Peer Community In Ecology

Glimmers of hope for the Eurasian lynx in Western Europe

Elodie Vercken *based on peer reviews by* ***Hector Ruiz*** *and* ***Henrik Andren***

Sarah Bauduin, Estelle Germain, Fridolin Zimmermann, Sylvia Idelberger, Micha Herdtfelder, Marco Heurich, Stephanie Kramer-Schadt, Christophe Duchamp, Nolwenn Drouet-Hoguet, Alain Morand, Laetitia Blanc, Anaïs Charbonnel, Olivier Gimenez (2025) Modelling Eurasian lynx populations in Western Europe: What prospects for the next 50 years? bioRxiv, ver. 4, peer-reviewed and recommended by Peer Community in Ecology.
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The conservation of large carnivores remains a challenge for biodiversity conservation (Ingeman et al. 2022), as they combine strict ecological requirements (large territories, sensitivity to human disturbance) with coexistence conflicts with human activities (livestock farming, hunting, risk perception). Although the Eurasian lynx is currently considered as "least concerned" by the IUCN Red List, this favorable status conceals major disparities between the remaining historical population nuclei in Northern and Eastern Europe and small, isolated populations in Western Europe resulting from reintroduction programs for which long-term persistence remains in jeopardy (Chapron et al. 2014). Several ambitious conservation programs have been launched to try and improve the long-term demographic status of these still fragile populations (e.g., Swiss Lynx Project, French National Action Plan for the Eurasian Lynx), and conservation actors have a dire need for modelling of population dynamics to project demographic trajectories and compare scenarios of alternative conservation actions (Gatti 2022). A major challenge for making accurate demographic predictions is that lynx are characterized by extensive territories, and their demographic processes are expected to be strongly dependent on landscape characteristics. To address this challenge and capture the complexity of interactions between landscape structure and lynx dispersal, survival and reproduction, Bauduin et al. (2025) develop here a spatially explicit individual-based model for the four Western European populations of Eurasian lynx: Alps, Jura, Vosges and Black Forest. They use fine-scale data on movement and habitat use as well as road collisions to build a detailed spatial layer of habitat suitability and collision risk to predict the demographic trajectory and spatial repartition of the four Western European core populations over the next 50 years. Their simulations reveal an optimistic outlook offer for the future of the lynx : the sizes of the four population cores

are predicted to increase steadily until stabilization at saturation within 20-40 years. Furthermore, the four populations are expected to act as a functional metapopulation, with regular exchanges of individuals between adjacent populations.
These results open up a wide range of perspectives. First, different conservation scenarios (e.g., reintroduction strategies, landscape evolution, changes in fragmentation) can be run using the framework of the model and compared to identify priority actions. Second, the predictions of lynx expansion into new areas (like Italian and French Alps) can be used to anticipate potential usage conflicts and develop coexistence strategies to improve social acceptance of the species in these target areas. Although genetic information and the effects of inbreeding depression were not included in the model and could significantly lower the predicted growth rates in the long term, the conclusions are robust to a wide range of parameter values, and can be used both to inform lynx conservation strategies and to provide a priceless basis for the development of other SE-IBM for large mammals in human-inhabited landscapes.

References:

Bauduin S, Germain E, Zimmermann F, Idelberger S, Herdtfelder M, Heurich M, Kramer-Schadt S, Duchamp C, Drouet-Hoguet N, Morand A, Blanc L, Charbonnel A, Gimenez O. 2025. Modelling Eurasian lynx populations in Western Europe: What prospects for the next 50 years?https://doi.org/10.1101/2021.10.22.465393

Chapron G, et al. 2014. Recovery of large carnivore in Europe's modern human-dominated landscapes. Science 345: 1517-1519 https://doi.org/10.1126/science.1257553

Gatti S. 2022. National Action Plan for the Eurasian Lynx: restoring the Lynx to a favorable conservation status un France (2022-2026), 176 p.

