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Where to go? Habitat preferences and connectivity at a crossroad of European brown bear metapopulations

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A B S T R A C T

Natural habitats become increasingly degraded and fragmented due to rapid human expansion. The decreasing availability of high-quality habitats combined with a lack of connectivity among suitable patches and the low permeability of human-transformed landscapes endangers the survival of many species. Understanding the environmental conditions favoring a species' distribution and the identification of movement corridors between populations is crucial for sustainable conservation and management. Serbia is the only European country inhabited by three different brown bear metapopulations, highlighting its crucial geographical position for establishing functional connections among these metapopulations. We used species distribution modeling to predict suitable habitats for the three bear metapopulations in Serbia at two spatial scales (5 and 1 km^2). We combined the predictions from each metapopulation to define suitable habitats for range expansion. Further, we created landscape resistance maps to identify possible connectivity areas to promote gene flow between these metapopulations. Our results highlight that 1) the underlying processes of bear habitat selection at the coarse scale differ between metapopulations, mainly due to the differences in habitat availability; 2) > 60% of areas predicted as suitable for bears in Serbia are currently still unoccupied; 3) the south-eastern part of Serbia represents a key area for the connectivity between bear metapopulations in the future. However, the presence of several movement barriers, such as highways, highlights the need to implement adequate mitigation measures to increase habitat permeability. Because bears are a useful umbrella species for conservation actions, improvement of habitat quality and permeability will also positively affect many other species in this region.

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1. Introduction

Expansion of human activities into wildlife habitats together with rapid development of infrastructure has led to the transformation of natural habitats into a network of fragmented and isolated patches (Bennett, 2003). Habitat connectivity is among the most

Fig. 1. Distribution range of brown bear metapopulations (Carpathian, Dinaric-Pindos, East-Balkan) in Serbia and southeastern Europe (Source: https://www.iucnredlist.org/species/41688/121229971).

important factors affecting the viability of wildlife populations, especially in recent years, when human-derived habitat degradation and fragmentation has reached critical levels that threaten the survival of many species (Fisher and Lindenmayer, 2007; Cushman et al., 2013; Saura et al., 2014; Mateo-Sánchez et al., 2014). As a result, many species with large area requirements exist in

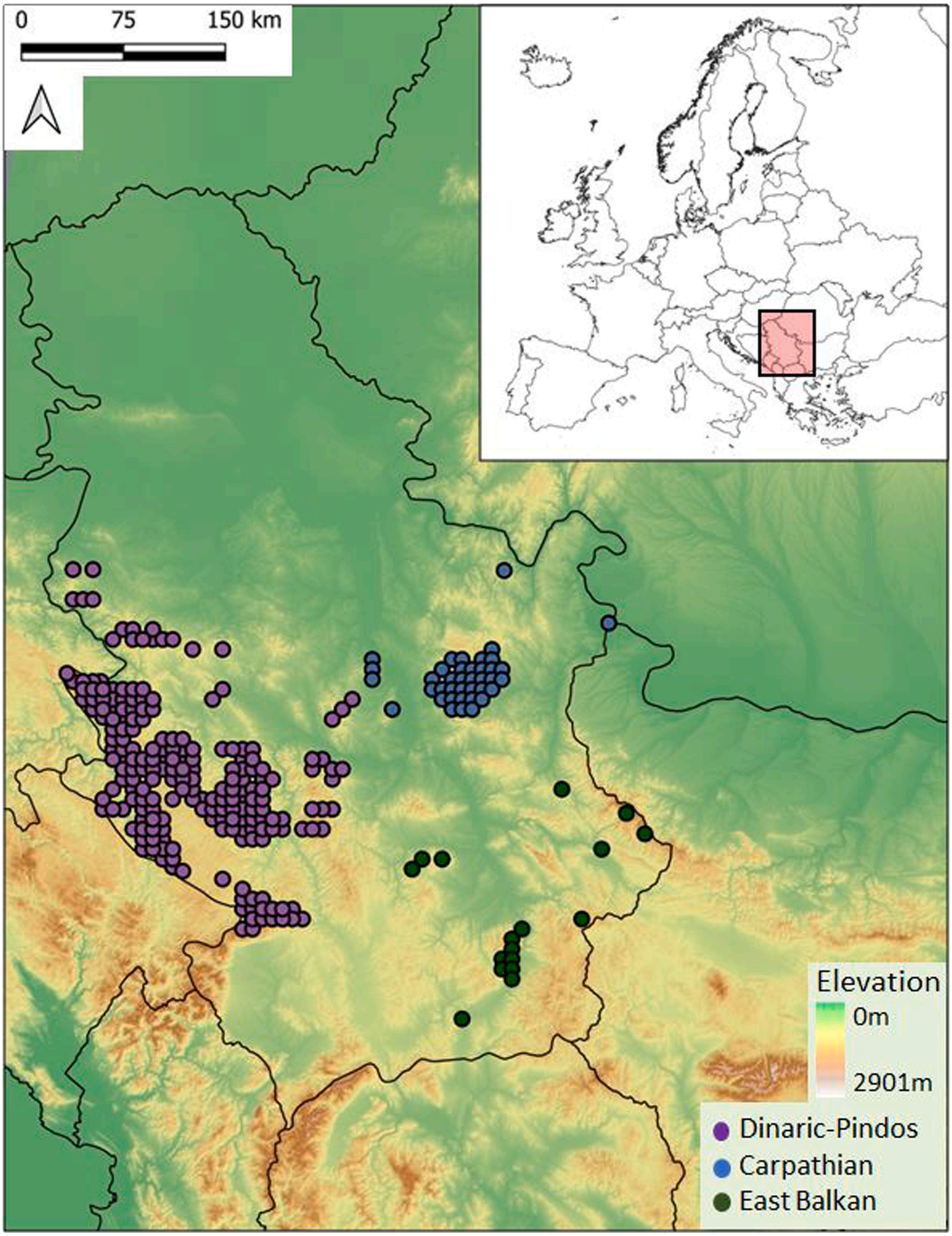

Fig. 2. Distribution of brown bear occurrence data at the regional 5 × 5 scale collected in Serbia, 2007–2021. The color-coding of the data points refers to data collected in different brown bear metapopulations (Dinaric-Pindos, Carpathian, East Balkan) in Serbia.

