Limited cougar recolonization of eastern North America predicted by an individual-based model

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ABSTRACT

As carnivores recolonize parts of their historical range, and such recolonization is increasingly recognized for its ability to reconfigure and revitalize degraded ecosystems, understanding where and when range expansion may continue is useful for facilitating scenario planning and identifying roles for conservation measures.

We developed an individual-based model to predict carnivore range expansion and applied it to cougars (*Puma concolor*) in North America between 2023 and 2100. We parameterized our model with empirical movement, demographic, and survival data, and validated its performance by hindcasting nine observed recolonization events from the 1990s – 2023.

Our model accurately recreated historical recolonization events and forecasted cougars reclaiming 2.1 % of unoccupied range by 2100, mostly in boreal Canada. Of currently unoccupied states/provinces ("jurisdictions"), only Manitoba received universal support across model runs for hosting a breeding population by 2100. Oklahoma, Minnesota, Kansas, and Iowa, requiring dispersal across nonhabitat, had 30 %, 30 %, 11 %, and 2 % probability of recolonization, respectively. No other jurisdictions were forecast to be recolonized.

Mortality from harvest in Midwestern source populations and vehicle collisions dominated outcomes for eastward-moving females. Simulated management scenarios eliminating such hunting and adding nine wildlife crossing structures, however, did not significantly change recolonization probability.

In areas where current cougar range abuts unoccupied breeding habitat, we estimated slower rates of expansion, varying from 2 to 3 km·yr^{-1}, yielding roughly 150–230 km of linear expansion in those regions by 2100.

Our mechanistic model and underlying empirical data provide a credible and transferable approach to forecast carnivore range expansion.

1. Introduction

Carnivores are recolonizing parts of their former ranges around the globe (Chapron et al., 2014; Larue et al., 2012; Pyare et al., 2004), altering socio-economic and ecological systems (Gilbert et al., 2017; Kuijper et al., 2016; Pettersson et al., 2021). Carnivore return can bring both positive (e.g., reduced ungulate-vehicle collisions) and negative (e. g., increase livestock depredation) socioeconomic impacts (Gilbert et al.,

2017; Landon et al., 2019). Understanding factors influencing such recolonization is useful for both strategic natural resource management and conservation efforts, particularly given the focus on carnivores as potential agents of ecosystem rewilding (i.e., the revitalization or restoration of ecosystem function; Sandom et al., 2013, Hobbs et al., 2024). Predicting recolonization, however, can be challenging, given the complexity of interacting processes involved, including spatiotemporal variation in mortality risks, habitat selection and movement characteristics during dispersal, and potential reliance upon stepping-stone populations amid hostile nonhabitat (Bocedi et al., 2014; Fletcher et al., 2019). Moreover, the interactions arising between a species' biology (e.g., dispersal distances and demographic rates) and the landscape the animals must traverse make recolonization patterns highly system-specific (Barros et al., 2016).

Range expansion can occur across nonhabitat ("matrix expansion") or contiguous breeding habitat ("contiguous expansion"), and the factors controlling expansion rate for each are distinct (Bocedi et al., 2014). If mortality while traversing nonhabitat is low, for example, matrix expansion can outpace contiguous expansion, because breeders travel farther to find suitable habitat (Bocedi et al., 2014). High mortality in nonhabitat, conversely, can slow or preclude matrix expansion. Contiguous expansion, meanwhile, is mediated predominately by demographic variables, including reproductive rate, dispersal probability, and settlement probability (Hastings et al., 2005).

Recolonization predictions typically focus on identifying suitable breeding habitat (e.g., Smith et al., 2016) and dispersal corridors (e.g., LaRue and Nielsen, 2008), or predicting range expansion using spatially-explicit stage matrices with fixed dispersal kernels (e.g., Larue and Nielsen, 2016; Petracca et al., 2023). These approaches address important components of recolonization, but risk neglecting underlying processes, such as different mortality rates during dispersal in the population core versus the colonization front.

