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Supporting Reintroduction Planning: A Framework Integrating Habitat Suitability, Connectivity and Individual-Based Modelling. A Case Study With the Eurasian Lynx in the Apennines

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ABSTRACT

Aim: Reintroducing carnivores is a widely used approach to restore the natural integrity of ecosystems. Species distribution models (SDMs) and connectivity analyses are valuable tools for planning reintroductions and identifying release sites but are rarely combined. We propose a new framework combining SDMs, connectivity modelling and individual-based models (IBMs) to assess the feasibility of various reintroduction scenarios. As a case study, we applied this framework to plan a potential reintroduction of the Eurasian lynx (*Lynx lynx*) to the Apennines by: (i) assessing niche overlap between potential source and target populations; (ii) integrating habitat suitability and connectivity to select release sites and (iii) evaluating reintroduction outcomes through IBMs.

Location: Apennines, Peninsular Italy.

Methods: We combined niche overlap analysis, ensembles of fine-tuned SDMs and circuit-theory techniques to model connectivity. Then, we integrated suitability and connectivity predictions within a GIS environment to identify the optimal release sites under different scenarios. Finally, we used IBMs to assess population viability, site occupancy and dispersal.

Results: Niche overlap suggested that the Carpathian lynx populations may serve as a valid reintroduction source. Integrating habitat and connectivity models highlighted the most functional sites in the Central (CA) and Northern Apennines (NA). A scenario with individuals released in both CA and NA did not outperform the single-area scenarios. Releasing individuals only in CA showed long-term feasibility but a higher risk of isolation, while release only in NA would not result in viable populations in the long term, despite closer proximity to suitable areas in the Alps.

Main Conclusions: Our framework can help practitioners with integrating functional connectivity within the selection of release sites for species reintroductions. We recommend incorporating demography, as well as dispersal and settlement phases, when evaluating reintroduction scenarios. This approach identifies critical mortality areas, predicts population size, site occupancy and connectivity and enhances decision-making for successful reintroductions.

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1 | Introduction

Large carnivores have faced population declines and range contractions due to habitat loss, fragmentation, persecution and reduced prey abundance (Linnell et al. 2009; Ripple et al. 2014). Despite historical declines, populations of Eurasian lynx (*Lynx lynx*; hereafter 'lynx'), brown bear (*Ursus arctos*) and grey wolf (*Canis lupus*) have increased in Europe over the past few decades, returning to areas where they previously went extinct (Cimatti et al. 2021). This conservation success stems from coordinated legal protection, specific management measures, rural abandonment, habitat improvement, recovery of natural prey, favourable public opinion and reintroduction/translocation programmes, the latter particularly relevant for the lynx (Cimatti et al. 2021; Skorupski et al. 2022).

Reintroductions and translocations are key components of biodiversity conservation efforts (Seddon et al. 2014). While reintroductions may lead to unexpected ecological dynamics, decisions regarding when, where and how to reintroduce are often based on limited empirical data, although some practical guidelines exist (e.g., IUCN 2013). To partially counter data deficiency, ecological models informed with available knowledge about species' ecology have been applied to predict the possible outcomes of reintroductions before investing in the latter (Bellis et al. 2021; Finn et al. 2024). In most cases, this approach relies on species distribution models (SDMs) to identify suitable areas for reintroduction. Nonetheless, standard SDMs do not consider factors like functional connectivity and dispersal capability (Hunter-Ayad et al. 2020). The need for mechanistic models, which simulate processes like dispersal, demography and evolution, stimulated the development of individual-based models (IBMs), rapidly implemented in evaluations of alternative reintroduction scenarios (e.g., Ovenden et al. 2019).

Reintroducing large carnivores poses significant challenges, particularly concerning public acceptance (Linnell et al. 2009). For example, hunters' concerns about their impact on ungulate populations and lynx predation on livestock can lead to conflicts and illegal killings (Breitenmoser-Würsten et al. 2007; Vandel et al. 2006). However, reintroducing an apex predator can benefit ecosystems by restoring the integrity of the highest trophic levels in local food webs, reducing densities of herbivores and/or mesopredators, supporting biodiversity and enhancing ecosystem stability (Bakker and Svenning 2018; Ritchie and Johnson 2009). Additionally, large carnivores offer economic and ecosystem services, influencing scavenger subsidies, disease dynamics, carbon storage, crop production (Ripple et al. 2014) and providing ecotourism opportunities (Penteriani et al. 2017). Despite increasing success in the translocation of large carnivores, only 66% of individuals survive the first 6 months and 37% reproduce (Thomas et al. 2023). The integration of habitat and connectivity modelling has the potential to further improve decision-making when choosing optimal release locations, thus contributing to the success of reintroduction programs.

Reintroductions have been key to the lynx's recovery in Europe, with some subpopulations fully reconstituted (Linnell et al. 2009). Once widespread across Eurasia (Werdelin 1981), the lynx went extinct in much of Europe due to habitat changes, persecution and prey loss (Breitenmoser 1998). Historically, only the Scandinavian, Eastern Baltic, Carpathian and Balkan populations survived. The recovery of other European populations required reintroductions over the past 50 years, as natural recolonisation was unlikely due to limited ecological corridors (Linnell et al. 2009), and some populations also needed reinforcements to counteract the lack of natural gene flow (Pazhenkova et al. 2025). Despite some unsuccessful reintroductions due to poor planning and scarcity of guidelines, several populations have become established, such as the Dinaric, Alpine, Bohemian-Bavarian-Austrian, Harz and Jura populations (Linnell et al. 2009; Mueller et al. 2022).

In Italy, the lynx currently occurs only in the Eastern Alps, along the border with Slovenia, with few individuals belonging to the Alpine population. Besides the Alps, the lynx in Italy historically also inhabited the Apennines, as indicated by paleontological and cultural evidence (Cherin et al. 2013; Ghezzo et al. 2015). Previous continent-wide habitat-modelling studies on the lynx suggested potential suitability of the Apennines, which represent one of the largest suitable, but currently non-occupied areas within the species' historic range in Europe (Oeser, Heurich, Kramer-Schadt, Mattisson, et al. 2023; Serva et al. 2023). Furthermore, the Apennines are characterised by increasing abandonment of rural activities, contributing to low human densities in inland areas, a factor that could further support the presence of the lynx (Cimatti et al. 2021; Ripari et al. 2022). Thus, the Apennines could represent one of the possible sites for future lynx reintroductions to contribute to the recovery of this apex predator in the European forest ecosystems.