metapopulations, making them vulnerable to reduction in gene flow, demographic stochasticity, and extinction (Lande, 1988; Hanski, 1998; Melbourne and Hastings, 2008). The long-term viability of such metapopulations largely depends on establishing functional connectivity across fragmented landscapes (Lancaster et al., 2016; Cushman et al., 2018). Conservation strategies commonly rely on the designation of protected areas, which, even if essential, may not be enough to preserve metapopulations (Coetzee, 2017). Furthermore, as many wide-ranging species occur across areas with different political jurisdictions and population management regimes, conservation strategies must be carried out at the appropriate scale to ensure long-term population viability (Inman et al., 2013). Thus, determining a species' current and potential distribution as well as identifying suitable habitats and movement corridors is crucial for sustainable management and conservation (Akçakaya et al., 2007; Martin et al., 2012; Zarzo-Arias et al., 2018; Kouchali et al., 2019).

Large carnivores, such as the brown bear (*Ursus arctos*), grey wolf (*Canis lupus*), and Eurasian lynx (*Lynx lynx*), used to have a pan-European distribution but were hunted to extinction or strongly reduced up until the beginning of the 20th century (Boitani and Linnell, 2015). Due to changes in conservation attitudes especially in the second half of the 20th century, populations of these species are currently recovering and recolonizing former distribution areas across Europe (Chapron et al., 2014; Ordiz et al., 2021). Due to the lack of suitable and reasonably large protected areas, the conservation of large carnivores must mainly occur outside of protected areas in coexistence with humans (Chapron et al., 2014). Large carnivores are wide-ranging species that require large areas but are able to coexist with humans in areas with moderate human densities and activities (Chapron et al., 2014). However, due to the high fragmentation of European landscapes, maintenance of connectivity and gene flow between populations is of crucial importance for the conservation of viable large carnivore populations (Crooks and Sanjayan, 2006; Dixon et al., 2007; Mateo-Sánchez et al., 2014; Fletcher et al., 2018).

Brown bears exist in 10 metapopulations across human-modified landscapes in Europe (Swenson et al., 2000; Zedrosser et al., 2001; Penteriani et al., 2018). Bears have very large spatial requirements, i.e., male home ranges can be up to several thousand square kilometers (Dahle and Swenson, 2003; Ćirović et al., 2015), and are highly affected by habitat loss and fragmentation (Nellemann et al., 2007; Calvignac et al., 2009; de de de Gabriel Hernando et al., 2021). Therefore, improving habitat permeability and establishing connectivity between suitable habitat patches and populations is a priority for brown bear conservation in Europe. Serbia is located in south-eastern Europe and is of special strategic importance for bear conservation, as it is the only country where three of the largest European metapopulations, i.e., Carpathian, Dinaric-Pindos, and East-Balkan, have a potential contact zone (Kaczensky et al., 2013; Chapron et al., 2014; see also Fig. 1). Therefore, the identification of suitable areas and habitats in Serbia where these metapopulations could expand to and potentially inter-connect, presents a unique opportunity for brown bear conservation in Europe.

We used habitat suitability models with a maximum entropy approach (MaxEnt) to analyze bear habitat selection patterns at a coarse regional (5 ×5 km) and a fine local scale (1 ×1 km) in an area where three European brown bear metapopulations (from now on referred to as populations) meet in Serbia. We aimed to 1) determine which environmental variables drive bear habitat selection in each population, due to different habitat availabilities; 2) create a combined prediction to define suitable bear habitats and possible expansion areas in Serbia; 3) explore areas of possible population connectivity based on landscape resistance; and 4) compare the results with the current distribution of bear populations and the existing network of protected areas in Serbia to evaluate if these areas could function as stepping stones to guide in population connectivity.

2. Material and methods

2.1. Study area and bear metapopulations

The study was conducted in Serbia, which is located in southeastern Europe (Fig. 1) and covers 88,361 km^2. The country is characterized by lowlands (from 28 to 200 m above sea level; 36.7% of the territory) in the north and mountainous areas in the rest of the country, including the Dinaric Mountain Range, the Serbian part of the Carpathian Mountain Range, the Balkan Mountain Range, and the mountains of the Vardar region (Pavlović et al., 2018). Forests occupy 25.6% of the territory, mainly composed of deciduous and mixed beech-coniferous forests, and to a lesser extent coniferous forests. The rest of the territory is occupied by developed agricultural lands (39.7%) and other lands, including undeveloped agricultural and barren lands or infrastructure areas, among others (34.7%; Statistical Yearbook of the Republic of Serbia 2021). Topographic differences can be observed among the mountainous part of the country, where the south and west are characterized by higher and steeper terrain (up to 2656 m at Mt. Djeravica), compared to the east (up to 1339 m at Mt. Beljanica). Serbia has a continental climate with temperatures ranging from − 20 °C in winter up to 40 °C during summer and a mean annual precipitation of 724 mm (Smailagić et al., 2013; Pavlović et al., 2018).