Here, we develop an individual-based model (IBM) for predicting carnivore range expansion and apply it to cougars (*Puma concolor*) in North America. IBMs offer a process-based approach for generating predictions of range expansion by relying on empirical ecological data to incorporate complexity of the underlying processes. Such models can incorporate spatially realistic landscapes, interaction among agents, adaptation, and learning (McLane et al., 2011; Railsback and Grimm, 2011). IBMs can be parameterized and calibrated using empirical data and validated by matching observed patterns, including historic recolonization events, bolstering their credibility. IBMs have been applied to diverse topics in wildlife ecology, including territory formation (Sells and Mitchell, 2020), gene flow (Landguth et al., 2017), and management scenario planning (Crevier et al., 2021), and are increasingly recognized as a useful tool for recolonization and invasion forecasting (Hauenstein et al., 2019; Pili et al., 2022; Recio et al., 2020).

Cougars once existed across the breadth of North America (Cardoza and Langlois, 2002), but were restricted to the West and Florida by 20th century eradication campaigns (Nesslage et al., 2006). Recently, however, new breeding populations have been documented in portions of the species' historic range, and cougar sightings have increased across the Midwest and East, including a male dispersal as far as Connecticut (Hawley et al., 2016; Larue et al., 2019). Cougar range expansion has taken place via both contiguous expansion in Alberta and matrix expansion across the broader Midwest (Jenks, 2018; Knopff et al., 2014; Larue et al., 2012; Morrison et al., 2015), and habitat suitability predictions suggest potential continuation via both avenues (Larue and Nielsen, 2011; O'Malley et al., 2024; Winkel et al., 2022; Yovovich et al., 2023). Rates of spread in these distinct habitat types, however, remain unclear, given uncertainty in both mortality rates while traversing nonhabitat (Crone et al., 2019) and how demographic rates influence expansion (Hastings et al., 2005).

We developed a modeling framework that generates empirically-founded predictions of carnivore range expansion and used this framework to identify likely timing and locations of continued cougar

recolonization. We drew upon published demographic information and cause-specific mortality rates, as well as existing empirical data of dispersal movements. We then validated our model by hindcasting recolonization of nine Midwestern populations from the 1990s through present day. Additionally, we explored the potential influence of two management scenarios, reduced Midwest hunting and constructing new road crossing structures, on recolonization probability. The resulting model provides a case study for understanding the role of contiguous versus matrix spread during carnivore recolonization, offers a template for predicting range expansion and recolonization among other wildlife species, and generates actionable, continent-scale predictions for a high-interest, recolonizing carnivore across a human-dominated landscape in the Global North.

2. Methods

Here, we summarize the development, design, and implementation of our IBM. A complete description following the Overview, Design concepts, and Details (ODD; Grimm et al., 2020) format is available in Appendix S1. We parallelized simulations in Python 3.10 on an AMD Ryzen 75800H 3.20 GHz processor; median runtime per simulation was 30.8 h.

2.1. Model summary

2.1.1. Model purpose and overview

The purpose of this model is to predict spatiotemporal dynamics of cougar recolonization in Midwestern and Eastern North America. Specifically, the model addresses the questions:

1) What is the relative importance of different source populations for recolonization?
2) Which mortality sources most inhibit females from reaching unoccupied habitat?
3) Where and with what probability can we expect cougars to establish populations outside their current breeding range?

The model simulates individual cougars dispersing from current cougar range, incurring mortality risk during dispersal, establishing territories upon reaching suitable habitat, and reproducing upon encountering a mate. Cougars "born" into the model undergo these same processes, enabling range expansion via stepping-stone populations. The model operates at a daily timestep on a 5 km grid of North America. All processes are parameterized, calibrated, and validated using empirical data. To validate the model, we hindcasted recolonization of Midwestern populations during the 1990s and 2000s and compared simulated recolonization timing with observed dates. A thorough description of each of these processes and the other empirical patterns we used to validate the model is available in Appendix S1; we summarize each below.