Here, we introduce a new coherent modelling framework (Figure 1), termed MDS ("Model, Define, Simulate"), that may assist practitioners in designing effective reintroduction plans by: (i) modelling niche overlap between the source population and the potential target population (ii) estimating habitat availability for the target species in the reintroduction area by coupling SDMs-based habitat suitability estimates with quantification of the functional connectivity amongst suitable areas; (iii) implement IBMs to evaluate the medium-to-long term viability of reintroduced population under alternative reintroduction scenarios. This framework permits to assess critical parameters to avoid reintroduction failures, such as the inappropriate number of individuals to be released and the misidentification of areas hosting enough high-quality habitat to sustain the introduced populations (MacDonald 2009; Thomas et al. 2023). To showcase the applicability of the MDS approach to a concrete potential reintroduction, we evaluated the feasibility of the lynx reintroduction in the Apennines. Specifically, we first estimated the potential for natural recolonisation of the Apennines from the Alps. Next, after modelling habitat availability and connectivity, we identified the best reintroduction areas (i.e., those with high habitat functionality) in the Apennines. Finally, we used IBMs simulations to evaluate several reintroduction scenarios, providing baseline guidance on how to establish a viable lynx population in the Apennines for the next 60 years.

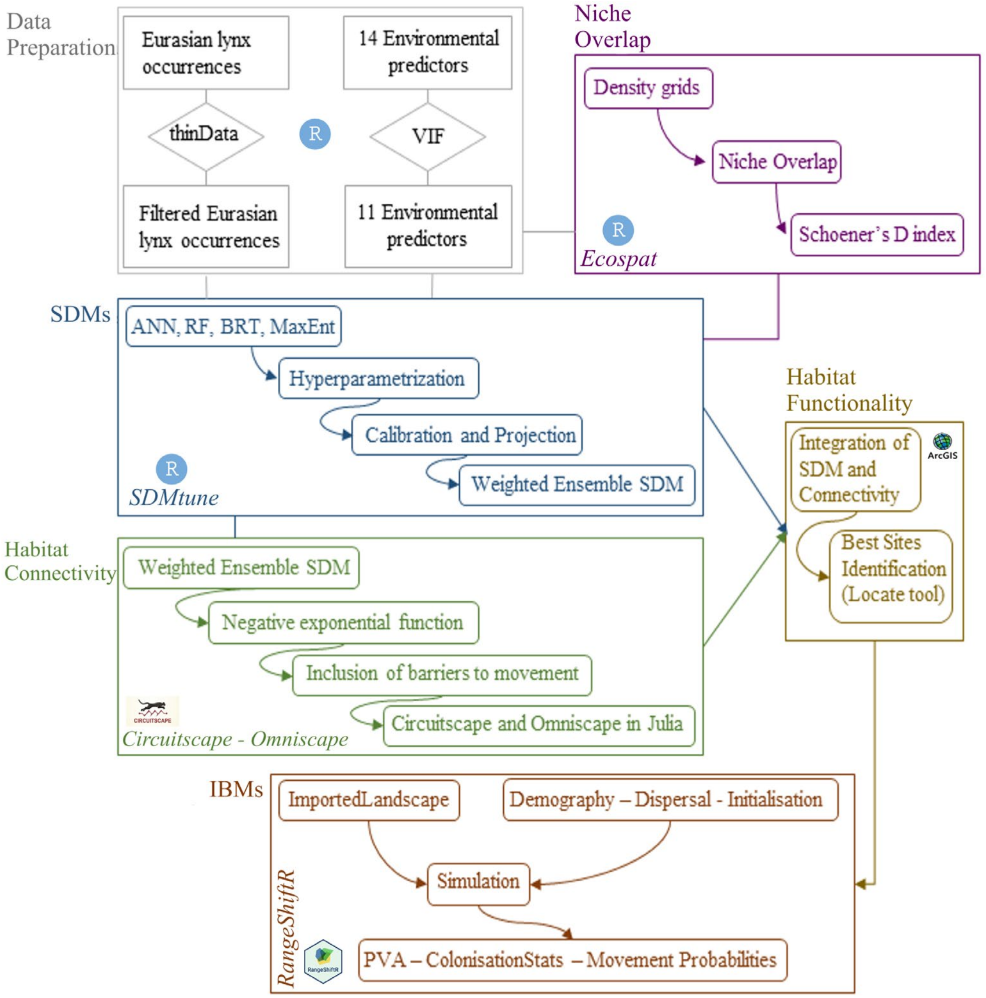

FIGURE 1 | The MDS framework: Full workflow adopted for assessing reintroduction scenarios.

2 | Material and Methods

2.1 | Study Area and Target Species

The target study area is the Apennines, a 1200 km long calcareous mountain range crossing Italy. The Apennines feature many protected and forested areas with low human density and, contrarily, a high density of wild ungulates, including the roe deer (*Capreolus capreolus*), which is the main prey for lynx in Europe (Khorozyan and Heurich 2023). The target species is the lynx, once present in the Apennines but now limited to the Alps in Italy. Given that most reintroductions in Western Europe over the past 50 years involved individuals from the Carpathian population, we considered Southern and Central Europe (excluding regions with other subpopulations like the Scandinavian, Karelian and Baltic) as a second study area for SDMs calibration.

The lynx, with an estimated 9000–10,000 individuals in Europe, is classified by the IUCN Red List as "Least Concern". However, subpopulation statuses vary, with some "Critically Endangered" and others "Endangered" (von Arx 2020). Data on the lynx distribution included records from previous studies and additional occurrences retrieved from various sources (e.g., citizen science data, published technical reports), within the Carpathian lynx range (both native and reintroduced populations) (Appendix S1, Table S1).

2.2 | Environmental Predictors

We selected bioclimatic, topographic, human-related and habitat-related variables previously shown to be relevant to lynx ecology (Čonč et al. 2024; Filla et al. 2017; Oeser, Heurich, Kramer-Schadt, Andrén, et al. 2023; Ripari et al. 2022; Serva et al. 2023). Specifically, we considered 12 candidate predictors: Elevation, retrieved from a Digital Elevation Model (DEM) at 90 m resolution (ESA 2024); Slope, computed within ArcGIS Pro (ESRI Inc. 2024); Terrain Ruggedness Index (TRI); Tree Cover (TC) (Hansen et al. 2013); Human Footprint Index (HFI) (Mu et al. 2022); Snow Cover; Mean Annual Temperature (BIO1); Precipitation Seasonality (BIO15); Forest Integrity Index (FII) (Grantham et al. 2020); NDVI; Human Impact, created as a distance layer from highways, major roads and urban areas (Iannella et al. 2024); Night Light. The predictors were obtained from WorldClim (ver. 2.1) (Fick and Hijmans 2017), Google Earth Engine (Gorelick et al. 2017) and Geomorpho90 (Amatulli et al. 2018). For BIO1 and BIO15, we also downloaded future projections from WorldClim (ver. 2.1, 30 arc-sec resolution) to three different time horizons (2030, 2050 and 2070), considering, for each of them, the Shared Socioeconomic Pathways (SSPs) 2.45, 3.70 and 5.85 to take into account all but one (SSP 1.26, the most optimistic) of the different trajectories (Riahi et al. 2017). To reduce the variability linked to the use of individual General Circulation Models (GCMs) in future projections (Stralberg et al. 2015), we merged SDMs' projections resulting from three different GCMs, namely, the IPSL-CM6A-LR (Boucher et al. 2020), the MPI-ESM1-2-HR (Müller et al. 2018) and the MIROC6 (Tatebe et al. 2019). Full details on the predictors used are available in Appendix S1, Table S2.