Serbia is the only European country inhabited by three different brown bear populations (Fig. 2), which indicates its crucial geographical importance for establishing connectivity and enhance the long-term conservation of the species in Europe. Brown bears are strictly protected in Serbia. Bears in the western and south-western part of the country are part of the large Dinaric-Pindos population, with an estimated size of > 3000 individuals distributed from Slovenia in the north to Greece in the south (Kaczensky et al., 2013; Chapron et al., 2014). The current population size estimate in the Serbian segment of the Dinaric-Pindos population is 60 ± 10 individuals (Kaczensky et al., 2013). The eastern part of the country is inhabited by bears belonging to the Carpathian population, which Serbia shares with Romania, Ukraine, Poland, and Slovakia. This is the largest European bear population with an estimated population size of > 7000 individuals (Kaczensky et al., 2013; Chapron et al., 2014). The current population size estimate for this population in Serbia is 6 individuals (Kaczensky et al., 2013). Individuals in the south-east of Serbia are part of the East-Balkan population with ~ 600 individuals distributed in Bulgaria, North Macedonia, Greece, and Serbia. This is the smallest population segment in Serbia and it is estimated at 2–3 individuals (Kaczensky et al., 2013). Latest data from the Serbian National Bear

Management Plan indicate an increase in both the number of individuals and range of all three populations in Serbia (Ćirović and Paunović, 2018), however, no connectivity or gene flow between the populations has been documented (Bogdanović et al. 2021).

2.2. Statistical analysis

Species distribution modeling (SDM) is commonly used to associate a species' known distribution data with environmental variables that describe it's occurrence (Anderson et al., 2003; Elith and Leathwick, 2009; Cassini, 2011). These models provide the opportunity to study habitat suitability of a species' potential range and to focus conservation efforts in areas that are most cost-effective for the long-term survival of the species (Martin et al., 2010; Mateo-Sánchez et al., 2014). We used two types of bear presence data: 1) GPS telemetry data, and 2) occurrence locations collected directly by remote cameras or indirectly (i.e., feces, footprints, hair). Remote cameras were located in all areas with bears in Serbia and an occurrence location was defined as the photograph of a bear for at least one time. Telemetry data included GPS locations (1 h relocation interval) of 20 brown bears from the Dinaric-Pindos and Carpathian populations monitored during 2007–2021 (Bogdanović et al. 2021). The permit for capture and handling was provided by the Serbian Ministry of Environmental Protection (license number: 353–01–127 1053/2019–04). To evaluate potentially suitable habitats for bears, we used coarse (5 ×5 km) and fine (1×1 km) grid cell sizes, because bears might be affected by environmental characteristics at different spatial scales (Mateo-Sánchez et al., 2013; Zarzo-Arias et al., 2019). At both the coarse and fine spatial scale, we selected the center coordinates of the grid cells with at least one bear occurrence. These coordinates were used as "bear presence" input data in our models.

2.3. Environmental variables

We used 12 environmental variables related to topography, land cover and human infrastructure (Table 1).

Elevation data (DEM) were obtained from DIVA GIS website (https://www.diva-gis.org/gdata), and mean aspect of slopes was estimated using Geographic Information System software (QGIS, version 3.16.15; QGIS Development Team, 2020). Transportation network data (highways, local roads, forest roads, hiking trails) and water bodies (rivers and streams) were obtained from the Geofabrik website (https://download.geofabrik.de/europe/serbia.html). Variables containing distances to habitat features were calculated as the Euclidean distance from each cell centroid to the nearest habitat feature in question. We calculated variables containing percentages of vegetation land cover classes based on the CORINE Land Cover Map of Europe (1:100.000) (available at: https://land.copernicus.eu/pan-european/corine-land-cover). Protected areas cover 6914 km^2 (7,81%) of Serbia ranging from 1133 km^2 (Stara Planina Mountain) to 9 km^2 (Mali Vršački Rit) (information provided by the Institute for Nature Conservation of Serbia, https://www.zzps.rs/).

We checked for spatial correlation and variance inflation factor (VIF) between variables to avoid inaccurate model predictions (Snee, 1977; Peterson et al., 2007). In case of high Pearson correlation coefficients (>0.7) and high VIF's (>5) we retained the variable that was more important for bear biology according to the scientific literature (Trisurat et al., 2012; Zarzo-Arias et al., 2019). For the final modeling procedure, we used a total of 10 uncorrelated variables: elevation, distance to water bodies, distance to first-order (highways), second-order (regional and local roads) and third-order (forest roads and hiking trails) roads, distance to urban areas, % forest, % shrubland, % pasture, and % human infrastructure (e.g., industrial areas, green urban areas, sport facilities).

2.4. Modeling habitat suitability

To predict suitable bear habitats, we used the maximum entropy modeling approach (MaxEnt version 3.4.1; Philips et al., 2007) called from the statistical environment R (version 4.0.4; R Core Team, 2021) using the packages dismo (version 1.3.5; Hijmans et al., 2021) and ENMeval (version 0.3.1; Muscarella et al., 2014). This method is commonly used for modeling species distribution and predicting potentially suitable habitats (Zarzo-Arias et al., 2019; Evcin et al., 2019; Rozhnov et al., 2020). To obtain the best model structure, we created candidate models for each bear population with all feature type combinations (i.e., linear, quadratic, product,

Table 1
Description, source, and original format of 12 environmental variables used to evaluate habitat suitability in three brown bear metapopulations in Serbia. Variables marked with * are correlated and removed from further modelling.