2.1.2. Cougar initiation in current range

We defined current/occupied range as areas hosting at least one documented cougar reproduction event circa April 2023. To simulate cougar dispersal from current range, we drew upon demographic and population density estimates from the literature (Table S1.7). Since these values can be estimated using different methods and can vary across ecoregions, we averaged values across available studies (Table S1.6). In short, we multiplied adult female population density (1.03 ind/100km²) by the area currently occupied by cougars (1,862,550 km²) and maternity rate (1.21 kittens per female per year) to generate the number of kittens born per year in North America (23,213). We assumed no seasonal pulse in reproduction and divided the result by 365 to achieve mean daily cougars born, which we multiplied by the survival rate (0.48) to dispersal age (14.5 months) for mean number of cougars reaching dispersal age per day (30.5). We assumed a 1:1 sex

ratio surviving to dispersal age and multiplied the result by sex-specific dispersal rates (F = 0.41, M = 0.90) to account for philopatry, yielding a daily mean of 13.31 males and 8.72 females dispersing from their natal territories each day across North America. For references and a complete description of these calculations, see Appendix S1, Tables S1.6, S1.7, and S1.8.

2.1.3. Movement

We simulated movement using a step selection function (SSF; Thurfjell et al., 2014, Signer et al., 2017) fit to GPS-collar data of 74 dispersing cougars (Fig. S1.6; 63M, 11F). Collar data were collected between 2002 and 2022 across 15 western study areas (see Appendix S1 for capture/handling/permitting information). Using a daily fix interval and 500 m pixel resolution for environmental covariates, we evaluated cougar response to land cover type, Normalized Difference Vegetation Index (NDVI), terrain metrics, human population density, rivers, and roads (Table S1.4). Of these, the top performing model (selected using the Deviance Information Criterion) retained Topographic Position Index (TPI), NDVI, population density, cropland, and roads (Table S1.5). We used this top model to generate a habitat kernel (Fig. S1.7; Signer et al., 2017), which we downsampled to 5-km resolution for transferability to the IBM.

Determining a cougar's location at time t + 1 required incorporating the above habitat kernel, a movement kernel comprising turning angle, step length, and bearing relative to the cougar's starting location, and a roads kernel that weighted cells according to the speed limit and number of lanes crossed to reach them, multiplied by the road selection coefficient from the SSF (Fig. S1.8). Since several of these kernels varied according to the cougar's current (and, in the case of turning angle, previous) location, the model calculates them anew for each distinct step. Each kernel is generated within 30 km of the animal's location (i.e., the maximum daily distance traveled by a GPS-collared dispersing cougar) and multiplied together to generate the final surface of selection probabilities for that step. The model then randomly draws a cell within 30 km, weighted by selection probabilities, to determine the animal's next location.

2.1.4. Mortality

Simulated cougars incur cause-specific mortality risk during dispersal, die upon reaching 10 years of age, and upon establishing territories incur daily mortality risk reflecting 4 % and 14 % annual mortality for adult males and females, respectively (Logan and Runge, 2021). We chose these mortality risk values because they are the most robust (i.e., largest sample size) published survival estimates of which we are aware that are (a) sex-specific, (b) limited to adults, and (c) obtained from a non-hunted population (or during a period without hunting). We emphasize that simulated cougars only incur these mortality rates after establishing territories, and many cougars die before this, during dispersal. Mortality during dispersal arises from harvest, nonharvest mortality (i.e., human-caused mortality excluding harvest and roadkill), roadkill, and natural causes.

We calibrated jurisdiction-specific mortality risk from harvest using state and provincial juvenile harvest records (representing dispersers) from 2011 to 2020. Each cell in current range in jurisdictions where harvest is permitted was assigned a mortality probability from harvest, and we iteratively ran simulations until median annual simulated jurisdiction harvest matched observed values (Fig. S1.3). We assigned mortality risk from nonharvest mortality following the same procedure, except nonharvest mortality was not restricted to areas of current range.

We parameterized roadkill mortality risk using 42 roadkill observations across the Western U.S. and 1577 observations of successful road crossing from our GPS-collar dataset. For each location, we extracted the number of lanes and speed limit and used the machine-learning technique support vector machines (SVM; James et al., 2017) to predict mortality probability for all North American roads (Fig. S1.9). Simulated cougars incur cumulative mortality risk from all roads intersecting a

step, evaluated after the cougar has "made the decision" to cross the road; i.e., behavioral response to roads is evaluated prior to mortality (Fig. S1.10).

We calibrated mortality risk from natural causes using the ratio of deaths labeled "natural" or similar (e.g., "male cougar," or "intraspecific killing") to harvest deaths in published studies (Table S1.1). This yielded a ratio of 108 natural:169 harvest deaths (i.e., 0.62 natural deaths for every harvest death). We multiplied this proportion by jurisdiction harvest deaths and followed the same calibration procedure described for harvest to assign mortality risk from natural death within current range.

