Biological Conservation 291 (2024) 110498

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Functional connectivity and the current arrangement of protected areas show multiple, poorly protected dispersal corridors for the Eurasian lynx

Mattia Iannella, Maurizio Biondi, Davide Serva *

Department of Life, Health and Environmental Sciences, University of L'Aquila, Via Vetoio— Coppito, L'Aquila, L'Aquila 67100, Italy

ARTICLE INFO

Keywords:
Habitat connectivity
Lynx lynx
Metapopulation dynamics
Large carnivores
Dispersal corridors
Europe

ABSTRACT

Landscape connectivity is essential for the conservation of large carnivores, particularly in highly fragmented landscapes. Despite was nearing extinction, the Eurasian lynx (*Lynx lynx*) recovers in Europe, owing to reintroduction projects that have re-established several subpopulations. However, some of these subpopulations are small and isolated, possibly incurring into reduced genetic diversity. To establish a functional metapopulation in Europe, facilitating lynx movements is crucial, and connectivity modeling could support the identification of optimal solutions to connect these subpopulations. Here, we assessed habitat connectivity for the Eurasian lynx in current and future scenarios, between the European subpopulations, applying two different modeling approaches, namely Circuit theory-based and least-cost path techniques. Moreover, we evaluated the potential of European Protected Areas (EPAs) to form an ecological network able to connect lynx subpopulations. Our results show that several connections occur between Jura, Alpine, Bohemian-Bavarian-Austrian (BBA), and Dinaric populations, while Balkan is less connected. Moreover, the Carpathian population has the potential to act as a source for the BBA subpopulation, if properly connected. We report that, currently, only 21 % of the crucial corridors are covered by EPAs, and those are often disturbed by human infrastructures. High connectivity among EPAs occurs in Central and Eastern Europe, and among the Carpathian, BBA and Alpine subpopulations. However, unprotected areas appear between the Carpathian, the BBA, the Baltic, and the Balkans subpopulation. To enhance those connections, we test the Agenda 2030 goals, and find those functional for management actions focusing on dispersal corridors, also proving that transboundary cooperation is pivotal.

1. Introduction

Despite the historical reduction in large carnivores' population size (Dirzo et al., 2014; Ripple et al., 2014), some recoveries have been recently documented in Europe (Chapron et al., 2014; Ingeman et al., 2022).

The reasons encompass different aspects: first, coordinated legislation shared by many European countries (Habitat Directive 92/43/EEC; Bern Convention), as well as some context-specific management measures, such as economic incentives for livestock protection, practices that permit a coexistence between human activities and large predators (Dickman et al., 2011), and a more favorable public opinion towards those (Chapron et al., 2014). Another important factor that led the large carnivores to recover is the rural-area abandonment (Ustaoglu and Collier, 2018), which in turn favored the increase of wild ungulates' population densities across Europe (Linnell et al., 2020).

In this context, the Eurasian lynx, a top predator once widely distributed across Europe and Asia (Sommer and Benecke, 2006), came close to extinction in the last centuries due to human persecution, loss of ungulate prey, and habitat changes (Breitenmoser, 1998), indeed now recovering (Chapron et al., 2014). Historically in Europe (by the mid-20th century), the species managed to survive only in four areas (i.e., in Scandinavia, Carpathian Mountains, Southern Balkans, and east-Baltic drainage (Von Arx et al., 2004)), but after recent recoveries, current estimates place the number of Eurasian lynx individuals at about 8.000–9.000 (Von Arx, 2020).

Despite this recovery, some subpopulations (in accordance with Von Arx, 2020), are still 'endangered' and 'critically endangered', especially the reintroduced ones, with a small number of individuals (Von Arx et al., 2021). One of the main problems concerning the Eurasian lynx conservation regards the isolation of the small subpopulations in Central and Eastern Europe, and of the larger Carpathians population (Lucena-Perez et al., 2020). In fact, this isolation led to the high genetic differentiation observed nowadays between subpopulations (Gajdárová et al.,

* Corresponding author.
E-mail address: davide.serva@graduate.univaq.it (D. Serva).

https://doi.org/10.1016/j.biocon.2024.110498
Received 11 October 2023; Received in revised form 1 February 2024; Accepted 7 February 2024

2023), and to the very low genetic diversity among them, especially in the reintroduced ones (Mueller et al., 2022). This low genetic variability is due to the low exchange of individuals between subpopulations. Indeed, Europe is among the continents most modified by man (Williams et al., 2020), due to the high anthropization and the high population density, which lead to an elevated level of habitat fragmentation. Habitat fragmentation could cause large gaps that limit both the potential population size and the natural expansion (Zimmermann and Breitenmoser, 2007). This evidence is also noted in some Eurasian lynx subpopulations, which despite the availability of suitable habitat, struggle to expand (Molinari-Jobin et al., 2010; Müller et al., 2014). Moreover, large carnivore conservation necessitates large spatial requirements (Gittleman, 2001), and the consequent problem is whether there is enough suitable habitat for viable and ecologically functional subpopulations (Packer et al., 2013).

Finding the key corridors to favor connectivity between and within lynx subpopulations is of crucial importance for their conservation. In particular, the main conservation strategy's objective would be to create a functional viable metapopulation across West and Central Europe that would prevent future genetic erosion (Mueller et al., 2022).

The existing network of the European Protected Areas (EPAs, after Staccione et al. (2023)) could favor an exchange of individuals between subpopulations. EPAs connectivity is necessary to facilitate large-scale ecological processes and to favor the persistence of viable populations (Saura et al., 2018). Previous studies showed the importance of EPAs as source areas for the Eurasian lynx, with the probability of presence decreasing drastically outside these areas (Müller et al., 2014). However, for what concern the Eurasian lynx, previous analysis shows that lynx's habitat is mostly protected in Sweden, Finland, and Romania (Santini et al., 2016). In recent years several theoretical and technical studies have been published to restore and support landscape connectivity (Correa Ayram et al., 2016; Ersoy et al., 2019; Iannella et al., 2021). Various software applications and algorithms can model ecological corridors. Circuitscape and Omniscape use electronic circuit theory to assess connectivity in a heterogeneous landscape (McRae et al., 2008; Landau et al., 2021). These approaches treat the landscape as a resistance surface, where the "current" flows between nodes across the resistant surface, following different modeling options (McRae et al., 2008). Circuit-theory techniques gained more support and popularity among conservationists and ecologists because they are not limited by the "route-selection" assumption (i.e., random-walk theory) (Dickson et al., 2019).

The aims of this study were: (1) to address the ecological connectivity between the European subpopulations of Eurasian lynx to identify the potential ecological corridors; (2) to evaluate the ecological connectivity of the EPAs with reference to lynx ecology; (3) to assess the measure in which protected areas could facilitate lynx dispersion and movements, both in the current arrangement and considering an expansion of EPAs' surface in accordance with the European Union's Biodiversity Strategy for 2030.

2. Material and methods

2.1. Target species and study area

The target species is the Eurasian lynx *Lynx lynx*, a predator widely distributed from Europe to Central Asia up to Siberia, overall classified as "Least Concern" by the IUCN Red List. In this study, we refer to the European subpopulations some of them reported as 'Critically Endangered' (i.e., Balkan, Bohemian-Bavarian-Austrian (BBA), Vosges-Palatinian subpopulations) and 'Endangered' (i.e., Alpine and Jura subpopulations) (Von Arx, 2020). For the purposes of the present research, we gathered occurrence data from the work of Serva et al. (2023) (Supplementary Material Table A1). To get the populations' range, we applied a buffer (10 km radius) around each occurrence with the "Buffer" tool on ArcGIS Pro managed by ESRI (ESRI Inc, 2023), refining the polygons when needed. The subpopulation ranges obtained were then compared to the reported ones (Kaczensky et al., 2021) (Supplementary Fig. A1).

We focus on European subpopulations of Eurasian lynx; thus, the main study area is Europe, including all the countries for which a biogeographic contiguity occurs, even at the farthest borders (e.g., Belarus and western Russia).

2.2. Populations' connectivity modeling in Circuitscape and connectivity change index

For the aims of the present study, we inferred the landscape connectivity through the Circuitscape application implemented in Julia language (v1.6.7) (Hall et al., 2021). This software, which results in great performances when computing large landscapes' connectivity, takes advantage of the circuit theory models, which are proven to have better performance than other approaches (Anantharaman et al., 2019; McClure et al., 2016). The inputs that Circuitscape requires are a resistance (or conductance) layer, and some source/target locations (i.e., nodes) (McRae et al., 2008). Using this data, it produces a current map that reflects the landscape connectivity as the expected net probability of an individual to move between two nodes (McRae et al., 2008).