Layer name	Layer description	Source	Format
Altitude		DIVA-GIS	Raster
Slope*		ArcGIS	Vector
Roads 1	Distance to nearest highways	GEOFABRIK	Vector
Roads 2	Distance to nearest local roads	GEOFABRIK	Vector
Roads 3	Distance to nearest forest roads and trails	GEOFABRIK	Vector
Water	Distance to nearest water bodies	GEOFABRIK	Vector
Urban	Distance to nearest infrastructure	CORINE Land Cover	Vector
Forest	% of forests per grid cell	CORINE Land Cover	Vector
Pasture	% of pastures per grid cell	CORINE Land Cover	Vector
Scrub	% of scrubs per grid cell	CORINE Land Cover	Vector
Infrastructure	% of infrastructure per grid cell	CORINE Land Cover	Vector
Agroland*	% of agriculture per grid cell	CORINE Land Cover	Vector

threshold, hinge (Phillips et al., 2006, Philips et al., 2007)), each one run over a set of regularization multipliers ranging from 0 to 19. We applied the same set of 10 environmental variables in all models. We used 500 iterations, a convergence threshold of 10^{-5}, values from all grid cells for the entire area as background, and the c-loglog format as model output, which allows us to interpret predictions as probability of bear occurrence ranging from 0 (unsuitable habitats) to 1 (highly suitable habitats) (Phillips, Dudík, 2008). We used Akaike's Information Criterion corrected for small sample sizes (AICc) to select the most parsimonious model for each population (Akaike, 1974; Burnham and Anderson, 2002). All models within 2 Δ AICc units were considered as equally good, and we considered the model with the least number of parameters as the most parsimonious (Burnham and Anderson, 2002; Zarzo-Arias et al., 2019). We obtained the percentage contribution of each variable to the model based on a heuristic method provided by default by MaxEnt (Phillips et al., 2006). Finally, we created one final model by combining the predictions from all bear populations (hereafter combined model). For that purpose, we retained only the highest predicted habitat suitability values from each population at both scales (Zarzo-Arias et al., 2022). Further, we defined a suitable/not-suitable threshold as the mean predicted suitability value for grid cells with confirmed bear presence.

2.5. Model validation

We used the area under the curve (AUC) of the receiver operating characteristics (ROC) curve for evaluating model performance (Fielding and Bell, 1997; Phillips et al., 2006). AUC values range from 0 to 1, where values close to 0.5 indicate that the model performance is not better than the random model (Phillips et al., 2006), while values from 0.7 to 0.9 indicate models with moderate performance, and values above 0.9 denote excellent predictive ability (Pearce and Ferrier, 2000). We followed Muscarella et al. (2014) for model execution and used a 'Checkerboard1′ method to separate presence data into training and testing bins for *k*-fold cross validation. To ensure the best possible model performance, we calculated two additional evaluation metrics recommended for presence-only models. First, the Boyce index indicates the extent to which model predictions differ from random distribution of the observed occurrences (Boyce et al., 2002). This index varies between − 1–1, where positive values suggest that observed predictions are consistent with the distribution of presence in the evaluation dataset, and models with an index close to 1 are considered as the best performing models (Hirzel et al., 2006). Second, the Mean Absolute Error (MAE) represents the mean absolute difference between model predictions and target value (Konowalik and Nosol, 2021). The jackknife procedure and the heuristic method provided by

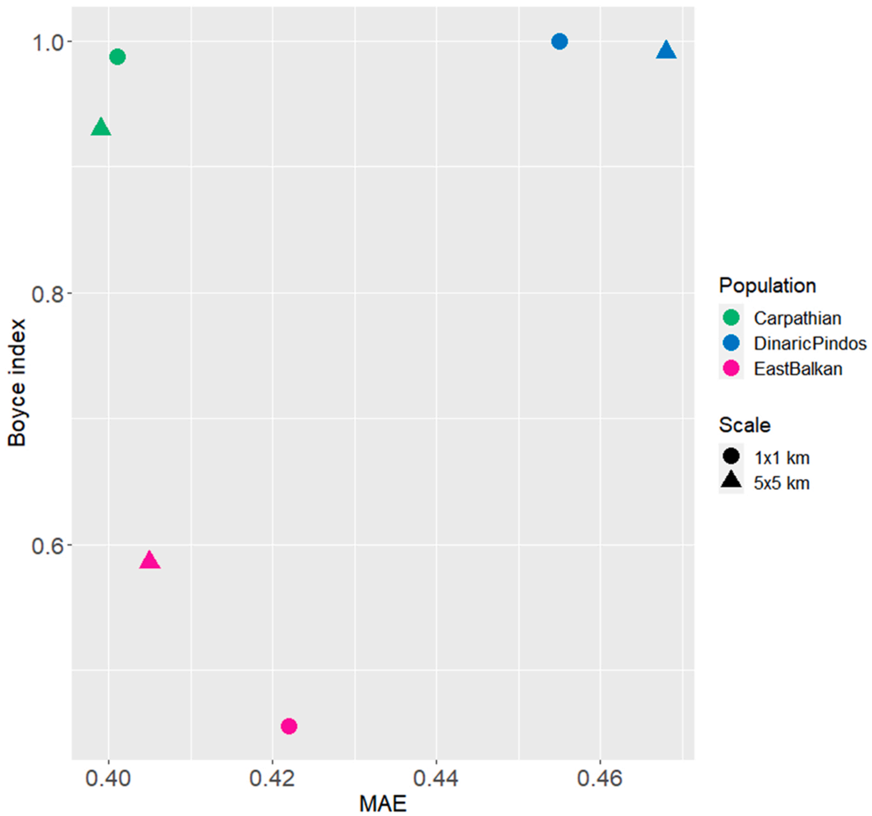

Fig. 3. Model performance based on Boyce index (showing the extent to which model predictions differ from random distribution of the observed occurrences) and Mean Absolute Error (MAE, mean absolute difference between model predictions and target value) values for three brown bear metapopulations (depicted in different colors) at different spatial scales (depicted in different shapes) for bear occurrences gathered in Serbia between 2007 and 2021.

MaxEnt were used to assess the relative importance of the environmental variables as the proportional contribution of each variable to the model (Phillips et al., 2006).