2.1.5. Territory establishment

In the model, cougars establish territories within current range according to fixed cell- and sex- specific probabilities, and in potential range according to territorial dynamics observed in wild cougars. Establishment probabilities in current range were calibrated to match observed sex-specific dispersal distances (Fig. S1.2), thereby controlling the number of dispersers leaving current range.

In potential range, simulated cougars establish territories only if their establishment keeps local sex-specific density under observed values (i.e., 1.03 females/100 km^2 for females and 0.65 males/100 km^2 for males), and male cougars must also be within 15 km of an established female cougar. In this way, males continue dispersing until they have encountered (i.e., passed within 15 km of) a potential mate.

2.1.6. Reproduction

Reproduction occurs in the model if an established female occupying potential range is within 15 km of an established male. In addition, a female only reproduces if at least 32 months of age (i.e., mean age to first litter; Logan and Runge, 2021), and at least 18.9 months have passed since her last reproduction (i.e., mean reproductive interval; Table S1.6), or she has not previously reproduced.

Upon reproduction, an average of 1.247 kittens are introduced to the model at the mother's location (i.e., mean litter size of 2.6 multiplied by the survival rate to independence of 0.48; Tables S1.6 and S1.7). Offspring have a sex ratio of 1:1 and gestate for 90 days, then become philopatric with a probability of 0.41 (females) and 0.10 (males). Philopatric offspring establish immediately if their establishment would not increase the local density above sex-specific thresholds (see 2.5 *Territory establishment*) and are otherwise removed from the model to maintain realistic population densities. Upon reaching dispersal age (14.5 months; Logan and Runge, 2021), dispersing offspring begin moving.

2.2. Hindcasting midwestern recolonization

To validate recolonization timing predictions, we compiled timing of observed recolonization events in the Midwestern USA and Canada from 1995 to 2023 (Table 1). We then ran the model for 40 years (i.e., 14,600 timesteps), starting in 1995, with recolonized habitat patches excluded from the area considered current range (i.e., current range defined circa 1995; Fig. 1a). We ran 100 iterations and extracted locations and timesteps of reproductive events (hereafter "litters") that occurred within known recolonized patches. For each patch and iteration, we determined year of the first litter in that patch; if no litters occurred for a patch during that iteration, we assigned the year 2035 (i.e., end of the simulation). We then calculated median and 95 % quantile hindcasted first litter dates for each patch across iterations and compared these with observed recolonization dates.

2.3. Predicting range expansion

To predict continued range expansion, we ran simulations from 2023 to 2100 (i.e., 77 years, 28,105 timesteps) with current range circa 2023 (Fig. S1.11). We ran 100 simulations in this configuration and for all simulated cougars extracted locations and timesteps of initiation/birth,

Table 1

Comparison between observed date range and individual-based model (IBM) hindcasted recolonization timing of Midwestern populations. Date ranges are based on either first documented reproduction (Beaver Hills, NW Saskatchewan, Cypress Hills, Pine Ridge, and Niobrara River Valley), or the period during which cougar sightings began increasing substantially (Porcupine Hills, Missouri Breaks, Badlands, and Black Hills).

Population	IBM median date (95 % interval)	Observed date range	Reference
Beaver Hills, AB	2013 (1998 – Inf)	2002–2004	Haughian, 2005
North Battleford region, SK	2013 (1999 – Inf)	2014–2016	Saskatchewan Ministry of Environment, 2018
Porcupine Hills, SK	2035 (2014 – Inf)	2015–2017	Saskatchewan Ministry of Environment, 2018
Cypress Hills, AB/SK	2003 (1997–2022)	2005–2007	Bacon, 2010
Missouri Breaks, MT	1997 (1996–2000)	1995–2000	U.S. Fish and Wildlife Service, 1995, 1998, & 2001
Badlands, ND	2001 (1997–2021)	2000–2005	Status of Mountain Lion Management in North Dakota, 2022
Black Hills, SD	1998 (1997–2001)	1995–2000	Jenks, 2018
Pine Ridge, NE	1998 (1997–1998)	2006–2007	Nebraska Mountain Lion Management Plan, 2017
Niobrara River Valley, NE	2026 (2000 – Inf)	2014–2017	Nebraska Mountain Lion Management Plan, 2017

reproduction, mortality, and territory establishment.