We initially checked pairwise correlation amongst predictors through the 'layerCor' function of the 'terra' R package (Hijmans et al. 2024), leading to the exclusion of Slope from model fitting. Multicollinearity was further evaluated through a stepwise Variance Inflation Factor analysis ('vifstep' algorithm of the 'usdm' R package (Naimi 2015)), selecting VIF ≤ 10 as threshold for retaining the candidate predictors (Guisan et al. 2017) (Appendix S1, Figure S3). According to the VIF analysis, the remaining candidate predictors were found to be non-collinear.

All variables were resampled to a resolution of 300 m using Google Earth Engine and the 'terra' R package (R Core Team 2024).

2.3 | Ecological Niche Modelling and Niche Overlap

The occurrence dataset was filtered using the 'thinData' function of the 'SDMtune' R package (Vignali et al. 2020) to maintain a single occurrence per raster cell, reducing spatial autocorrelation (Sillero and Barbosa 2021).

Species distribution models (SDMs) were generated through the 'SDMtune' R package, which permits to fit SDMs through four machine learning algorithms—artificial neural networks (ANN), boosted regression trees (BRT), MaxEnt and random forest (RF)—and tune them by searching for the best hyperparameters with a real-time chart display (Vignali et al. 2020). To fit ANN, BRT and RF, pseudoabsences were created through the 'biomod2' R package (Thuiller et al. 2016) using the Surface Range Envelope algorithm (quantile = 0.05), generating 13,000 pseudoabsences (ratio pseudoabsences:occurrences equalling 10:1) (Barbet-Massin et al. 2012). Differently, to feed the MaxEnt algorithm, ~20,000 background points were randomly drawn from the study area. Presences and pseudoabsences were merged and randomly split into training (80%) and test (20%) datasets, using the function 'trainValTest' available in the 'SDMtune' R package. Model tuning was performed on the training dataset, taking advantage of the 'optimizeModel' function from 'SDMtune': this permitted to select the best values for critical hyperparameters of each algorithm, based on area under the curve (AUC) scores computed within a 4-folds random cross-validation scheme (on the training dataset). The optimised SDMs were projected across both study areas (Central and Southern Europe, and the Apennines) under the current environmental conditions, and only to the Apennines under the future scenarios. The final ensemble models (current and future) were then generated through a weighted mean of predictions from the single SDMs, based on the respective AUC and TSS scores on the test data (20%) previously excluded from model tuning. Full details about SDMs' tuned parameterisation are available in Appendix S1, Table S4. Finally, the ensemble model was validated using independent GPS telemetry data from the Dinaric population (Krofel et al. 2025), belonging to the Carpathian subspecies.

The standard ODMAP protocol for reporting SDMs' implementations (Zurell et al. 2020) is available, for our modelling pipeline, in Appendix S2. The 'ecospat' R package (Di Cola et al. 2017) was used to assess environmental overlap between the potential distribution of the lynx in the Apennines (as estimated through the ensemble model) and the range of the Carpathian population. In the Apennines, we generated 300 random points within pixels with very high predicted suitability, while for the Carpathian population we used the occurrences within its range. Environmental variability within the two regions was then summarised into two orthogonal axes through a Principal Component Analysis (PCA). Finally, the 'ecospat.niche.overlap' function was used to generate kernel-smoothed grids showing density of occurrence in environmental space for each potential range, subsequently measuring the corresponding overlap through the Schoener's D index.

2.4 | Connectivity Analyses

A resistance layer spanning the Alpine biogeographic area, and the Italian peninsula was created by transforming the predicted habitat suitability according to the negative exponential function of Keeley et al. (2016). Barriers such as major roads, urban areas, rivers and lakes were assigned the highest resistance value and were later merged through the 'Mosaic to New Raster' tool in ArcGIS Pro (ESRI Inc. 2024).

Connectivity was computed using Circuitscape in Julia (version 1.9.2), a circuit-theory technique shown to perform better than other approaches (Anantharaman et al. 2019). Circuitscape requires a resistance layer and source/target locations (nodes) (McRae et al. 2008), producing a current map reflecting landscape connectivity as the expected net probability of movement between nodes, considering a random-walk scenario (McRae et al. 2008).

In the Alps, lynx occurrences were used as focal nodes. In the Apennines, where lynx does not currently occur, the most suitable areas (i.e., showing suitability beyond the 90th percentile of predicted values within the ensemble SDM) were individuated, and their centroids were then used as focal nodes for the Apennines: the assumption is that these areas will be the ones selected by lynx individuals in a scenario of natural recolonisation. Circuitscape was initially run in 'pairwise' mode, computing current for every node pair, so that each node served as both source and destination (McRae et al. 2008). To test a different scenario, a second Circuitscape run was performed in 'advanced' mode, computing connectivity from sources (i.e., Alps' nodes) to destinations (i.e., Apennines' nodes) only.

To test a different scenario of connectivity, without the potential influence related to the position of focal nodes (e.g., Koen et al. 2014), we used Omniscape v.0.5.8 in Julia (Landau et al. 2021). Omniscape iteratively computes connectivity within a moving window, where the center pixel is the destination and pixels within the window are sources. Users can specify whether to use all pixels as sources or only those with certain resistance values. Omniscape then applies Circuitscape in 'advanced' mode for each target pixel (Landau et al. 2021). For this analysis, we used a resistance-based omnidirectional connectivity assessment, by using 'souce_from_resistance = True' in the initialisation file.

Lastly, Circuitscape in 'pairwise' mode was run again, this time limiting the analysis to the Apennines, to compute connectivity between potentially suitable areas based on the ensemble SDM.

2.5 | Habitat Functionality and Potential Reintroduction Areas

To identify potential reintroduction sites, habitat suitability predicted by the ensemble SDM and the connectivity layer resulting from Circuitscape in 'pairwise' mode were integrated using the 'Suitability Modeller' tool in ArcGIS Pro (ESRI Inc. 2024). This tool helps the user to find the best sites for establishment/reintroduction purposes, based on several user's defined criteria. In our case, habitat suitability and functional connectivity were the considered criteria; the corresponding layers were transformed and weighted (see below) to produce a final layer, which serves as input for selecting optimal sites. The algorithm can be further informed with spatial requirements such as the total area needed by a target species, the number and size of sites and their reciprocal distance.