Since Circuitscape requires those inputs, we use the Species Distribution Models (SDMs) from Serva et al. (2023) as the conductance raster. Briefly, to obtain those SDMs, a "couple and weigh" framework (Iannella et al., 2021) was applied after the climatic modeling. Thus, different types of predictors relevant to the Eurasian lynx were used, namely some climatic, topographic, human disturbance, and habitat-related ones (Serva et al., 2023). These SDMs are comparable to others recently developed for the current scenario (Oeser et al., 2023b), confirming their reliability.

To deepen the precision of our analyses, we further refine the so-obtained conductance raster, by applying target species' specific connectivity information. In fact, we used the function 'Mosaic to new raster' in ArcGIS Pro 3.1 (ESRI Inc, 2023) to merge the weighted SDMs to the road's spatial information (highways and major roads), incorporating these as barriers, as recent research demonstrated them to be the most relevant variable limiting the dispersal of Eurasian lynx (Mueller et al., 2022; Ripari et al., 2022). We repeated the same process to incorporate the built-up areas as barriers (Ripari et al., 2022). Moreover, we added lakes and bigger rivers, setting these barriers as less constraining than anthropogenic barriers. We then transformed the resulting conductance layer with a negative exponential function following the approach of Keeley et al. (2016) setting the *c* factor to 4.

We ran Circuitscape selecting the 'pairwise' option: in this mode, connectivity is evaluated between each pair of nodes (in this case, the subpopulation's ranges), so that each pair is both the source and the destination node (McRae et al., 2008). Setting this parametrization ensures that also barriers inside the subpopulation ranges are considered. We infer the connectivity for different scenarios, the current, 2050, and 2070, based on respective SDMs obtained from Serva et al. (2023).

The connectivity maps obtained for the different scenarios were then compared using the Standardized Connectivity Change Index (SCCI) (Iannella et al., 2021). This index returns values ranging from loss (−1) and gain (+1) of connectivity, summarizing the effect of future changes on the inferred landscape corridors.

2.3. EPAs' connectivity assessment for the Eurasian lynx

To complement Circuitscape analysis, we used ArcGIS Pro's 'Optimal region connections' (ORC) tool. ORC identifies optimal least-cost paths between input points by converting conductance layers into cost surfaces. Then, for the least-cost corridors of the European study area, we used the EPAs centroids as input features. We applied it to identify least-cost corridors within the study area, using EPAs centroids larger than 40 km^2 (approximating the minimum home range for the Eurasian lynx) that intersected subpopulation ranges (Suppl. Fig. A1). The tool lets the users define an input barrier feature, which is completely impassable. Built-up areas from the Corine Land Cover (https://land.copernicus.eu/en/products/corine-land-cover) map were designated as impassable barriers, given their significance as disturbances for Eurasian lynx (Mueller et al., 2022). We decided to use the EPAs centroids as input for the least-cost path given the great importance of the input features for the analysis and considering the possible limitations of the dataset (built upon citizen science data, literature records, and data from national repositories). Thus, the resulting least-cost corridors are not affected by the species movement, leading to a fixed pattern of connectivity. Corridors were generated for both present and future projections to detect variations. To assess these differences, we devised a dedicated index, presented in its formula:

$$ORC\,CostChange = log\left[\left(\frac{Cost\ current - Cost\ future}{Cost\ current + Cost\ future}\right)\cdot relative\ dist\right],$$

where *relative dist* $= (dist/maxdist)\cdot 100$

The formula is designed to normalize spatial data, allowing for comparison across different territories. ORC generates linear outputs with varying costs and geographies for each line segment. As these outputs change over time, it's challenging to spatially compare current and future ORC results, necessitating the normalization of data to a range of -1 to $+1$. Thus, the overall assessment of variation between scenarios is possible by calculating the distance between each of the two ORCs' segments, also assessing their cost every time. Again, to give normalized values, we use a relative distance standardization to have the possibility of comparing changes from small to great landscapes (and their respective connectivity). Finally, since there may be great variation in each landscape/timeframe, we use a log normalization.

To better assess the connectivity between the EPAs, considering their importance for the lynx (Müller et al., 2014; Heurich et al., 2018), we used the Omniscape connectivity algorithm (McRae et al., 2016). Since its development, Omniscape is gaining more popularity and it has been used in various contexts and at different scales (Jennings et al., 2020; Choe et al., 2021; Belote et al., 2022; Cameron et al., 2022). This software produces maps of omnidirectional connectivity, and it is based on circuit theory. Omniscape applied iteratively the Circuitscape "advanced" mode algorithm, with a moving window with a specific radius, based on species dispersal ability (Landau et al., 2021). We used the same resistance layer applied in Circuitscape, but selecting EPAs greater than 40 km^2 (reported as the minimum home range detected for the Eurasian lynx, following Breitenmoser-Würsten et al. (2007)) as sources. In this way, we obtained a connectivity assessment of EPAs with reference to the Eurasian lynx.

2.4. Quantitative and qualitative EPAs' assessment

To check whether the current EPAs could work as an ecological network to connect the different European lynx populations, we evaluate the quantitative coverage of the critical corridors, and the qualitative characteristics of the EPAs considering the main aspects that could influence the Eurasian lynx's habitat selection.

We identified the crucial corridors for the Eurasian lynx movement between subpopulations using the 90th percentile values of our Circuitscape model. Then, we used the 'Pairwise Intersect' tool of ArcGIS Pro to identify the overlapping areas, i.e., critical corridors protected by EPAs. Moreover, considering the Target 1 of the Biodiversity section of the Agenda 2030, i.e., legally protect a minimum of 30 % of the EU land's area, integrating ecological corridors, we applied a buffer to every EPAs to increase its extension by ~34 %. Thus, we repeated the intersect analysis with these 'increased' EPAs.

To assess whether protected areas meet the most important requirements to protect the movement of the Eurasian lynx (Ripari et al., 2022; Oeser et al., 2023a), we select three main variables inside the EPAs: forest cover (FC), human footprint index (HFI), and terrain ruggedness index (TRI) (as a proxy of the availability of refuges).

Indeed, we download the FC data at a precision of ~30 m (Hansen et al., 2013). As a measure of human disturbance, we downloaded the recent global HFI layer (Mu et al., 2022) at a resolution of ~1 km. Finally, the TRI was obtained from the work of Amatulli et al. (2018), at a resolution of ~1 km. We resampled the Forest Cover layer (FC) (Hansen et al., 2013) in order to match the other raster's resolution, and then we performed the 'Zonal Statistic' tool in ArcGIS Pro to calculate the mean value of each layer inside each EPA polygon before and after the increased surface.

To assess if the EPAs are in general more suitable for lynx movements, we compared the values of the above-mentioned layers inside the EPAs, with the values outside the EPAs, extracted with random points generated at a minimum distance of 1 km, through the tool 'Extract multi-values to Points' in ArcGIS Pro. We first selected the EPAs inside the minimum convex polygon that encloses all the subpopulations. We then performed in R studio (R Core Team, 2023) a *t*-test (after checking for normality and homoscedasticity of data) to check for significative differences ($p = 0.05$) between Circuitscape connectivity values resulting inside and outside EPAs.

3. Result

3.1. Circuitscape results

Starting from 2164 total occurrences, we obtained the subpopulation ranges that reflect the real situation of the Eurasian lynx in Europe (Fig. 1a).

The resistance layer shows the best conditions in the main European mountains' ranges, and in the northern part of the study area, while Central and Southern Europe shows a more fragmented landscape with higher resistance to movements, mainly due to the high density of human infrastructures (Fig. 1a).