We used six metrics to evaluate spatiotemporal recolonization dynamics, which cumulatively address the questions: 1) How likely is recolonization in each currently unoccupied jurisdiction, and what is the relative importance of source populations for such recolonization? 2) How quickly will contiguous range expansion proceed in areas where unoccupied habitat abuts current range? 3) What factors impede recolonization?

First, for all jurisdictions currently unoccupied by cougars, we calculated the proportion of simulations in which each jurisdiction supported the birth of at least one litter. We did this on a decadal basis, yielding, for example, the probability of Minnesota hosting a reproducing cougar population during the decade 2041–2050 (the decade ending in 2030 was truncated to begin in 2023). We then bootstrapped these proportions 500 times to generate confidence intervals (Fig. 2).

Second, to evaluate connectivity across the Midwest and relative importance of source populations for recolonization, we extracted origin jurisdiction for every female establishing a territory in currently unoccupied jurisdictions. We summed these values for each jurisdiction pair in each simulation and took the mean across simulations. To visualize connectivity, we mapped segments connecting the start and end locations of these recolonizing females (Fig. 3). We included the currently unoccupied portion of Nebraska in these calculations to evaluate continued within-state eastward expansion.

Third, to estimate the rate of range expansion in contiguous habitat, we identified regions of northern Saskatchewan, Florida, and Texas that were consistently colonized during model runs (white boxes in Fig. 4). We extracted year and location of first litters born in each region for each simulation, and in the case of ties we calculated centroids. We then calculated the distance and elapsed time from this litter to all other litters born in that region during the simulation, and extracted the farthest litter born. In the case of multiple equidistant farthest litters, we retained the earliest. We then calculated the rate of range spread as the distance from the first to farthest divided by the elapsed intervening time and bootstrapped these rates 500 times across simulations for each region.

