Eurasian lynx populations in Western Europe: What prospects for the next 50 years?

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Abstract

Persistence of viable populations may be uncertain for large carnivore species, especially for those established in human-dominated landscapes. Here, we studied the Eurasian lynx in Western Europe established in the Upper Rhine metapopulation (i.e., Jura, Vosges-Palatinian and Black Forest populations) and in the Alpine population. These populations are currently considered as endangered or critically endangered due to high anthropogenic mortality and isolation. We assessed lynx persistence over a 50-year time horizon by implementing a spatially-explicit individual-based model while accounting for road mortality and habitat selection. For the Alpine and Jura populations, forecasts showed a steady growth rapidly reaching a stabilization phase with high resident female occupancy, and a positive growth for the newly re-established Vosges-Palatinian population. Moreover, this population showed a difference in female occupancy between the northern part, where a recent reintroduction program was conducted in the Palatinate Forest, and the southern part. Only the group of individuals in the Black Forest had an irregular growth probably due to the small number of only male lynx at start of the simulation and poor connectivity to surrounding populations. Exchanges of individuals between populations were limited, and the Jura population played the role of a crossroad. Persistence of lynx in Western Europe seems likely on a large scale over the next 50 years. However, lynx persistence in the southern part of the Vosges-Palatinian population and in the Black Forest appears challenging without long-term conservation management.

Keywords: *Lynx lynx*, population persistence, spatially-explicit individual-based model

Introduction

The Eurasian lynx (*Lynx lynx*) was eradicated in most of Europe between the 17th and 20th centuries. The main reasons for its disappearance were habitat degradation, human persecution and a decrease in prey availability (Breitenmoser et al., 2000). The species has recently recolonized parts of its historical range in Central and Western Europe thanks to different reintroduction programs which started in the 1970s. Nowadays there are ten or eleven (depending on the author) identified lynx populations in Europe (Chapron et al., 2014; von Arx, 2020), and the species benefits from a conservation status across its whole range area. Although the species is considered as “least concerned” at the European level of the IUCN Red list, its status greatly differs from one population to another, even though they share similar threats, mostly habitat fragmentation, illegal killings and collisions with vehicles (von Arx, 2020). Long-term persistence remains notably uncertain for the Alpine population (France and Switzerland) and for the Upper Rhine meta-population, which encompasses the Jura population (France and Switzerland), the Vosges-Palatinian population (France and Germany) and few individuals located in the Black Forest and its surroundings (e.g., the Swabian Alb, Germany) (Drouet-Hoguet et al., 2021; Germain and Schwoerer, 2021; Herdtfelder et al., 2021; Idelberger et al., 2021; Molinari-Jobin et al., 2021). These populations are currently defined as endangered (Jura and Alpine) or critically endangered (Vosges-Palatinian) (von Arx, 2020). Indeed, the populations forming the Upper Rhine meta-population remain currently small and isolated. Only a few exchanges between them and with the Alpine population are documented, most likely because of habitat fragmentation and little functional connectivity (Morand, 2016; Zimmermann and Breitenmoser, 2007). Low female dispersal rates and movements most likely slow population expansion due to their risk-shy nature compared to male lynx (Port et al., 2021). This situation, added to the common origin of the reintroduced individuals from the Carpathian population (Breitenmoser et al., 1998; Vandel et al., 2006), may lead to high inbreeding within populations (Breitenmoser-Würsten and Obexer-Ruff, 2003; Bull et al., 2016; Premier et al., 2020).

In this context, wildlife conservationists, scientists and policy-makers face significant challenges for lynx conservation when individuals inhabit human-dominated landscapes. To inform decision-making processes for population conservation, several studies have used individual-based models (IBMs). These bottom-up models flexibly integrate species demography (dispersal, territory establishment, reproduction, mortality) and how animals interact with their inhomogeneous environment (e.g., habitat selection, collisions, illegal killings) and other individuals, while accounting for individual characteristics (e.g., sex, age, dispersal status).

Population-level results emerge from the individual-level simulations (Railsback and Grimm, 2012). These models are used for the management and conservation of large and small carnivores (e.g., Hradsky et al., 2019; Kramer-Schadt et al., 2011, 2005, 2004; Marucco and McIntire, 2010). Recent applications of IBMs for the lynx species allowed estimating illegal killing (Heurich et al., 2018), linking movements and genetic diversity (Premier et al., 2020) and evaluating reintroduction scenarios (Ovenden et al., 2019; Philips, 2020).

Lynx are large carnivores with large spatial requirements (Breitenmoser-Würsten et al., 2007). They are territorial and live in large connected forested areas (Vandel and Stahl, 2005; Zimmermann and Breitenmoser, 2007), which sustain large prey populations (Basille et al., 2009). Natural barriers (e.g., large waterbodies) as well as anthropogenic barriers (e.g., urban areas, highways) limit lynx movements (Schadt et al., 2002). Roads are complex infrastructures acting as semi-permeable movement barriers (Klar et al., 2006; Zimmermann and Breitenmoser, 2007) as well as an important source of mortality (Bencin et al., 2019; Ceia-Hasse et al., 2017). Therefore, a major modelling challenge when simulating lynx populations is to account for movements over large areas and consequently, for the impact of landscape characteristics on different demographic processes such as dispersal, territory establishment and survival rates. Because simulation rules in IBMs are defined at the individual level, these models appear as a great tool to integrate the complex interactions between landscape characteristics and both lynx demographic and spatial processes to simulate population changes on a large scale.

Our study aimed to assess the long-term persistence of the Eurasian lynx in the large range area delimited by the Upper Rhine meta-population and the Alpine population using the available population status in 2018. We build a spatially-explicit IBM that integrates up-to-date information on lynx ecology while accounting for habitat preferences and the risk of collisions with vehicles. We implement our model in the R programming language and share it publicly with open-source code allowing full reproducibility and its adoption by ecologists and conservationists. We use this model to forecast the fate of lynx populations over a 50-year time horizon. Finally, we provide several population metrics that help in diagnosing the long-term species persistence in its most western range area.

Material and Methods

Study area and populations

We conducted the study on Eurasian lynx (*Lynx lynx*) populations located in France, Germany and Switzerland (Fig. 1). The three main populations inhabiting the vast mountainous and forested areas of these countries are the Vosges-Palatinian (France-Germany), the Jura (France-Switzerland) and the Alpine (France-Switzerland) populations (von Arx, 2020). Some individuals were also observed in the Black Forest and its surroundings (e.g., Swabian Alb) in Germany (Fig. 1), but were not considered as a lynx population *per se* (von Arx, 2020). Therefore, we should refer to “mountain ranges” when speaking of the Vosges-Palatinate, Jura, Alps and Black Forest with its surroundings, but for simplicity and clarity, we will use “populations” throughout our paper.

The Jura and Alpine populations originated from individuals reintroduced in Switzerland in the 1970s (Breitenmoser et al., 1998; Vandel and Stahl, 2005), followed by a natural recolonization of the territories westward. After the complete decline of the Vosges-Palatinian population in the 18th century, a reintroduction of 21 lynx occurred in the southern part of the Vosges Mountains (France) between 1983 and 1993 (Vandel et al., 2006). Only 10 individuals contributed to the lynx local establishment (Vandel et al., 2006) without conclusive stabilization

(Charbonnel and Germain, 2020). Since 2016, the lynx has been back in the Palatinate Forest (Germany) thanks to a new reintroduction program finalized in 2020 (Scheid et al., 2021; Schwoerer, 2021) with a few individuals that already moved to the Vosges Mountains (Scheid et al., 2021; Schwoerer, 2021). Finally, only a few male individuals have been observed in the Black Forest area since 2013, most of them coming from the Swiss Jura Mountains (Mitarbeitende der Stiftung KORA, 2017; MLR, 2019; Wölfl et al., 2021). Lynx regular occurrences are yearly documented by the three countries.

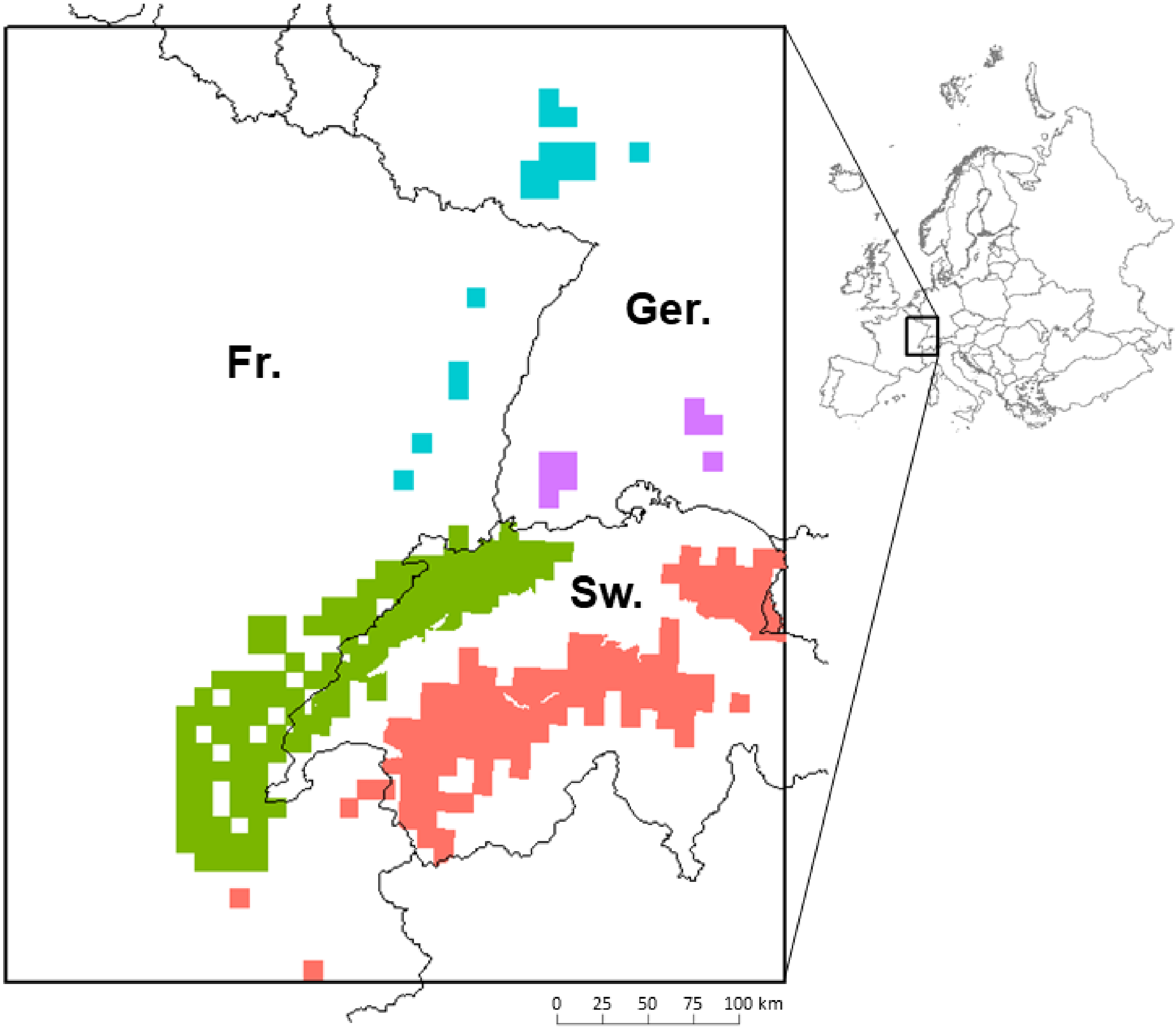

Figure 1: Eurasian lynx presence as available in 2017-2018 in France (Fr.), Germany (Ger.) and Switzerland (Sw.) in the study area (black rectangle). Data for France cover the period from 01/04/2013 to 31/03/2017 (OFB Réseau Loup-Lynx), for Germany from 01/05/2017 to 30/04/2018 (Bundesamt für Naturschutz) and for Switzerland from 01/01/2015 to 31/12/2017 (KORA). We used a standardized 10x10 km grid from the European Environment Agency for France and Germany, and a grid derived from the 1:25,000 map for Switzerland). The four colors are for the four different populations: the Vosges-Palatinian population (blue; 1,800 km^2) with cells in France (Vosges Mountains) and Germany (Palatinate Forest), the Black Forest population (purple; 900 km^2) in Germany, and the Jura (green; 12,057 km^2) and the Alpine (red; 11,190 km^2) populations with cells in France and Switzerland. Top right corner inset: Europe with the location of the study area.

Lynx population persistence

Based on previous works by Kramer-Schadt et al. (2004, 2005, 2011), we built a spatially-explicit individual-based model (SE-IBM) to simulate lynx populations dynamics and dispersal, while accounting for the risk of lynx-vehicle collisions and lynx habitat preferences. A SE-IBM is an IBM where individual responses to behavioral rules are constrained by environmental characteristics. Our lynx SE-IBM is made of four components (Appendix A). The first component represents the impact of road network on lynx survival via predicted collision probabilities. The second component represents the impact of land cover on lynx space use with the definition of different lynx habitat types. These first two components are spatial layers influencing the behavioral rules followed by simulated lynx individuals. The third component represents the initial lynx populations made of lynx individual's location and characteristics used to launch the SE-IBM. The fourth component details all SE-IBM rules including lynx demography, dispersal movement and territory establishment. A complete description of the four model components is available in Appendix A, and the SE-IBM structure following the Overview, Design concepts, and Details (ODD) protocol (Grimm et al., 2010, 2006) is provided in Appendix B.