The raster correlation performed between the conductance layer and the cumulative current map shows a little correlation ($r = \sim 0.34$). The corridor network obtained from Circuitscape for all the European subpopulations of Eurasian lynx in the current scenario shows higher connectivity in Northern Europe, where some large corridors link the Karelian, the Scandinavian, and the Baltic subpopulations (Fig. 1b). In contrast, in Central and Southern Europe there is generally lower connectivity. Despite this, some key corridors able to connect the central European subpopulations of lynx are highlighted (Fig. 1b). Thus, good connectivity values are noted between the Dinaric and Alpine subpopulations, in the southwestern part of Slovenia, and between the subpopulation in the Harz range and the BBA subpopulation, despite the distance of ~250 km. A slight connectivity is noted between the Carpathian and Bohemian-Bavarian-Austrian subpopulations, and a longer strip of connectivity links the Carpathian and the Harz subpopulations (Fig. 1b). In contrast, between the Jura and Alpine subpopulations, despite the short distance, there is low connectivity (Fig. 1b), and the same process affects the Vosges Palatinian subpopulations, linked with only two corridors with the Jura subpopulations (Fig. 1b). In Eastern Europe, Carpathians, Dinaric, and Balkan subpopulations are connected by various corridors between Kosovo, Montenegro, and southern Serbia (Fig. 1b).

The future corridor networks computed with Circuitscape show some differences compared to the current one (see Supplementary Material Figs. A2, A4 for maps detail). In both future scenarios, bigger increases in landscape connectivity concern Alpine, Jura, Dinaric, and Balkan subpopulations (Figs. 2a and c), but connectivity increase also between Alpine, Dinaric, and Balkan subpopulations for 2050 projection (Fig. 2b) and between Scandinavian and Carelian subpopulations for 2070 (Fig. 2d). Within subpopulations, a major decrease concerns the Carelian, Harz, Scandinavian, and Baltic subpopulations (Figs. 2a and c), where the current connectivity is high. At between subpopulations level,

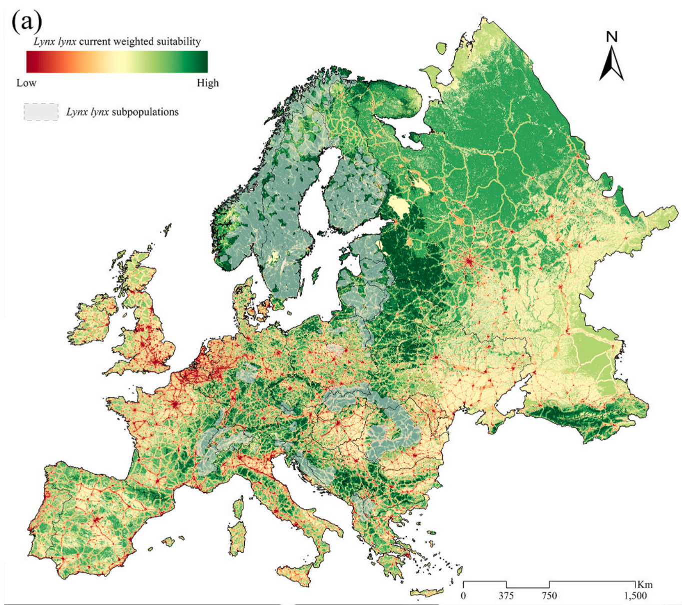

Fig. 1. (a) The final conductance map obtained from the habitat suitability map from Serva et al. (2023) merged with the built-up areas, the main roads, and the water features, and (b) the cumulative current map obtained from Circuitscape in the 'pairwise' mode for the current scenario. In transparency the subpopulation ranges obtained from the occurrences.

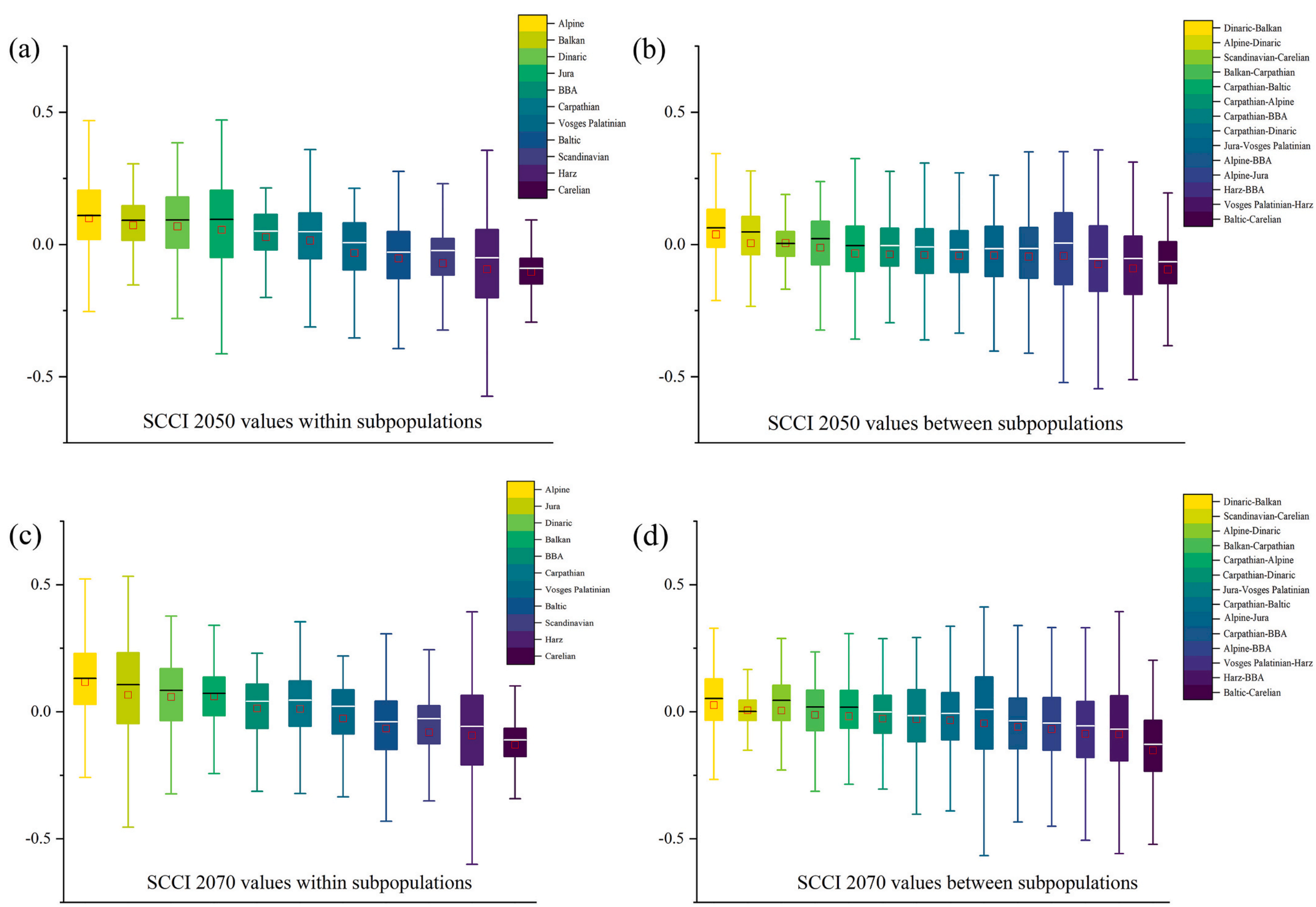

Fig. 2. Circuitscape SCCI values for future scenarios: a) SCCI values within subpopulations for 2050 scenarios. b) SCCI values between subpopulations for 2050 scenarios. c) SCCI values within subpopulations for 2070 scenarios. d) SCCI values between subpopulations for 2070 scenarios.

there are some decreases in both future projections between Baltic States and Finland, and between Harz, BBA, and Vosges Palatinian subpopulations (Figs. 2b and d). Overall, the two future scenarios are similar to each other and show only very small differences.

3.2. Connectivity assessment of EPAs

3.2.1. Landscape connectivity obtained from Omniscape

The cumulative current map obtained from Omniscape using the EPAs as sources shows great amount of current in Central Europe, between Germany and Poland, in the Pyrenees, and in Greece (Fig. 3a). While the last ones are of less interest for the Eurasian lynx conservation, the first ones are more important, with a patch matching the Harz subpopulation, and with some areas with moderate-high connectivity towards the BBA and Vosges-Palatinian subpopulations (Fig. 3a). The Alpine subpopulation appears to be connected to the Dinaric one, but corridors to the nearest Jura subpopulations are missing (Fig. 3a). Still focusing on Central Europe, the normalized current map shows a possible ecological network connecting the Harz and the Carpathian subpopulations, through the BBA subpopulation (Fig. 3b). Furthermore, the good connectivity highlighted from Circuitscape between the Dinaric and Alpine subpopulations is confirmed (Figs. 1b and 3b).