Fourth, for jurisdictions containing unoccupied habitat that abuts occupied habitat (i.e., Alberta, Saskatchewan, and Texas), we mapped annual cell-specific probability of establishment. To do this, we calculated earliest year in each simulation a litter was born in each 5×5 km cell, then took the median across simulations. We applied a moving-
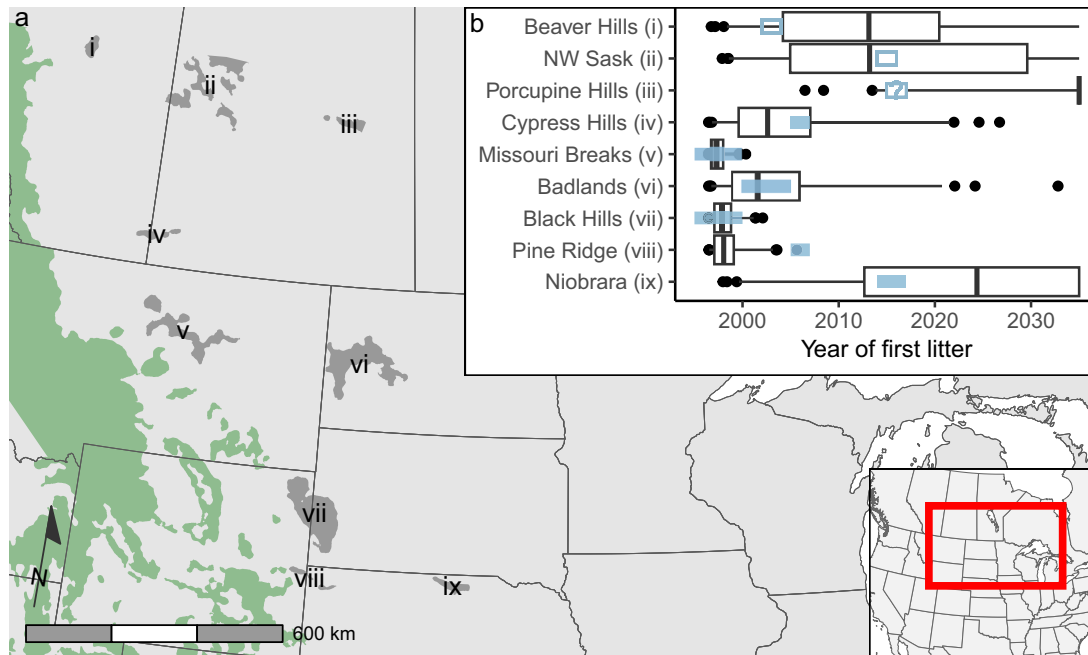
Fig. 1. Location (a) and recolonization timing (b) of Midwestern populations, as observed (blue boxes) and hindcasted by the IBM (boxes and whiskers). In (b), filled blue boxes indicate date range of first reproduction when followed by establishment of breeding populations, unfilled blue boxes indicate single observations of reproduction with no subsequent information on breeding populations, and the question mark for Porcupine Hills indicates no documented reproduction of which we are aware, but the region is considered to host a breeding population by local authorities. The boxplot represents the year of first reproduction summarized across 100 simulations; if no recolonization occurred, the year 2035 (i.e., end of simulation) was assigned. Boxes indicate interquartile range, whiskers indicate 95 % quantile limits. In (a), locations of midwestern populations are in grey, with distribution circa 1995 in green.
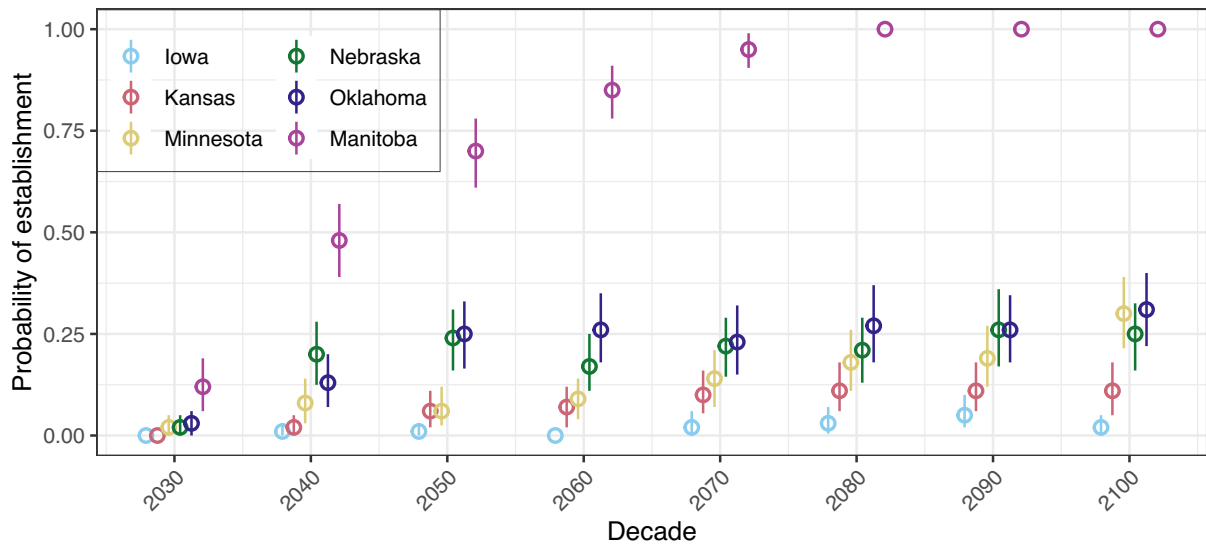
Fig. 2. Probability of establishment in currently unoccupied states/provinces, calculated as the proportion of simulations yielding at least one litter born during the decade ending in the indicated year. Ninety-five percent confidence intervals were calculated from 500 bootstrap iterations. In Nebraska, calculations excluded currently occupied areas; Alberta and Saskatchewan are not included because both contain areas where current range abuts potential range and simulated establishment therefore happens nearly immediately.
