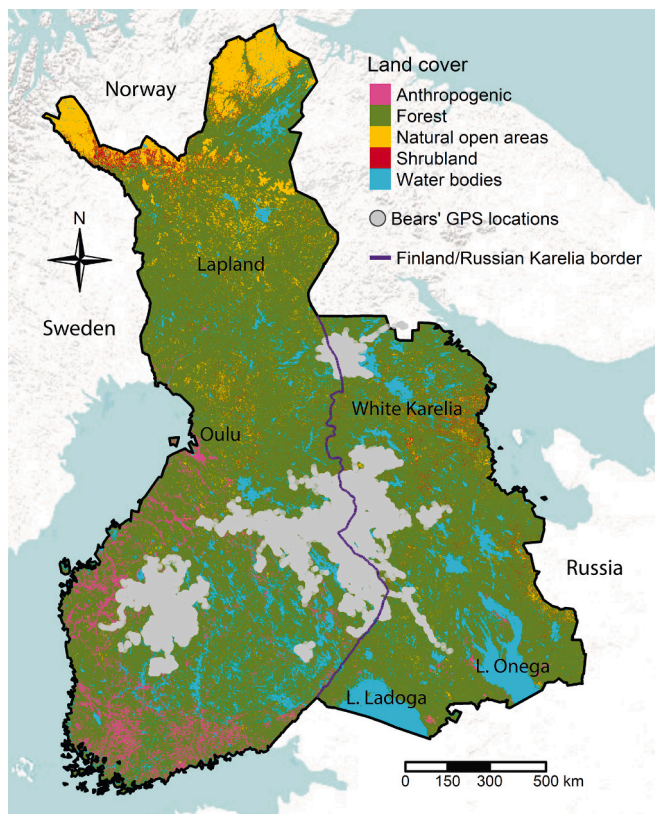
connectivity (Kopatz et al., 2021). This finding has been attributed to several factors in the reindeer husbandry region of northern Finland compared to the south, such as lower bear density, relatively higher harvest rates, and a lower proportion of females that could produce dispersing males (Kojola et al., 2020). In addition, there may be functional habitat barriers to long-distance dispersal by Karelian bears into the Scandinavian population (Kopatz et al., 2012; Schregel et al., 2012). Nonetheless, a comprehensive analysis of the quality and heterogeneity of the habitat matrix (sensu Revilla et al., 2004) in the Karelian population range has been lacking.

The transboundary Finnish-Russian Karelian bear population provides the opportunity to explore the potential overlooked effects of hunting, which may transform connectivity areas into mortality traps. Therefore, the general aim of this study was to assess potential landscape connectivity for Karelian brown bears and examine whether hunting-mortality risk affects intra-population connectivity, potentially limiting bear settlement near the Karelian-Scandinavian population border and thereby reducing subsequent dispersal toward Scandinavia. Specifically, our objectives were to identify: (1) potential movement corridors that may facilitate gene flow from the Karelian to the Scandinavian population, and (2) high hunting-mortality risk areas within the Finnish bear population range. To this end, we adopted a two-dimensional modelling framework (Naves et al., 2003; Nielsen et al., 2006) by making use of extensive, long-term datasets from the Karelian population. To achieve the first objective, we analysed telemetry data from bears in Finnish and Russian Karelia, conducting a step-selection analysis (Avgar et al., 2016) to estimate a resistance surface and model landscape connectivity using electrical circuit theory (McRae et al., 2008; Zeller et al., 2012). For the second objective, we used locations of legally harvested bears in Finland and applied resource selection functions (Boyce and McDonald, 1999; Nielsen et al., 2004) to model hunting-mortality risk to be subsequently integrated with the previously identified corridor areas. This study provides valuable insight into the combined effects of environmental features, landscape resistance, and a novel investigation of hunting pressure on connectivity. Ultimately, it offers spatially explicit outputs relevant to the long-term conservation and viability of the Karelian bear population.

## 2. Materials and methods

### 2.1. Study area and brown bear data

The boundaries of Finland and the Russian Karelia region defined our study area, totalling more than 500,000 km<sup>2</sup> (Fig. 1). However, we focused on Finland alone for the hunting-mortality risk analysis (see below). Approximately 81% of the entire study area consists of low-lying land below 200 m altitude. About 77% of the territory is covered by forests: located in the boreal vegetation zone (Ahti et al., 1968), they are composed mainly of coniferous Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, mixed with broad-leaved trees, such as birches *Betula* spp. and Eurasian aspen *Populus tremula*. Lakes and wetlands, such as swamps and peat bogs, also characterise the landscape extensively, covering around 13% of the land area. Russian Karelia has an overall lower anthropogenic impact than Finland, with a percentage of anthropogenic land and road density roughly ten and five times lower, respectively (e.g., average road density within Finland: 1.77 km/km<sup>2</sup>; average density within Russian Karelia: 0.35 km/km<sup>2</sup>). From 2002 to 2013, 71 brown bears were captured throughout the study area (115 total captures, including recaptures), and each bear was fitted with a GPS collar (Televilt, Lindesberg, Sweden; Vectronic Aerospace GmbH, Berlin, Germany). Bear capture, handling, and collaring (for details see e.g., Penteriani et al., 2021) met the guidelines issued by the Animal Care and Use Committee at the University of Oulu, with all permits provided by the provincial government of Oulu and the Regional State Administrative Agency (OYEKT-6-99, OLM-01951/Ym-23, ESAVI/3229/04.10.07/2013). The GPS collars were programmed to collect one