3.2.2. Least-cost corridors obtained from ArcGIS Pro

The least-cost corridor analysis for all the Eurasian lynx subpopulations in the current scenario shows a complex pattern of corridors (Fig. 3c). Within each subpopulation, there are generally cheaper corridors, while the corridors between subpopulations appear to be expensive, especially those connecting western and eastern subpopulations in Central and Southern Europe (Fig. 3c). The future cost

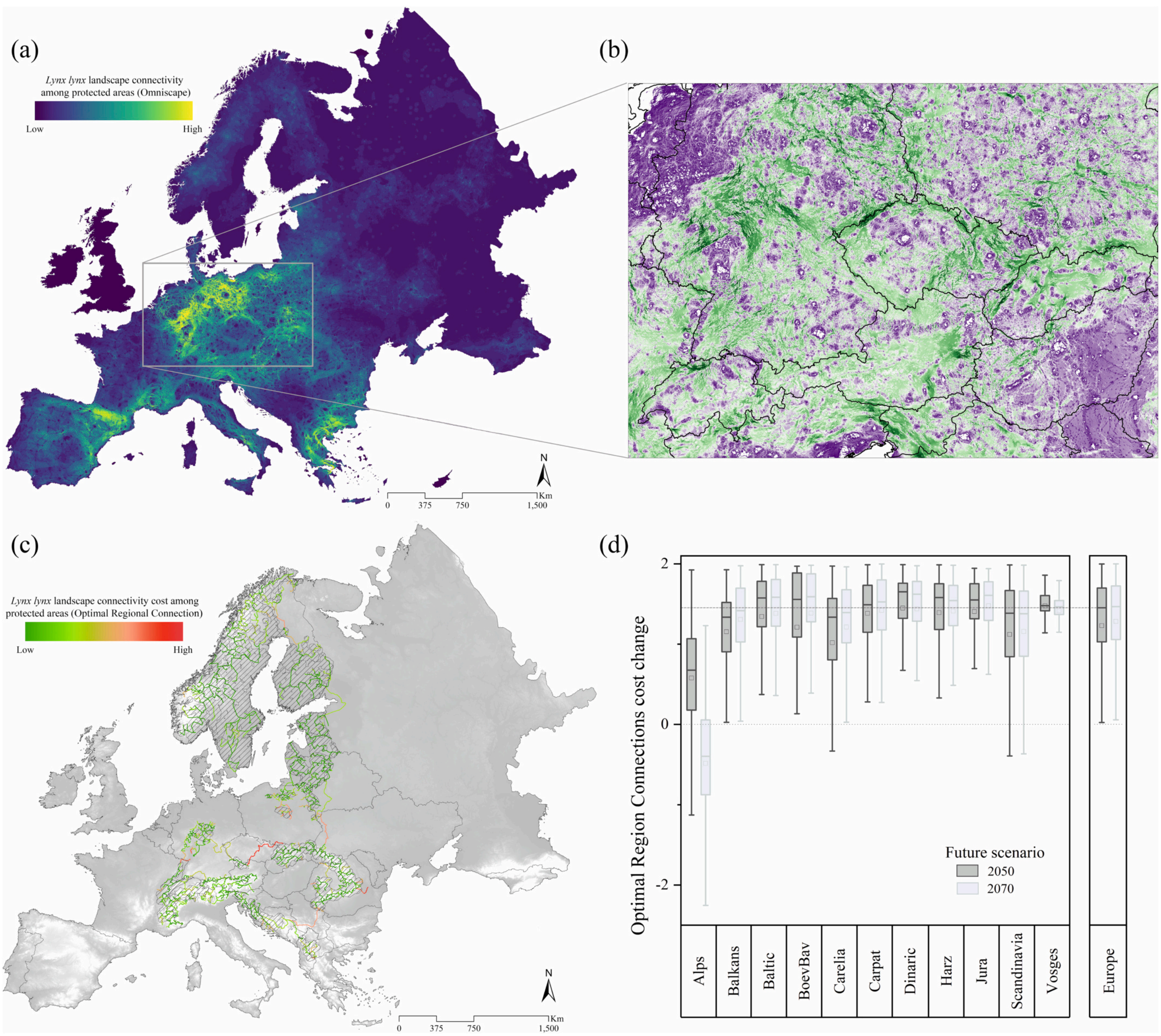

Fig. 3. Landscape connectivity between EPAs for the Eurasian lynx. a) The cumulative current map between EPAs obtained from Omniscape. b) The inlay for Central Europe of the normalized current map from Omniscape: green zones are the areas with a channelized flow, i.e., possible corridors. c) The least-cost corridors obtained from the Optimal Region Connections in ArcGIS Pro between the EPAs inside the subpopulation's ranges. d) The least-cost path cost change for all the European subpopulations of Eurasian lynx in the future scenarios. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

changes of the least-cost corridors show a general increase for all the subpopulations, especially for the 2070 scenario, except for the Alpine subpopulation (Fig. 3d). Thus, indicating the possibility of a decrease in EPAs' connectivity for the Eurasian lynx.

3.3. *Qualitative and quantitative assessment of EPAs for Eurasian lynx movements*

When comparing the considered variables' asset (HFI, FC, TRI) inside and outside the EPAs enclosed by the Minimum Convex Polygon obtained by the lynx subpopulations, we found a significative increase in FC inside the EPAs ($p = 0.05$) (Fig. 4a). Furthermore, considering the current EPAs network, the crucial corridors obtained from Circuitscape (Supplementary Material Fig. A6) are covered for 179,652 km^2 (~21 % of all crucial corridors). Currently, a lack of protection to the crucial corridors occurs between the Dinaric and the Balkan subpopulations in Eastern Europe, and between the Carpathian and the BBA subpopulations in Central Europe. An increase in the surface of the EPAs following the European Union's Biodiversity Strategy for 2030 would cover 533,725 km^2 (~62 % of all crucial corridors) of the crucial corridors for the Eurasian lynx. The increase of the EPAs' surface would keep similar conditions considering the HFI and TRI, but with a different amount of the FC (Fig. 4b). The data of connectivity maps relative to the 'inside and outside' assets of the EPAs within the minimum convex polygon of all the subpopulations (Supplementary Material Fig. A7) showed normal distribution and homoscedasticity. The *t*-test performed over those data shows that inside the EPAs there is greater connectivity than outside (with a significance level of 0.05) (Fig. 4c). To better summarize the spatial asset of the analyses reported above, we report in Fig. 4d a scheme.

4. Discussion

Recognizing the importance of landscape connectivity as a crucial conservation strategy effectively reduces the negative consequences of habitat loss and fragmentation (Fletcher et al., 2016). Connectivity enhances individual movement, supporting dispersal, migration, and gene flow, thereby promoting population recolonization or establishment in previously unoccupied areas (Hilty et al., 2012). Additionally, connectivity is pivotal in sustaining viable metapopulations and contributes to the demographic rescue of small, isolated populations (Haddad et al., 2015). The Eurasian lynx, known for thriving in human-dominated landscapes, serves as a conservation model for large carnivores at a landscape scale (Carter and Linnell, 2016). Recent findings indicate low genetic diversity and high inbreeding rates in reintroduced lynx populations (Huvier et al., 2023; Mueller et al., 2020, 2022), emphasizing the need to enhance connectivity both between and within subpopulations. This study takes the initial step towards establishing a functional metapopulation of Eurasian lynx in fragmented landscapes of Eastern and Central Europe by assessing landscape connectivity at these two levels.