Ingeman, K.E., Zhao, L.Z., Wolf, C. et al. 2022. Glimmers of hope in large carnivore recoveries.Sci Rep 12, 10005 https://doi.org/10.1038/s41598-022-13671-7

Reviews

Evaluation round #2

DOI or URL of the preprint: https://doi.org/10.1101/2021.10.22.465393
Version of the preprint: 3

Authors' reply, 18 March 2025

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Decision by Elodie Vercken, posted 27 February 2025, validated 27 February 2025

Thanks a lot to the authors for the great job they did working on this revised manuscript. I sent this new version back to Henrik Andren, whose comments on the first version of the manuscript resulted in significant changes in the methods and results of the study. He still raised a couple minor issues regarding model presentation/data availability, which I reckon should be adressed. Once this is done, I will gladly recommend the manuscript.

I mark this decision as a request for revision, to give you a bit of time to adress these last comments, and for me to work on the recommendation text so the

Reviewed by Henrik Andren, 14 February 2025

I think the authors have answered most of my questions in the revised version of the manuscript.

However, I still miss some information and data presentation what would improve the manuscript. I am happy that the Tables (A1 and A2) now are include, but I still miss some information to be able to use the models in other areas. We should have the aim that studies could be repeated by someone else. Therefore, we need to know the range and measurement units of variables included in the models. I think it would be very interesting to make the predicted maps (Figure A1 & A2) for another study area.

In the Appendix there are detailed descriptions of the models. However, I miss the mean, std and range (min – max) and the measurement units for all the variables included. Please include a new table with that. If I should use the logistic regression for collision probability (Table A1), then I need to know the measurement units. I used to coefficients from Table A1 and had to guess what ranges different variable should have.
It would be great to make a similar map in another landscape (as Figure A1).

I have the same problem with the model in Table A2. Please include a new table the mean, std and range (min – max) and the measurement units for all the variables.
How does occupancy model look like (the math behind it)? There is no intercept1
I tested with a logistic regression but could not get any predicted "lynx occupancy values" that were reasonable.

The threshold of 0.01 for a "lynx occupancy value" to be "breeding habitat" looks very low. Maybe it can be explained by the model structure (math for the model) and the range for the included variables.

I miss a key figure. How is the population development in the four populations? Figure 3 reports the growth rate, and it is about 1 (stable population) after 30 years in Alps and Jura and after 45 years in Black Forest and Voges-Palatinate. But what are the population sizes? I think the population sizes for each population at saturation (lambda = 1) is very important to report from a conservation point-of-view. The conclusion in the summary (Lines 57-58, "Finally, persistence of lynx in Western Europe seems likely on a large scale over the next 50 years.") depends very much on the population sizes in the different "sub-populations". Thus, I think one should report them (a figure with population development).

Some details.
It would be good to have the same colours in figures 1, 3 and 4 (Alps is red in all of them, but Jura, Black Forest and Vosges-Palatinate have colours).

On lines 519 – 520 The conclusions start with "forecast the lynx populations over the next 50 years", but there is no description of the population size over the years in different areas.

Evaluation round #1

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Authors' reply, 06 December 2024

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Decision by Elodie Vercken, posted 22 February 2022, validated 22 February 2022

Recommendation under minor revisions

Dear Authors, Thank you very much for submitting your work for recommendation in PCI Ecology. Your manuscript has been evaluated by two reviewers and myself, and we all concur that it is of excellent quality. The topic (prediction of long-term demography of a large carnivore in Europe) is most engaging, both on the scientific and social dimensions. The impressive amount of data, the level of details in spatial modelling, and the very clear and detailed description of modelling methods were all acknowledged as major strengths of your work, which has the potential to be of interest to a wide community of ecologists and conservationists. I would be most happy to recommend this work for PCI Ecology, provided you can address the minor concerns raised by the different evaluators, in particular:

- A few more details seem to be necessary on the different regression models used to build the collision and habitat layers, and on the evaluation of breeding territories
- The discussion could use a couple of clear conclusions on the factors most critical for population growth and expansion, at present it is difficult to understand clearly why the population fails to colonize the entire available habitat
- Some perspectives on the potential evolution of the landscape: agricultural lands vs forest covers, new road or infrastructure projects, key dispersal routes, … Don't hesitate to ask if any of the reviewers' comments are unclear to you, or if I can help in any way. I sincerely hope our comments are helpful to you and contribute to improving the manuscript further. **Download recommender's annotations**