We ran 200 replicates of the lynx SE-IBM forecasting the populations over 50 years. We used a different initial population (Appendix A) at each replicate to avoid bias due to initial locations of simulated individuals. Initial populations were created based on real monitoring data (Appendix A). We defined a burn-in phase of 10 years after the start of the simulation (i.e., this phase is not included in the conclusions of the analyses) to let the population settle down and start with a stable system. We removed all mortalities during the first year of simulation to allow all individuals to find a territory, if they can, without dying while doing so. To evaluate lynx persistence, we analyzed a) population growth rates, b) establishments outside of the lynx native population, and c) female territory occupancy.

a) We extracted the number of individuals in each population, for every year and for each replicate. Then, we calculated the growth rate for each replicate and each population over the simulated years as the number of individuals at time *t* divided by the number of individuals at time *t*-1. Furthermore, we calculated the mean growth rate per year and per population, and the 95% confidence interval of the mean over the 200 replicates.

b) We extracted the number of times individuals established their territory in a population area not corresponding to the one they were born in (“Population layer”, Appendix A) for every year and for each replicate. We did not account for individuals which moved to another population area during their dispersal but finally came back to their native population area to establish, nor those which died in another population area while dispersing. We calculated the cumulative sum of these movements over the simulated years for each replicate and for each movement type (e.g., from the Alpine to the Jura population, from the Jura to the Vosges-Palatinian population). Then, we calculated the mean and 95% confidence interval of the mean across all replicates.

c) We extracted female territory locations at the last year of simulation for each replicate. We focused on female territories as male territories are based on those of the females. We assigned a “1” to each cell of the gridded study area (1 km^2) that was occupied by a female territory and a “0” otherwise. Finally, we estimated territory occupancy by calculating the mean value per cell from these rescaled maps over the 200 replicates. We also did a visual validation of our model predictions using GPS and VHF tracks from several collared female residents that we overlaid on the resulting territory occupancy map (details in Appendix C).

Results

Population growth rates

Simulations predicted similar growth rate patterns for the Alpine, the Jura and the Vosges-Palatinian populations, with a growth rate above 1 (i.e., growing phase) slowly decreasing towards reaching 1 (i.e., stabilization phase). The Alpine and Jura populations had very similar patterns with their maximum growth rates equal to 1.04 (sd = 0.06) and 1.03 (sd = 0.07) at the 13th and 14th year of simulation, respectively. They both quickly reached a stabilization phase and fluctuated a little over the final time span of the simulation. The Vosges-Palatinian population had the highest growth rate, equal to 1.11 (sd = 0.21), in the 10th year of the simulation. This population stabilized later than the Alpine and Jura populations. The Black Forest population had a more fluctuating growth rate over the simulation. It reached a minimum of 0.87 (sd = 0.49) at the 15th year of simulation and a maximum of 1.37 (sd = 0.62) at the 25th year of simulation; confidence intervals around mean growth rates were large and much larger than in other populations.

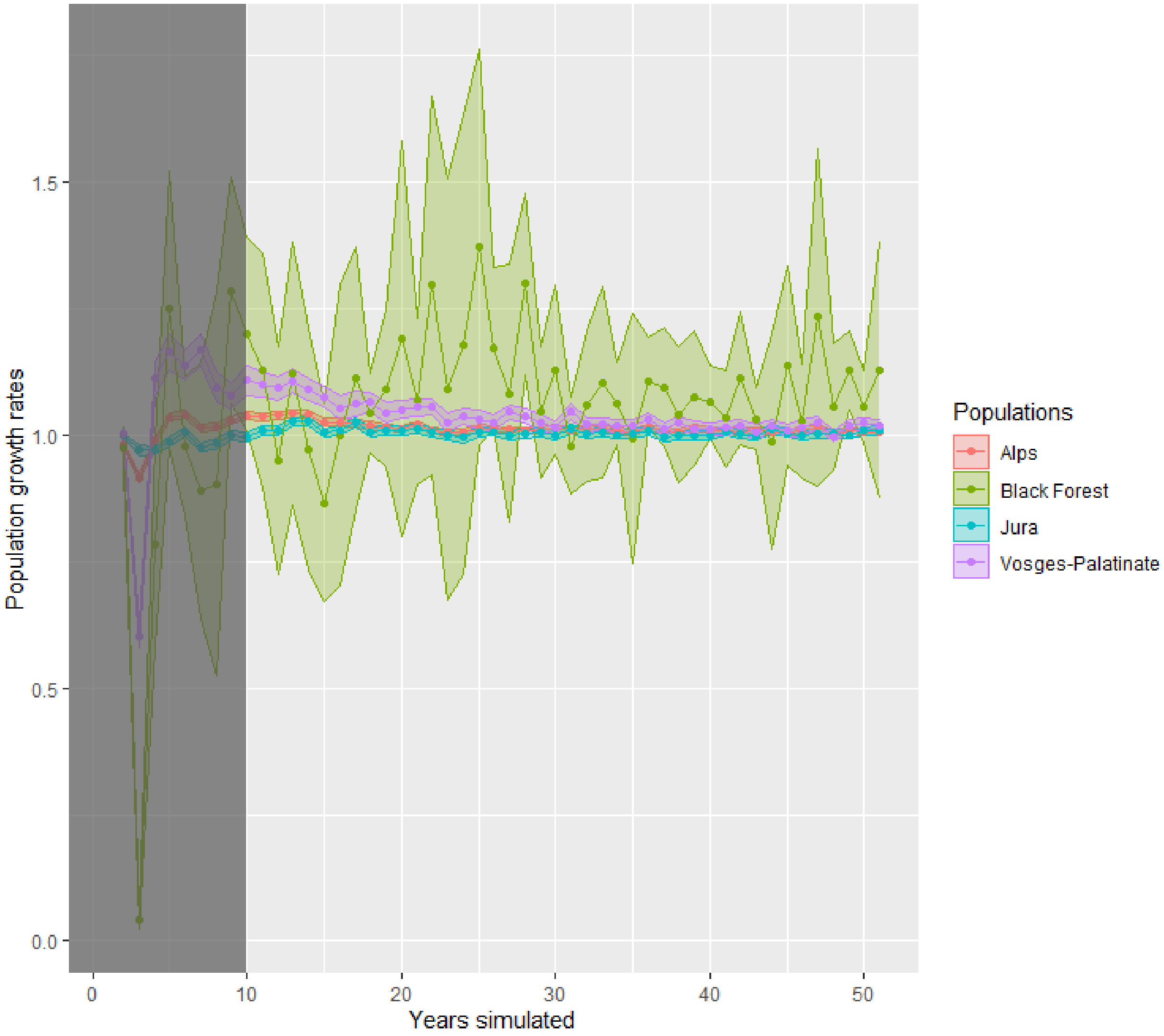

Figure 2: Annual rates of increase over the simulated years for each population. The grey area represents the 10-year burn-in phase. Points are mean over 200 replicates and envelopes are 95% confidence intervals from 200 replicates.

Lynx establishments outside their native populations

The cumulative number of lynx establishments in a population area different from their native one showed that the Jura population is at the center of lynx movements between populations. The most important movement was for individuals born in the Jura population going to establish themselves in the Alpine population. After 50 years, the Jura population had, on average across all replicates, 2.0 individuals (sd = 1.7) leaving to settle in the Alpine population over the whole simulated period, 1.0 individuals (sd = 1.6) leaving to settle in the Vosges-Palatinian population, and 0.3 individuals (sd = 1.1) leaving to settle in the Black Forest. The Alpine population showed a movement of 1.2 individuals on average (sd = 1.4) leaving to settle in the Jura population over the simulated period of 50 years. There were only a few movements from the Vosges-Palatinian (0.3 individuals on average, sd = 0.7) or from the Black Forest (0.2 individuals on average, sd = 0.8) populations towards the Jura to establish. There was no exchange of individuals simulated between the Alpine, the Vosges-Palatinian and the Black Forest populations.

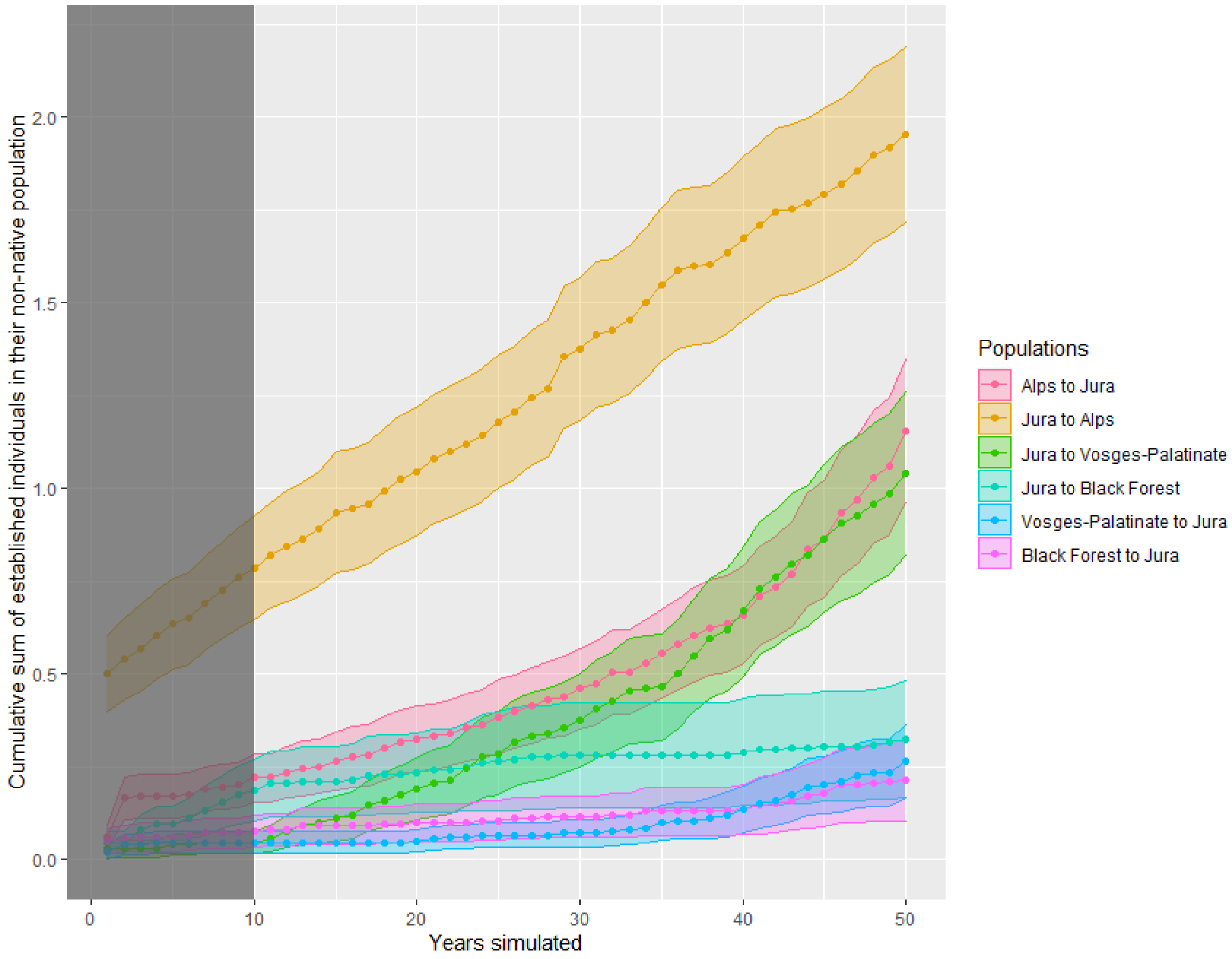

Figure 3: Cumulative number of lynx establishments outside of their native populations over 50 simulated years. Colors represent different directions from the native populations to those where individuals established. We did not represent pairs of populations for which there were no exchange between them. The grey area represents the 10-year burn-in phase. Points are mean over 200 replicates and envelopes are 95% confidence intervals around the mean from 200 replicates of cumulative sums over years for each pair of populations.

Territory occupancy

At the end of the simulation period, female territories were predicted to cover most of the Jura (mean = 0.45, sd = 0.35) and the Alps (mean = 0.60, sd = 0.27) with a very high frequency across replicates. Most of the area that sustained territories had a mean territory occupancy of over 0.8 (maximum value for the Alpine population = 0.98, maximum value for the Jura population = 0.97). There were very contrasting values in predicted female territories for the Vosges-Palatinian population (mean = 0.23, sd = 0.33). Female territories were established with a very high frequency of occurrence across the replicates in the Palatinate Forest in Germany (maximum value = 0.94), whereas territories were established less frequently in the southern part of the Vosges Mountains in France. Finally, mean territory occupancy was the lowest for the Black Forest population (mean = 0.03, sd = 0.02, maximum value = 0.09).

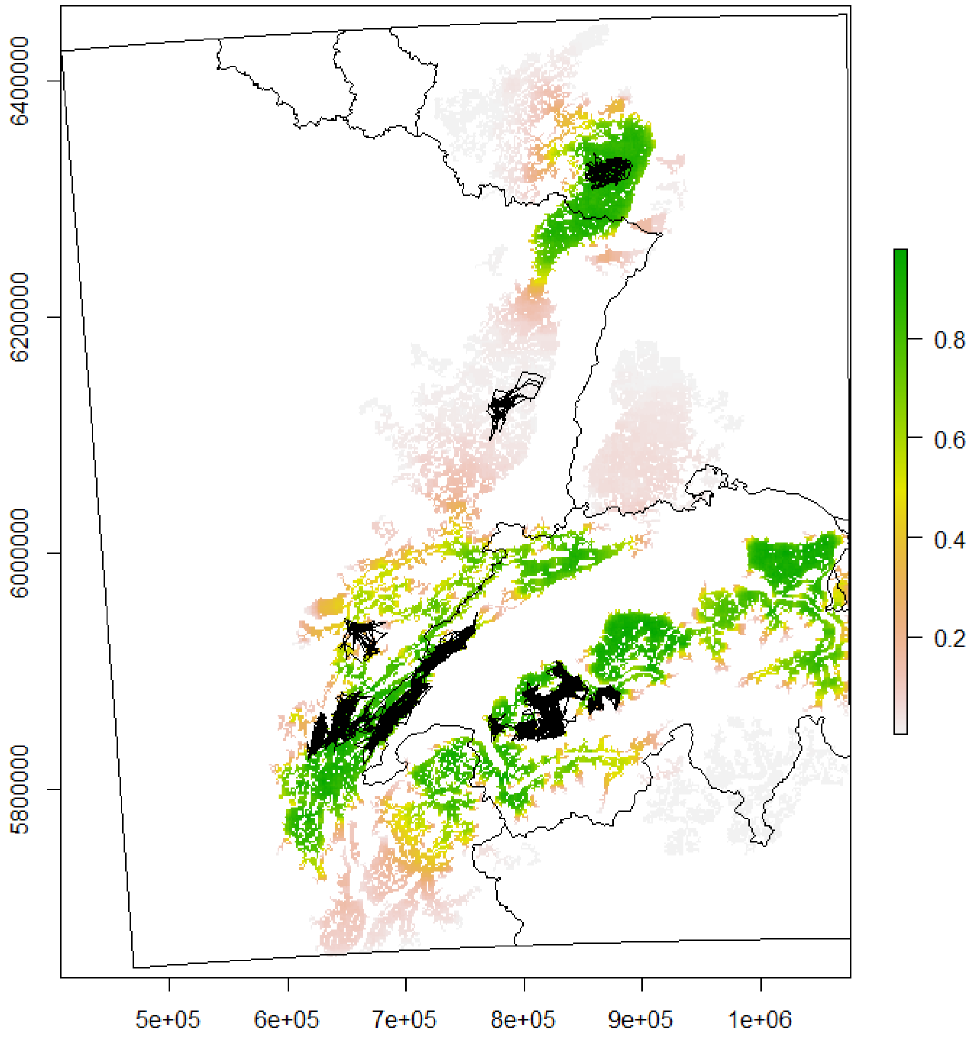

Figure 4: Occupancy by female territories over the study area at the last year of simulation. Values between 0 and 1 are mean occupancy probability per cell of 1 km^2 over 200 replicates (e.g., cell with value equal to 1 were always occupied in all simulation replicates). GPS and VHF recorded paths for female residents are overlaid as thin black lines. A zoom of the different areas with telemetry data is presented in Appendix C.