Regarding European corridors identified by Circuitscape, a key

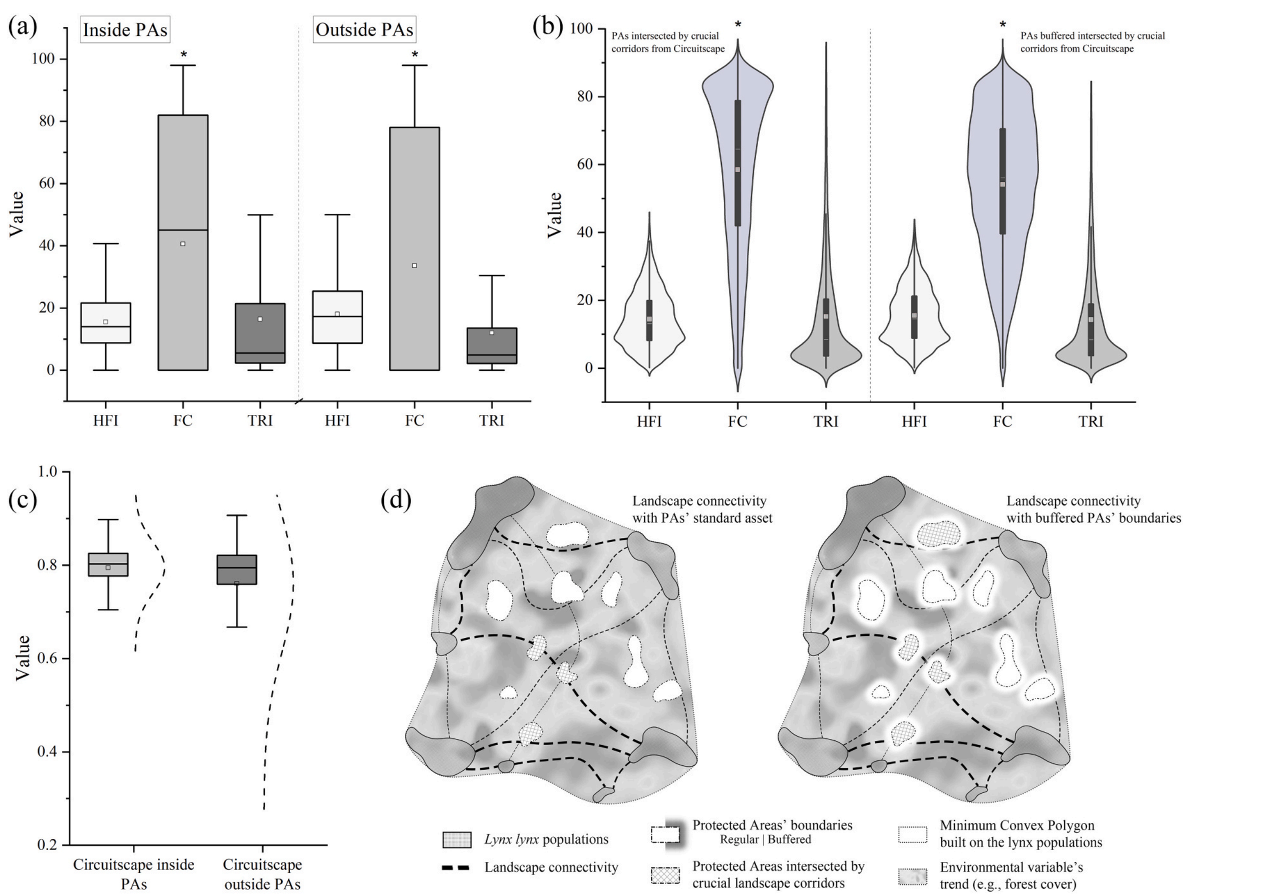

Fig. 4. Qualitative assessment of EPAs for the Eurasian lynx. a) The values of the Human Footprint Index (HFI), Forest Cover (FC), and Terrain Ruggedness Index (TRI) inside and outside the EPAs intersected from the minimum convex polygon enclosing all the subpopulations. b) The values of HFI, FC, and TRI, between current EPAs intersecting the crucial corridors for the Eurasian lynx, and the same EPAs with an increased surface of ~34 % (following Agenda 2030 objectives). c) The value of the cumulative current map obtained from Circuitscape (normalized to a 0–1 scale), inside and outside EPAs. d) The protected areas to which we refer in the previous figures: on the left, the current structure of the EPAs included within the minimum convex polygon that enclosed all the populations (Supplementary Material Fig. A7); right, buffered EPA with ~30 % surface area increase. The filled EPAs are those intersected by corridors crucial for the Eurasian lynx.

distinction emerges between the northern subpopulations, including Scandinavian, Karelian, and Baltic lynx subpopulations, and others. Our findings reveal strong connectivity among these northern subpopulations through multiple corridors, which are expected to persist in future scenarios (Fig. 1b). In contrast, central and western European subpopulations exhibit lower current connectivity in the present scenario, with predictions of increased connectivity only for some subpopulations in future projections. However, a clear connection between the Dinaric and the south-eastern Alpine area appears, confirmed by the least-cost corridors and the Omniscape outputs (Fig. 1 b, Fig. 3 a, and c), consistent with findings from previous studies (Favilli et al., 2023). These corridors are crucial for establishing a viable lynx population within the Alps. To achieve this, it is essential to establish functional corridors connecting the Alpine subpopulation with the BBA and the Jura subpopulations. Despite their spatial proximity, our current predictions indicate only a few corridors, and while others may emerge in the future (Supplementary Material Figs. A3, A5), these subpopulations face significant barriers linked to human infrastructures, and limited protected areas (Supplementary Material A6). The BBA subpopulation plays a vital role in linking Alpine, Harz, and Carpathian lynx subpopulations, making it crucial for Eurasian lynx conservation in Central Europe (Heurich et al., 2018). Effective habitat preservation measures can facilitate natural expansion from BBA subpopulations due to good habitat connectivity (Magg et al., 2016). Furthermore, to support this expansion, efforts are needed to combat illegal killings, a major threat stagnating this subpopulation (Heurich et al., 2018).

Given the recent evidence of extremely low genetic diversity in the Jura subpopulation (Huvier et al., 2023), urgent individual exchange is required. Between Alpine and Jura subpopulations, approximately 80 km apart, we find a viable corridor between the Upper Jura Regional Nature Park and the Bauges Prealps, even if various barriers separate these subpopulations, such as roads, large urban areas, and lakes.

The Harz subpopulation shows good connectivity with the BBA subpopulation, with corridors maintained in all future projections (Figs. 1b, 2b, and d). Despite moderate human disturbance, effective conservation measures can establish a vital link with the BBA subpopulation, essential for Harz subpopulation conservation (Mueller et al., 2020). For example, considering the anthropogenic disturbance between these subpopulations, and the concomitant presence of unprotected areas, new protected stepping-stones areas would be important to favor an exchange of individuals. These actions are needed especially considering the impact of illegal hunting on the BBA subpopulation (Palmero et al., 2021). On the contrary, the network between the Alpine, Jura, Vosges Palatinian, and Harz subpopulations does not seem to be viable, due to artificial habitat fragmentation (Gimenez et al., 2019). The critically endangered Balkan subpopulation is connected to the Dinaric population by corridors poorly covered by EPAs, and a natural connection is improbable, even if moderate connectivity occurs (Fig. 1b). In Central Europe, the larger Carpathian population shows moderate genetic diversity (Mueller et al., 2022) and has the potential to serve as a source for other subpopulations, particularly the isolated BBA subpopulation (Gajdárová et al., 2023). Although two main potential routes appear with relatively high predicted connectivity between these subpopulations, still they are not actually connected (Gajdárová et al., 2023). Thus, additional protected areas are needed to ensure the effectiveness of these routes, especially considering that these potential corridors are mostly unprotected (Supplementary Material Fig. A6). So far, there is only one report of the dispersal of a male from the Carpathians close to the BBA subpopulation, demonstrating such long-distance dispersal for the lynx (Gajdárová et al., 2021), so appropriate management actions could enhance a more conspicuous individuals' flow.

Protected areas play a vital role in the survival and stable reproduction of the Eurasian lynx, as complete protection within them enhances survival probabilities (Müller et al., 2014; Palmero et al., 2021). Our connectivity results from Omniscape align with findings by Saura et al. (2018), indicating higher connectivity in Germany, Poland, and France, compared to EPAs in the northern and eastern European regions (Fig. 3a). These great differences in the connectivity analysis between subpopulations range are also related to the Omniscape analysis itself, in which the higher connectivity between EPAs detected in Central Europe is partly related to their higher abundance, i.e., higher number of input nodes for the connectivity analysis, despite the higher habitat fragmentation. Similarly, the lower connectivity in Northern Europe, despite the lower anthropogenic impact, is partly related to the lower numbers of EPAs. These good connectivity values between protected areas of Central and Western Europe for the Eurasian lynx, combined with its dispersal capacity, with individuals capable of moving almost 170 km (i.e., from the Harz subpopulation to the vicinity of the BBA subpopulation) (Gajdárová et al., 2021), indicate that there is the possibility of gene flow between these subpopulations, if proper management actions are provided. Thus, it is essential to enhance permeability in unprotected areas between EPAs for lynx conservation. Additionally, lynx suitable habitat is more protected in Sweden and Finland, followed by Romania, where the species has a 'favorable' status (Santini et al., 2016), even if the connectivity among the EPAs is low. This underscores the need to bolster habitat protection in Central and Eastern Europe, especially in corridor-affected regions. Given the lynx's sensitivity to human disturbance (Ripari et al., 2022), relying solely on EPAs is insufficient to ensure subpopulation connections.