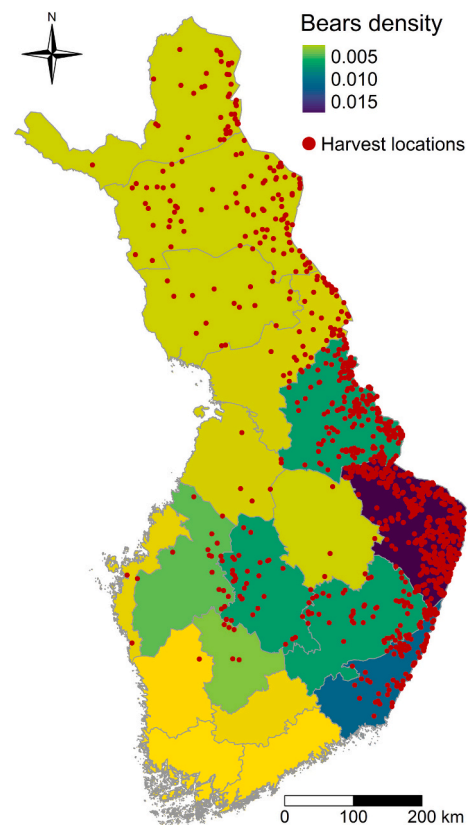
**Fig. 1.** The study area is defined by the boundaries of Finland (~338,000 km<sup>2</sup> land area) and the Russian Karelia (~170,000 km<sup>2</sup>). GPS locations of 71 brown bears captured and monitored in central-western and eastern Finland and Finnish-Russian Karelia between 2002 and 2014 are shown, overlaid on the five-category land-use layer derived from the 2015 *Copernicus* Global Land Cover (see Appendix A.2). Although GPS data occur across three clusters, they belong to the same Karelian population (Kopatz et al., 2014, 2012; Schregel et al., 2012), which is distributed virtually continuously throughout Russian Karelia, north-eastern Finland, and central-western Finland (Heikkinen et al., 2024; Kojola et al., 2020). Basemap credits: © 2009 Esri – World Terrain Base. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

location at a rate of 1, 2, or 4 h (i.e., 6–24 locations/day; Falcinelli et al., 2024), with these schedules allowed to vary within the same collar's deployment. Signals from satellite transmitters were recorded by the ARGOS satellite system (<https://www.cls.fr/en/cls-group/>). Following D'Eon et al. (2002), we excluded all 2-D fixes (~8%) to screen data from high location errors (Bjørneraas et al., 2010). Additionally, we excluded fixes collected during the denning period (i.e., most typically, mid-November to April).

Although estimates of landscape connectivity are most reliable when based on species dispersal data (Elliot et al., 2014; Vasudev et al., 2015), such data are notoriously difficult to obtain (Zeller et al., 2018); in our sample, for instance, only three collared individuals were confirmed to disperse (see subsection 2.4.3). Therefore, in line with several landscape-connectivity studies (e.g., Abrahms et al., 2017; Maiorano et al., 2019; Ziólkowska et al., 2016), we used intra-range direct movements to model resistance to movement (see below), as they are considered a useful proxy for dispersal movement (Zeller et al., 2018, 2012). This approach was particularly suitable for our study population, as during the study period, it was expanding into the Finnish range (Kojola et al., 2006, 2003), with many bears exhibiting extensive movements typical of non-resident individuals (Appendix Table S1). Additionally, movement patterns in Karelian bears have previously been shown to be largely unaffected by sex, age, or reproductive status

(Lamamy et al., 2022; Penteriani et al., 2025, 2022, 2021), although these studies did not include many subadult dispersing individuals. For subsequent Step Selection Analysis (ISSA), we thus prepared a consistent dataset by filtering and resampling all locations at a 2-h fix rate with a flex of 15 min to include those locations on the margin. The final dataset included 38,907 GPS locations collected from 2002 to 2014 from 37 brown bears: adult females (9562), adult males (5524), females with cubs (11,815), subadult females (7076), and subadult males (4930); mean number of locations per individual  $\pm$  SD =  $1052 \pm 884$  (Appendix Table S1).

In Finland, the bear annual hunting season starts on 20 August and stops on 31 October, with harvest limited by regional quotas (Kojola et al., 2020). Hunters generally fill a form about every harvested bear, including information about the geographic coordinates of the kill site and the bear's sex, and it is sent to the Natural Resources Institute Finland (Luke) (Kojola et al., 2021, 2020). Although data on legally harvested bears within Russian Karelia are available (see Kopatz et al., 2014), these are few, and kill site coordinates are missing or represent very rough, approximate locations. Additionally, information for estimating hunting-related covariates (see subsection 2.5.1) is not available for the Russian territory. For these reasons, we investigated hunting-mortality risk for bears in Finland alone. We filtered bear harvest locations for the same years of our GPS data (i.e., 2002–2014) and excluded cubs-of-the-year from the dataset because (a) they are not present in the GPS data, and (b) their space use is not independent of their mother (i.e., autocorrelated data; Steyaert et al., 2016a). After filtering, a total of



**Fig. 2.** Average bear density (number of bears/km<sup>2</sup>) across regions of the Finnish Wildlife Agency (see Appendix A.8 for all details and the other hunting-related covariates). Red dots represent all retained bear hunting mortality locations ( $n = 1174$ ; 2002–2014, and cubs-of-the-year excluded). Note that, despite the low bear density in northern Finland (i.e., Lapland; Fig. 1) — similar to that in the two more southern regions of central Finland — this area still shows a relatively high number of mortality locations compared to those central regions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1174 hunting mortality locations were included in the final dataset (Fig. 2).

## 2.2. Digital environmental covariates

For landscape connectivity and hunting-mortality risk analyses, we selected an extensive set of environmental covariates according to their potential ecological relevance for our species in the study area. All covariates were derived from free-downloadable spatial datasets (Appendix Table S2) and converted to raster layers with a spatial resolution of 100 m. We aggregated these covariates into four categories: (1) topographic, which included Terrain Ruggedness Index and Topographic Position Index; (2) landcover (*Copernicus* Global Land Cover; Buchhorn et al., 2020), which comprised the four continuous land-use covariates anthropogenic areas, forest, natural open areas, and shrubland, all expressed as proportional coverages within a 700-m radius buffer. The radius value was chosen based on the average 2-h step length pooled over all individuals (Osipova et al., 2019); (3) forest-related, which contained Tree Canopy Cover and forest height (also a proxy for forest age) (GLAD laboratory; <https://glad.umd.edu/>), as well as distance from forest edge; and (4) human-related, which included four distance variables, i.e., distance from main roads, secondary roads, all (combined) roads, and human habitations (road network from OpenStreetMap; OpenStreetMap contributors, 2023) (see Appendix A.2 for complete information on environmental covariates, including their preparation and source). We processed all data and performed all spatial/statistical analyses in R version 4.4 (R Core Team, 2024) and QGIS version 3.3 (QGIS Development Team, 2023).