Discussion

The well-established Alpine and Jura populations

The model predicted a steady growth of Alpine and Jura populations, quickly reaching a stabilization phase indicating that they may soon be at carrying capacity. However, carrying capacity could be higher than what we found in our simulations, depending on the strength of density-dependence processes (Zimmermann et al., 2007). Although we assumed that the number of individuals an area can support is mainly defined by female territory size, our model does not include a relationship between lynx behavior and density. Yet, studies found that lynx density also influences home range sizes (Pesenti and Zimmermann, 2013), and differently for females and males (Aronsson et al., 2016). For instance, in the North-Western Swiss Alps, lynx territories were much larger in the 80s when lynx density was lower compared to the 90s (Breitenmoser-Würsten et al., 2001). The Alpine and Jura areas could therefore support more individuals if density-dependent mechanisms occur. On the other hand, threats that we did not include in the simulations, such as low genetic diversity (concerning the Alpine population in particular; Stiftung KORA, 2021) or illegal killing (Arlettaz et al., 2021), may slow the predicted growth.

The Jura population as the crossroad of Western Europe lynx movements

The Jura population was found to be the only population connected by lynx exchanges with all the other populations. However, individual exchanges were estimated very low, with only a few individuals moving from their native population to establish their territory in another one over the 50 years. In Switzerland, only a few lynx movements between the Alpine and Jura populations have been observed until now despite a large camera trapping effort over the years. These two populations also differ genetically, suggesting very few exchanges between them (Breitenmoser-Würsten and Obexer-Ruff, 2003). When inspecting model output maps (Fig. 4), individuals are contained in the Swiss Alps, restricted to an area of good habitat almost totally surrounded by less favorable habitats (Appendix A, Fig. A.3). However, individuals have recently started to settle permanently on the Swiss Plateau (between Alps and the Jura Mountains) predicted with less favorable habitats. Some have even reproduced successfully (F. Zimmerman, pers. comm.), indicating potential connections between the two populations. On the other hand, our model suggests connectivity between the Jura and Alpine populations on the French side with a continuity of a few forested corridors until the Chartreuse Mountains in the Alps (Zimmermann and Breitenmoser, 2007). Many observations were made via camera traps of lynx moving between the southern part of the Jura population and the Chartreuse Mountains (Bailly, 2021). However, movement barriers (e.g., highways) may prevent connections with the rest of the Alpine populations in Switzerland.

Lynx movements from the Jura to establish within the Vosges-Palatinian population may be possible but rare (one case on average simulated over 50 years). This is coherent with field monitoring that highlighted the presence of only a male in the south of the Vosges Mountains coming from the Jura Mountains during the winter 2014-2015 (Chenesseau and Briaudet, 2016; Hurstel and Laurent, 2016). Connectivity between these two populations remains far from optimal because of multiple barriers (e.g., highways, railroads and rivers) that impede lynx dispersal between the two mountain ranges and increase collision risk (Morand, 2016; Zimmermann and Breitenmoser, 2007).

Regarding the Black Forest (including the adjoining Swabian Alb area), six males are known to have immigrated from the Swiss side of the Jura population since 2013 (unpublished data, Forest Research Institute Baden-Wuerttemberg; Drouet-Hoguet et al., 2021; Mitarbeitende der Stiftung KORA, 2017) as well as two males from the Northeastern Alps (Herdtfelder et al., 2021). Simulated lynx movements towards the Black Forest seem therefore largely under-estimated in our model, probably because we only accounted for individuals who successfully established. Dispersal of individuals from the Jura or the Alps towards the Black Forest area may have been simulated but if individuals did not establish successfully, they were not recorded. Moreover, male establishment is driven by female presence in our model, and because the Black Forest population did not have any female, new males arriving could not establish and were doomed to die while searching for females. A more realistic rule for male establishment would be to let them search for females but still allow them to settle after a defined period of time, even without females. It happens quite regularly that males show territorial behavior even without females (M. Herdtfelder, pers. comm.).

The increasing Vosges-Palatinian population

Projections for the Vosges-Palatinian population showed a growth over the next 50 years. However, there was a difference between the northern part of the population range (Northern Vosges in France and Palatinate Forest in Germany) predicted with high resident female occupancy compared to the low occupancy predicted from Central to Southern Vosges. The lynx reintroduction program in the Palatinate Forest conducted since 2016 and the arrival of new individuals colonizing the Northern Vosges and regions more to the south (Schwoerer 2021 ; Scheid et al. 2021) are currently one of the main inputs. Lynx abundance was initially a bit higher in this smaller part of the Vosges-Palatinian population (i.e., 11 individuals in the Palatinate Forest compared to 8.4 individuals on average in the Vosges Mountains in France). The habitat quality in the Vosges Mountains and the Palatinate Forest appears favorable for lynx establishment (Appendix A, Fig. A.3). However, the lack of functional connectivity between the Jura and the Vosges-Palatinian populations on one hand, and within the Vosges Mountains on the other hand, may explain the difficulty for lynx to colonize the Vosges Mountains elsewhere than in the Northern Vosges from the Palatinate Forest. Indeed, lynx movements between Jura and Vosges-Palatinian populations are possible, but so far very scarce. In the same way, functional connectivity between the Northern Vosges and the rest of the area may also be altered by anthropogenic barriers, for example at the *Col de Saverne* where this forest bottleneck is fragmented by both a highway and high-speed railway (Klar et al., 2006; Morand, 2016; Scheid et al., 2021). However, movement is possible as lynx from the Palatinate Forest are known to have crossed this pass, some even going back and forth (Idelberger et al., 2021; Scheid et al., 2021). Lynx reintroduced in the Palatinate Forest could therefore reinforce the Vosges Mountains part of the population if functional connectivity would allow it.

Because our model does not include human attitudes towards the species, we warn against its blind use to assess the effect of reinforcement on lynx long-term persistence without accounting for the human dimension component. Illegal killings, as they occurred after the 90's reintroduction program in the southern part of Vosges Mountain (Vandel et al., 2006) as well as more recent ones (Germain, 2020) may be an additional mortality that the model does not account for. The extent of acceptance towards species reinforcement from some local stakeholders is an important element (Charbonnel and Germain, 2020). In this case, we recommend that our model be extended to include the dynamics of the whole socio-ecosystem (Behr et al., 2017; Guerrero et al., 2018).

The isolated Black Forest

Growth rates were very heterogeneous along the simulated time period and confidence intervals around the mean were large for this population. This is due to the demographic stochasticity which impacted the Black Forest population a lot because of its small size when starting the simulation compared to other populations. The model simulated only a few lynx movements from the Jura population to the Black Forest, which did not contribute much to population growth, and female established with a very low rate after 50 years. These results tend to show that the Black Forest population is unlikely to be soon recolonized by lynx, especially considering that observed individuals are only males (Drouet-Hoguet et al., 2021; Port et al., 2021). For instance, no female lynx has been observed until now dispersing from Jura to Black forest crossing the Rhine valley that separates the Black Forest from the Jura population, probably due to their risk-shy nature compared to males (Port et al., 2021). Monitoring data from 2021 indicate that one female from the very eastern Alpine population crossed this barrier for the first time (M. Herdtfelder, pers. comm.). Using IMBs, Herdtfelder (2012) showed that population reinforcement with lynx females might be one solution considering that habitat is of good quality in this area. Again, if our model was to be used to assess this strategy, it would need to incorporate human dimensions.

Model limitations

Although model predictions passed the validation step (Appendix C), several aspects of our IBM could still be improved. The habitat layer is defined in categories with strict “barriers” that the simulated lynx cannot cross whereas the species may be tolerant of human activities (Basille et al., 2009; Bouyer et al., 2015). Lynx may live near urban areas and cross small lakes (F. Zimmermann, pers. comm.). In that context, the habitat layer could be improved by being defined as a continuous variable representing a degree of preference or permeability of the landscape to avoid prohibiting the movement through certain landscape elements. The habitat layer could also be improved by accounting for roads and their associated structures as movement barriers (e.g., highways difficult to cross, over-pass facilitating the movement) instead of only mortality sources (Klar et al., 2006; Marchand et al., 2017). In our model, lynx movement is not impeded by roads. The inclusion of permeability of these linear barriers to the lynx movements may help to refine the behavior rules (Marchand et al., 2017). We could also redefine the movement behavior rules to be sex or age-dependent. Indeed, females seem more conservative (i.e., disperse close to their natal range) compared to males and some males are able to disperse over long distances (Port et al., 2021).

Perspectives for assessing lynx conservation strategies

Our model used to evaluate lynx population persistence could be applied to better understand aspects of lynx conservation that we did not include yet, such as illegal killings (Heurich et al., 2018). Moreover, thanks to its individual-based structure, a genetic component could also be included to track relatedness between individuals and allow studying inbreeding risk and Allee effects (Premier et al., 2020). Our model could also be used to test the effect of different scenarios, either by modifying the lynx populations (e.g., illegal killings, reintroduction programs) or the landscape (e.g., green bridges, roads construction, habitat destruction or restoration) and assess the potential benefits or negative effects on lynx population persistence. Modifications of road networks to improve connectivity, such as the removal of road segments or the addition of overpasses (i.e., green bridges), could be tested. Then, their effect could be included through a new layer of collision probabilities and the population persistence calculated accordingly. Similarly, other modifications of land cover (e.g., restoring forest areas) could also be tested. This model could be very useful for stakeholders working on corridors and the reduction of lynx-vehicle collisions as well as reintroduction programs and species acceptance.

Conclusion

In this paper, we built and analyzed a spatially-explicit individual-based model to forecast the fate of lynx populations over the next 50 years. Our results suggest that exchanges of individuals between populations to establish new territories were limited, and emphasize that the Jura population plays the role of a Western Europe crossroad. Overall, lynx persistence in the Upper Rhine meta-population and the Alpine population over the next 50 years seems likely on a large scale. However, lynx persistence in the southern part of the Vosges-Palatinian population and in the Black Forest appears more challenging without long-term conservation planning like improving connectivity or reintroduction programs.

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Appendix A – Detail of the lynx spatially-explicit individual-based model

A complete description of the model following the Overview, Design concepts, and Details (ODD) protocol (Grimm et al., 2010, 2006) is provided in Appendix B.

Our lynx spatially-explicit individual-based model is made of four components (Fig. A.1). The first component represents the impact of road network on lynx survival via predicted collision probabilities. The second component represents the impact of land cover on lynx space use with the definition of different lynx habitat types. These first two components are spatial layers influencing the behavioral rules followed by simulated lynx individuals. The third component represents the initial lynx populations made of lynx individual’s location and characteristics used to launch the SE-IBM. The fourth component details all SE-IBM rules including lynx demography, dispersal movement and establishment.