To feed the 'Suitability Modeller', the habitat suitability layer (weight = 60%, expert-based evaluation) was transformed to a 0–1 scale using a simple linear function, while the connectivity map for the Apennines (weight = 40%) was transformed according to an MSLarge function (which is similar to a logistic growth function), emphasising large values using mean and standard deviation multipliers (ESRI Inc. 2024). After obtaining the final integrated layer, defined as 'habitat functionality' *sensu* Van Moorter, Kivimäki, Panzacchi, et al. (2023), this was used to feed the 'Locate' tool to identify the best release sites for the reintroduction of the lynx in the Apennines. Specifically, the tool was run considering three major scenarios: (1) minimum distance of 10 km between sites; (2) no minimum distance between sites; (3) no minimum distance but sites cannot be inside protected areas (PAs). The latter scenario was specifically aimed at identifying potential key areas for the lynx where new potential PAs could be established. Furthermore, the spatial constraints imposed to the tool when identifying the 30 best release sites were altered five times for each scenario, varying the total reserved area (i.e., the total area encompassing all the 30 sites) from 2800 km^2 to 4400 km^2. This setting permitted to reduce potential biases related to the user's choices, resulting in 15 different scenarios overall (Appendix S1, Table S5). The 450 release sites identified in this manner (30 sites × 15 scenarios) were merged into a single layer. The minimum and maximum site areas imposed to the algorithm were 45 and 120 km^2, respectively, with an average of ~80 km^2, based on female lynx home-range sizes in the Alps (Molinari-Jobin et al. 2007).

2.6 | Individual-Based Modelling and Reintroduction Scenarios

The 'RangeShiftR' R package (Malchow et al. 2021), based on RangeShifter 2.0 (Bocedi et al. 2021) was used to produce IBMs and subsequent Population Viability Analysis (PVA). 'RangeShiftR' is a spatially explicit, individual-based simulation platform that models species' range dynamics, patch connectivity and complex local population dynamics, accounting for inter-individual variability and evolutionary processes (Bocedi et al. 2021; Malchow et al. 2021). The package is modular, allowing the users to define the Landscape settings and add parameters for Demography, Dispersal, Genetics, Initialisation, Simulation and Output modules. The ensemble SDMs reclassified into ten habitat quality classes following a natural breaks classification (e.g., Arenas-Castro and Sillero 2021), each with specific carrying capacities and mortalities, was used as imported landscape. We used a dynamic landscape approach, where four different landscapes were considered to account for the potential climate change effects during the simulations: briefly, the habitat quality layer was substituted after 5 (2030 projection), 25 (2050 projection) and 45 years (2070 projection). For the Stochastic Movement Simulator (SMS), four cost layers (one for each projection) were provided based on the reclassified resistance layers used in the connectivity analyses.

Simulations were run under a patch-based model. All the patches identified through the 'Locate' tool were initially loaded, some specific sites were delimited and three scenarios were then explored, namely reintroductions occurring in: two regions (Northern and Central Apennines); Central Apennines only; Northern Apennines only. Species-specific parameters were set based on previous studies (Guilfoyle et al. 2023; Ovenden et al. 2019) (Appendix S1, Table S6). For each reintroduction scenario, two simulations were performed, changing the type of environmental stochasticity: (1) temporal uncorrelated (i.e., 'white noise') stochasticity and (2) temporally correlated (i.e., 'red noise' stochasticity), both affecting the growth rate parameter (Malchow et al. 2021). For all the simulations, we used an individual list file, where the user can provide a specific list with the details of the reintroduction scenario: number of individuals in each patch, their age, sex and life stage. We simulated: (1) 10 individuals released in both the Central and Northern Apennines (3 males and 7 females, adults between 3 and 4 years); (2) 20 individuals in both reintroduction areas (6 males and 14 females, adults between 3 and 4 years); (3) differential release in the two areas (15 individuals in the Central Apennines, 20 in the Northern Apennines, keeping fixed the sex ratio and the age). Finally, all simulations were replicated considering enhanced mortality during dispersal steps to make possible negative events (e.g., poaching, roadkill) be reflected in the IBMs' outputs. The outcome of each simulation was evaluated positively based on the population abundance, i.e., > 50 individuals including adults, sub-adults and juveniles (Zimmermann and Breitenmoser 2007).

3 | Results

3.1 | Habitat Suitability and Connectivity in the Apennines

The final dataset after the thinning procedure contained 1373 occurrences. The AUC of the fitted SDMs spanned from 0.92 of the ANN to 0.97 of the RF algorithms (Appendix S1, Figure S7). Response curves are consistent with lynx's ecology (Appendix S1, Figure S8). In all algorithms, elevation and BIO1 were the most important variables, followed by TRI and BIO15 (Appendix S1, Figure S9).

A moderately high niche overlap (Schoener's D index = 0.73) emerged between the potential lynx distribution in the Apennines and that of the Carpathian lynx in its current range (Figure 2b). This niche overlap is also suggested by the relative importance estimates of the predictors used to fit the SDMs (Appendix S1, Figure S10).

The ensemble SDM, calibrated on the Carpathian lynx range (Appendix S1, Figure S11), which was validated through the use of GPS telemetry data (Appendix S1, Figure S12), projected to the Apennines, highlighted several suitable patches, mainly in the Northern and Central Apennines, with several potential stepping-stone areas in between (Figure 2b), even if from the Carpathian lynx-based model, the Apennines appear less suitable than areas where the lynx already occurs. Furthermore, most of the suitable patches in the Central Apennines at least partially overlap with large PAs and are located in mountain areas with low human disturbance (Figure 2b). Future projections of habitat suitability in the Apennines showed a constant decrease through the years, especially in the Northern Apennines (Appendix S1, Figure S13).

Landscape connectivity in the Apennines, as estimated in Circuitscape, showed several fine-scale, high-connectivity corridors in Central Apennines, while predicted connectivity was more 'diffused' in the northern part of Northern Apennines (Figure 2c). Importantly, areas with moderate connectivity appeared between the two sectors (Figure 2c), suggesting the possibility for the lynx to disperse through the Apennines. Landscape connectivity between the Alps and the Apennines was generally low, regardless of the algorithm used (Appendix S1, Figure S14), making a natural recolonisation of the Apennines unlikely under current conditions, while medium-to-high connectivity emerged within both the Alpine and Apennine regions.

3.2 | Habitat Functionality and Reintroduction Sites

High values of habitat functionality, indicating areas being both suitable and well connected, occurred in the Northern and Central Apennines, while the southern part of the mountain chain appears less 'functional' for the lynx (Figure 3a).