2.6. Connectivity analysis

To identify potential connectivity areas between populations, we performed landscape resistance analysis following Mateo-Sánchez et al. (2014). We created a landscape resistance surface which reflects how difficult it is for an animal to move through a location (observed as a cell in a raster map) as a function of its environmental features (Adriaensen et al., 2003; Mateo-Sánchez et al., 2014). From the combined model, we obtained the predicted habitat suitability value for each cell in our study area (Phillips et al., 2006), and defined landscape resistance as the inverse function of this value according to the formula $(R`/R`min)^2$, where R` is 1-HS (HS: habitat suitability value for each cell) and R`min is the minimum value of 1-HS across the entire study area (Mateo-Sánchez et al., 2014). As a result, we obtained a unique resistance value for each cell (i.e., the cost of crossing it), where the lowest resistance values match the most suitable habitats.

3. Results

3.1. Model evaluation and variable contribution

Our results showed that two of three population models performed well in predicting habitat suitability. Specifically, the Dinaric-Pindos and Carpathian population models showed high reliability, while the East-Balkan model showed poor predictive ability at both spatial scales (Boyce index of 0.586 and 0.456, respectively), likely due to the small sample size (15 and 25 presence grids, respectively) (Fig. 3; Table S1). We therefore, removed this model from further analyses. In general, altitude and forest were the most important variables determining bear habitat suitability (Table 2).

Dinaric-Pindos population: The best performing model at the coarse scale (5 ×5 km) had a Boyce index of 0.98 and MAE of 0.466, and the fine scale model had values of 1 and 0.458, respectively. These values indicate high quality predictions (Fig. 3; Table S1). The best performing model at both scales had mean AUC values of 0.910 and 0.937, respectively, indicating a high accuracy in distinguishing suitable from unsuitable bear habitats (Table S1). The variables contributing most to the coarse scale model were altitude (63%, Table 2), followed by percentage of forest cover, and distance to first- and third-order roads (Table 2). The other remaining variables had a negligible contribution (Table 2). For the fine scale (1×1 km) model, altitude was the most important variable for habitat suitability (69%, Table 2). Other variables had only minor contributions (Table 2).

Carpathian population: The best performing model at the coarse scale had a Boyce index of 0.93 and MAE of 0.399, while the fine scale model had values of 0.988 and 0.401, respectively (Fig. 3; Table S1). The best performing model had a mean AUC value of 0.850 at the coarse scale and 0.960 at the fine scale (Table S1). Percentage of forest cover (64%, Table 2) was identified as the most important variable on the coarse scale. The variables percentage of scrub cover, altitude, and distance to first-order roads had moderate contributions (16%, 7% and 6%, respectively; Table 2), while the contribution of the remaining variables was negligible. In comparison, the fine scale model was most affected by altitude (38%) and the percentage of forest cover (37%, Table 2), while % of scrub cover and distance to primary roads had moderate contributions (8% and 6%, respectively, Table 2).

Table 2

Variable contribution for coarse (5×5 km) and fine scale (1 ×1 km) models that predict habitat suitability for the Dinaric-Pindos and Carpathian brown bear metapopulations in Serbia. Darkest colors refer to maximum (orange) and minimum (blue) variable importance.

Scale	5km		1km	
Population	Dinaric-Pindos	Carpathian	Dinaric-Pindos	Carpathian
Altitude	63	7	69	38
Forest	11	64	4	37
Scrub	2	16	1	8
Pasture	0	2	0	0
Infrastructure	2	0	0	0
Dist. Water	0.6	4	8	4
Dist. Urban	4	0.3	1	4
Dist. Road1	6	6	6	6
Dist. Road2	5	0.1	5	2
Dist. Road3	7	1	6	1

3.2. Habitat suitability

To define which habitats are suitable for all bear populations as well as areas that could promote population connectivity, we used a common model based on the highest prediction values from the Dinaric-Pindos and Carpathian models for each grid at both scales. We excluded the Eastern Balkan model from this analytical step due to its poor predictive ability (Fig. 3; Table S1). Suitable habitats were predicted using a threshold (mean predicted suitability for all confirmed presence cells) of 0.57 for coarse scale and 0.58 for the fine scale, i.e., all areas with values higher than this threshold were treated as suitable for bears. At the coarse scale, the common model identified a total of 9400 km^2 (11.5% of the territory of Serbia) as suitable bear habitat, mostly in the southern half of the country (Fig. 4, left panel; Table 3). Based on the presence data, bears occupy 7.6% of the total territory of Serbia, which equivalents to 35.4% of the identified suitable habitats (Table 3). This leaves a substantial portion of suitable habitats (6075 km^2) available for potential population expansion. The fine scale model (1×1 km) predicted a smaller area of suitable habitat (4451 km^2; 5.1% of the entire study area), of which 24.4% is already occupied by bears (representing 2.4% of the entire area of Serbia). Results at both scales indicate that about 60% of current bear occurrences appear within protected areas (Fig. 4, right panel; Table 3).

3.3. Connectivity

Our coarse scale model predicted habitat suitability values ranging from 0 to 0.88, which resulted in resistance values ranging from 0.9 to 59 (Fig. 5). The landscape resistance map at the coarse scale predicted several areas feasible to connect suitable habitats, especially in the southern part of the country. For the fine scale model, habitat suitability values ranged from 0 to 0.94, which resulted in resistance values ranging from 0.9 to 204 (Fig. 5). The fine-scale results indicate that predicted connectivity areas in the south-east are not continuous but suggest potential corridors for the connection between the three bear populations. The Radan Mountain is the only protected area that lies within this potential connectivity area, highlighting its importance as a 'stepping stone' for the connection between European metapopulations (Fig. 5). In addition, our results suggest several potential barriers for bear movement from west to east due to transportation infrastructure, especially a highway in the southeast (Fig. 5).