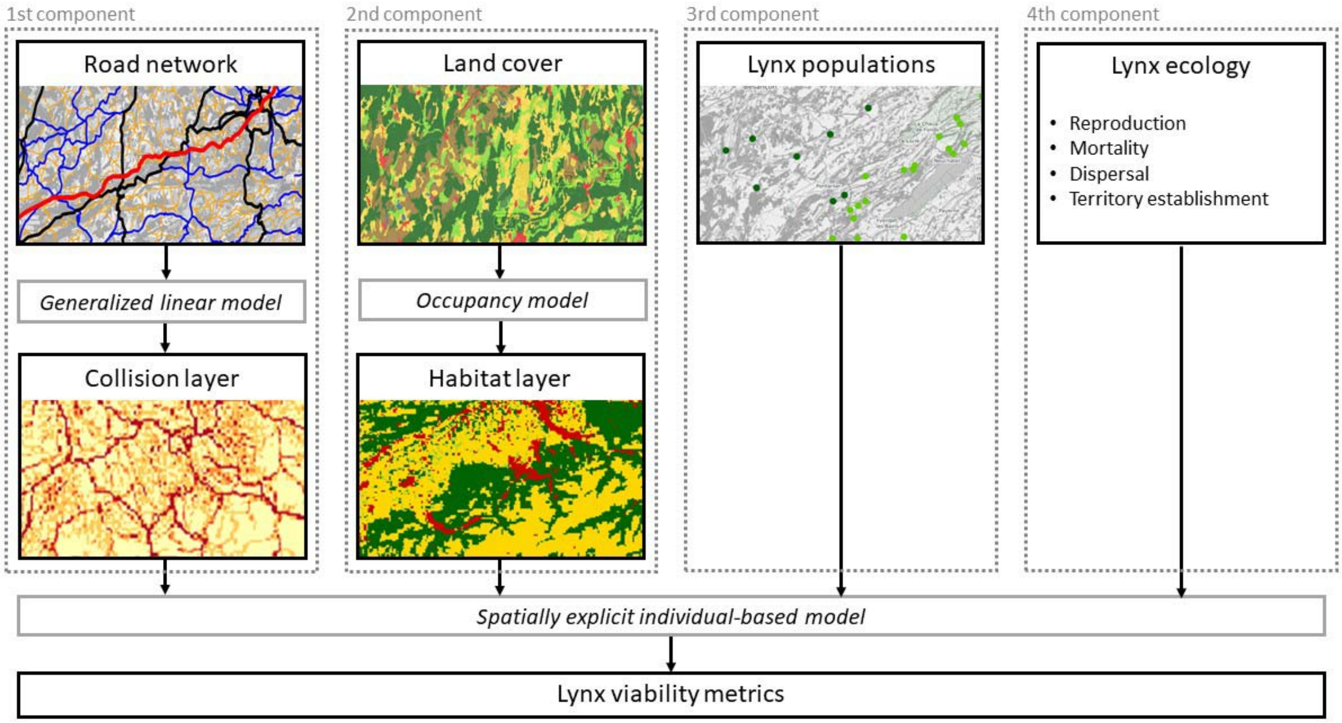

Figure A.1: The four components of the lynx SE-IBM. The first component represents the impact of road network on lynx survival through vehicle collision. A generalized linear model predicted collision probabilities ("Collision layer", Fig. A.2). The second component represents the impact of land cover on the lynx populations. A site-occupancy model predicted lynx habitats influencing lynx movement ("Habitat layer", Fig. A.3). The third component represents lynx populations with individuals' locations and characteristics (Fig. A.4). The fourth component encompasses all ecological rules and SE-IBM parameters. All four components are included in the SE-IBM to simulate lynx populations and assess their persistence with different metrics.

Impact of road network (SE-IBM 1st component)

We first built a risk model to predict collision probabilities between lynx and vehicles within the 1 km² resolution gridded study area. We used lynx mortality events recorded by the wolf-lynx monitoring framework implemented in France (Duchamp et al., 2012), Réseau Loup-lynx https://www.loupfrance.fr/suivi-du-loup/reseau-loup-lynx/) to train a logistic regression explaining lynx collisions using lynx presence and both road and environmental characteristics (Visintin et al., 2018, 2017). We used the IGN route500 © for France (IGN ROUTE 500, 2018) and OpenStreetMap© for the other countries (Geofabrik OpenStreetMap, 2014) as data sources to extract total road length per cell and the type of road of the longest road segment in each cell. We classified the road segments as "highways" (i.e., "Type autoroutier" in route500 © data, "motorway", "motorway_link", "trunk" and "trunk_link" in OpenStreeMap data), "main road" (i.e., "Liaison principale" in route500 © data, "primary" and "primary_link" in OpenStreeMap data), "secondary road" (i.e., "Liaison régionale" in route500 © data, and "secondary" and "secondary_link" in OpenStreeMap data) and "local road" (i.e., "Liaison locale" in route500 © data, "tertiary", "tertiary_link" and "unclassified" in OpenStreeMap data). For environmental characteristics, we used Corine Land Cover© at 100 m of resolution for all Europe (Copernicus, 2012) to calculate the proportion of urban area in each cell (i.e., human presence). The best model identified included total road length, type of road of the longest road segment and the proportion of urban area. Distance to highways and human density were also tested to explain lynx-vehicles collisions but were not significant. We used this model to predict a collision probability between 0 and 1 in each cell of our study area to create the "Collision layer" (Fig. A.2). Lynx presence was also included as explanatory variable in the model. To predict collision probabilities, we defined the lynx as present everywhere on the gridded study area because simulated individuals in the SE-IBM suffer from collision probability on the cells they are located. Study area grid cells without road intersecting them have a zero collision probability.

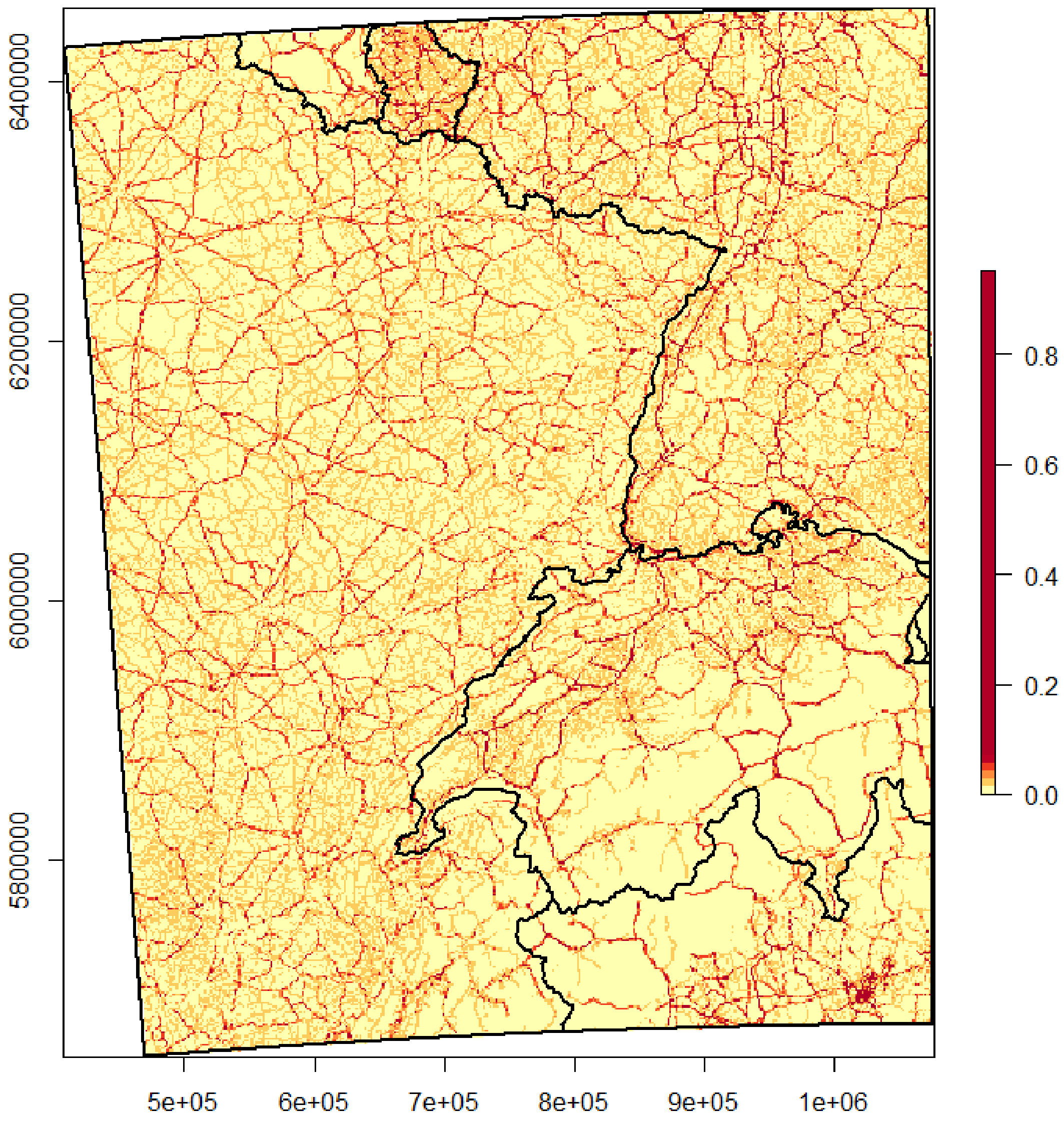

Figure A.2: "Collision layer" with collision probabilities between lynx and vehicles estimated between 0 and 1 (yellow to red color scale). Collision probabilities are assigned to each cell of the gridded landscape over the whole study area (black rectangle) used in the lynx SE-IBM using the collision model. Limits of the countries (main text, Fig. 1) are overlaid in black over the map.

Impact of land cover (SE-IBM 2^{nd} component)

We built a habitat model to define a habitat type for each cell within the 1 km² resolution gridded study area. We used a multi-year occupancy model (Isaac et al., 2014; Outhwaite et al., 2018) to explain regular lynx presence using land cover types important to lynx (agricultural fields, forest and open land), the distance to highways (Basille et al., 2013), and human density. The model was calibrated using French data for the lynx presence from 1994 to 2017 (data: Réseau Loup-Lynx https://www.loupfrance.fr/suivi-du-loup/reseau-loup-lynx/) and then predicted over our entire study area. We used used Corine Land Cover© at 100 m of resolution for all Europe (Copernicus, 2012) to calculate the proportion of agricultural and cultivated fields, forest, pasture and open land in each cell. We used the IGN route500 © for France (IGN ROUTE 500, 2018) and OpenStreetMap© for the other countries (Geofabrik OpenStreetMap, 2014) as data sources to calculate the distance from each cell center to the nearest highway. We also used IGN© data for France (IGN ADMIN-EXPRESS-COG, 2018) and NASA© data for the other countries (CIESIN GPWv4, 2015) to calculate the mean human density per cell. The best model identified to explain lynx presence included presence of agricultural fields, forest, and open land, distance to highways and human density. Shrub cover and road length were also tested to explain lynx presence but were not significant. We used this model to predict lynx occupancy probability in our entire gridded study area for the year 2017. We then categorized the cells to obtain a habitat layer with the four habitat types defined by the habitat categorization of Kramer-Schadt et al. (2004): “breeding”, “dispersal”, “matrix” and “barrier” (Fig. A.3). All cells where lynx occupancy was predicted as non-null (above or equal a threshold of 0.01) were considered “breeding” habitat. All forested areas not already “breeding” habitat were considered as “dispersal” habitat. Cells with more than half of their surface covered by water or urban area defined by Corine Land Cover© (Copernicus, 2012) were considered “barrier” for lynx movements. The rest was considered “matrix” area (i.e., habitat not favorable for lynx but that can be traversed by dispersers). The map of categorized cells for our study area defined the “Habitat layer” used in the SE-IBM (Fig. A.3).

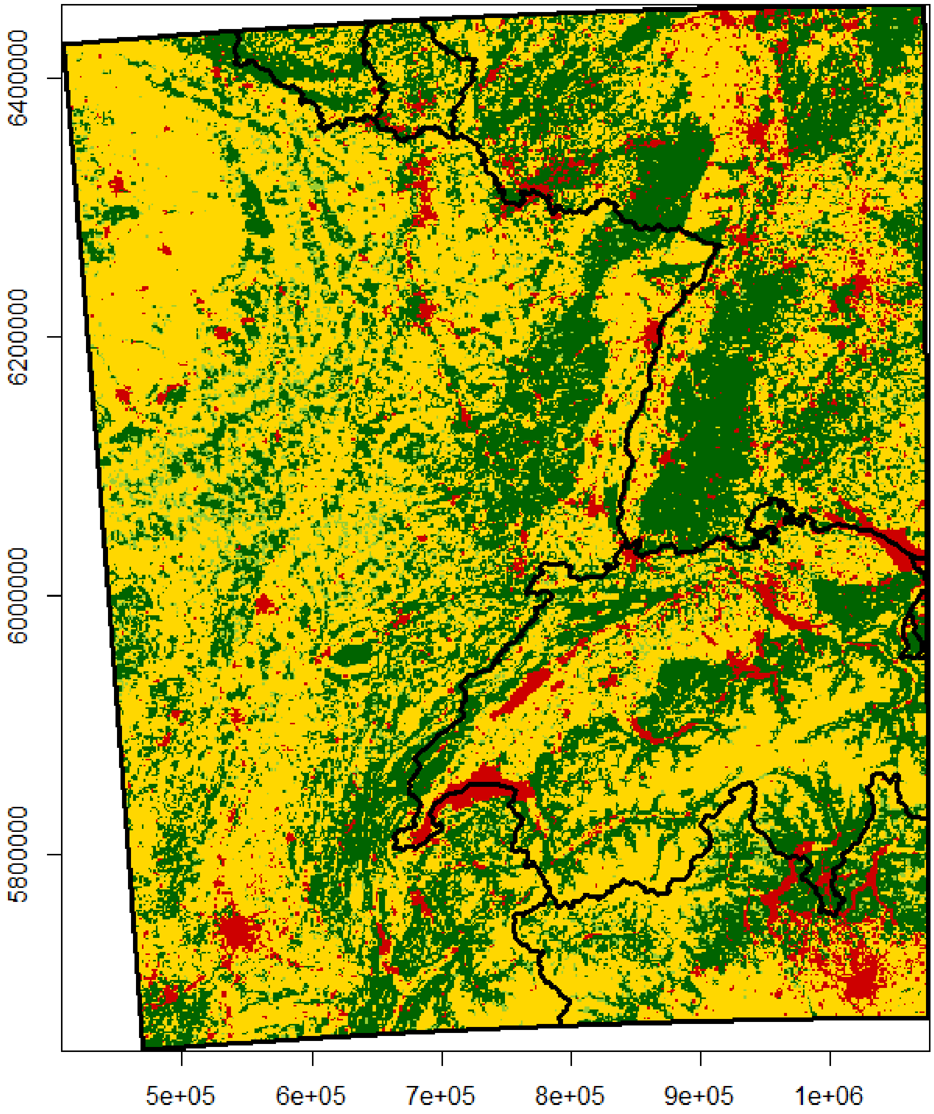

Figure A.3: “Habitat layer” with lynx habitat types as breeding habitat (dark green), dispersal habitat (light green), matrix (yellow) and barrier (red). Habitat types are assigned to each cell of the gridded landscape over the whole study area (black rectangle) used in the lynx SE-IBM using the habitat model. Limits of the countries (main text, Fig. 1) are overlaid in black over the map.