The 450 potential suitable release sites for lynx reintroduction in the Apennines identified through the 'Locate' tool were mainly distributed in Northern and Central Apennines, with some important stepping-stone areas between these two areas, with only one site in the Southern Apennines (Figure 3b). Despite some differences between the tested scenarios, some areas were selected more frequently by the

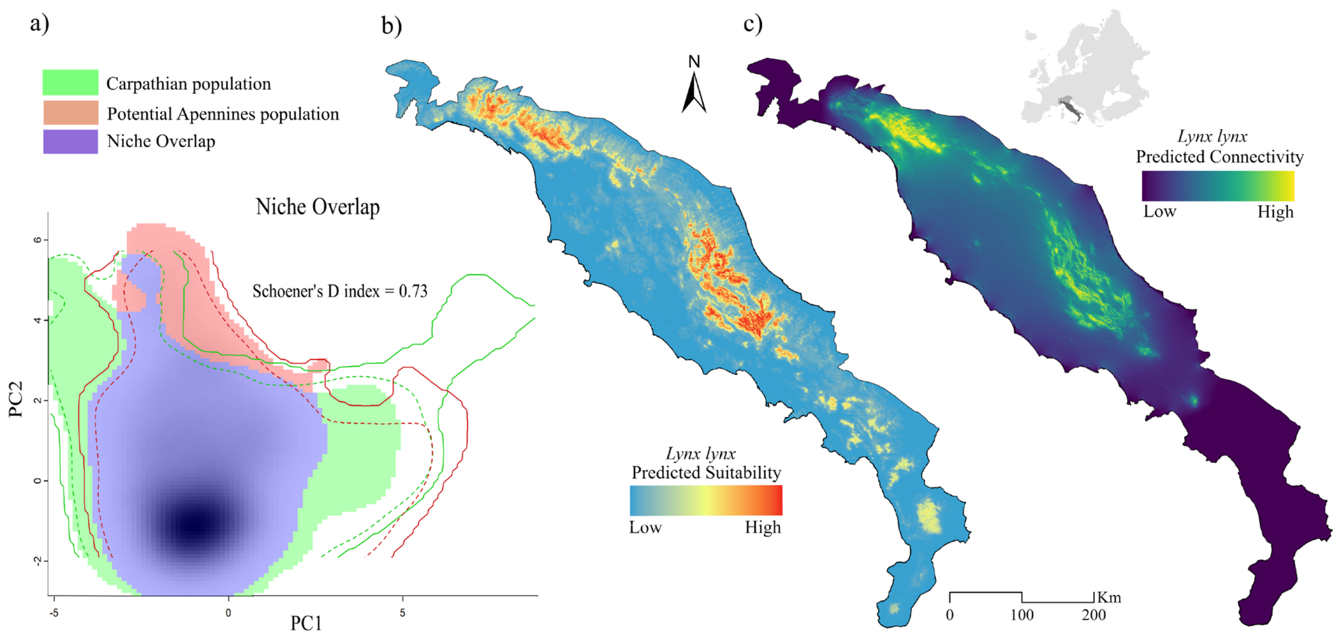

FIGURE 2 | Niche overlap (blue) between potential lynx distribution (i.e., high-suitability areas) in the Apennines (red) and the Carpathian lynx range (green) (a); predicted habitat suitability, resulting from the ensemble SDM, for the lynx in the Apennines (b); predicted connectivity (c), estimated using as focal nodes the most suitable areas detected from the habitat suitability layer.

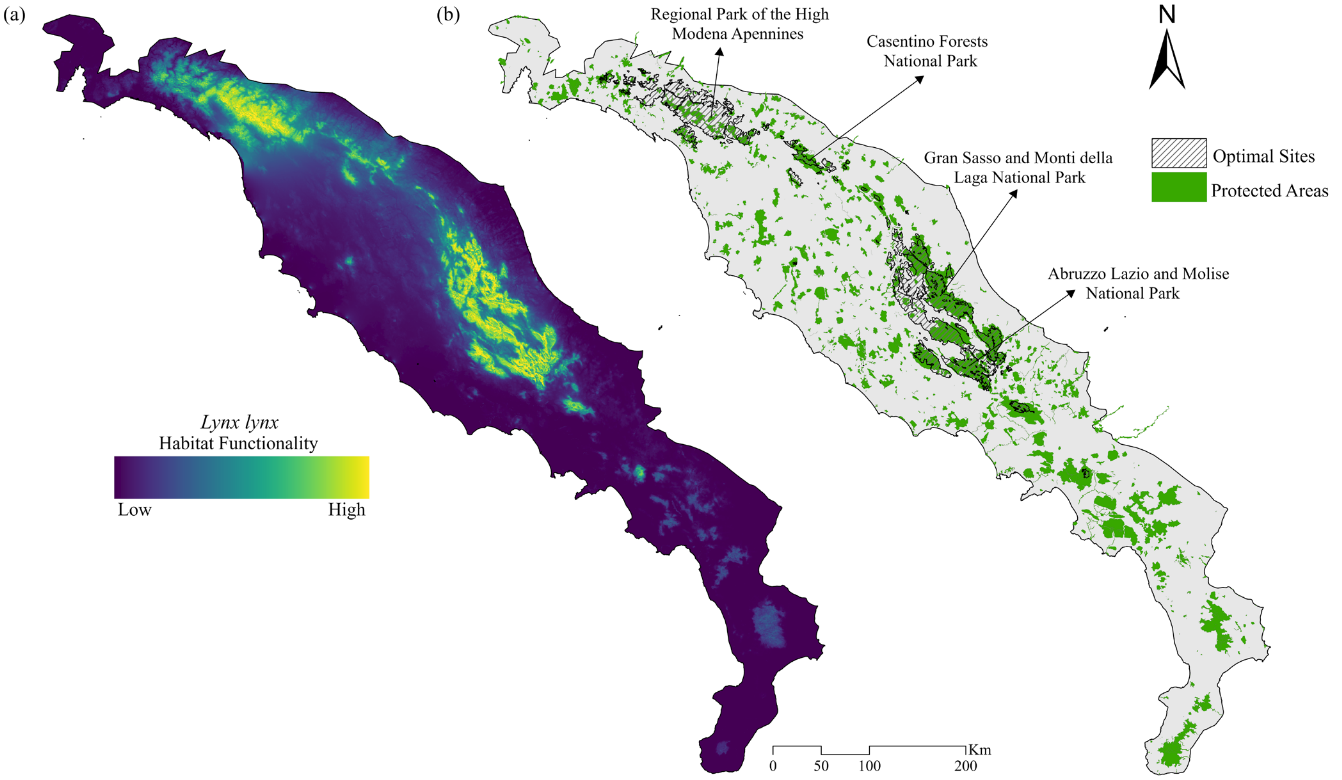

FIGURE 3 | (a) Habitat functionality for the lynx in the Apennines, estimated by integrating the ensemble SDM's predictions and the habitat connectivity layer; (b) the best reintroduction sites (hatched polygons) identified through the ArcGIS Pro 'Locate' tool under fifteen different scenarios, overlapped with PAs (green polygons).

algorithm (Appendix S1, Figure S15). Furthermore, the best identified sites partially overlap with PAs, particularly those of Central Apennines (67%), followed by those of Northern Apennines (33%).

3.3 | Population Viability Analyses and Reintroduction Scenarios

The best reintroduction scenarios, leading to an estimated population size of ~70 individuals after 60 years, involved the reintroduction of ~10 individuals in the Central Apennines, or 20 individuals in the Central and Northern Apennines, with several sites showing high occurrence probability in both areas (Figure 4a,b). A faster colonisation process was predicted in the Northern Apennines, while in the Central Apennines some long-distance patches were predicted to be colonised only after more than 50 years (Figure 4c).

