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Letter to the editor

Reply to Thornton and Murray: Models for Canada lynx conservation planning require nuance

Thornton and Murray (2024; hereafter TM) sought to further our understanding of historical and future Canada lynx (*Lynx canadensis*) habitat in the contiguous USA to guard against shifting baseline syndrome and aid conservation planning for this federally threatened species. We commend the intent of this exercise, however several issues limit the application of TM to lynx conservation, including model design and validation, extensive extrapolation, ambiguous source data, and plausibility of the results.

1. Problems with the contemporary model

The TM analysis rests on the accuracy of a lynx distribution model created with contemporary data to predict both past and future distributions in the contiguous USA. However, this contemporary model included overly broad vegetation covariates, few training data from the area of inference, and lacked adequate validation. Canada lynx is a specialist species requiring specific forest composition and structure (Ruggiero et al., 2000). Relevant vegetation categories for capturing lynx habitat in the TM model were "semi-natural/natural woodland" and "boreal/coniferous forest" from their 'land use' and 'biome' covariates, respectively, which can encompass a wide range of forest conditions and likely pushed the model toward over-prediction of lynx habitat. Training data for the contemporary model, derived largely from northern locations, were spatially mismatched from the area of prediction in the contiguous USA. Ironically, as co-authors of Olson et al. (2021), TM were aware of contemporary lynx distribution models within the prediction area, built on thousands of high quality occurrence observations and validated with hundreds of independent detections (e.g., withheld GPS locations, camera detections, genetic samples). Finally, the contemporary TM model was apparently not validated before using it for prediction (only the backward forecasting was validated), nor was the model presented to the reader for visual inspection. These missed steps are critical as our present understanding of lynx distribution is also our best understanding. Any model used to predict past or future lynx distributions should first be shown to appropriately describe the present distribution.

2. Extensive extrapolation

This manuscript extrapolates the contemporary model extensively in time (over a century) and space (contiguous USA). Regardless of the covariates or training data employed, extrapolation like this is inherently precarious and relies on a number of assumptions, including stationarity in animal-environment relationships. Clamping covariates in the zone of prediction to their original range (as TM did) does not remove this risk. Olson et al. (2021) demonstrate that even *regional* transferability of lynx habitat models within the *same* time frame is challenging, let alone across the continental and multi-century scales that TM make.

3. Interpretation of Lynx location data

TM use "reliable" historical records from McKelvey et al. (2000) instead of more stringent "verified records" to denote lynx occurrence. McKelvey et al. noted that even with verified records the population dynamics of lynx, and behaviors that result from those dynamics, "… increases our uncertainty concerning the meaning of an occurrence, or even many occurrences." Lynx make large exploratory movements or even become nomadic, especially following peaks in their population cycles. TM assume that a lynx occurrence record, whether it is reliable or verified, indicates suitable habitat for a lynx population.

TM state that these data quality issues were "minor," claiming that if observations occurred in marginal habitat (e.g., from dispersing or nomadic individuals) (1) the model should have predicted lower scores in those locales, and (2) the locations in potentially anomalous habitat should register at different times from cyclic peaks in Canada than locations in currently occupied habitat. In our opinion data quality is a central issue because (1) the model would only generate lower scores if it was a sensitive model of lynx habitat suitability (capable of discerning residency from nomadism, for example), and (2) peaks produce waves of individuals that travel in both occupied and marginal habitat, thus providing potential for occurrences to rise and fall relatively synchronously in both habitat types, especially for a species as vagile as lynx. Furthermore, TM seem to interpret all occurrence data as indicative of occupancy, inferring importance to the habitat underlying them. However, these occurrence data include a mix of resident, dispersing, and nomadic lynx. Even multiple occurrence records in a given area that may indicate occupancy by one or a few individuals cannot be equated with a resident, viable population, nor is the habitat underlying such individuals necessarily critical as inferred by TM. Ambiguous occurrence data do not transform into reliable models of distribution.

4. Plausibility

Numerous blocks of modeled historical habitat with high relative habitat suitability values (e.g., > 0.5) were predicted to occur in Arizona, New Mexico, Nevada, South Dakota, and California (TM Fig. 3), which is untenable based on known habitat and climatic requirements for lynx and snowshoe hares. Even within more reasonable areas of lynx habitat such as Colorado, Utah, the Greater Yellowstone Area (GYA), Minnesota, and New England, large areas of predicted historical habitat by TM occur in dry conifer systems, montane shrub, deciduous forest, or other cover types that lack adequate snowshoe hare densities to support a lynx population. If these areas were (or will be as in TM Fig. 5) lynx

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habitat, a shift in vegetative systems, or a shift in lynx-hare habitat preference would be required in about 100 years. A shift like this is ecologically implausible.

5. Conservation

TM conclude that lynx range covered 254 % more area historically than at present, identifying northern Utah, central Idaho, GYA, and parts of northeast Minnesota as important lynx habitat that is currently unoccupied. However, at least in Idaho, Utah, and some parts of the GYA, recent models built and tested on spatially congruent data suggest that these areas are marginal habitat, and not suitable for persistent occupancy by lynx (Olson et al., 2021). Furthermore, several lynx from the Colorado reintroduction dispersed to these areas, but did not remain (Devineau et al., 2010; Fig. 1). We suggest that TM's approach of extrapolating northern data, combined with the use of ambiguous historical occurrence data to verify results, dilutes a more appropriate, nuanced, and complex view of these regions and the forest types they contain. It is an oversimplification to classify such modeled areas as "lynx habitat" then claim lynx distribution has shrunk because these areas do not currently contain resident populations. Ultimately, effective lynx conservation requires focused action in forested landscapes that promote occupancy, especially those areas also resilient to climate change. We disagree that suspect characterizations of historical lynx habitat should be equally considered alongside well-studied contemporary understandings. There is strong literature from substantial lynx research throughout the contiguous US over the last 25 years that should be used to qualify the over-generalized conclusions of TM for conservation decision-making.

CRediT authorship contribution statement

Jacob S. Ivan: Conceptualization, Writing – original draft. **Karen E. Hodges:** Conceptualization, Writing – review & editing. **Joseph D. Holbrook:** Conceptualization, Writing – review & editing. **Ron A. Moen:** Writing – review & editing. **Lucretia E. Olson:** Conceptualization, Writing – review & editing. **John R. Squires:** Conceptualization, Writing – review & editing. **Jennifer H. Vashon:** Writing – review & editing.

Declaration of competing interest

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

Data availability

No data was used for the research described in the article.

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