## 2.3. Habitat selection modelling

### 2.3.1. Generation of available steps

For each observed step, i.e., the line connecting two successive GPS locations (Turchin, 1998), we first calculated its length and turning angle using the R package *adehabitatLT* (Calenge, 2006). As we were interested in characterising habitat selection by bears associated with active movements rather than limited movements or stationary states (e.g., feeding and resting), we excluded consecutive locations below a threshold distance from each other from the analysis. Specifically, we used the step length-based approach of Ziolkowska et al. (2016) to select the “active” steps indicating directional movement, i.e., all steps  $\geq 300$  m ( $n = 15,480$ ) (Appendix A.3). Next, we paired each retained step with 10 random steps generated using a parametric sampling method and an iSSA approach (Avgar et al., 2016). In detail, step lengths were drawn through a uniform distribution within a minimum distance of 300 m and a maximum corresponding to the 99th percentile of the observed step length distribution (i.e., 5410 m). Turning angles of random steps were sampled from a von Mises distribution ( $\mu = -0.019$ ,  $\kappa = 0.713$ ) fitted by maximum likelihood estimation to observed turning angles using the R package *circular* (Agostinelli and Lund, 2024). We finally extracted the above-mentioned environmental covariates at the endpoints of each observed and random step, as averaging predictors along steps may overestimate landscape resistance, especially at reduced fix rates (Thurfjell et al., 2014; Ziolkowska et al., 2016). To verify that using 10 random steps per used step adequately characterised availability (Benson, 2013; Northrup et al., 2013), we refitted models (see below) using increasing numbers of available locations (1–20) and found that coefficient estimates stabilised at this value (Appendix A.3).

### 2.3.2. Step-selection analysis

We checked all environmental covariates for collinearity using Pearson's correlation coefficient threshold of  $r \geq |0.65|$  (Ziolkowska et al., 2016). The pairs of correlated variables were tree canopy cover with forest height ( $r = 0.76$ ), distance to main roads with distance to human habitations ( $r = 0.65$ ), and distance to secondary roads with distance to all roads ( $r = 0.98$ ). We took correlation into account in

building the candidate model set, such that pairs of correlated variables were not included in the same model (Corradini et al., 2021; Peck et al., 2017) (Appendix Table S4).

We fitted a set of 12 ecologically plausible step-selection function models using mixed conditional logistic regression (Duchesne et al., 2010) (Table 1). Specifically, we implemented the method proposed by Muff et al. (2020) via the R package *glmmTMB* (Brooks et al., 2017), making use of the Poisson trick and treating intercepts as a random effect with a large, fixed variance. The model structure was as follows: (1) used (1) and available (0) steps as the response variable; (2) each used step with its associated 10 random steps as the stratum; (3) five “core” environmental covariates as predictor variables, i.e., the four land-use covariates and forest height, representing the effects of land use and forest structure; (4) one or more additional environmental covariates characterising the different candidate models; (5) step length as a predictor, to reduce bias in estimated model coefficients (Forester et al., 2009). All continuous predictors were standardised using Min-Max normalisation (i.e., subtraction of the minimum value and division by the range) to facilitate the comparison of parameter estimates and convergence of models (Grueber et al., 2011); and (6) bear ID as a random slope with respect to all included covariates, to accommodate inter-individual heterogeneity (Muff et al., 2020) (further details in Appendix A.4). We evaluated all candidate models through corrected Akaike's Information Criterion (AIC<sub>c</sub>) scores (Burnham and Anderson, 2002), selecting only the most parsimonious model for inference. To assess the predictive power of this model, we finally used k-fold cross-validation as introduced by Boyce et al. (2002), modified by splitting the data by individual, i.e., cross-validation blocked by individual (Roberts et al., 2017).

## 2.4. Landscape connectivity modelling

### 2.4.1. Calculation of the resistance surface

Using the coefficients ( $\beta$ ) of the top iSSF model and spatial

**Table 1**

Model selection results based on the corrected Akaike's Information Criterion (AIC<sub>c</sub>) for step-selection function models. For each candidate model, the included environmental covariates, degrees of freedom (*df*), difference in AIC<sub>c</sub> values between models ( $\Delta$ AIC<sub>c</sub>), Akaike weight (*wi*), and log-likelihood (logL) are reported. Model M10 outperformed all other models ( $\Delta$ AIC<sub>c</sub> > 2) and received a weight of one. Model numbers correspond to Appendix Table S4.

Model ID	Covariates	<i>df</i>	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	<i>wi</i>	logL
M10	Core + DFE + DMR + DSR	18	299,203.3	0.0	1.00	-149,583.6
M7	Core + DMR + DSR	16	299,304.5	101.3	0.00	-149,636.3
M12	Core + TRI + TPI + DFE + DR + DHH	22	299,393.2	189.9	0.00	-149,674.6
M11	Core + DFE + DR + DHH	18	299,433.2	229.9	0.00	-149,698.6
M9	Core + DR + DHH	16	299,516.4	313.1	0.00	-149,742.2
M5	Core + DMR	14	299,618.5	415.2	0.00	-149,795.2
M6	Core + DSR	14	299,777.7	574.4	0.00	-149,874.8
M8	Core + DHH	14	299,856.9	653.6	0.00	-149,914.5
M4	Core + DFE	14	300,053.3	850.0	0.00	-150,012.6
M3	Core + TRI + TPI	16	300,103.9	900.6	0.00	-150,035.9
M1	Core + TRI	14	300,112.3	909.0	0.00	-150,042.2
M2	Core + TPI	14	300,131.3	928.0	0.00	-150,051.6

*Note:* Core covariates comprised the four land-use covariates (anthropogenic areas, forest, natural open areas, and shrubland) and forest height. TRI = Terrain Ruggedness Index; TPI = Topographic Position Index; DFE = Distance to Forest Edge; DMR = Distance to Main Roads; DSR = Distance to Secondary Roads; DR = Distance to all Roads; DHH = Distance to Human Habitations. All models also included step length as a predictor to reduce bias in estimates of model coefficients (see text).

environmental covariates ( $x$ ), we first predicted a movement permeability surface spanning the entire study area, calculating the selection score for each raster cell by the equation  $w(x) = \exp.(\beta_1x_1 + \beta_2x_2 + \dots + \beta_nx_n)$  (Hofmann et al., 2021; Thurfjell et al., 2014). Following Squires et al. (2013), we then included only the range of predicted scores within the 5th–95th percentiles of their original values. For ease of interpretation, we normalised the final permeability surface to a range between 0 and 1 (Hofmann et al., 2021). Our permeability model was also based on within-home-range movements, whereas dispersing bears may be more tolerant of lower-quality habitat compared to resident/non-dispersing bears (Abrahms et al., 2017; Elliot et al., 2014; Mateo-Sánchez et al., 2015). To account for this difference, we thus transformed the permeability surface using the equation  $R = 100 - 99 * ((1 - \exp.(-c * H)) / (1 - \exp.(-c)))$  where  $R$  is the resistance,  $H$  is the habitat permeability, and  $c$  is a constant (i.e.,  $c_8$  negative exponential transformation; Keeley et al., 2016). This transformation is well suited to calculate resistance derived from telemetry data as it assigns high resistance values to only the lowest habitat permeability values (Carroll et al., 2020; Zeller et al., 2018).