The single-site reintroduction scenario (in both case involving the reintroduction of ~10 individuals) focusing on Central Apennines performed better than the one centered in Northern Apennines, despite the higher colonisation time, due to high occurrence probability in most patches and higher predicted population size (Figure 4d,e,g,h). Moreover, simulating reintroduction only in Northern Apennines produced the smallest population after 60 years, with a strong reduction after 25 years, mainly due to the lower habitat quality due to climate change effects, resulting in fewer patches occupied (Figure 4g–i). Considering simulations with increasing mortality (Appendix S1, Figure S16), as expected, smaller populations resulted in every reintroduction scenario, with lower occurrence probability (average percent reduction ± SD = 25% ± 7) and longer colonisation time (average percent increase ± SD = 23% ± 9). In contrast, changing the type of environmental stochasticity and seeding more individuals did not significantly affect the results (Appendix S1, Figures S17 and S18).

3.4 | Movement Probabilities

Dispersal heatmaps obtained from the IBMs highlighted those parts of the landscape matrix that are predicted to be frequently used for dispersal, showed high values of movement probability outside the patches selected for the reintroduction, both in Northern and Central Apennines, under different simulation conditions (Figure 5a–c). However, interesting differences emerged between the two areas, with movements in Northern Apennines primarily clustered close to the reintroduction patches, while in Central Apennines individuals were predicted to disperse farther, especially northwards (Figure 5a–c).

Considering different scenarios of environmental stochasticity did not significantly change the results, except when simulating increased mortality (Figure 5c). In this latter scenario, movement probabilities were higher around the reintroduction patches, and some corridors disappeared in Central Apennines, like those connecting the patches around the "Majella National Park" to the "Gran Sasso and Monti della Laga National Park" (Figure 5c). Focusing on Central Apennines, multiple corridors

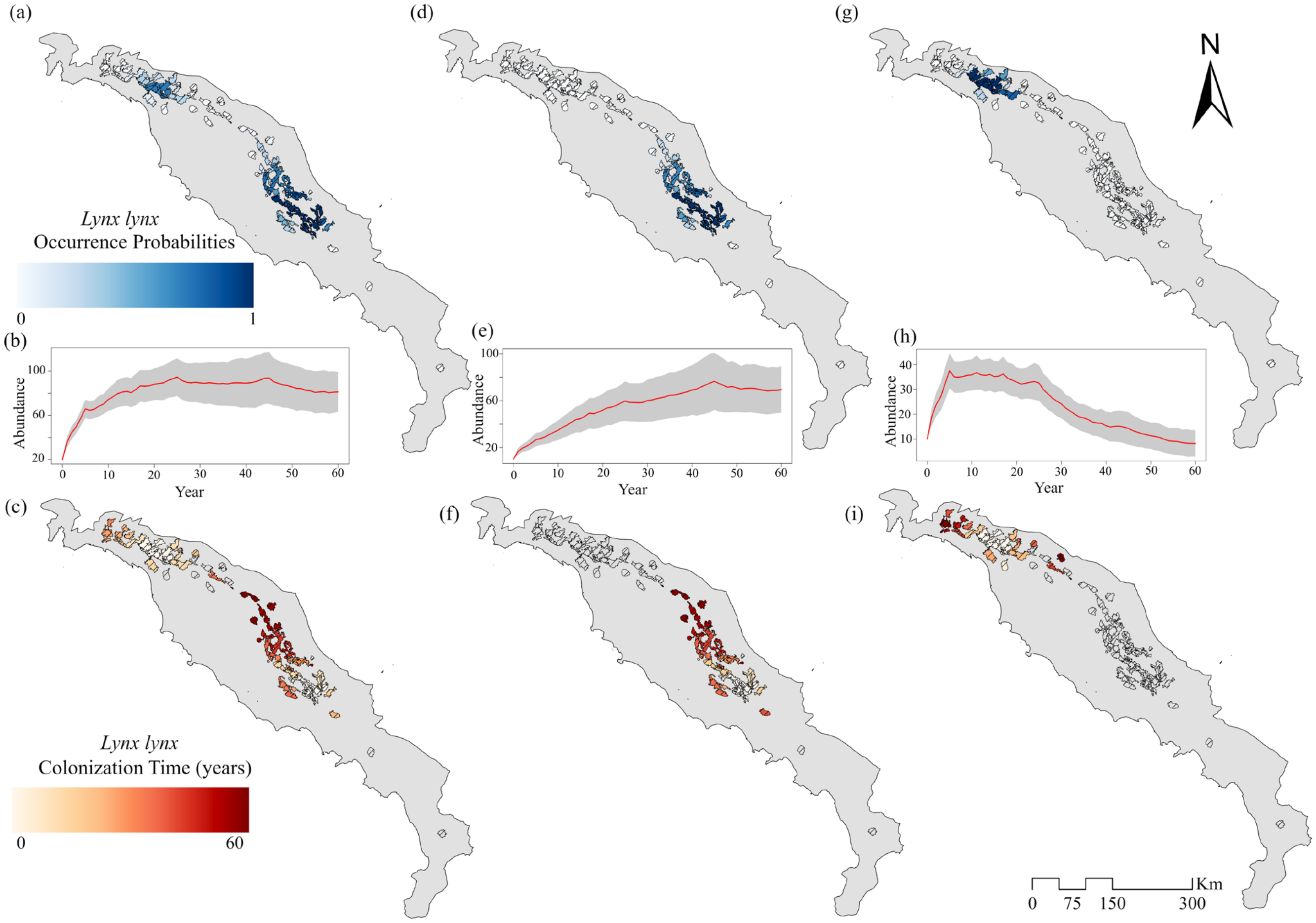

FIGURE 4 | Colonisation stats and Population Viability Analysis (PVA) for different reintroduction scenarios. Specifically, occurrence probability, PVA chart (i.e., predicted abundance over time) and colonisation time are shown for a reintroduction starting in: (left) both Northern and Central Apennines (panels a, b and c); (center) Central Apennines only (panels d, e and f); (right) Northern Apennines only (panels g, h and i).

can connect most of the suitable patches, especially between "Abruzzi Latium and Molise National Park" and "Sirente-Velino Regional Park" (Figure 5d).

4 | Discussion

4.1 | A New Framework to Identify Sites for Reintroduction Purposes

Using the potential lynx reintroduction to the Apennines as a case study, we developed the MDS framework for identifying the best release sites for reintroduction purposes and assessing the feasibility of such conservation efforts. By combining spatially explicit predictions derived from SDMs and connectivity analyses with individual-based modelling (IBMs), we demonstrated how such an integrated modelling approach could help in defining reintroduction scenarios and testing their probability of success.

Maintaining or restoring ecologically effective densities of large carnivores is crucial for preserving ecosystem structure and function (Ripple et al. 2014). Reintroducing the lynx to the Apennines, for instance, could help limit ungulate and mesocarnivore populations, support endangered scavengers and potentially trigger trophic cascades by affecting wild ungulates (Elmhagen et al. 2010; Ripple et al. 2014). However, reintroducing large carnivores poses challenges, particularly related to spatial requirements and resource availability, including prey (Wolf and Ripple 2018).