Various factors, including roads, particularly highways, act as barriers that impede the Eurasian lynx's movement, leading to population separation on a small scale (Zimmermann et al., 2007). Some of the identified corridors intersect with highways and major roads, necessitating specific management actions. Thus, our results offer valuable insights for prioritizing mitigation measures, such as overpasses, to reduce the effect of these barriers on the lynx's movements.

The limited size of certain EPAs in Central Europe poses a challenge due to the Eurasian lynx's extensive spatial requirements, making long-term subpopulations health unsustainable (Palmero et al., 2021). Expanding EPA's coverage in line with the European Union's Biodiversity Strategy for 2030 is a crucial initial step, ensuring enhanced protection for corridors, particularly in Central and Eastern Europe. Our results indicate that a random expansion of EPA's surfaces could lead to increased forest cover. However, it is important to note that our circular buffer approach may not accurately represent the real expansion for all EPAs. As an alternative strategy, other conservation measures could include the establishment of new, peculiar EPAs acting as stepping-stones in areas where high connectivity between subpopulations is predicted (Fig. 1b).

Concerning natural or human-mediated connectivity, as a tool to ensure the long-term survival of the Eurasian lynx subpopulations in Eastern and Central Europe, it is important to consider the current evolutionary significant units (ESU). Actually, there are six lineages, three of which are in Europe: the Northern lynx (*L.* l. *lynx*), the Carpathian lynx (*L.* l. *carpathicus*), and the Balkan lynx (*L.* l. *balcanicus*) (Kitchener et al., 2017; Lucena-Perez et al., 2020; Mueller et al., 2022). Thus, it is important to favor connectivity among the subpopulations that belong to the same ESU (Schmidt et al., 2011). Considering the Balkan subpopulation, previous studies have demonstrated the similarity with the Carpathian lynx present in the Dinaric area, which could therefore be used as a source to favor the exchange of individuals between these populations (Bazzicalupo et al., 2022; Melovski et al., 2022).

The analysis of ecological connectivity is crucial for designing effective ecological networks and evaluating the efficacy of protected areas. Nonetheless, overcoming the obstacles that impede the integration of connectivity into conservation planning, including the validation of connectivity models and enhancements in field data collection and sharing among researchers, is essential (Correa Ayram et al., 2016). Meta-analyses by Fletcher et al. (2016) and Resasco (2019) have shown that ecological corridors positively impact movement across diverse species and organizational levels, reinforcing the notion that investing in corridor creation and maintenance is beneficial for biodiversity conservation.

Previous studies that validated circuit-theory algorithms with empirical data demonstrated their effectiveness in the identification of dispersal corridors (McClure et al., 2016). The recent findings of individuals belonging to Baltic, Harz, and Carpathian subpopulations, in the vicinity of the BBA subpopulation (Gajdárová et al., 2021), partly support our landscape connectivity models' outcomes. Moreover, our connectivity results have been confirmed from other sensitivity analyses repeated with different input data (Supplementary Material Figs. A8, A9).

Given the Eurasian lynx's dispersal ability, especially in Central Europe (Mueller et al., 2020; Gajdárová et al., 2021), and its adaptability (Filla et al., 2017), establishing dispersal corridors is a viable management option to enhance the conservation status of isolated and endangered subpopulations. Previous studies have shown that even a small number of individuals can increase genetic diversity in small populations (Bull et al., 2016). Furthermore, the BBA subpopulation case-study indicated that full protection, sufficient food supply and suitable permeable habitat supported population recovery (Gajdárová et al., 2023). Our approach, which assesses connectivity using various techniques and considers both the target species and protected areas, offers utility for species with similar spatial requirements. In conclusion, our findings can inform conservation and management strategies at multiple scales, potentially aiding the creation of a functional metapopulation in Central Europe and preserving the small and isolated populations of Eurasian lynx. Moreover, these results can support managing existing protected areas, which are essential for promoting Eurasian lynx expansion. However, effective conservation requires tackling poaching and illegal killing outside protected areas, and given the species' extensive mobility, international cooperation is imperative.

CRediT authorship contribution statement

Mattia Iannella: Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization. **Maurizio Biondi:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Conceptualization. **Davide Serva:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Formal analysis, Data curation, Conceptualization.

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

All the datasets and the spatial data generated during the current study are available from the corresponding author (davide.serva@graduate.univaq.it) on reasonable request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110498.

References

Amatulli, G., Domisch, S., Tuanmu, M.-N., Parmentier, B., Ranipeta, A., Malczyk, J., Jetz, W., 2018. A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. Sci Data 5, 180040. https://doi.org/10.1038/sdata.2018.40.

Anantharaman, R., Hall, K., Shah, V., Edelman, A., 2019. Circuitscape in Julia: High Performance Connectivity Modelling to Support Conservation Decisions.

Bazzicalupo, E., Lucena-Perez, M., Kleinman-Ruiz, D., Pavlov, A., Trajçe, A., Hoxha, B., Sanaja, B., Gurielidze, Z., Kerdikoshvili, N., Mamuchadze, J., Yarovenko, Y.A., Akkiev, M.I., Ratkiewicz, M., Saveljev, A.P., Melovski, D., Gavashelishvili, A., Schmidt, K., Godoy, J.A., 2022. History, demography and genetic status of Balkan and Caucasian *Lynx lynx* (Linnaeus, 1758) populations revealed by genome-wide variation. Divers. Distrib. 28, 65–82. https://doi.org/10.1111/ddi.13439.

Belote, R.T., Barnett, K., Zeller, K., Brennan, A., Gage, J., 2022. Examining local and regional ecological connectivity throughout North America. Landsc. Ecol. 37, 2977–2990. https://doi.org/10.1007/s10980-022-01530-9.

Breitenmoser, U., 1998. Large predators in the Alps: the fall and rise of man's competitors. Biol. Conserv. 83, 279–289.

Breitenmoser-Würsten, C., Zimmermann, F., Molinari-Jobin, A., Molinari, P., Capt, S., Vandel, J.M., Breitenmoser, U., 2007. Spatial and social stability of a Eurasian lynx *Lynx lynx* population: an assessment of 10 years of observation in the Jura Mountains. Wildl. Biol. 13 (4), 365–380.

Bull, J.K., Heurich, M., Saveljev, A.P., Schmidt, K., Fickel, J., Förster, D.W., 2016. The effect of reintroductions on the genetic variability in Eurasian lynx populations: the cases of Bohemian–Bavarian and Vosges–Palatinian populations. Conserv. Genet. 17, 1229–1234.

Cameron, D.R., Schloss, C.A., Theobald, D.M., Morrison, S.A., 2022. A framework to select strategies for conserving and restoring habitat connectivity in complex landscapes. Conservation Science and Practice 4, e12698. https://doi.org/10.1111/csp2.12698.

Carter, N.H., Linnell, J.D., 2016. Co-adaptation is key to coexisting with large carnivores. Trends Ecol. Evol. 31, 575–578.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346, 1517–1519. https://doi.org/10.1126/science.1257553.

Choe, H., Keeley, A.T.H., Cameron, D.R., Gogol-Prokurat, M., Hannah, L., Roehrdanz, P. R., Schloss, C.A., Thorne, J.H., 2021. The influence of model frameworks in spatial planning of regional climate-adaptive connectivity for conservation planning. Landsc. Urban Plan. 214, 104169 https://doi.org/10.1016/j.landurbplan.2021.104169.

Correa Ayram, C.A., Mendoza, M.E., Etter, A., Salicrup, D.R.P., 2016. Habitat connectivity in biodiversity conservation: a review of recent studies and applications. Prog. Phys. Geogr. 40, 7–37.

Dickman, A.J., Macdonald, E.A., Macdonald, D.W., 2011. A review of financial instruments to pay for predator conservation and encourage human–carnivore coexistence. Proc. Natl. Acad. Sci. 108, 13937–13944.