#### 2.4.2. Potential connectivity

Landscape connectivity was modelled by applying circuit theory in Circuitscape.jl (Anantharaman et al., 2020; McRae et al., 2008) (see Appendix A.5 for details on circuit theory). To focus on general connectivity (i.e., regional movement corridors; García-Sánchez et al., 2022), we adopted an omnidirectional approach based on the method in Boudreau et al. (2022). Therefore, we placed a set of source points randomly across the study area to represent locations of individual bears travelling randomly through the landscape. Since connectivity is always higher near focal nodes (McRae et al., 2008), we performed random sampling for source points weighted on their habitat permeability score. We selected 250 source points (i.e., density of 0.05/100 km<sup>2</sup>), corresponding roughly to 15% of the number of bears estimated in Finland during our study period. As Circuitscape models movement between each pair of nodes separately, we used the *all-to-one* mode to acquire cumulative connectivity between all point pairs: the resulting map represents the overall potential connectivity for a bear moving randomly through the landscape, regardless of the movement direction. The cumulative current density map was log-transformed (e.g., Buchholtz et al., 2020; Merrick and Koproński, 2017; Zeller et al., 2016) and then linearly rescaled from 0 to 100 to ease its interpretation. To assess the sensitivity of the final map as a function of the number/location of source points, we repeated the analysis with 200 and 300 points (further details and corresponding results in Appendix A.5).

We used zonal statistics to analyse landscape features associated with the highest current densities (García-Sánchez et al., 2022). For this zonal analysis, we reclassified the final current map into five categories using the Jenks natural breaks classification method, where 1 indicates the category most constraining bear movement (i.e., current flow) and 5 the most favourable category. For management purposes, corridors are often identified from a connectivity model by taking an upper percentage of connectivity values (Dutta et al., 2022; Maiorano et al., 2019; Zeller et al., 2018). Following this approach, we finally delineated corridors by taking the top 15% of the final current surface (Appendix Table S5).

#### 2.4.3. Model evaluation

We assessed the fit of our connectivity model using dispersal data from three subadult males and two complementary evaluation methods, i.e., a null model comparison and a random path comparison (McClure et al., 2016; Zeller et al., 2018). Specifically, model performance was evaluated by: (1) comparing empirical connectivity values at observed dispersal locations against those expected under a null (isolation-by-distance) model, and (2) testing whether observed dispersal paths followed areas of higher predicted connectivity than randomly-generated alternative paths (for all details, see Appendix A.7). All connectivity

analyses were performed in Circuitscape version 5.13 through Julia version 1.10 (Anantharaman et al., 2020).

### 2.5. Modelling hunting mortality risk

#### 2.5.1. Hunting-related covariates

Using available data on Finnish wildlife hunting, we derived three hunting-related covariates indicating, for each Finnish Wildlife Agency region: (1) average bear density (Fig. 2), estimated annually from 2007 to 2014; (2) average density of registered hunters, estimated annually from 2007 to 2014; and (3) the bear hunting quota for 2014, i.e., the only year available (see Appendix A.8 for details). We considered as predictors the above hunting-related covariates along with land-use covariates, tree canopy cover, distance from forest edge, and distance from all roads, i.e., the environmental covariates expected to exert the greatest effect on bear occurrence (Grueber et al., 2011; Zuur et al., 2010).

#### 2.5.2. Resource selection functions

To model hunting-mortality risk, we used a Resource Selection Function (RSF) approach following the guidelines in Fieberg et al. (2021). We sampled 100 times as many random locations as the number of mortality locations within the 100% minimum convex hull of all mortality locations after masking water bodies. We then checked for collinearity among the selected covariates using the same criterion described above (see subsection 2.3.2). Average bear density correlated with bear hunting quota ( $r = 0.81$ ), forest correlated with both natural open areas ( $r = -0.72$ ) and distance to forest edge ( $r = -0.68$ ); therefore, we retained bear density, open areas, and distance to forest edge for modelling due to their easier interpretation in a management context.

We fitted a global RSF model using weighted logistic regression with the R package *gmmTMB* (Brooks et al., 2017). The model structure was as follows: (1) used (1) and available (0) locations as the response variable; (2) the above covariates as predictor variables, standardised with Min-Max normalisation; and (3) a weight of 1 and 5000 assigned to used and available locations, respectively, as this ensures that RSF coefficients are estimated correctly according to an inhomogeneous Poisson point process model (Fieberg et al., 2021; Fithian and Hastie, 2013; Warton and Shepherd, 2010). For model selection, we employed a multi-model inference approach through full averaging of models with  $\Delta AIC_C < 2$  (Burnham and Anderson, 2002; Grueber et al., 2011) using the R package *MuMIn* (Bartoń, 2024). The final model predictive performance was evaluated using k-fold cross-validation by dividing the data randomly, i.e., random cross-validation (Boyce et al., 2002).

Based on the model's coefficients and the above equation (subsection 2.4.1), we predicted hunting-mortality risk for bears across Finland, curtailing predicted scores between the 5th and 95th percentile of their original values and then linearly rescaling from 0 to 100 to ease interpretation. Accordingly, we identified areas with the highest hunting-mortality risk as those comprising the top 15% of predicted risk values (Dutta et al., 2022). We then overlapped these areas with previously modelled corridors (Ghoddousi et al., 2021) and calculated the percentage of corridor area within Finland that included high-mortality-risk areas. All manuscript maps were created with the R package *tmap* (Tennekes, 2018).

## 3. Results

### 3.1. Brown bear habitat selection

Model M10 was the most parsimonious habitat selection model; in addition to land-use covariates and forest height (i.e., “core” covariates), this model included distance to forest edge, main roads, and secondary roads (Table 1). According to this model, Karelian brown bears selected forests with high canopy height when travelling (Table 2). They also selected anthropogenic and natural open areas, but did not seem to

**Table 2**

Values of coefficients ( $\beta$ ) and 95% confidence intervals (CI) for the most parsimonious mixed conditional logit model (i.e., M10, Table 1) comparing used steps to randomly generated steps. Numbers in bold represent effects with a  $P$ -value  $< 0.01$ .