Our approach assesses several important prerequisites for planning reintroductions. It measures niche overlap between environmental conditions in source and target areas, ensures the identification of the best release sites and evaluates the success and threats of various reintroduction scenarios. So far, most reintroduction studies involved the use of SDMs alone to define the most suitable areas (e.g., Bellis et al. 2021; Finn et al. 2024; Osborne and Seddon 2012; Treves et al. 2022). However, for many species, connectivity is as important as suitability for the long-term persistence of a population but is often ignored or considered separately (e.g., Iannella et al. 2024). Moreover, the improved accessibility of IBMs is a significant step forward, as it allows researchers and conservationists to evaluate the various reintroduction scenarios considering the specific ecology of the target species.

We encourage the use of this framework, at least partially, when planning reintroductions, as crucial information for decision-making can be obtained. Indeed, the use of these integrated

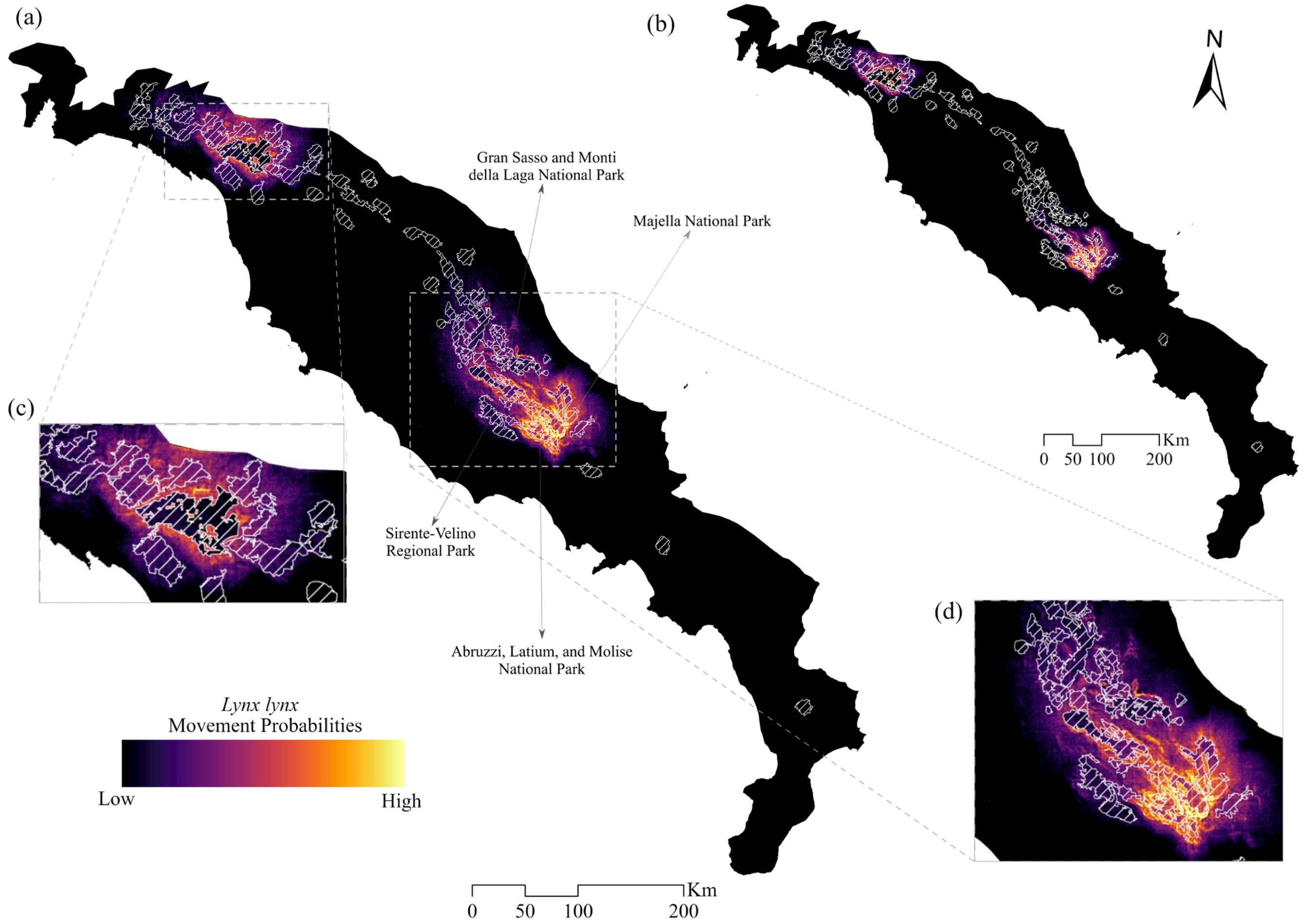

FIGURE 5 | Dispersal heatmaps representing the predicted movement probabilities across the landscape matrix considering: (a) 'red-noise' environmental stochasticity; (b) 'red-noise' environmental stochasticity and increased mortality; (c and d) two zoomed-in maps for the Northern and Central Apennines, respectively. Hatched areas are the optimal reintroduction sites identified in the habitat functionality layer.

modelling tools permits accounting for critical demographic, landscape and dispersal factors that affect the probability of reintroduction success, thus supporting decision-making through an accurate quantification of the uncertainties related to different reintroduction scenarios. The integration of habitat suitability and habitat connectivity is a key step in determining the potentiality of a site for reintroduction. For a species like the lynx, connectivity between suitable patches is crucial (Kramer-Schadt et al. 2004; Zimmermann and Breitenmoser 2007). However, few studies have used frameworks to integrate these two parameters (Van Moorter, Kivimäki, Noack, et al. 2023). Here, we propose a new approach to achieve this, developed for ArcGIS software but easily implementable in other GIS and modelling environments. Furthermore, we underline the importance of considering the target species' ecology and requirements when determining the best release sites for reintroduction, which can be achieved by adding IBMs to the decision process, as in our MDS framework.

4.2 | Double-Site vs. Single-Site Reintroduction Scenarios in the Northern and Central Apennines

Despite the great dispersal ability of the lynx, especially males (Gajdárová et al. 2021; Zimmermann et al. 2005) connectivity analyses between the Alps and the Apennines revealed low connectivity, making natural recolonisation unlikely under the current conditions, also considering the small population in the Western Alps. Thus, reintroduction is currently the only viable option for the lynx's return to the Apennines. Selecting optimal release sites and assessing potential movements of translocated individuals are critical for successful reintroduction (Devineau et al. 2010). In our study, simulations including reintroduction in both Central and Northern Apennines were the only ones ending with successful colonisation of most patches in both areas. However, this scenario resulted in the same future abundance as when simulating reintroduction only in Central Apennines, mainly due to the fast population decline predicted for the sites in the Northern Apennines (Figure 4). Furthermore, this double-site scenario would be more challenging due to the long distance between sites and the greater resources needed to sustain reintroduction and subsequent monitoring in two areas. Therefore, this scenario is probably the less realistic in practice, considering the monitoring and financial efforts that would be required, and should be considered with these limitations in mind. If a single-site reintroduction is chosen, the Central Apennines are the only option, as this would result in a viable population in the long term, potentially capable of expanding northward. The presence of large, well-connected PAs in this area further supports this strategy. Although a viable lynx population is proposed to range between 50 and 100 individuals (Zimmermann and Breitenmoser 2007), a greater population in well-connected habitats would better avoid inbreeding and protect against unexpected population declines, such as those following disease outbreaks (Breitenmoser 1998). Our simulations, however, suggest that lynx from the Central Apennines would not naturally colonise the Northern Apennines within 60 years, risking long-term isolation, as seen in other reintroduced lynx populations in Europe (Mueller et al. 2022). To mitigate this, creating a stepping-stone network to facilitate lynx movement between the Northern and Central Apennines or managing the population through occasional translocations would be necessary.