Lynx initial populations (SE-IBM 3rd component)

The initial populations to launch the SE-IBM were built with generated locations and characteristics for the lynx populations using the best data available at the time of the study (Fig. A.4). We used cells of regular lynx presence for France (for the time period of 01/04/2013 to 31/03/2017 from the Réseau Loup-Lynx, main text, Fig. 1), Switzerland (for the time period of 01/01/2015 to 31/12/2017 from the KORA, main text, Fig. 1) and Germany (for the time period of 01/05/2017 to 30/04/2018 from the Bundesamt für Naturschutz, main text, Fig. 1). In these cells, we extracted “breeding” and “dispersal” areas and sampled random lynx locations in these areas to locate individuals within the different populations. In France, we used the most reliable lynx density estimate (1.14 lynx per 100 km^2; Gatti et al., 2014) regardless of differences in local densities (Gimenez et al., 2019) to convert the area of regular presence into a number of individuals to create. Ninety-two individuals were generated and dispatched over “breeding” and “dispersing” areas in France: in the Vosges Mountains (500 km^2 of presence), in the French Jura (7,700 km^2 of presence) and in the French Alps (500 km^2 of presence). A density of 1.14 lynx per 100 km^2 may be an over- or an under-estimate of the lynx density in certain areas but in the absence of local density for each French population, we used this mean value. On average, this method led to 4.5 individuals in the French Alps (sd = 2.1), 77.0 individuals in the French Jura (sd = 3.4), and 8.4 individuals in the Vosges Mountains (sd = 2.7). In Switzerland, we generated 230 individuals distributed in the different areas of presence according to estimated local population sizes in 2017 (data: F. Zimmermann, pers. comm.). In Germany, 11 lynx (i.e., reintroduced lynx still alive and their offspring) were identified in the Palatinate at the end of April 2018 (Scheid et al., 2021) and four male lynx were identified in the Black Forest (Wölfl et al., 2021). Therefore, we generated 11 lynx in Palatinate Forest and 4 lynx in the Black Forest area.

Except for reintroduced individuals for which we knew their characteristics, we randomly assigned individuals' sex (male or female) according to ratio 1:1 usually observed at birth (Breitenmoser et al., 1993; Jedrzejewski et al., 1996). We also randomly assigned an age between 2 and 15 as lynx usually live until 15-17 years old (e.g., Breitenmoser-Würsten et al., 2007a). Age is defined as 0 for the first year of life, 1 during the second year of life, etc. For the Palatinate part of the Vosges-Palatinian population, we assigned known age and sex (5 females and 6 males). In the Vosges Mountains, only males were detected in 2017 thanks to the camera trap survey design implemented (Charbonnel and Germain, 2020) and no case of reproduction was reported during the years preceding our analyzes. We then only defined males for the individuals located in the Vosges part of the Vosges-Palatinian population, with ages randomly generated. We also only defined males for the Black Forest population. All generated individuals were defined as "disperser" to avoid the bias of defining territories by ourselves. They find their territories on their own as defined by the SE-IBM rules.

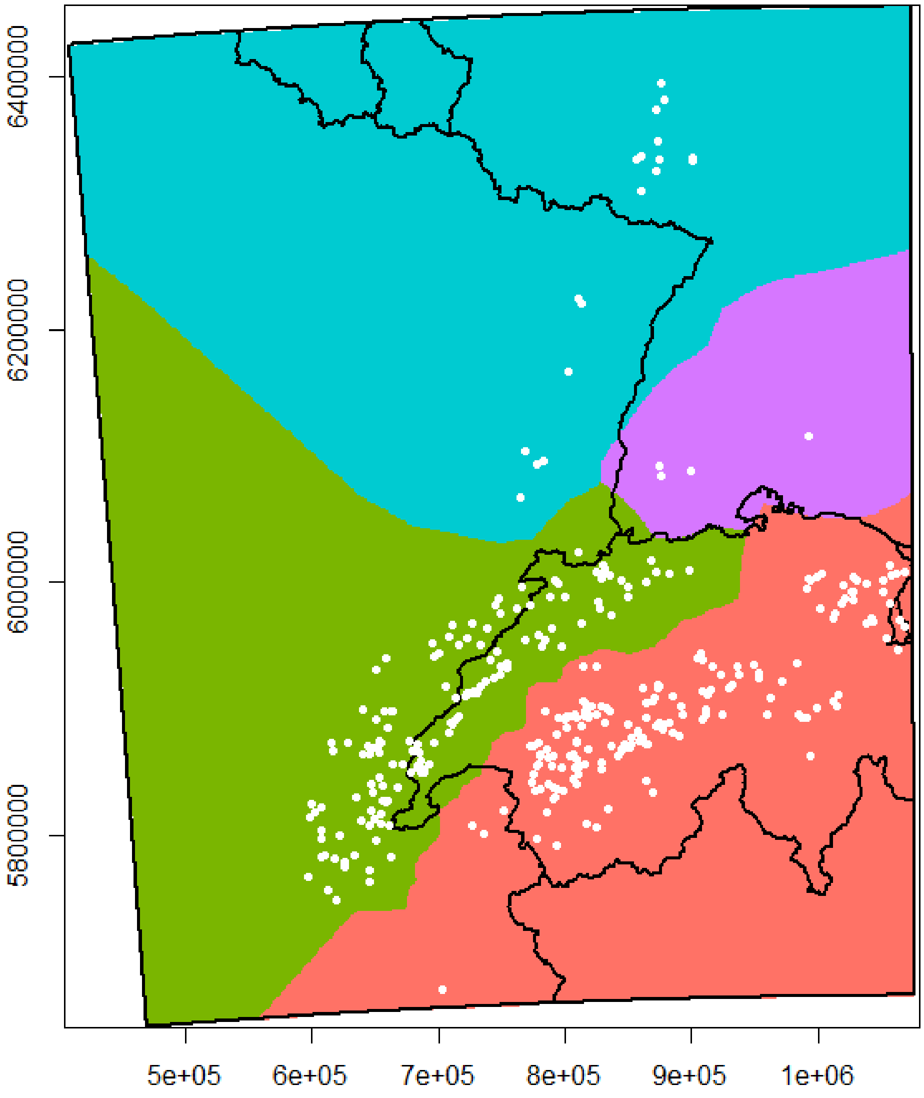

Figure A.4: “Population layer” with the example of an initial population over the whole study area (black rectangle) used in the lynx SE-IBM using the habitat model. Limits of the countries (main text, Fig. 1) are overlaid in black over the map. Areas for the Vosges-Palatinian (blue), Black Forest (purple), Jura (green) and Alpine (red) populations were defined using the cells of lynx regular presence as in 2017-2018. Each cell of the gridded study area was assigned the population from its closest cell of lynx regular presence. White dots represent one initial population (i.e., simulated lynx released at the beginning of one simulation replicate) generated using the cells of lynx regular presence, the density or number of lynx in each population and the habitat layer to place these theoretical individuals in breeding or dispersal habitats. A different initial population was used at each simulation replicate; we used the same cells of lynx regular presence, the same density or number of lynx in each population and the same habitat layer, only the generated locations, and chosen sex and age for unknown individuals, were different.

SE-IBM rules according to lynx ecology (SE-IBM 4th component)

Lynx individuals are simulated over a landscape represented as a grid of 1 km² resolution covering the whole study area and encompassing the four lynx populations (main text, Fig. 1). The gridded study area resolution corresponds to lynx's perceptual range (Haller and Breitenmoser, 1986) as well as to the resolution of previous lynx IBMs (Kramer-Schadt et al., 2011, 2005, 2004). Two variables characterize the gridded study area: a probability of lynx-vehicle collision between 0 and 1 ("Collision layer", Fig. A.2) and a habitat type among "breeding", "dispersal", "matrix", and "barrier" ("Habitat layer", Fig. A.3). Simulated individuals are characterized by their "disperser" (i.e., not established on a territory and in search of one) or "resident" status (i.e., established on a defined territory), their age and their sex.

Simulated resident individuals follow rules on a yearly time step (Fig. A.5). They do not move (i.e., their movement inside their territory is not simulated), they hold a territory and they may reproduce once a year. They suffer two types of annual mortality: a fixed baseline mortality and a spatial one derived from the collision layer. Simulated dispersing lynx follow rules on a daily time step (Fig. A.5). They do not have a territory yet and move every day along the gridded study area, searching for a place to establish themselves. Their dispersal movement (Fig. A.6) and search for a territory (Fig. A.7) are driven by the habitat layer. At each step individuals can die from the spatial mortality derived from the collision layer, and daily from a fixed baseline mortality.

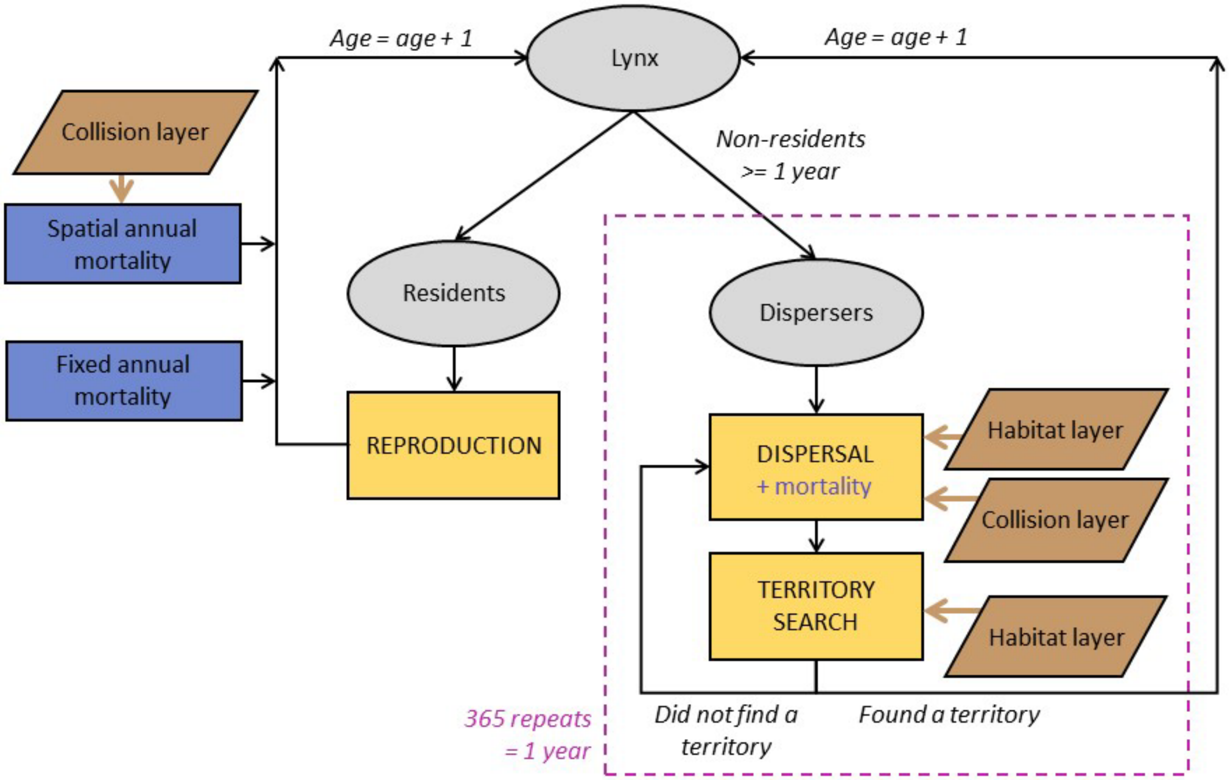

Figure A.5: Diagram of the main structure of the SE-IBM with the main events affecting both resident and dispersing simulated lynx. Grey circles represent individuals. Yellow boxes represent SE-IBM main events detailed in model description. Blue boxes and blue writing represent different mortality causes individuals suffer. Brown boxes represent environmental layers used in the SE-IBM and brown arrows point where behavioral rules are constrained by these layers. Black arrows indicate the flow of the model. Dispersers can go through dispersal and territory search every day during a year, as long as they do not find a territory (Figs. A.6 and A.7).

Lynx are solitary carnivores (i.e., each resident holds its own territory), except during reproduction (i.e., mating between male and female) and when females are raising their kittens

(Breitenmoser et al., 1993; Stahl and Vandel, 1998). Female residents reproduce with a probability of 0.81 if a resident male occurs on their territory (Breitenmoser-Würsten et al., 2007a; López-Bao et al., 2019). Females have 0.5 chance to be sexually mature at 1 year old, and they are all sexually mature at 2 years old. Males have 0.5 chance to be sexually mature at 2 years old, all being sexually mature at 3 years old (Breitenmoser-Würsten et al., 2007a; Kramer-Schadt et al., 2005; Kvam, 1991). In the wild, lynx litter size averages two kittens and can be up to four (Breitenmoser-Würsten et al. 2001; Lopez-Bao et al. 2019). However, around 50% of lynx kittens die before reaching the age of dispersal (Breitenmoser-Würsten et al., 2007a, 2001). We simulated that resident females up to 11 years old ("young" female in the SE-IBM model) produce 1 or 2 kittens, with a probability of 0.5 for each litter size, that will survive until becoming dispersers the following year (Henriksen et al., 2005; Kramer-Schadt et al., 2005). Senescence reduces litter size, therefore "old" females in the model (12 years old and older) produce 0 or 1 kitten with an equal probability of 0.5 (Henriksen et al., 2005; Kramer-Schadt et al., 2005). We defined that residents die from a fixed annual mortality (i.e., baseline mortality) with a probability equal to 0.1 (Breitenmoser-Würsten et al., 2007a; Heurich et al., 2018; Kramer-Schadt et al., 2005), which does not include the mortality due to vehicle collisions (i.e., spatial mortality added separately with the collision model) and illegal killing (i.e., unavailable estimates). We did not define an increase of mortality due to senescence but we set an age maximum of 20 years (Breitenmoser-Würsten et al., 2007a; Stahl and Vandel, 1998; von Arx et al., 2017). Residents can also die from a spatial annual mortality due to vehicle collisions inside their territory. This spatial mortality is specific to each resident and corresponds to mean collision probability inside their territory. If residents survive, they age by one year and the annual loop starts again and continues as long as the simulation lasts or until they die.