Covariate	$\beta$	CI
Anthropogenic areas	4.87	2.88; 6.85
Forest	5.57	4.41; 6.73
Natural open areas	1.76	0.42; 3.11
Shrubland	-1.13	-3.64; 1.37
Forest height	0.60	0.43; 0.77
Distance to forest edge	0.05	-0.78; 0.89
Distance to main roads	-0.45	-2.51; 1.62
Distance to secondary roads	-0.99	-3.38; 1.39
Step length	-9.59	-10.86; -8.31

avoid proximity to any roads, as well as to the forest edge (Table 2). Such a model had high predictive power (mean Spearman correlation coefficient across folds  $\pm$  SD =  $0.973 \pm 0.03$ ).

### 3.2. Landscape connectivity

Our prediction of the resistance surface showed marked differences across the study area (Fig. 3). Specifically, landscape resistance was lowest throughout central and southern Finland, as well as in the southernmost and westernmost parts of Russian Karelia. Here, low-resistance areas were fragmented mainly due to the widespread occurrence of lakes. Large, isolated areas of high resistance were present in the northernmost half of Russian Karelia (i.e., White Karelia) and northern Lapland in Finland. Accordingly, based on the final cumulative current density map, low-current-density areas were found throughout the northernmost regions of the study area (Fig. 4a). In contrast, areas of

high connectivity occurred in central-eastern Finland, along the southernmost Finnish-Russian border, and southern Russian Karelia (Fig. 4a). Similarly, corridors ran along the central-west coast of Finland and throughout central-eastern Finland, although more continuous and broader corridors stretched from the bordering area toward southern Russian Karelia beside Lakes Ladoga and Onega (Fig. 4b). The identified corridors featured, on average, areas with  $>90\%$  forest cover and a canopy cover of about 80%, and were relatively close (i.e.,  $< 300$  m) to roads (Appendix Table S5). On the contrary, low connectivity was mainly due to a combination of higher shrubs and open areas cover and lower occurrence of anthropogenic infrastructure. Model evaluation through dispersal data yielded partially contrasting results: the null isolation-by-distance model slightly outperformed the empirical connectivity surface at dispersal points, whereas observed dispersal paths showed higher mean connectivity values than the majority of randomised paths for all three individuals (see Appendix A.7 for details).

### 3.3. Hunting mortality risk

Four RSF models best described hunting-mortality risk for bears in the study area (Table 3). The probability of bears being hunted increased with bear density, at lower hunter density, and in proximity to roads (Table 3). Hunting-mortality risk was also lower in open areas at closer distances to the forest edge and increased at higher canopy cover (Table 3). Cross-validation suggested a high predictive performance for this model (mean Spearman correlation coefficient across folds  $\pm$  SD =  $0.936 \pm 0.03$ ). Our map of the predicted hunting-mortality risk (Fig. 5a) depicts this is highest mainly throughout central-eastern Finland and, to a lesser extent, in south-western Finland and central Lapland. By overlapping connectivity areas and the hunting mortality map, we found that about 44% of the Finland corridor area fell within zones of high mortality risk (Fig. 5b).

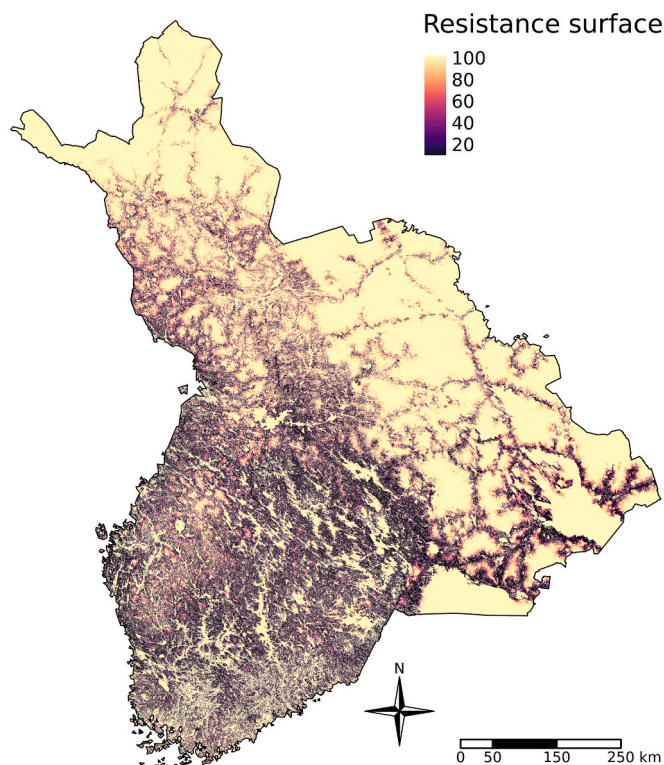
## 4. Discussion

By analysing movement data from Karelian brown bears combined with remotely-sensed environmental covariates, we found that landscape connectivity was greatest throughout central-eastern Finland and the southernmost Finnish-Russian border area, with major corridors running into southern Russian Karelia. Moreover, by analysing the spatial distribution of bear harvest locations within Finland, we estimated that hunting-mortality risk was highest in central-eastern Finland. These findings indicate that potential movement corridors in the northernmost regions of Finland are indeed limited, limiting the expansion of the Karelian population northwards and, in turn, reducing potential connectivity to Scandinavia. Remarkably, our results also suggest that hunting-mortality risk may further constrain intra-population connectivity by acting as a functional barrier (Ghoddousi et al., 2021; Taylor et al., 2006) to movements by Karelian bears.