Reviewed by Hector Ruiz, 07 February 2022

This is a very interesting article on predicting long-term persistence of Eurasian lynx (*Lynx lynx*) populations in central Europe. The article is very well written and clearly explained. I know SE-IBMs but I am far from being an expert and despite this, I was able to perfectly understand everything that has (and has not) been done and included in your model. All the details to make the model as realistic as possible (which should always be the main goal of predictive models) have been considered and taken into account. I have some thoughts/reflexions about some of the model limitations (most of which have already been explained by you in your manuscript) particularly regarding not having considered landscape and land use changes along your prediction time of 50 years (please see my comment below). Of course I agree with you that if you could have included data on poaching and genetics the model would have provided more realistic results. Sadly, that data is generally hard to obtain and thus difficult to incorporate in the models. Taking all this into account, I think that you have done a great job using what was available to predict the persistence of lynx populations in Central Europe. I think your article is very useful not only from the lynx ecology and conservation point of view but also to scientists and conservationists as a tool to run future SE-IBM with other species and in other environments. Congratulations! Everything looks fantastic so only a couple of minor comments and some reflexions are included.

L46: I would avoid the use of the word "viable" in your abstract. Persistence and viability are different concepts with different implications in ecology and your model would probably fit better with the concept of persistence (see my next comment).

L122: Persistence or viability? I think these concepts are greatly different. A population may persist with very bad genetic quality and very low population numbers; however that population may not be viable from a long-term perspective. As you are not including key viability components in your model (illegal mortality or genetic characteristics) I would probably talk about persistence and remove the word viable from the abstract as it may sound confusing.

L684 (Impact of Land Cover): I think your methods to determine the influence of land cover on lynx occupancy are fantastic. However, did you consider modelling habitat modification along the 50 year period to assess the effects on viability of lynx populations? I see in L1014 that you did not include variations in landscape in your

model. For example, one scenario may be that agriculture intensification continues growing and thus gaps between lynx populations get larger consequently complicating its viability. You explain in your introduction that habitat fragmentation is one of the main threats for lynx worldwide and thus these changes would be expected to have great implications. Another possibility would be that forest cover increases (as it may be the case in many areas of Europe), and thus connectivity among lynx populations would increase. Could you please explain why you did not use this approach? (model complication, lack of evidence, etc)? Land change across Europe in the last 50 years has been substantial and it is thus expected that something similar occurs in the next 50 as it has not been otherwise explained in the text. From a conservation (and prediction) point of view I think that considering the future changes in the European landscape inside and around lynx populations would make your predictions much more realistic, particularly when knowing that fragmentation can greatly impact lynx populations.

L691: Remove one "used"

L815: Change "kitty" for "kitten"

Reviewed by Henrik Andren, 15 February 2022

I think this is an important paper forecasting lynx occupancy in different regions in Western Europe. The paper is easy to follow. The appendix and model description are very well structured and follows Overview, Design concepts, and Details (ODD) protocol.

However, I have a problem to understand how the "breeding habitat" in habitat layer (Figure A3) can result in the occupancy layer (Figure 4). To me there is a miss-match between the two. Most of my questions are related to the differences between these two maps.

Black Forest and Vosges-Palatinian regions have the largest areas of continues "breeding habitat", whereas both Jura and Alpine have very fragmented "breeding habitat". But the modelling results in higher occupancy in Jura and Alps than Black Forest and Vosges-Palatinian.

Firstly, I wonder how female territories were established. A dispersing female establish a territory if she is in "breeding habitat" and the is enough unoccupied "breeding habitat" around she current position. The territory core area is 43.5 km2 in the Alpine region and 73 km2 in the other populations (from page 45, lines 885-900).
Must all the territory core area be "breeding habitat? If so, there are lots of small fragments of "breeding habitat" in Jura and Alpine regions that will never be occupied (Figure A3), as the fragments are smaller than the territory core area. If not so (i.e., the territory core area can contain other habitat types), how much of other habitat types (dispersal or matrix) can the territory core area contain?
If the territory core area can only be "breeding habitat" then it is very surprising that Black Forest and Vosges-Palatinian have a very low occupancy (Figure 4) and that Jura and Alpine have much higher occupancy.
In Figures 4 and C1 it is not possible to evaluate if recorded paths of female are also found outside "breeding habitat".