Dickson, B.G., Albano, C.M., Anantharaman, R., Beier, P., Fargione, J., Graves, T.A., Gray, M.E., Hall, K.R., Lawler, J.J., Leonard, P.B., 2019. Circuit-theory applications to connectivity science and conservation. Conserv. Biol. 33, 239–249.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J., Collen, B., 2014. Defaunation in the Anthropocene. science 345, 401–406.

Ersoy, E., Jorgensen, A., Warren, P.H., 2019. Identifying multispecies connectivity corridors and the spatial pattern of the landscape. Urban For. Urban Green. 40, 308–322.

ESRI Inc, 2023. n.d. ArcGIS pro 10.3. ESRI Inc, Redlands, California.

Favilli, F., Laner, P., Bertoncelj, I., 2023. Application of the continuum suitability index (csi) model to display the permeability of the alpine-dinaric landscape and to define intervention priorities for ecological linkages. Biodivers. Conserv. 32, 3237–3254. https://doi.org/10.1007/s10531-023-02651-6.

Filla, M., Premier, J., Magg, N., Dupke, C., Khorozyan, I., Waltert, M., Bufka, L., Heurich, M., 2017. Habitat selection by Eurasian lynx (*Lynx lynx*) is primarily driven by avoidance of human activity during day and prey availability during night. Ecol. Evol. 7, 6367–6381. https://doi.org/10.1002/ece3.3204.

Fletcher, R.J., Burrell, N.S., Reichert, B.E., Vasudev, D., Austin, J.D., 2016. Divergent perspectives on landscape connectivity reveal consistent effects from genes to communities. Curr. Landsc. Ecol. Rep. 1, 67–79. https://doi.org/10.1007/s40823-016-0009-6.

Gajdárová, B., Belotti, E., Bufka, L., Duľa, M., Kleven, O., Kutal, M., Ozoliņš, J., Nowak, C., Reiners, T.E., Tám, B., Volfová, J., Krojerová-Prokešová, J., 2021. Long-distance Eurasian lynx dispersal – a prospect for connecting native and reintroduced populations in Central Europe. Conserv. Genet. 22, 799–809. https://doi.org/10.1007/s10592-021-01363-0.

Gajdárová, B., Belotti, E., Bufka, L., Volfová, J., Wölfl, S., Mináriková, T., Hollerbach, L., Duľa, M., Kleven, O., Kutal, M., Nowak, C., Ozoliņš, J., Tám, B., Bryja, J., Koubek, P., Krojerová-Prokešová, J., 2023. Long-term genetic monitoring of a reintroduced Eurasian lynx population does not indicate an ongoing loss of genetic diversity. Global Ecology and Conservation 42, 2351–9894. https://doi.org/10.1016/j.gecco.2023.e02399.

Gimenez, O., Gatti, S., Duchamp, C., Germain, E., Laurent, A., Zimmermann, F., Marboutin, E., 2019. Spatial density estimates of Eurasian lynx (*Lynx lynx*) in the French Jura and Vosges Mountains. Ecol. Evol. 9, 11707–11715.

Gittleman, J.L., 2001. Carnivore Conservation. Cambridge University Press.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1 (2), e1500052 https://doi.org/10.1126/sciadv.1500052.

Hall, K.R., Anantharaman, R., Landau, V.A., Clark, M., Dickson, B.G., Jones, A., Platt, J., Edelman, A., Shah, V.B., 2021. Circuitscape in Julia: empowering dynamic approaches to connectivity assessment. Land 10, 301.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century Forest cover change. Science 342, 850–853. https://doi.org/10.1126/science.1244693.

Heurich, M., Schultze-Naumburg, J., Piacenza, N., Magg, N., Červený, J., Engleder, T., Herdtfelder, M., Sladova, M., Kramer-Schadt, S., 2018. Illegal hunting as a major driver of the source-sink dynamics of a reintroduced lynx population in Central Europe. Biol. Conserv. 224, 355–365.

Hilty, J.A., Lidicker Jr., W.Z., Merenlender, A.M., 2012. Corridor Ecology: The Science and Practice of Linking Landscapes for Biodiversity Conservation. Island Press.

Huvier, N., Moyne, G., Kaerle, C., Mouzon-Moyne, L., 2023. Time is running out: microsatellite data predict the imminent extinction of the boreal lynx (*Lynx lynx*) in France. Frontiers in Conservation Science 4.

Iannella, M., Console, G., Cerasoli, F., De Simone, W., D'Alessandro, P., Biondi, M., 2021. A step towards SDMs: a "couple-and-weigh" framework based on accessible data for biodiversity conservation and landscape planning. Divers. Distrib. 27, 2412–2427.

Ingeman, K.E., Zhao, L.Z., Wolf, C., Williams, D.R., Ritger, A.L., Ripple, W.J., Kopecky, K. L., Dillon, E.M., DiFiore, B.P., Curtis, J.S., Csik, S.R., Bui, A., Stier, A.C., 2022. Glimmers of hope in large carnivore recoveries. Sci. Rep. 12, 10005. https://doi.org/10.1038/s41598-022-13671-7.

Jennings, M.K., Zeller, K.A., Lewison, R.L., 2020. Supporting adaptive connectivity in dynamic landscapes. Land 9, 295. https://doi.org/10.3390/land9090295.

Kaczensky, P., Linnell, J.D.C., Huber, D., Von Arx, M., Andren, H., Breitenmoser, U., Boitani, L., 2021. Distribution of large carnivores in Europe 2012-2016: distribution maps for Brown bear, Eurasian lynx, Grey wolf, and wolverine. Zenodo. https://doi.org/10.5281/zenodo.5060137.

Keeley, A.T.H., Beier, P., Gagnon, J.W., 2016. Estimating landscape resistance from habitat suitability: effects of data source and nonlinearities. Landsc. Ecol. 31, 2151–2162. https://doi.org/10.1007/s10980-016-0387-5.

Kitchener, A.C., Breitenmoser-Würsten, C., Eizirik, E., Gentry, A., Werdelin, L., Wilting, A., Yamaguchi, N., Abramov, A.V., Christiansen, P., Driscoll, C., 2017. A revised taxonomy of the Felidae: the final report of the cat classification task force of the IUCN cat specialist group. Cat News Special Issue 11, 1–80.

Landau, V.A., Shah, V.B., Anantharaman, R., Hall, K.R., 2021. Omniscape.jl: software to compute omnidirectional landscape connectivity. Journal of Open Source Software 6, 2829.

Linnell, J.D.C., Cretois, B., Nilsen, E.B., Rolandsen, C.M., Solberg, E.J., Veiberg, V., Kaczensky, P., Van Moorter, B., Panzacchi, M., Rauset, G.R., 2020. The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. Biol. Conserv. 244, 108500.

Lucena-Perez, M., Marmesat, E., Kleinman-Ruiz, D., Martínez-Cruz, B., Węcek, K., Saveljev, A.P., Seryodkin, I.V., Okhlopkov, I., Dvornikov, M.G., Ozolins, J., Galsandorj, N., Paunovic, M., Ratkiewicz, M., Schmidt, K., Godoy, J.A., 2020. Genomic patterns in the widespread Eurasian lynx shaped by Late Quaternary climatic fluctuations and anthropogenic impacts. Mol. Ecol. 29, 812–828. https://doi.org/10.1111/mec.15366.

Magg, N., Müller, J., Heibl, C., Hackländer, K., Wölfl, S., Wölfl, M., Bufka, L., Červený, J., Heurich, M., 2016. Habitat availability is not limiting the distribution of the Bohemian–Bavarian *lynx Lynx lynx* population. Oryx 50, 742–752.

McClure, M.L., Hansen, A.J., Inman, R.M., 2016. Connecting models to movements: testing connectivity model predictions against empirical migration and dispersal data. Landsc. Ecol. 31, 1419–1432.

McRae, B., Popper, K., Jones, A., Schindel, M., Buttrick, S., Hall, K., Unnasch, R., Platt, J., 2016. Conserving Nature's Stage: Mapping Omnidirectional Connectivity for Resilient Terrestrial Landscapes in the Pacific Northwest. https://doi.org/10.13140/RG.2.1.4158.6166.

McRae, B.H., Dickson, B.G., Keitt, T.H., Shah, V.B., 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89, 2712–2724.