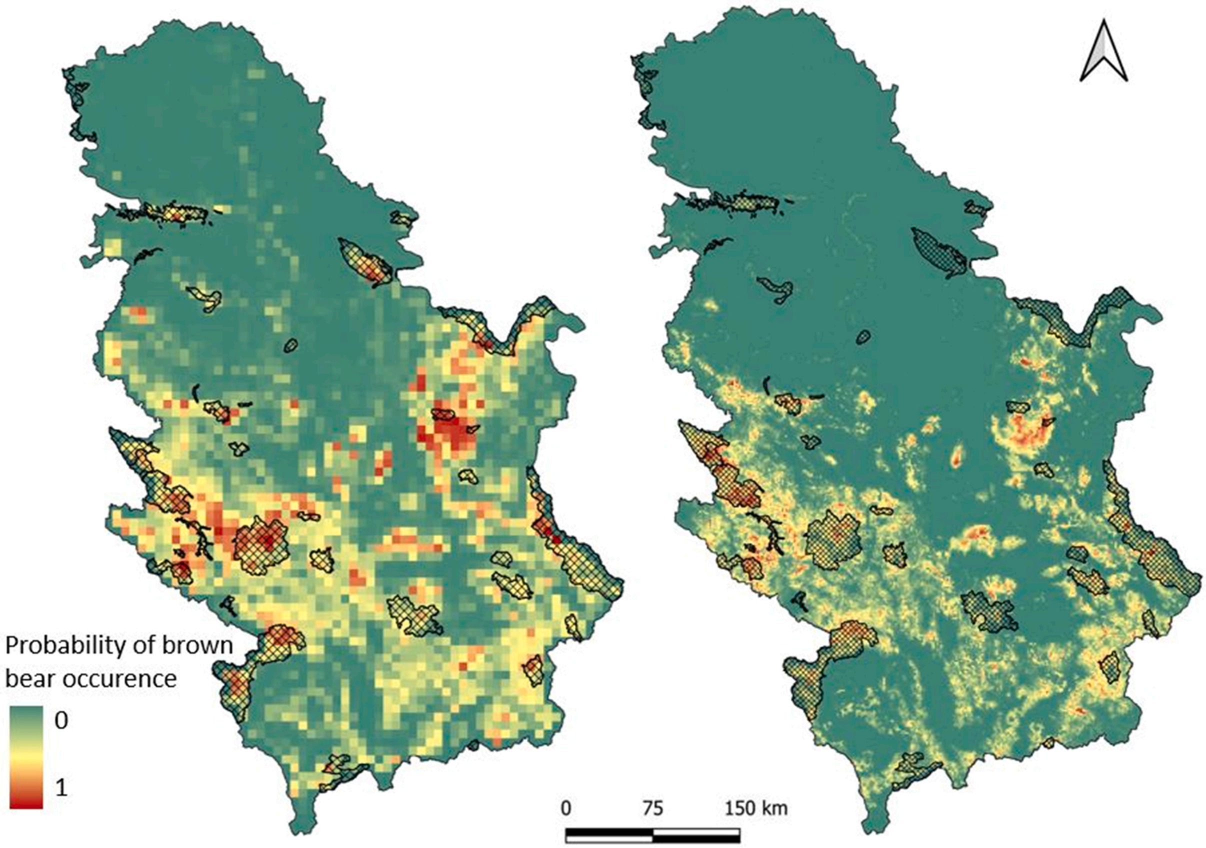

Fig. 4. Common Maxent models predictions of habitat suitability for brown bears in Serbia (based on data from the Dinaric-Pindos and Carpathian metapopulations) at a coarse (5 ×5 km, left) and fine scale (1 ×1 km, right). Hatched areas depict protected areas in Serbia. Predictions represent the probability of bear occurrence scaled from unsuitable (0, green) to most suitable habitats (1, red).

Table 3
Area and proportion of predicted unsuitable and suitable, occupied and unoccupied, and habitats inside and outside of protected areas for brown bears in Serbia at different spatial scales (5 ×5 km and 1 ×1 km) in Serbia. Numbers in parentheses with * refer to threshold values above which habitats were considered as suitable.

Categories	Common model			
	5×5 (0.57 *)		1×1 (0.58 *)	
	Area	%	Area	%
Suitable	9400	11.5	4451	5.1
Unsuitable	72,550	88.5	82,574	94.9
Total	81,950	100	87,025	100
Suitable occupied by bears	3325	35.4	1088	24.4
Suitable unoccupied	6075	64.6	3363	75.6
Total	9400	100	4451	100
Suitable occupied inside protection area	2075	62	602	55.3
Suitable occupied outside protection area	1250	38	486	44.7
Total	3325	100	1088	100

4. Discussion

The main goal of this study was to evaluate bear habitat selection at the intersection of three European metapopulations with the long-term goal to establish connectivity between these populations. We found that altitude and forest cover are the most important factors in bear habitat selection; however, there were differences in how bears from the different populations responded to their environments. Our results further show the availability of areas suitable for population expansion as well as highlight especially one area in south-eastern Serbia where functional connectivity between populations could be established. The results show that higher altitude areas and dense forests cover play an important role in brown bear distribution, and that the probability of bear presence at both analytical scales was negatively affected by human infrastructure. These results are consistent with previous results on bear habitat selection (e.g., Jerina et al., 2003; Posillico et al., 2004; Martin et al., 2012; Zarzo-Arias et al., 2018; Almasieh et al., 2019; Ahmadipari et al., 2021). In addition, our models revealed that the underlying drivers of bear habitat selection slightly differed between our studied populations, especially at the coarse scale. This is primarily due to the differences in the habitats available to each population in Serbia. Altitude best explained bear occurrence in the Dinaric-Pindos population, with most occurrences in areas > 1000 m. In comparison, forest cover was the most influential environmental variable for the Carpathian population. These differences are related to the generally higher altitudes in the Dinaric Mountain Range (west and southwest) compared to altitudes in the Carpathian Mountain Range (east) in Serbia. Furthermore, previous studies on brown bear habitat selection showed that bears avoid areas with high human disturbances (Nellemann et al., 2007; Zarzo-Arias et al., 2018; Almasieh et al., 2019; Morales-González et al., 2020). In general, human presence is lower at higher altitudes, which likely is the reason why bear habitat selection in the Dinaric-Pindos population was primarily driven by altitude. On the other hand, due to the lower altitudes in the east of Serbia, bears in these areas occupy more forested areas, which also provide shelter from human disturbances (Martin et al., 2010; Ordiz et al., 2011). Given that bear behavior is influenced by a wide range of environmental (Nazeri et al., 2012; Zarzo-Arias et al., 2018; Zeller et al., 2019) but also population factors (both intra and inter-specific interactions; Nellemann et al., 2007; Ordiz et al., 2020; García-Sánchez et al., 2022), there might be additional factors not considered in our analyses which may also influence bear habitat preferences.