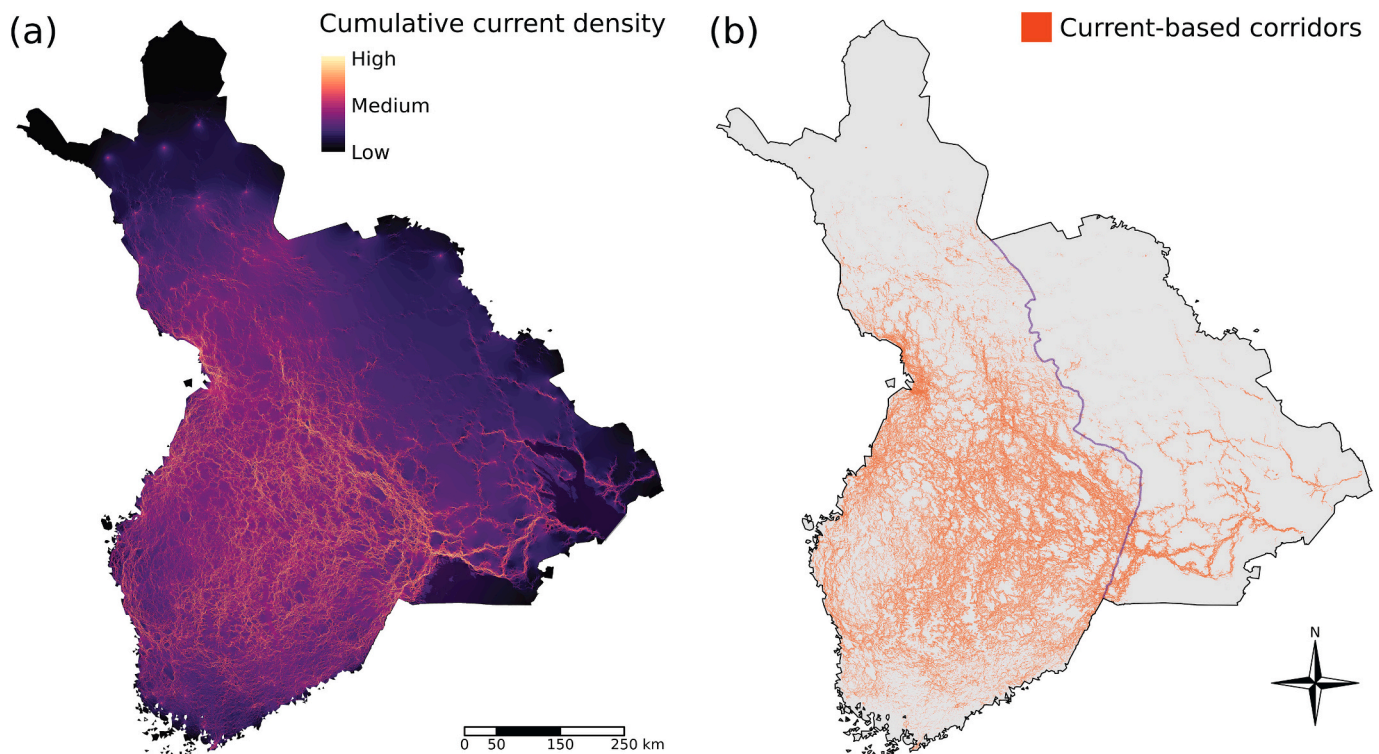
### 4.1. Landscape connectivity

Karelian bears strongly selected large and high stands of mature forest when travelling, possibly because these habitats offer refuge during movement (Swenson et al., 2023). This preference resulted in a good matching of high-connectivity areas with “closed” forests (i.e., with a canopy cover of more than 70%; Buchhorn et al., 2020), such as those occurring along the Finnish-Russian border in the so-called Green Belt area (Karivalo and Butorin, 2006; Linden et al., 2000). Although there are border fences all along the Russian border (Kopatz et al., 2012), the extensive transboundary movements observed for our collared bears (Fig. 1; Appendix Figs. S4, S6) indicate that these did not act as physical barriers and seem not to restrict movement and dispersal, contrary to what was reported for wolves (Aspi et al., 2009).

Additionally, brown bears preferred to move along areas near anthropogenic infrastructure, which may be associated with lower



**Fig. 3.** Resistance surface, scaled from 1 to 100, as estimated by applying a c8 negative exponential transformation (sensu Keeley et al., 2016) to the final permeability surface (see text for details). Landscape resistance was lowest in the whole of central-eastern Finland and the most southern and western parts of Russian Karelia.



**Fig. 4.** Cumulative current density map (a), obtained by log10 transforming and rescaling from 0 to 100 the Circuitscape output, and corridors map (b), as derived by taking the top 15% of current density values. The purple line in (b) delineates the border between Finland and Russian Karelia. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 3**

Model selection results based on the corrected Akaike's Information Criterion ( $AIC_C$ ) for resource selection function models. For each of the four competing models, the degrees of freedom ( $df$ ), difference in  $AIC_C$  values between models ( $\Delta AIC_C$ ), Akaike weight ( $w_i$ ), and log-likelihood ( $\log L$ ) are reported. For each covariate, the coefficient ( $\beta$ ), 95% confidence intervals (CI), and relative importance value (RIV) obtained by averaging this top model set ( $\Delta AIC_C < 2$ ) are reported. Numbers in bold represent effects with a P-value  $< 0.01$ .

Competing models	$df$	$AIC_C$	$\Delta AIC_C$	$w_i$	$\log L$
Bear density + DFE + DR + Hunters density + Open areas + TCC	7	31,212.5	0.00	0.36	-15,599.3
Bear density + DFE + DR + Hunters density + Open areas + Shrubland + TCC	8	31,213.2	0.66	0.26	-15,598.6
Anthropogenic areas + Bear density + DFE + DR + Hunters density + Open areas + TCC	8	31,213.4	0.90	0.23	-15,598.7
Anthropogenic areas + Bear density + DFE + DR + Hunters density + Open areas + Shrubland + TCC	9	31,214.3	1.79	0.15	-15,598.2

Covariate	$\beta$	CI	RIV
Intercept	-12.60	-13.13; -12.06	
Bear density	3.06	2.90; 3.23	1.00
Distance to forest edge	-3.08	-4.75; -1.41	1.00
Distance to roads	-4.21	-6.27; -2.15	1.00
Hunters density	-2.16	-2.54; -1.78	1.00
Natural open areas	-1.60	-2.65; -0.54	1.00
Tree canopy cover	0.61	0.37; 0.85	1.00
Shrubland	0.38	-0.64; 2.48	0.41
Anthropogenic areas	-0.15	-1.22; 0.41	0.38

Note: TCC = Tree Canopy Cover; DFE = Distance to Forest Edge; DR = Distance to all Roads.