Melovski, D., Krofel, M., Avukatov, V., Fležar, U., Gonev, A., Hočevar, L., Ivanov, G., Leschinski, L., Pavlov, A., Stojanov, A., Veapi, E., Mengüllüoğlu, D., 2022. Diverging ecological traits between the Balkan lynx and neighbouring populations as a basis for planning its genetic rescue. Mamm. Biol. 102, 1697–1708. https://doi.org/10.1007/s42991-022-00268-w.

Molinari-Jobin, A., Marboutin, E., Wölfl, S., Wölfl, M., Molinari, P., Fasel, M., Kos, I., Blažič, M., Breitenmoser, C., Fuxjäger, C., 2010. Recovery of the Alpine lynx *Lynx lynx* metapopulation. Oryx 44, 267–275.

Mu, H., Li, X., Wen, Y., Huang, J., Du, P., Su, W., Miao, S., Geng, M., 2022. A global record of annual terrestrial human footprint dataset from 2000 to 2018. Sci Data 9, 176. https://doi.org/10.1038/s41597-022-01284-8.

Mueller, S.A., Reiners, T.E., Middelhoff, T.L., Anders, O., Kasperkiewicz, A., Nowak, C., 2020. The rise of a large carnivore population in Central Europe: genetic evaluation of lynx reintroduction in the Harz Mountains. Conserv. Genet. 21, 577–587. https://doi.org/10.1007/s10592-020-01270-w.

Mueller, S.A., Prost, S., Anders, O., Breitenmoser-Würsten, C., Kleven, O., Klinga, P., Konec, M., Kopatz, A., Krojerová-Prokešová, J., Middelhoff, T.L., Obexer-Ruff, G., Reiners, T.E., Schmidt, K., Sindičič, M., Skrbinšek, T., Tám, B., Saveljev, A.P., Naranbaatar, G., Nowak, C., 2022. Genome-wide diversity loss in reintroduced Eurasian lynx populations urges immediate conservation management. Biol. Conserv. 266, 109442 https://doi.org/10.1016/j.biocon.2021.109442.

Müller, J., Wölfl, M., Wölfl, S., Müller, D.W., Hothorn, T., Heurich, M., 2014. Protected areas shape the spatial distribution of a European lynx population more than 20 years after reintroduction. Biol. Conserv. 177, 210–217.

Oeser, J., Heurich, M., Kramer-Schadt, S., Andrén, H., Bagrade, G., Belotti, E., Bufka, L., Breitenmoser-Würsten, C., Černe, R., Duľa, M., Fuxjäger, C., Gomerčić, T., Jędrzejewski, W., Kont, R., Koubek, P., Kowalczyk, R., Krofel, M., Krojerová-Prokešová, J., Kubala, J., Kusak, J., Kutal, M., Linnell, J.D.C., Mattisson, J., Molinari-Jobin, A., Männil, P., Odden, J., Okarma, H., Oliveira, T., Pagon, N., Persson, J., Remm, J., Schmidt, K., Signer, S., Tám, B., Vogt, K., Zimmermann, F., Kuemmerle, T., 2023a. Prerequisites for coexistence: human pressure and refuge habitat availability shape continental-scale habitat use patterns of a large carnivore. Landsc. Ecol. 38, 1713–1728. https://doi.org/10.1007/s10980-023-01645-7.

Oeser, J., Heurich, M., Kramer-Schadt, S., Mattisson, J., Krofel, M., Krojerová-Prokešová, J., Kuemmerle, T., 2023b. Integrating animal tracking datasets at a continental scale for mapping Eurasian lynx habitat. Divers. Distrib. 29, 1546–1560.

Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S., Pfeifer, M., Zander, K., Swanson, A., MacNulty, D., Balme, G., 2013. Conserving large carnivores: dollars and fence. Ecol. Lett. 16, 635–641.

Palmero, S., Belotti, E., Bufka, L., Gahbauer, M., Heibl, C., Premier, J., Weingarth-Dachs, K., Heurich, M., 2021. Demography of a Eurasian lynx (*lynx lynx*) population within a strictly protected area in Central Europe. Sci. Rep. 11, 19868.

R Core Team, 2023. R: A Language and Environment for Statistical Computing.

Resasco, J., 2019. Meta-analysis on a decade of testing corridor efficacy: what new have we learned? Current Landscape Ecology Reports 4, 61–69. https://doi.org/10.1007/s40823-019-00041-9.

Ripari, L., Premier, J., Belotti, E., Bluhm, H., Breitenmoser-Würsten, C., Bufka, L., Červený, J., Drouet-Hoguet, N., Fuxjäger, C., Jędrzejewski, W., Kont, R., Koubek, P., Kowalczyk, R., Krofel, M., Krojerová-Prokešová, J., Molinari-Jobin, A., Okarma, H., Oliveira, T., Remm, J., Schmidt, K., Zimmermann, F., Kramer-Schadt, S., Heurich, M., 2022. Human disturbance is the most limiting factor driving habitat selection of a large carnivore throughout continental Europe. Biol. Conserv. 266, 109446 https://doi.org/10.1016/j.biocon.2021.109446.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484.

Santini, L., Saura, S., Rondinini, C., 2016. Connectivity of the global network of protected areas. Divers. Distrib. 22, 199–211.

Saura, S., Bertzky, B., Bastin, L., Battistella, L., Mandrici, A., Dubois, G., 2018. Protected area connectivity: shortfalls in global targets and country-level priorities. Biol. Conserv. 219, 53–67.

Schmidt, K., Ratkiewicz, M., Konopiński, M.K., 2011. The importance of genetic variability and population differentiation in the Eurasian lynx *Lynx lynx* for conservation, in the context of habitat and climate change. Mammal Rev. 41, 112–124.

Serva, D., Iannella, M., Cittadino, V., Biondi, M., 2023. A shifting carnivore's community: habitat modeling suggests increased overlap between the golden jackal and the Eurasian lynx in Europe. Front. Ecol. Evol. 11, 1165968. https://doi.org/10.3389/fevo.2023.1165968.

Sommer, R., Benecke, N., 2006. Late Pleistocene and Holocene development of the felid fauna (Felidae) of Europe: a review. J. Zool. 269, 7–19.

Staccione, A., Brown, C., Arneth, A., Rounsevell, M., Essenfelder, A.H., Seo, B., Mysiak, J., 2023. Exploring the effects of protected area networks on the European land system. J. Environ. Manag. 337, 117741.

Ustaoglu, E., Collier, M.J., 2018. Farmland abandonment in Europe: an overview of drivers, consequences, and assessment of the sustainability implications. Environ. Rev. 26, 396–416.

Von Arx, M., 2020. IUCN Red List of Threatened Species: *Lynx lynx* (amended version of 2018 assessment). In: IUCN Red List of Threatened Species. https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T12519A177350310.

Von Arx, M., Breitenmoser-Würsten, C., Zimmermann, F., Breitenmoser, U., 2004. Status and conservation of the Eurasian lynx (*Lynx lynx*) in Europe in 2001. Kora 19, 1–319.

Von Arx, M., Kaczensky, P., Linnell, J., Lanz, T., Breitenmoser-Würsten, C., Boitani, L., Breitenmoser, U., 2021. Conservation status of the Eurasian lynx in West and Central Europe. The Eurasian lynx in Continetal Europe Special Issue N.14, 5–8.

Williams, B.A., Venter, O., Allan, J.R., Atkinson, S.C., Rehbein, J.A., Ward, M., Di Marco, M., Grantham, H.S., Ervin, J., Goetz, S.J., Hansen, A.J., Jantz, P., Pillay, R., Rodríguez-Buriticá, S., Supples, C., Virnig, A.L.S., Watson, J.E.M., 2020. Change in terrestrial human footprint drives continued loss of intact ecosystems. One Earth 3, 371–382. https://doi.org/10.1016/j.oneear.2020.08.009.

Zimmermann, F., Breitenmoser, U., 2007. Potential distribution and population size of the Eurasian lynx *Lynx lynx* in the Jura Mountains and possible corridors to adjacent ranges. Wildl. Biol. 13, 406–416.

Zimmermann, F., Breitenmoser-Würsten, C., Breitenmoser, U., 2007. Importance of dispersal for the expansion of a Eurasian lynx *Lynx lynx* population in a fragmented landscape. Oryx 41, 358–368.