Dispersers are individuals of 1 year old and older that do not hold a territory yet. Both dispersing males and dispersing females move on the gridded study area, one cell at a time, from one to 45 times per day (Fig. A.6), following the same rules. The number of steps individuals move per day is sampled, each day for each disperser, from a non-linear distribution defined by (Kramer-Schadt et al., 2004). Dispersers follow a correlated habitat-dependent walk in a two-step process: first, they favor their habitat preferences and then, maintain their previous direction with a certain probability (i.e., correlation factor; Kramer-Schadt et al., 2004). This movement process has been rigorously tested with inverse fitting, and “pattern-oriented modelling” (Kramer-Schadt et al., 2007) using telemetry data of 6 dispersing lynx (5 females and one male) followed in the Swiss Jura Mountains between 1988 and 1991. First, dispersers choose in which habitat type they will move next. Dispersers favor “breeding” and “dispersal” habitats without distinction between the two when moving and tend to avoid “matrix” habitats. By contrast, they never use “barrier” habitats. The choice to move into the habitat “breeding/dispersal” or “matrix” depends on the types of their 9 available cells for their next step (i.e., their 8 surrounding cells plus the one they are currently on as they also can choose not to move). If the 9 cells are all of one type, excluding the “barrier”, so they are either only “breeding/dispersal” (with or without “barrier”) or only “matrix” (with or without “barrier”), the only available habitat type is selected. If the available cells for an individual are a mix between “breeding/dispersal” and “matrix” habitats (with or without “barrier”), there is a probability of 0.03 times the number of “matrix” cells among the 9 ones, to choose the “matrix” habitat for the next step (Kramer-Schadt et al., 2004). For example, if an individual has 3 “matrix” cells available, there is a probability of 0.09 that it will choose a “matrix” cell for its following location. Second, once the habitat type is selected, the choice of the particular cell to move on, among the ones of the selected habitat type, is given by the correlation part of the movement. Individuals follow a correlated movement with a probability equal to 0.5, except for the first step of the day where there is no correlated movement (Kramer-Schadt et al., 2004). If the movement is not correlated, the choice of the next cell among the ones of the selected habitat type is random. If the movement is correlated, the chosen cell is the one maintaining the most of the individual’s current direction among the ones of the selected habitat type. The chosen cell is then where the simulated lynx is moving to. Dispersers try to minimize their time spent in “matrix” habitat and they can use their memory to return to a previously visited “breeding/dispersal” habitat when needed. Lynx do not move more than 9 cells inside “matrix” habitats, so if an individual already stepped 9 consecutive times in “matrix” cells and the chosen cell for its next step is again of “matrix” type, it will use its memory and return to the last “breeding/dispersal” cell visited (Kramer-Schadt et al., 2004). Finally, dispersers rotate towards their chosen cell and move on their center. Once dispersers move to their next cell, they may die from the spatial mortality due to vehicle collision. This spatial mortality is the collision probability from the collision layer for the cell of their new location. If dispersers survive, they search for a territory. If found, they stop moving, establish a territory, and become resident. Dispersers that do not find a territory to establish on their new location keep moving, as many steps during the day as simulated for them at the beginning of the day. At the end of the day, all individuals that dispersed during the day may die from a fixed daily mortality probability of 0.0007 (i.e., baseline mortality estimated by inverse fitting; Kramer-Schadt et al., 2004). Dispersers that have not established during the day can move and search for a territory every day during the year. At the end of the year, all individuals (i.e., the ones that are still dispersers and the former dispersers that found a territory and became residents) age by one year. Individuals still dispersing will do again this same loop and the new residents will do the annual loop, as long as the simulation lasts or until they die.

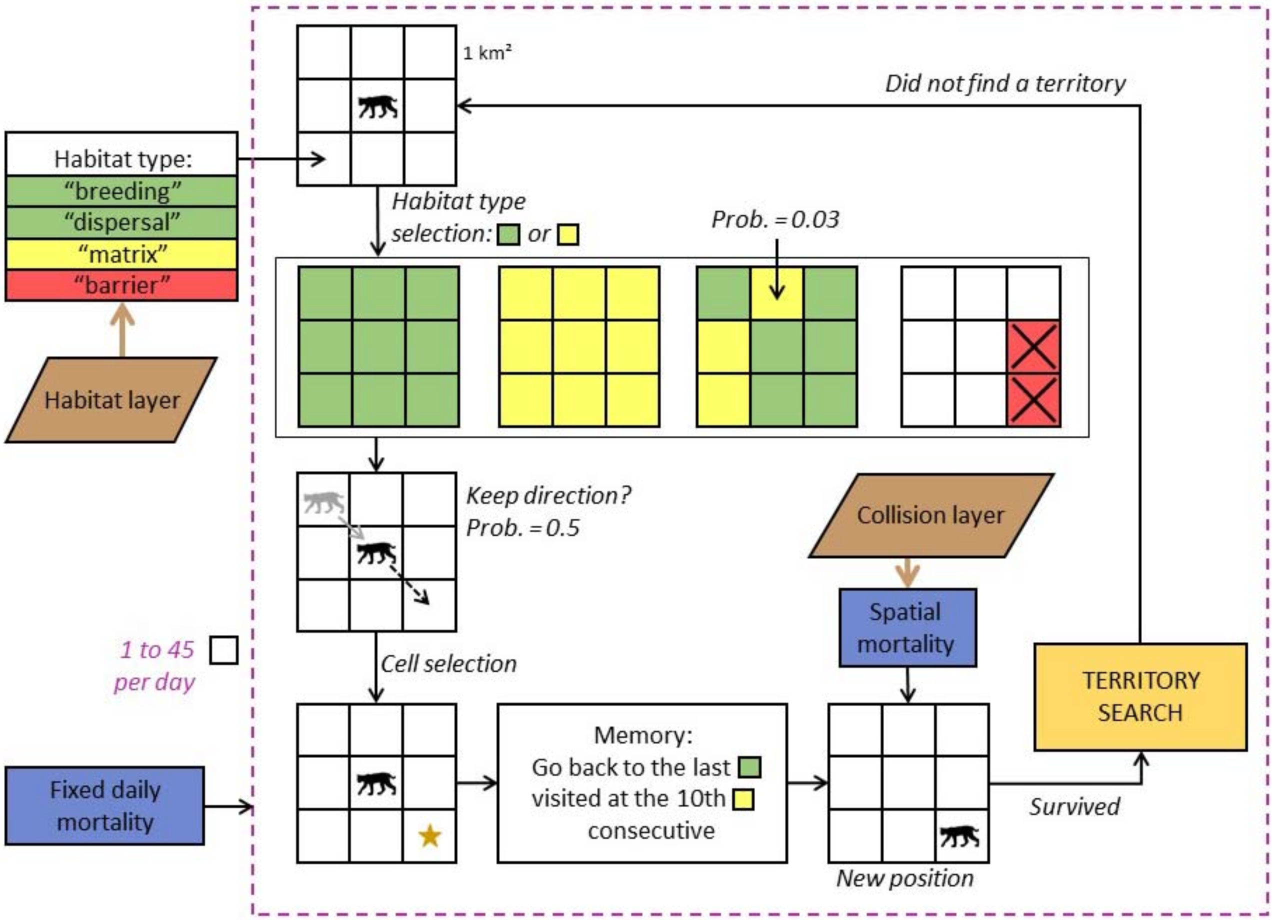

Figure A.6: Diagram of simulated lynx dispersal movement in the lynx SE-IBM. The loop represents one step. Individuals move one cell at the time per step, up to 45 a day or until they find a territory to establish (yellow box). Individual movement is constrained by habitat types in their surroundings defined by habitat layer (brown box), probabilities to step into different habitat types and to keep a direction (i.e., correlated movement), and their memory. Blue boxes represent mortalities an individual suffers, a spatial one each time reaching a new location, derived from the collision layer (brown box) and a daily one.

Dispersing individuals arriving at a new location have a different strategy to search for a new territory to establish regarding their sex (Fig. A.7). Females mainly look for good habitat (which represent high prey availability) while males search for breeding opportunities and seek female presence (Breitenmoser-Würsten et al., 2007b). Female dispersers need to be on a cell of habitat type “breeding”, defined by the habitat layer, and with enough unoccupied “breeding” habitats around their position to establish their territory. The size of the territory females need to define represents the territory core area (Kramer-Schadt et al., 2005) and depends on the population area where they are located in. We calculated these territory sizes to reach as: mean(95% kernel) – sd(95% kernel), where “95% kernel” represents the territory size of female residents calculated using a 95% kernel density (Heurich et al., 2018). When a female builds a territory, the cells used as the territory core area are no longer available for other females. Only the core areas are exclusive whereas an overlap between female territories on their edges is possible, as observed with telemetry data (Breitenmoser-Würsten et al., 2007b, 2001; Breitenmoser et al., 1993). Territory size to reach for the Alpine population is equal to 43.5 km^2 (mean home range computed with a 95% kernel = 76 km^2, standard deviation = 32 km^2; Breitenmoser-Würsten et al., 2001) and to 73 km^2 for the Jura population (mean home range computed with a 95% kernel = 119 km^2, standard deviation = 46 km^2; Breitenmoser-Würsten et al., 2007b). As we did not have a reliable estimate for the Vosges-Palatinian and the Black Forest populations, we assigned them the value of the Jura population due to the similarity of the habitat structure (Fig. A.3). The “population” layer in which population area individuals are located in (Fig. A.4). For that, each cell of the gridded study area was assigned the population of its closest cell of regular lynx presence. Once a female has established a territory, she becomes resident. If a resident male already established his territory nearby, the male includes the new resident female’s territory into his own, if he has less than three females already associated. Then, the two individuals may potentially reproduce the following year. That means, the male’s dispersal strategy to establish is female-dependent. At their new location, dispersing males check if they arrived inside the territory of a resident female available (i.e., with no male associated). If a male finds a female, he pairs with her and his territory becomes the same as the one from the female je joined. He also looks at nearby territories for up to three other available females to pair with. Males can pair with females whose territories are within the size of their maximum territories. The maximum distance between the male location and a female territory (i.e., a cell of her territory) is the radius of the mean territory size (estimated by 95% kernel density). It is equal to 6.6 km for males in the Alpine population (mean home range computed with a 95% kernel = 137 km^2; Breitenmoser-Würsten et al., 2001) and to 8.5 km for the other populations (mean home range computed with a 95% kernel = 226 km^2; Breitenmoser-Würsten et al., 2007b). If there are several females available for a particular male, the closest one(s) are chosen. The male can potentially reproduce the following year with every three females. The male territory is defined by the union of all the female territories he has paired with. If a disperser cannot find a territory to create (for female) or to join (for male) at their location, it continues dispersing. If all the females a male is paired with die, the male start to disperse again in search of new available female.

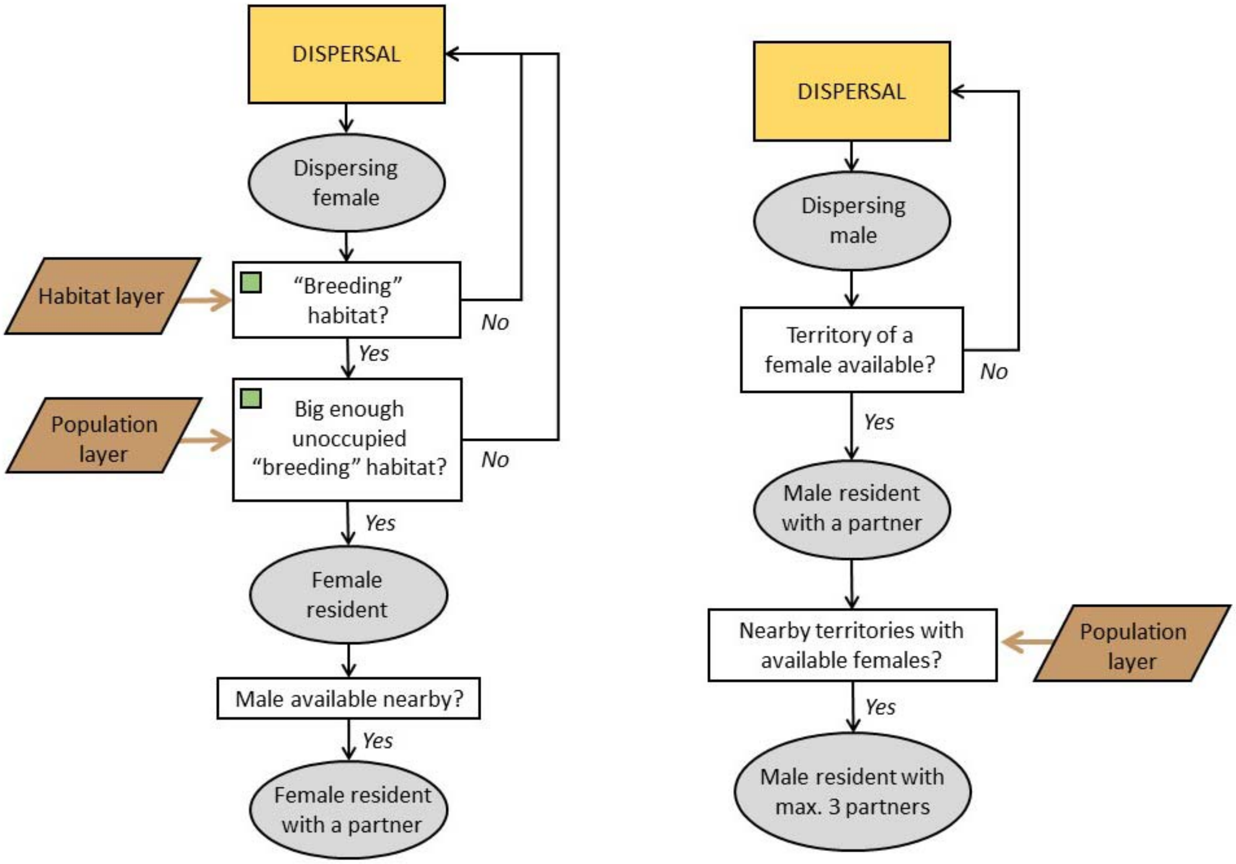

Figure A.7: Diagram of the territory establishment in the lynx SE-IBM separated by sex. The successive grey circles represent the successive status of the individual. Females are constrained by their surrounding habitat defined by the habitat layer (brown box). Males are constrained by female presence. The territory sizes females need to establish in "breeding" habitat and the maximum distance to which males can look for available female residents are constrained by the population in which the individuals are located (population layer; brown box).