movement costs (e.g., avoiding crossing numerous lakes and wetlands). This pattern agrees with our recent research showing that adult males in Finland used habitats close to anthropogenic areas to travel during the mating season (Falcinelli et al., 2024). More generally, this behaviour aligns with previous findings indicating that linear infrastructure and nearby areas may function as efficient travel routes for large carnivores (e.g., Dickie et al., 2020; Dickson et al., 2005; James and Stuart-Smith, 2000), even in our study area (Barry et al., 2020; Gurarie et al., 2011). In addition, developed and agricultural areas may represent relatively low-risk environments during the hunting season, as hunting-mortality risk is presumably lower near these areas (i.e., a human-shield effect; Steyaert et al., 2016b). This interpretation is consistent with the relatively high habitat suitability observed in areas closer to settlements during the hunting season (authors' unpublished data). Therefore, a reduced anthropogenic-area presence and a more extensive network of shrublands, open areas, and wetlands resulted in lower connectivity observed mostly within the northern Lapland and White Karelia (Russia) regions. As high bear density has been reported within Russian Karelia (i.e., 17 bears/1000 km<sup>2</sup>; Danilov, 2005), our results suggest this region may be less favourable for bears' long-range movement but still suitable for their presence, highlighting the importance of basing connectivity assessments on movement rather than habitat models (Ziółkowska et al., 2016).

The observed landscape connectivity patterns are supported by various studies showing high gene flow between Finland and Russian Karelia (Kopatz et al., 2014, 2012; Schregel et al., 2015; Tammeleht et al., 2010), as well as by historical bear monitoring data from both territories. In fact, bear immigration from Russian Karelia was primarily recorded in the eastern Finnish regions of Northern Karelia, Kainuu, and Koillismaa, whereas the immigration rate from the Kola Peninsula into eastern Lapland was much lower (Pulliainen, 1986). Also, corridors we detected within Russian Karelia were along the three isthmuses between the White Sea, Lakes Onega and Ladoga, and the Baltic Sea, assumed to connect Fennoscandia forests to Russian forests (Linden et al., 2000;

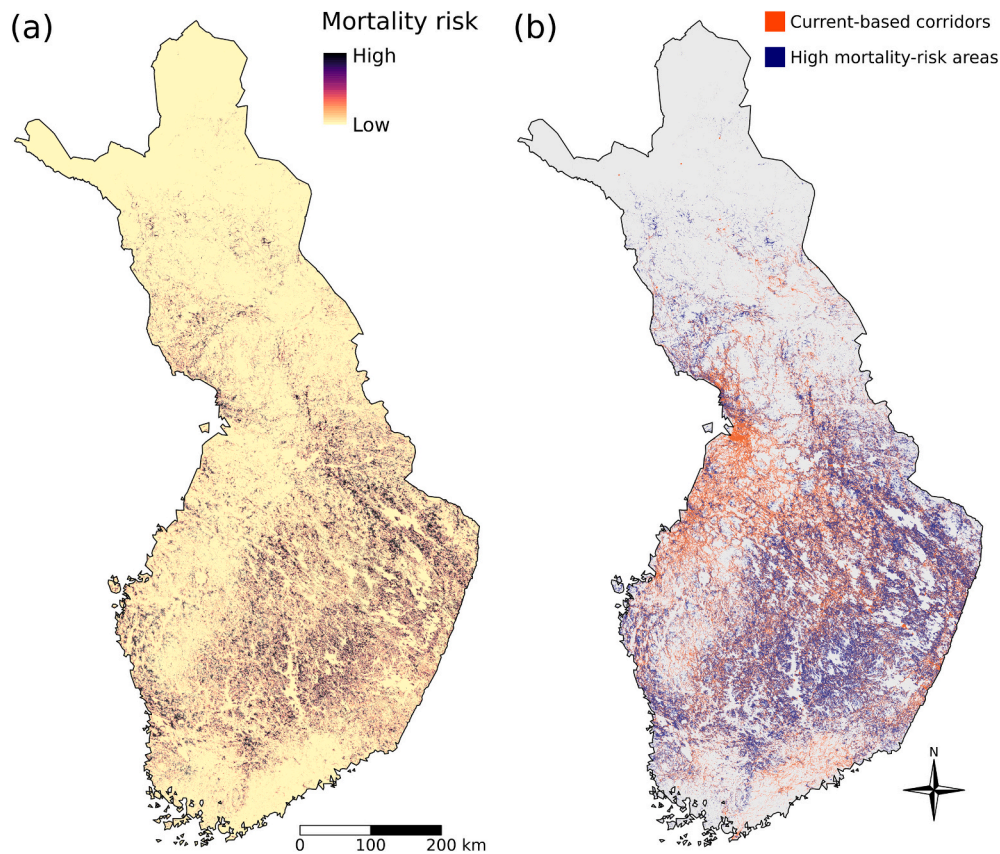


Fig. 5. Map of hunting-mortality risk (rescaled from 0 to 100) predicted for the whole of Finland (a), and high mortality-risk areas (delineated by taking the 15% maximum risk values) overlaid on current-based corridors in Finland (b).

Mayer et al., 2005; Muukkonen et al., 2009), and potentially used also by other large carnivores in the area (see Aspi et al., 2009; Danilov et al., 2018; Kojola et al., 2009).

#### 4.2. Hunting mortality as a functional barrier

Bear harvest locations were mainly concentrated in prime forest habitats close to roads, with a high bear density and low hunter density. Similar patterns have been documented for several other harvested species, such as the cougar *Puma concolor*, leopard *Panthera pardus*, moose *Alces alces*, and caribou (Brown et al., 2023; Dougherty et al., 2025; Pitman et al., 2015; Plante et al., 2017; Stoner et al., 2013), although these studies did not include direct measures of hunting effort. Almost half (i.e., ~44%) of Finland's corridor area overlapped with high mortality-risk areas, thus representing potential mortality traps. This finding suggests higher exposure to hunting-mortality risk for bears within corridors, supporting the conceptual framework of Panzacchi et al. (2016). According to these authors, corridors and barriers stand at the opposite ends of a *continuum* of permeability in which barriers may arise, for example, by reducing the width of passageways or increasing their resistance beyond critical thresholds (Panzacchi et al., 2016). Nevertheless, a large percentage of harvest locations (~65%) occurred outside corridors, indicating that high-mortality-risk areas as a whole may act as barriers limiting connectivity in our study system. This effect may result from both direct bear killing and spatio-temporal avoidance by bears of these high-risk areas (i.e., indirect behavioural effect), given their capability to perceive human-derived risk (e.g., Brown et al., 2023; Corradini et al., 2024; Ordiz et al., 2011).