My second major question deals with the "collision layer" (Figure A2) and how the collision probabilities are treated for resident and dispersing individuals.
Resident lynx suffer from a fixed baseline mortality (0.1; Table B1) and a spatial one derived from the collision layer (between 0 and 1) and the risk is on a yearly time step.
Dispersing lynx follow a daily time step also with a fixed mortality (0.0007; Table B1) and a risk of collisions. A daily mortality risk of 0.0007 correspond to a yearly mortality risk of 0.23 (1-(1-0.0007)^365), which is a reasonable yearly mortality. I estimated the population growth rate with the fixed mortality and reproduction given in table B1, but without the "collision risk", to about lambda = 1.25 (a realistic growth rate).

However, how is the collision risk layer used? Is it the same collision risk for residents (yearly time step) and dispersers (daily time step)? If so, the collision risk is very much higher (maybe unrealistic high) for dispersers than for residents. If not so, how is the collision risk estimated for the residents vs. dispersers? How is the collision risk estimated for a disperser moving several steps?

If residents (yearly time step) and dispersers (daily time step) have the same collision risk (but for very different time steps) then it can explain the very low occupancy of Black Forest and Vosges-Palatinian regions, although these areas have large continuous breeding habitat. The low occupancy can be explained by the very low probability of colonization of these areas (or very high collision risk for dispersers). The occupancy map (Figure 4) seems to be entirely a result of the "random initial population" (Figure A4) and dispersing between regions are almost impossible because of the very high collision risk. The number of successful establishments in non-native populations is very low (the cumulative number over a 50-year period is less than 2 for all regions; Figure 3). Is this extremely low establishment in non-native populations supported by data?

Page 11, line 225, Page 14 lines 265-266, and Page 17 line 288 – The populations go towards a stabilization phase indicating a carrying capacity. I should call it "saturation" instead of carrying capacity, as it is a result of "all" female territory core areas are occupied ("saturated"). I think it would be very interesting to report the population size (divided into females and males) at the stabilization phase for each region, as population size is more important for long-term persistence than occupancy and growth rate.
I also wonder about the fairly low occupancy reported for Jura and Alps (pages 14-15, lines 265-274; Jura = 0.45, Alps = 0.60). I wonder if this can be explained by the many small fragments of "breeding habitat" that are too small for a territory core area? It would be very interesting to know the maximum number of female territory core areas that can fit into different regions. What is the maximum possible occupancy (can it be 100 %), given that the fragment of breeding habitat has to be larger than the female territory core areas? This question is also related to the question above if a female territory core area can include also other habitat types (not only "breeding habitat" but also "dispersing habitat" and matrix).

How are the different regions (or "populations") delineated outside the core area (Figure 4)? For example, the "breeding habitat" west and northwest of the Jura and Vosges-Palatinian regions in Figure 4 are continuously getting more and more fragmented without a clear boarder. The regions ("populations") are spatially defined as one report occupancy for each region, but it is not described how the regions are spatially defined.

Can the model forecast important dispersal routes? It would be very interesting to report the routes that successful lynx have used, although there are very few of them. The dispersal routes in the SE-IBM might be very informative (better than for example circuitscape models).

Page 19, lines 339-341 – Lynx males settle and stay even without females (Samelius et al. 2012, J. Zool. 286: 120-130), but they move over very large areas (Aronsson et al. 2016). Thus, I fully agree that a more realistic rule would be than male stay in areas also without females. But hopefully the results are not sensitive to this rule.

Page 21, line 391 – Herdtfelder 2012 is not in the reference list.

Page 34, lines 667-668 – Is it possible to report the exact model for the "collision layer"? I guess it is a logistic regression and it would be interesting to the have the coefficients (intercept, total road length, type of road of the longest road segment and proportion of urban area) to be able to apply the "collision layer" in other study areas.

Page 36, lines 697-699 – Is it possible to report the exact model for regular lynx presence? I guess it is a logistic regression and it would be interesting to the have the coefficients (intercept, presence of agricultural fields, forest and open land, distance to highways and human density) to be able to apply the "lynx habitat layer" in other study areas.