The model is coded using R 4.1.0 (R Core Team, 2014). We used the package NetLogoR (Bauduin et al., 2019) to facilitate the IBM structure implementation in R language and the package SpaDES (Chubaty and McIntire, 2018) to schedule SE-IBM rules with different time units. We also used the packages data.table (Dowle and Srinivasan, 2019), randomcoloR (Ammar, 2019), raster (Hijmans and Van Etten, 2018), and testthat (Wickham et al., 2019).

Appendix B - Complete description of the lynx spatially-explicit individual-based model following the ODD protocol (Overview, Design concepts, and Details) developed by Grimm et al. (2006, 2010)

Overview

Purpose

The model simulates lynx population dynamics and dispersal, accounting for the impact of the road network via the risk of vehicle collisions and of the land cover to represent the lynx habitat preferences (Kramer-Schadt et al., 2005). Layers (i.e., maps) of collision probabilities, lynx habitats and lynx populations (Appendix A) are combined with SE-IBM rules simulating lynx dispersal (Kramer-Schadt et al., 2007, 2004) and demography (Kramer-Schadt et al., 2011, 2005).

Entities, state variables, and scales

The mobile entities of the model represent lynx individuals. Each simulated individual holds several characteristics:

- *id*: each lynx is unique and has a unique numerical identity (*id*);
- *heading*: direction of the lynx in degrees from 0 to 360 (0 is heading North) to one of its 8 neighboring cells (i.e., 0º, 45º, 90º, 135º, 180º, 225º, 270º, 315º);
- *location*: coordinates of the lynx current position;
- *previous location*: lynx hold in memory the coordinates of their previous position;
- *population*: the population area where the individuals are born among Vosges-Palatinate, Black Forest, Jura or Alps;
- *sex*: male or female;

- *age*: numerical value to represent the lynx age. This number represents the age as for humans with 0 for the first year of life, 1 for the second year of life, etc.;
- *status*: resident (i.e., established with a territory) or disperser (i.e., without a territory);
- *steps*: number of steps dispersing lynx have to do during the current day;
- *last dispersing location*: dispersing lynx hold in memory the coordinates of the last cell of habitat type “breeding” or “dispersal” they visited;
- *number matrix*: how many consecutive steps dispersing lynx move in “matrix” habitat;
- *male id*: for resident female only, the *id* of their male associated if they have one;
- *number females*: for resident male only, the number of resident females associated they have. It cannot be more than 3;
- *road mortality territory*: mean collision probability inside its territory;

Simulated lynx progress on a gridded study area of 1 km² resolution encompassing the four populations of interest: Vosges-Palatinian, Black Forest, Jura and Alpine, over Germany, France and Switzerland (main text, Fig. 1). The gridded study area resolution corresponds to the lynx perceptual range (Haller and Breitenmoser, 1986) and original resolution for the lynx individual-based models (Kramer-Schadt et al., 2011, 2005, 2004). The gridded study area holds four different variables:

- *collision probability* (from the collision layer): cells crossed by roads have an estimated probability of fatal collision with lynx, a value between 0 and 1. The collision probability is equal to 0 for cells with no road in it;
- *habitat type* (from the habitat layer): each cell is of one of the following habitat types: “breeding”, “dispersal”, “matrix” or “barrier”;

- *individual territory*: this variable holds the *id* of the female residents for the cells included in their territories.

Process overview and scheduling

At the beginning of each simulated year, lynx individuals are differentiated by their resident or disperser *status* (Appendix A, Fig. A.5). Residents progress on a yearly time step while dispersers progress on a daily time step. Resident lynx may reproduce and kittens are born. Then, residents may die from a fixed annual baseline mortality and from a spatial annual mortality, the latter being defined by the mean *collision probability* inside their territories. All these happen once in the year. Dispersing lynx move on the gridded study area (Appendix A, Fig. A.6) and their simulation time step is daily. A number of *steps* to move per day is generated for each dispersing lynx at the beginning of each day. All dispersers move simultaneously, one step (i.e., cell) at the time, following a correlated habitat-dependent movement influenced by the *habitat type*. After each step, dispersing lynx may suffer from a spatial mortality given by the *collision probability* at their new location. Then, the surviving ones search for a place where establish their territory (Appendix A, Fig. A.7). Dispersing females are constrained by the *habitat type* in their surroundings to establish a new territory while dispersing males are constrained by the presence of available resident females for reproduction (Breitenmoser-Würsten et al., 2007b). Dispersing lynx that do not establish a territory continue to disperse during their set number of *steps* per day, and every day during the year until establish one. At the end of each day, lynx that dispersed suffer from a fixed daily baseline dispersal mortality. At the end of a year, all lynx *age* are incremented by one and their *status* is updated if applicable.

Simulated lynx *id*, *population*, and *sex* variables do not change during a simulation. Their *heading*, *location*, *previous location*, *last dispersing location*, *number matrix*, *male id*, *number* *females* and *road mortality territory* may change at every dispersal step. The *steps* variable is updated each day, and *age* and *status* are updated once a year. There is no modeling of the landscape during the simulation, therefore the *collision probability* and *habitat type* are constant during one simulation. However, the *territory id* may change at every step (i.e., each time there is a new territory created).

Design concepts

Basic principles

Our lynx SE-IBM is an assemblage of four components: three spatial layers and an existing individual-based model (Kramer-Schadt et al., 2011, 2007, 2005, 2004) parameterized with field data and inverse model fitting (Appendix A, Fig. A.1). The *collision probability* layer and the *habitat type* layer are output maps from a collision model and a habitat model (Appendix A). The population layer was generated using presence data and estimated number of lynx (Appendix A).

Emergence

Simulated males and females follow the same rules, except for the territory establishment where females are constrained by the habitat and males by the presence of females (Breitenmoser-Würsten et al., 2007b). In an area with few individuals, females have many possibilities of empty land to establish. On the other hand, males will have to move further to find one of the few females available, inducing longer dispersal movement and higher chances of dying. However, in a very dense area, this can be reverse. Females will have to move further to find free land whereas males, if they are not too numerous, may move less as they may have many females around them to pair with. If there are many males, all females may be already taken, inducing again longer dispersal for the males.

To breed, residents are constrained by the presence of a partner on their territory and both individuals need to be in age of reproduction. The presence of a suitable partner depends on their past dispersal movement and territory search, and if they could establish a new territory or not. Reproduction success is therefore stochastic, as well as the number of kittens. All this will modify the number of new individuals in the population.

Residents and dispersers are subject to a fixed baseline and spatial mortality. Both mortalities are stochastic and the spatial one depends on the location of the individuals (i.e., *collision probability* at their location). The location of the individuals depends on their current or past dispersal movement that depends on the *habitat type*. All this will modify the number of individuals dying each year.

Adaptation

There is no adaptation in the SE-IBM (e.g., no density-dependent rules). All individuals follow the same behavioral rules regarding dependent on their inner and environmental characteristics.

Objectives

Simulated lynx do not have adaptive traits and they do not have a final goal to reach. They take decisions at each time step based only their current characteristics and their environment to fulfill an immediate goal (e.g., where to move next).

Learning

Simulated lynx try to minimize their time spent in poor habitat quality. When they step into “matrix” habitat, they store the position they just left (i.e., their last position in good habitat so either in “breeding” or “dispersing” habitat) and start counting how many consecutive steps into "matrix" they do. At the 10th step, if the chosen cell is still located into "matrix", simulated lynx will use their memory to find and move back to their last location of good habitat.

Prediction

Simulated lynx cannot predict the future nor have a global view of the study area. Both residents and dispersers sense the current state of their environment and population in their immediate surroundings and react to this information only. For example, dispersing lynx move, making decisions based only on their immediate surroundings. They cannot anticipate their path nor have a global view of their environment to make advantageous decisions for the long term (e.g., they cannot find a better territory and/or more quickly).

Sensing

Simulated lynx can sense the *habitat types* and the *individual territories* of their surroundings. Dispersers establishing a territory and trying to find a partner can sense other individuals: it knows who hold nearby territories and the characteristics of these individuals, such as their *sex* and the availability to pair with.

Interaction

There is a tacit competition between dispersing individuals during the territory search. Dispersers evaluate their surroundings before establishing one at the time (in a random order each time). The first female in the list looking for a territory has therefore more chance to find empty space to establish than the last female. Similarly, the first male in the list looking for an available female to join has more chance to find a partner than the last male.

Residents also interact with each other for reproduction. If a male and a female resident in age of reproduction are on the same territory, they may reproduce and produce new individuals. However, this interaction does not affect any of the individuals (i.e., a reproduction event does not change the characteristics of the concerned individuals).

Stochasticity

The model involves several stochastic processes. Regarding demography, both reproduction (i.e., the reproduction event itself and the number of kittens) and mortality (both fixed baseline and spatial for both residents and dispersers) are defined with probabilities and therefore outcomes vary between individuals. During dispersal, the choice of the *habitat type* to select when there is a mix of “breeding/dispersal” and “matrix” habitats in the lynx surroundings depends on the probability to step into “matrix”. Then, there is also stochasticity in the choice of the next location within the selected *habitat type*, as the choice to follow a correlated movement or not are defined by probabilities, as well as the choice of the next location among those available if the movement is not correlated. Finally, the number of steps dispersing simulated lynx must move during a day is sampled from a probability distribution and so, the outcomes are not the same for all individuals all the time.

Collectives

When a resident male finds one or several available resident females, he may pair and reproduce with them. Every year, the pairs persist unless one of the lynx dies and therefore frees the other one to find another partner.

Individuals belong to populations. The two rules different between populations are the size of the territory females have to reach and the maximum size of territory males can hold (i.e., how far can they look for females). Other than that, no rule is defined at the population level and the population affiliation does not affect the individual progress. Individual progress according to their own characteristics.

Observation

The state of all alive simulated individuals (i.e., their location and characteristics) and of the *individual territory* map are available at the end of each yearly time step. All disperser movements are also recorded on a single map over the whole simulation time. Events changing the demography are saved each year: which individuals died and how (i.e., from the fixed baseline mortality or from collision), which individuals reproduce, who are the kittens, and which individuals became residents.

Details

Initialization

At the beginning of the simulation, a grid covering the whole study area (main text, Fig. 1) with a resolution of 1 km^2 is created. The values from the habitat layer and the collision layer are transferred to the gridded study area variables *habitat type* and *collision probability*. The variable *individual territory* is set to missing value (NA) everywhere. *Collision probability* on the borders of the grid are set to 1 so that individuals reaching the borders of the study area die instead of bouncing on the border. We assumed that these individuals would have left the study area and therefore are removed from the population even if it is not unlikely that they, or others, may come back.

Using the population layer, a lynx population is created with unique *id* for each individual, *location*, *population*, as well with a *sex* and *age* (when known from field data) for some individuals. A simulated individual cannot start in "matrix" or "barrier" habitats. Therefore, if some individuals' *location* are located in these habitats, they are relocated to the closest cell of "breeding" or "dispersal" habitat. At the start of the simulation, individuals cannot have a *previous location* or a *last dispersing location*, so we used their current *location* for these two variables. For individuals with unknown *sex* or *age* (no field data), a random *sex* (male or female with ratio 1:1) and *age* (between 2 and 15) is randomly given. A random *heading* (i.e., initial direction) is given to each individual, between 0° and 360°. At the start, all individuals have a disperser *status*, 0 *steps* to do, 0 steps done in "matrix" (*number matrix*) and 0 for *road mortality territory*. As all individuals are dispersers, no couples are made so *male id* for the females are set to NA and the *number females* for males are set to 0 (Table B1).

The parameter values used in the SE-IBM to represent the dynamics and dispersal of the Eurasian lynx in our study area (main text, Fig. 1) are provided in Table B.1.