We found that suitable areas predicted at the coarse spatial scale were almost twice the size compared to the fine spatial scale (9400 km^2 vs 4451 km^2; Table 3). This can be related to the fact that the bear is a highly mobile species that usually reacts to the environment at large spatial scales (Mateo-Sánchez et al., 2014, Zarzo-Arias et al., 2018) leading to large areas being predicted as generally suitable. However, habitat use on finer scales may better reflect preference or avoidance of certain habitat features, which are expressed by fine scale movement decisions by bears. Mateo-Sánchez et al. (2014) suggested that topography and human factors were the main drivers of habitat suitability for bears at larger scales, while results at finer scales relate more to variables associated with habitat configuration and edge effects.

Our results provide information about possible directions of bear population expansion (primarily in western, eastern and south-eastern areas of Serbia), which suggests that adequate management measures should be put in place before bears start occupying these areas and conflicts typical for this area start occurring. Our results further show that a considerable portion (~6000 km^2 and ~3000 km^2 at coarse and fine scale, respectively) of habitat predicted as suitable is available for bear populations to increase in size and range. However, most of these areas are fragmented by roads, which pose a threat for connectivity if bears avoid crossing roads or are regularly killed when attempting to cross them (Proctor et al., 2012; Straka et al., 2012; Mateo-Sánchez et al., 2014). Therefore, the main focus of mitigation measures should be to improve habitat permeability and connectivity between fragmented habitat patches, allowing undisturbed movement of animals with large home ranges, such as brown bears.

More than half of the occupied suitable habitats are located inside protected areas, which shows a good overlap between the protected area network and the current bear distribution. Bears tend to avoid human activities both spatially and temporally (Martin et al., 2010; Ordiz et al., 2013; Hertel et al., 2016). Given that human activities are generally limited in protected areas, they could function as important refuges (or stepping stones for connectivity) for bears and other species (Worboys et al., 2010). However, there are also plenty (~35%) of habitats predicted as suitable outside of protected areas, especially in the southwest (around Zlatibor, Zlatar, Jadovnik and Golija protected areas) and the east of the country (around Južni Kučaj protected area). Potential expansion of the