Our connectivity analysis pooled GPS locations collected both during and outside the hunting season, whereas the mortality-risk model directly reflects hunting pressure. This temporal mismatch should be

acknowledged when interpreting the spatial overlap between corridors and high-risk areas. Moreover, in brown bears, the mating season (approximately May–July) is a key period for functional connectivity, as adult males in particular increase their movements and subadults initiate natal dispersal (Swenson et al., 2023); yet this period does not overlap with the hunting season. Nevertheless, subadults may experience delayed dispersal and initiate long-distance movements after the mating season (Støen et al., 2006), potentially travelling during the hunting period; notably, one of our dispersing males began its movement toward Russian Karelia during the hunting season (Appendix A.7). Additionally, adult males in Finland have been previously shown to perform large daily displacements also during the post-mating period, which fully overlaps with the hunting season, and to select areas farther from roads only during the hunting season (Falcinelli et al., 2024). This behaviour, which suggests active avoidance of high-risk areas during this period, may partly influence the extent of overlap between corridors and high-risk areas. Therefore, the asymmetrical gene flow detected between the Karelian and Scandinavian bear populations could presumably be explained by a combination of factors, primarily the lower bear density and reduced landscape connectivity in Finnish Lapland (Kopatz et al., 2021), as well as higher hunting risk in central-eastern Finland.

Interpopulation connectivity and gene flow in large carnivores are primarily mediated by dispersing subadult individuals, whose movement behaviour and habitat selection may differ markedly from those of resident animals, including in brown bears (Elliot et al., 2014; Thorsen et al., 2022; Vasudev et al., 2015). Consequently, the limited inclusion of dispersing individuals in our dataset represents a limitation when interpreting connectivity in a strict demographic sense. Nevertheless, many collared bears performed wide-ranging, non-resident movements, and predicted connectivity showed encouraging agreement with

movements from the few dispersers available for model evaluation (Appendix A.7), supporting the relevance of the inferred permeability patterns. Future research should build upon our results by obtaining GPS-based movement data from Karelian bears during natal dispersal for a more complete understanding of inter-population connectivity and gene flow across Fennoscandia.

#### 4.3. Management and conservation implications

Our integrated analyses provide information on the effect of landscape structure and hunting-mortality risk on bear movements to help inform conservation measures and management actions for Karelian brown bears and, more generally, for the Fennoscandian bear population. Our spatially explicit outputs can be directly used to guide policy-making, including determining where to focus on maintaining/restoring connectivity or refining harvest management (e.g., quotas and territory restrictions) across jurisdictions with different levels of mortality risk. In this context, a key conservation area seems to be central-western Finland and the Oulu sub-region, characterised by extensive corridor areas and a relatively low mortality risk level. Since these regions are located just south of the western Finland-Sweden border, they could actually boost connectivity between the two bear populations in Fennoscandia. By contrast, connectivity toward Russia is mediated by fewer, more spatially defined corridors than in central/southern Finland, suggesting that these pathways warrant strong protection, particularly given Russia's high bear density and their potential role in facilitating movements into Fennoscandia.

Given bears' preference to move along large and mature forest patches, forest management should minimise extensive clear-cutting and fragmentation. Boreal forests in Finland underwent extensive clear-cutting operations mostly from 1950 to 1980, while the human influence on Russian Karelia forests has grown over recent decades, mainly due to increasing demand for wood material from Finland itself (Mayer et al., 2005; Muukkonen et al., 2009). To mitigate fragmentation effects, Linden et al. (2000) emphasised the strategic role of establishing a continuous "forest bridge" across Finland toward Sweden. Considering the brown bear umbrella effect (Steenweg et al., 2023), conservation and restoration of large-scale forest connections would provide protection and benefits even to other forest-dwelling species of the taiga (Linden et al., 2000; Määttä et al., 2022), e.g., by ensuring continuous gene flow between Fennoscandian and Russian populations.

Based on the overall results of this work, it may be desirable to reduce hunting pressure throughout Finland by (a) limiting harvest in areas identified as critical for connectivity, and (b) specifically giving legal protection to all bear family groups (Kojola et al., 2021, 2020; Kopatz et al., 2021), as well as to solitary subadults. These demographic groups play a crucial role as potential sources of immigrant individuals from Finland to Scandinavia, given that most juvenile male bears disperse from their natal ranges as 2-year-olds (Støen et al., 2006; Zedrosser et al., 2007). However, Finnish legislation currently grants legal protection only to family groups with cubs-of-the-year, a measure that remains ineffective because cubs are frequently mistaken for yearlings and consequently shot by hunters (Kojola et al., 2021). Moreover, subadult males dominate harvest statistics, and male-biased mortality is particularly pronounced in the reindeer husbandry region (Kojola et al., 2020).

Although hunting-mortality risk in northern Finland was mainly concentrated in central Lapland, overall mortality risk for bears may still be higher in these northernmost areas. Within reindeer husbandry regions, brown bears and other large carnivores can kill substantial numbers of reindeer calves, and the consequent illegal hunting can have a significant effect on their populations (Andrén et al., 2006; Liberg et al., 2012; Persson et al., 2009; Sivertsen et al., 2016). Future research should thus quantify the extent of brown bear illegal hunting within the Finnish reindeer area while increasing predator tolerance by local communities through the development of new damage prevention and

compensation strategies (Rasmus et al., 2020). Our two-dimensional modelling approach could be extended to the whole Scandinavian peninsula, using bear movement and mortality data from that region too (see Steyaert et al., 2016a). Finally, this approach should possibly be combined with spatially explicit human dimensions models (e.g., Behr et al., 2017; Mayer et al., 2023) in order to foster coexistence between humans and brown bears within the Fennoscandian reindeer husbandry area.

#### CRediT authorship contribution statement

**Daniele Falcinelli:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Paolo Ciucci:** Writing – review & editing, Methodology, Funding acquisition, Data curation, Conceptualization. **María del Mar Delgado:** Writing – review & editing, Methodology, Funding acquisition, Data curation, Conceptualization. **Ilpo Kojola:** Writing – review & editing, Data curation. **Samuli Heikkinen:** Writing – review & editing, Data curation. **Alexander Kopatz:** Writing – review & editing, Data curation. **Daniele De Angelis:** Writing – review & editing, Investigation. **Vincenzo Penteriani:** Writing – review & editing, Methodology, Funding acquisition, Data curation, Conceptualization.

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#### Declaration of competing interest

All 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.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2026.111818>.

#### Data availability

The datasets used in this study are available from the corresponding author upon reasonable request due to conservation reasons.

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