Human-wildlife conflicts, especially in areas where these predators have been absent, may also arise, leading to retaliatory killings that significantly affect lynx populations (Heurich et al. 2018; Premier et al. 2025). Although lynx generally pose less risk to livestock compared to wolves and bears, concerns about their impact on wild ungulates and competition with hunters often drive low acceptance and poaching (Breitenmoser et al. 2010). To mitigate human-wildlife conflicts and reduce the probability of poaching, selecting PAs as reintroduction sites is recommended. The size of PAs, along with low human disturbance and high prey density, is a key factor for large carnivore persistence (Wolf and Ripple 2018), and in Europe generally, PAs are too small for hosting large carnivores' populations (Santini et al. 2016). In our study, the most optimal reintroduction sites overlapped with PAs, even though the model was not specifically informed of their presence. This overlap may enhance lynx survival, particularly during the vulnerable initial reintroduction phase, as previous studies have shown (Vandel et al. 2006; Linnell et al. 2009; Heurich et al. 2018).

In our analysis, we used lynx occurrences from the Carpathian lynx range to calibrate the SDM, since most reintroductions in the past have used this population as a source (Linnell et al. 2009). Furthermore, the low size of other populations in Western and Central Europe does not allow the collection of individuals for reintroduction purposes, especially considering that some of these populations have been reinforced recently with individuals from the Carpathians (e.g., Topličanec et al. 2022). A potential limitation of our results concerns the mixed types of data sources used to calibrate the model, which include opportunistic observations, monitoring reports and camera traps. Nonetheless, predictions from the obtained SDM are coherent with those of SDMs calibrated at the continental scale in previous studies (Serva et al. 2023; Oeser, Heurich, Kramer-Schadt, Mattisson, et al. 2023). Moreover, our SDM was also validated on an independent GPS telemetry dataset, showing a good correspondence between predicted habitat suitability and lynx occurrence. Another key point is related to the lower habitat suitability values of the Apennines when compared to other areas (e.g., Dinaric and Carpathian ranges). No formal proposals currently exist for lynx reintroduction to the Apennines, and the primary aim of this study is to showcase the potential (and limitations) of the presented framework, rather than to provide concrete plans for a lynx reintroduction in the Apennines. Nonetheless, our results support the theoretical feasibility of lynx reintroduction in the Central Apennines, reaffirming the suitability of these areas for the species, as identified by previous larger-scale studies (Oeser, Heurich, Kramer-Schadt, Mattisson, et al. 2023; Serva et al. 2023) and providing further guidance on optimal release sites and potential connectivity.

4.3 | Limitations and Future Perspectives

To enhance the usability of our framework, it is important to acknowledge certain limitations. First, several subjective decisions were made throughout the modelling process, each carrying implicit assumptions (e.g., SDMs assume that species are in equilibrium with their environment). At each step of our workflow, specific methodological choices were made from the creation of SDMs (e.g., selection of pseudo-absence generation methods, cross-validation approaches and ensemble modelling techniques) to the computation of connectivity (e.g., using Circuitscape instead of alternative methods) and their subsequent integration (e.g., applying specific transformations and weight assignments). While each analysis inherently involves fundamental assumptions, it is crucial to emphasise that these methodological steps are user-driven decisions. Consequently, the primary focus of our approach should be on the use of habitat suitability and connectivity indices and their integration to feed the IBMs.

Therefore, we recommend not focusing excessively on the specifics of each step in our workflow but rather on developing indices that effectively represent landscape suitability and connectivity, integrating them to identify the most functionally important sites. This can be achieved through various approaches (e.g., Van Moorter, Kivimäki, Noack, et al. 2023), while key site prerequisites (e.g., total area, distances, constraints) remain species-specific. Similarly, implementing IBMs requires carefully selecting species-specific parameters that best capture not only demographic aspects but also dispersal and settlement dynamics.

Another key point is related to the implemented climate change scenarios, where we changed only the two bioclimatic variables, as future projections of habitat or human-related variables are less available. So even if our IBMs are developed by considering potential climate change effects, other potential changes, such as forest cover, prey availability, potential competitors and human footprint were not considered. Thus, we stress the importance of such data to further improve the reliability of predictive models in future scenarios.

Other potential barriers to successful reintroductions include genetic isolation, a small number of released individuals, poor selection of released individuals, inadequate feasibility studies and insufficient knowledge of the species' ecological needs (MacDonald 2009; Thomas et al. 2023). This study addresses these concerns by assessing connectivity, determining optimal release numbers and identifying suitable reintroduction sites. As for the optimal release numbers, we obtained a stable population starting from both 15 and 10 individuals in the Central Apennines, while in the Northern Apennines, even 20 individuals were predicted to be unable to create a mid-term sustainable population.

However, the main aim of this study is more related to the framework than to the effective reintroduction of the lynx in the Apennines. In fact, in Europe several lynx populations remain endangered (von Arx et al. 2021), and current conservation measures and economic investments, such as those required in case of translocation/reintroduction projects, should be prioritised towards the existing populations to ensure their long-term persistence. Another limit proved by our framework is related to the results of this study that the lynx population in the Apennines would likely remain isolated from the closest population (i.e., the Alpine and Dinaric), which would in the long term probably require genetic management with periodic reinforcements (Pazhenkova et al. 2025).

In conclusion, this study provides a new framework that could support reintroduction projects and help decision-making for this pivotal conservation measure. By evaluating habitat suitability and connectivity, we first identified optimal sites for reintroduction and then simulated and evaluated different reintroduction scenarios. Moreover, niche overlap helped in the identification of the potential population source. Our analysis suggests that a single-site reintroduction in the Central Apennines would be most effective. Niche overlap showed the Carpathian lynx as a plausible source for this reintroduction. However, public acceptance and political support are essential for the success of reintroducing a large carnivore like the lynx in Europe's human-dominated landscapes.

Author Contributions

D.S., M.K. and M.I. conceived the ideas. D.S., F.C. and M.I. designed the methodology and analysed the data. D.S., M.K. and M.B. collected the data. D.S. wrote the original draft. D.S., M.K., F.C. and M.I. reviewed and edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.59zw3r2km.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.