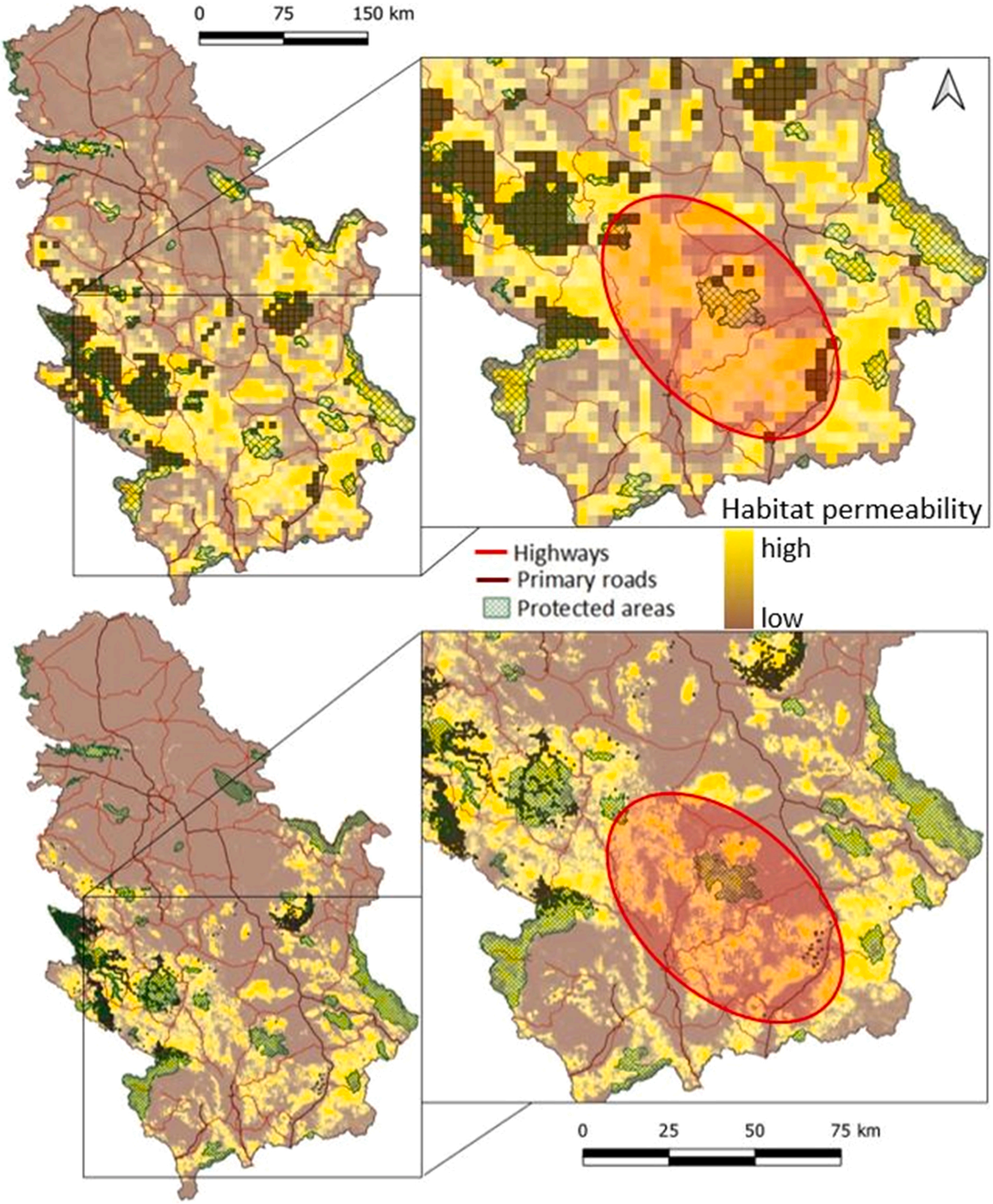

Fig. 5. Landscape resistance maps showing the areas of potential connectivity (red circle) between three European brown bear metapopulations (brown squares depict bear occurrence data) in Serbia. The upper map shows results at a coarse (5 ×5 km) spatial scale, and the lower map results at a fine (1 ×1 km) scale. Areas with lowest resistance values and thus highest permeability for bears are shown in yellow. Green hatched areas depict protected areas in Serbia.

protected areas network in Serbia could consider including habitats important for brown bears, which has been proposed as a good conservation measure in several other regions (Jerina et al., 2003; Nazeri et al., 2012; Mukherjee et al., 2021). The ongoing expansion of the European Union's Natura 2000 network can be particulary important in this regard.Considering that the conservation of bears in Europe must occurr in a human-dominated landscape, their long-term survival depends on their ability to coexist with humans (Zedrosser et al., 2001; Chapron et al., 2014; Morales-González et al., 2020). Our result can be used as a starting point to identify priority areas where appropriate measures need to be put in place before conflicts arise. Furthermore, given the importance of brown bears as an umbrella species for conservation actions, protecting their habitats will also benefit many other endangered species.

Bears in Serbia are at the intersection of three large European bear populations, and therefore crucial to establish gene flow between these populations (Bogdanović et al. 2021). Our results highlight that gene flow is possible in the southern part of the country, which points to the key role of Serbia for long-term conservation of brown bears in Europe. An area especially suitable for connectivity shows good overlap with the „Radan Mountain" Nature Park, which could promote movement of bears from the Dinaric-Pindos population towards the East Balkan and Carpathian populations, and vice-versa. Yet, the habitat permeability analysis revealed that this area intersects with several local and national roads. The major highway, which is located in the central part of the country, will likely represent the most important barrier for bear movement and dispersal, together with the natural terrain formation of the Morava River valley. Numerous studies have shown that roads (Alexander et al., 2005; Riley et al., 2006; Koreň et al., 2011; Mateo-Sánchez et al., 2014) are a major barrier for movement of wildlife, especially fenced highways. These high-volume and high-speed motorways pose a particular threat to species with large home ranges, such as brown bears, leading to a reduction in genetic exchange (McCown et al., 2009; Karamanlidis et al., 2012). Therefore, special attention should be paid to mitigate the effects of these movement barriers. Wildlife underpasses and overpasses combined with road fencing are effective mitigation measures for reducing wildlife-vehicle collision, but also for increasing road permeability for animal movement (Clevenger and Waltho, 2000; Huijser, McGowen, 2010; Huijser et al., 2016; Rytwinski et al., 2016). Given their high costs, such activities must be well designed and placed in the most cost-effective places for species of concern (Kaczensky et al., 2003). Our results can serve as an important guide to highlight the most significant areas where mitigation measures would have the greatest effect on increasing habitat permeability. The rapid expansion of the national transportation network in Serbia, especially the construction of a new highway (Miloš the Great), poses a new serious threat for bear conservation. This highway under construction will pass through parts of the Dinaric-Pindos bear distribution range and prevent the connection with populations to the east (Easter-Balkan and Carpathian populations). In general, a crucial part of all long-term bear conservation programs must be to minimize habitat loss and fragmentation as well as to improve the quality and connectivity of suitable habitats (Swenson et al., 2000; Chapron et al., 2014; Morales-González et al., 2020).

5. Conclusion

Our results are of crucial importance for the long-term conservation of brown bears in Europe, as they highlight the unique possibility to connect three different bear metapopulations in south-eastern Europe. Because bears require large areas of suitable habitat, conservation strategies must focus on preventing further habitat fragmentation and loss as well as on improving connectivity among existing occupied areas (Swenson et al., 2000; Chapron et al., 2014; Mateo-Sánchez et al., 2014; Almasieh et al., 2019; Kouchali et al., 2019). Our results identify areas and landscape corridors important for genetic connectivity between bear metapopulations and provide suggestions for areas in Serbia where connectivity should be improved. Protected areas generally provide suitable habitat for bears but are often too small to support a sustainable population. Our results suggest that improving connectivity between protected areas, despite their small size, could be part of a strategy to improve overall landscape connectivity and habitat suitability that is also beneficial for far-ranging species, such as bears. However, large-scale and long-term conservation of population connectivity must mainly occur in the human-dominated landscape outside of protected areas (Chapron et al., 2014). Therefore, we highly recommend to evaluate current national conservation policies in order to define and appropriately manage landscape connectivity in Serbia as well as in adjacent countries, also by increasing the number and connectivity of protected areas. Furthermore, improving habitat suitability and connectivity for bears will also benefit the long-term conservation of several other species.

Authors' contributions

NB, AZA and DĆ conceived the ideas and designed methodology; NB and DĆ collected the data; Final analyses were conducted by NB and AZA; NB led the writing of the manuscript and AZA, DĆ, AZ and AGH revised it extensively. All authors contributed substantially to the study and gave final approval for publication.

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Declaration of Competing Interest

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

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02460.

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