Parameter	**Explanation**	**Value**	**Reference**
endTime	Number of years to simulate the lynx populations.	50	By default
pRepro	Probability of reproduction for a couple (one resident female and one resident male associated on the same territory, both in age of reproduction).	0.81	(Breitenmoser-Würsten et al., 2007a; López-Bao et al., 2019)
nKittyYoungF	Number of kittens that survive until the age of dispersal when the female is considered "young" (maxAgeYoungF	1 or 2 (with equal	(Breitenmoser-Würsten et al., 2007a, 2001;

	parameter).	probability for each value)	Henriksen et al., 2005; Kramer-Schadt et al., 2005; López-Bao et al., 2019)
nKittyOldF	Number of kittens that survive until the age of dispersal when the female is considered "old" (maxAgeYoungF parameter).	0 or 1 (with equal probability for each value)	(Breitenmoser-Würsten et al., 2007a, 2001; Henriksen et al., 2005; Kramer-Schadt et al., 2005)
maxAgeYoungF	Age maximum for a female to be considered "young".	11	(Henriksen et al., 2005)
minAgeReproF	Age minimum at which all resident females can reproduce (i.e., are sexually mature). One year younger, only half of the females are mature.	2 (3rd year of life)	(Breitenmoser-Würsten et al., 2007a; Henriksen et al., 2005; Kvam, 1991)
minAgeReproM	Age minimum at which all resident males can reproduce (i.e., are sexually mature). One year younger, only half of the males are mature.	3 (4th year of life)	(Kvam, 1991)

pMortRes	Fixed annual baseline probability of mortality for resident lynx (without the risk of collisions included).	0.1	(Breitenmoser-Würsten et al., 2007a; Heurich et al., 2018)
ageMax	Age maximum a lynx can reach.	20	(von Arx et al., 2017)
xPs	Exponent value of the power function to define the daily step distribution. This distribution is used to sample a number of steps per day to move for dispersing lynx.	11	(Kramer-Schadt et al., 2004)
sMaxPs	Maximum number of steps dispersing lynx can do in one day.	45	(Kramer-Schadt et al., 2004)
pMat	Probability of stepping into “matrix” cells. This probability is multiplied by the number of “matrix” cells available for a dispersing lynx to define its probability to choose this habitat type for its next location.	0.03	(Kramer-Schadt et al., 2004)
pCorr	Movement correlation probability for dispersal movement.	0.5	(Kramer-Schadt et al., 2004)
pMortDisp	Fixed daily baseline probability of mortality for dispersing lynx (without the risk of collisions included).	0.0007	(Kramer-Schadt et al., 2004)

nMatMax	Maximum number of consecutive steps a dispersing lynx can do into “matrix” habitat. After this number of steps, disperser can use its memory to find and move in the last good habitat visited (“breeding” or “dispersal” habitat).	9	(Kramer-Schadt et al., 2004)
coreTerrSizeFAlps	Territory size (in km^2) females located in the Alpine population need to reach.	43.5	(Breitenmoser-Würsten et al., 2001; Heurich et al., 2018)
coreTerrSizeFJura	Territory size (in km^2) females located in the Jura population need to reach.	73	(Breitenmoser-Würsten et al., 2007b; Heurich et al., 2018)
coreTerrSizeFBF	Territory size (in km^2) females located in the Black Forest population need to reach.	73	(Breitenmoser-Würsten et al., 2007b; Heurich et al., 2018)
coreTerrSizeFVP	Territory size (in km^2) females located in the Vosges-Palatinian population need to reach.	73	(Breitenmoser-Würsten et al., 2007b; Heurich et al., 2018)
terrSizeMAlps	Maximum territory size (in km^2) males	137	(Breitenmoser-

	located in the Alpine population can reach.		Würsten et al., 2001)
terrSizeMJura	Maximum territory size (in km^2) males located in the Jura population can reach.	226	(Breitenmoser-Würsten et al., 2007b)
terrSizeMBF	Maximum territory size (in km^2) males located in the Black Forest population can reach.	226	(Breitenmoser-Würsten et al., 2007b)
terrSizeMVP	Maximum territory size (in km^2) males located in the Vosges-Palatinian population can reach.	226	(Breitenmoser-Würsten et al., 2007b)
nFem	Maximum number of resident females a resident male can pair with and potentially reproduce with.	3	(Kramer-Schadt et al., 2005)

Table B.1: Parameter values used in the SE-IBM.

Input data

See Appendix A.

Submodels

Reproduction: A female resident in *age* of reproduction (1 or 2 years old, see Table B1) with a resident male associated, also in *age* of reproduction (2 or 3 years old, see Table B1), may reproduce and have offspring. There is a Bernoulli trial for the reproduction success with a mean probability of 0.81 (Table B1). If the couple reproduces, the female can produce 1 or 2 kittens with equal probability (Table B1) if she is “young” (11 years old or younger; Table B1) or 0 or 1 kitty with equal probability if she is “old” (12 years old or older; Table B1). Kittens obtain a unique *id*. The *sex* of the kittens is randomly chosen between male and female with ratio 1:1 (Table B1). Their *location*, *heading* and *last dispersing location* are the ones from their mother. Their *previous location* is NA. Their *population* is not the one of their parents but the one of the territory where they are born. Their *age* is 0, their *status* is resident (i.e., they stay with their mother and cannot disperse at this age), their *steps* and *number matrix* are 0, their *male id* is NA, and their *number females* and *road mortality territory* are 0.

Mortality: Resident individuals may die from a fixed baseline annual mortality and a spatial mortality using a Bernoulli trial. Mortality rate for all residents is equal to 0.1 (Table B1) for the fixed baseline mortality. We did not simulate an effect of senescence but we set an age maximum (20 years; Breitenmoser-Würsten et al., 2007a; Stahl and Vandel, 1998; von Arx et al., 2017) and all individuals reaching this age die. Resident individuals may also die from spatial mortality, the mortality rate for female residents is the mean *collision probability* of the cells inside of their territory (*road mortality territory*). For male residents, spatial mortality rate is the mean *road mortality territory* of all his paired females.

When a resident female dies, her territory disappears (i.e., her *id* is removed from the *individual territory* study area variable) and the local male resident loses one female. If this male did not have other females, he becomes disperser again to look for new available female resident as male home ranges are adjusted to mate availability (Breitenmoser-Würsten et al., 2007b). If the dead female had kittens during the year, they all die too. When a male resident dies, its paired females become available to reproduce with other males.

Demography: All individuals' *age* increment of 1. The *status* of the offspring of the year changes from resident to disperser.

Dispersal: A number of steps to do during the day is sampled every day from the distribution defined by Kramer-Schadt et al. (2004), one per dispersing individual. Dispersers move one cell per step, into one of their 8 neighboring cell or their current cell (i.e., so a total of 9 potential cells for their next location). First, there is a selection of the habitat type each disperser chooses for its next location. Among those 9 cells, all cells of "barrier" type are removed from the potential choices. As individuals cannot be on "barrier" habitat, it cannot happen that all 9 cells are "barrier". For a dispersing individual, if all his cells are of "breeding" or "dispersal" type, this type ("breeding/dispersal" without distinction between the two) is selected. If all his cells are of "matrix" (i.e., habitat not favorable for lynx), this type is selected. If the cells are a mix of "breeding/dispersal" and "matrix", there is a Bernoulli trial of mean 0.03 (Table B1) times the number of "matrix" cells among the 9 to select the "matrix" habitat type.

Second, there is the choice of the cell for the next location, among all cells of the selected habitat type. If there is only one cell of the selected type, the disperser goes on this one (for example, if the selected cell type is "breeding/dispersal" and there is only one cell of "breeding/dispersal" habitat, all other cells being "matrix" or "barrier", therefore the only cell of "breeding/dispersal" is selected). Otherwise, there is a choice either random or governed by a correlation movement to select the cell. The first step of the day is never correlated, otherwise there is a Bernoulli trial of mean 0.5 (Table B1) to determine if the movement is correlated for each individual for each step. If there is no correlation of the movement, the choice for the cell is done with an equal probability for all the cells of the selected type. If the movement is correlated, the rotating angle between the individual's heading and each cell of the selected type is calculated. There is a preference for the cell minimizing this rotating angle. If the cell that the individual is on is of the selected habitat type (i.e., this cell can be selected for the individual's next step which will make the lynx stay at its current location), the preference for this cell is equal to the preference for the cells inducing a rotation of +/- 90 degrees, to favor a forward movement. The selected cell is the one with the highest preference (i.e., smallest rotation movement).

Third, if the selected cell is of "matrix" type, the individuals check how many consecutive steps they have done in "matrix" habitat (*number matrix*). If a disperser has already step 9 consecutive times (Table B1) in "matrix" and this 10th consecutive step is in "matrix" too, it used its memory and select, for its next location, the last visited cell of good habitat ("breeding" or "dispersal"), stored in his memory (*last dispersing location*) (Kramer-Schadt et al., 2004).

Finally, all dispersers rotate towards their selected cell and move to the center of it. They update their *previous location* with the coordinates of the cell they were before moving. If their new location if of type "breeding" or "dispersal", this location is stored in their memory for the *last dispersing location*, and their *number matrix* is reset to 0. If their new location is of type "matrix", their *number matrix* increments of 1.

Now, disperser may be also subject to spatial mortality. There is a Bernoulli trial for each disperser with mean equal to the *collision probability* value of their new location. Dispersers that do not die from spatial mortality search for a new home range to establish (*searchTerritory* sub-model). At the beginning of the simulation, all initial individuals were created as dispersers because we did not have data on lynx territories Thus, we decided to let simulated individuals establish their initial territories. Individuals needs some time to do so, therefore we did not apply any mortality during the first year of simulation to allow dispersers to establish their territories.

The dispersal movement is done until all dispersing individuals have reached their number of steps to do during the day, or they have established a territory and are now resident, or they died from spatial mortality. At the end of the day, all individuals that were dispersers at the beginning of the day (even the ones that established a territory during the day) may die from a fixed daily baseline mortality. There is a Bernoulli trial of mean 0.0007 (Table B1) for each individual. If some of the individuals dying established a territory during this day, there is an update of their characteristics similarly as the death of resident individuals. As the spatial mortality, there is no fixed daily baseline mortality applied the first year of the simulation.

SearchTerritory: Dispersing individuals arriving at a new location search for a territory to establish, one at the time, and females first (i.e., male establishment depending on female territories). One at the time, in a random order each time, females evaluate their surroundings to establish their territory. Females needs to be on a cell of “breeding” type that is not already included in any territory to start creating their own. Then, they need to have enough empty contiguous cells of “breeding” habitat to create a big enough territory (Table B1). When enough empty contiguous cells of “breeding” habitat are present, females establish their territory and becomes resident. Otherwise, they stay disperser and keep dispersing. After a female establishes her territory, all the cells of this territory become occupied and are not available anymore for the other females. The female *id* is given to the *individual territory* study area variable for all cells in her territory. The mean *collision probability* of the territory is calculated and given to the female for her *road mortality territory*. Then, the female checks if there is a resident male around. If there is a male not further than the radius of the maximum territory size for the male (Table B1) and he has less than three females associated, she pairs with him. Then, she obtains the male *id* for her *male id* and the *number females* of the male increments of 1.

After all dispersing females tried to establish, dispersing males try to disperse of their own, one at the time in a random order each time. Each male checks if the cell they are currently on is located inside the territory of an available female (i.e., without male associated yet). If there is one, the male pairs with this female and becomes resident. His territory is the same one as the female and its *number females* is set to 1. The female obtains the male *id* for her *male id* variables. Then, the male also looks if there are other nearby available females to pair with, as far as the radius of its maximum territory size (Table B1). He can pair with up to three available females. The male territory represents the union of all the female territory with which he paired with. His *road mortality territory* is the mean value of the *road mortality territory* of all the females he paired with.

Appendix C – Model validation using telemetry data

We performed a qualitative validation of the lynx model predictions using tracks from collared female residents. The map below (Fig. C.1) shows the simulated territory occupancy with darker green colors representing areas most often occupied by female territories across simulation replicates (main text, Fig. 4). We overlaid GPS and VHF paths from collared female residents on the map. Data for the Vosges-Palatinate consist in 2 females in the Palatinate Forest (Germany) and 1 in the Vosges Mountains (France) (locations recorded in 2017-2018; Scheid et al., 2021). Data in the Jura represent 4 females in France and 13 in Switzerland (locations recorded in 1988-1998; Breitenmoser-Würsten et al., 2007b). Data in the Alps (Switzerland) represent 16 females (locations recorded in 1997-2000; Breitenmoser-Würsten et al., 2001). We show the full study area and 4 zoomed areas on the telemetry locations. Overall, the realized movements and territory emergence inferred from field data were coherent with the frequencies across simulation replicates of the territories defined by simulated lynx. Most of the recorded tracks were located in cells with a high frequency of territory occupancy and very few were located in cells where no territories were simulated.

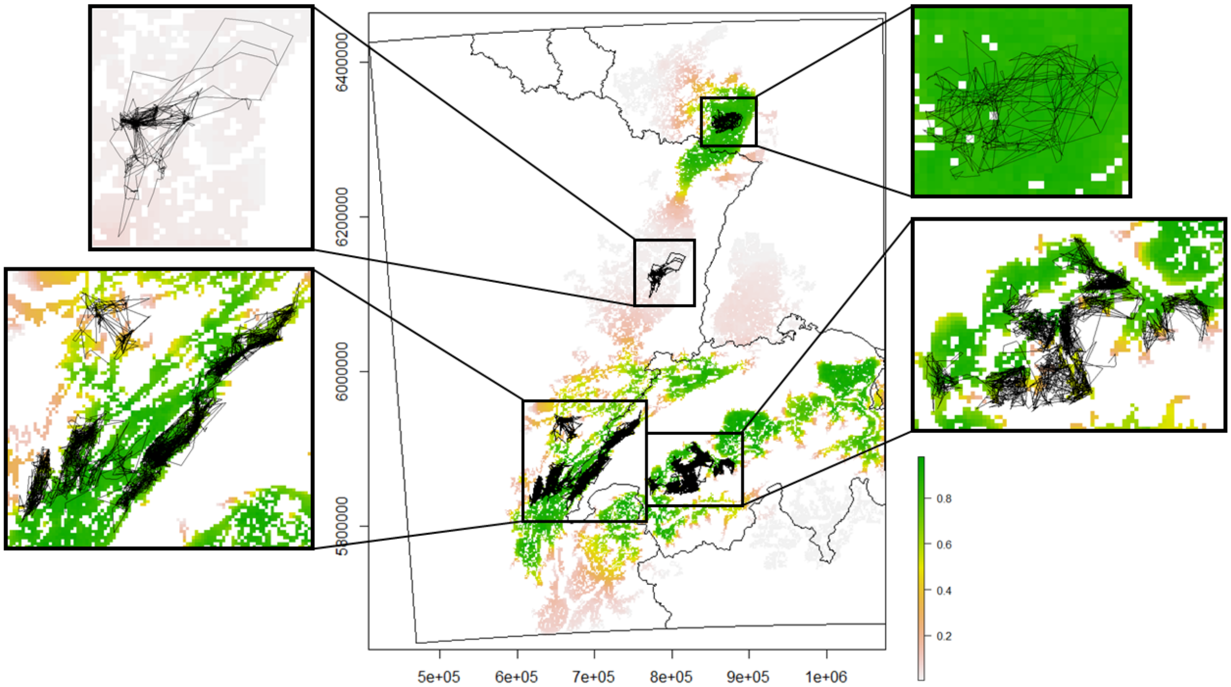

Figure C.1: Occupancy by female territories at the last year of simulation over the whole study area (black rectangle) used in the lynx SE-IBM using the habitat model. Limits of the countries (main text, Fig. 1) are overlaid in black over the map. Values between 0 and 1 are mean occupancy probability per cell of 1 km^2 over 200 replicates (e.g., cell with value equal to 1 were always occupied in all simulation replicates). GPS and VHF recorded paths for female residents are overlaid as thin black lines. A zoom of different areas are presented on the sides of the central map.

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