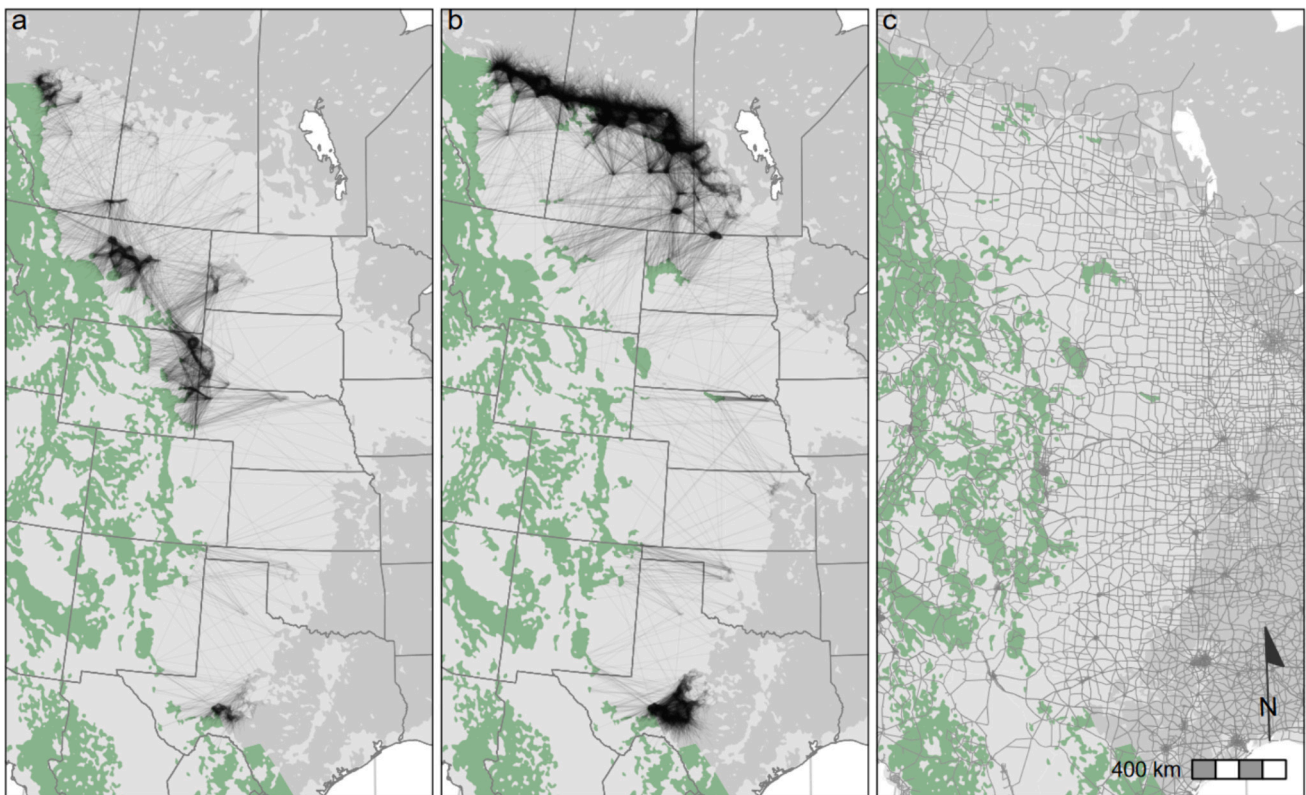

Fig. 3. Segments connecting simulated natal and adult territories among female cougars that established territories in unoccupied habitat, from (a) midwestern hindcasting simulations (i.e., 1995–2023), and (b) eastward forecasting simulations (i.e., 2023–2100). Segments are partially transparent to illustrate relative abundance of connections between habitat patches, and only territory establishments within 15 km of unsuitable habitat are shown to emphasize connections between isolated patches rather than within patches. Note actual recolonization during recent decades by comparing current range (green) in panels (a) and (b). Roads, based on the National Transportation Atlas Database (U.S. Department of Transportation, 2022), are shown in (c). Segments from 20 simulations for each run type are shown to facilitate interpretability. Current range in Alberta, based on Knopff et al. (2014), is circa 2010 and has likely expanded since.

window smoothing function and binned the result by decade, yielding a visual representation of range expansion in contiguous habitat (Fig. 4).

Fifth, to characterize constraints on recolonization, we determined cause-specific mortality for female dispersers that began moving toward unoccupied habitat but failed to either reach suitable breeding habitat or to reproduce. To do this, we extracted all females initiated within 30-km of any female's initiation that did successfully reach unoccupied habitat (effectively excluding females that originated too far west). From these
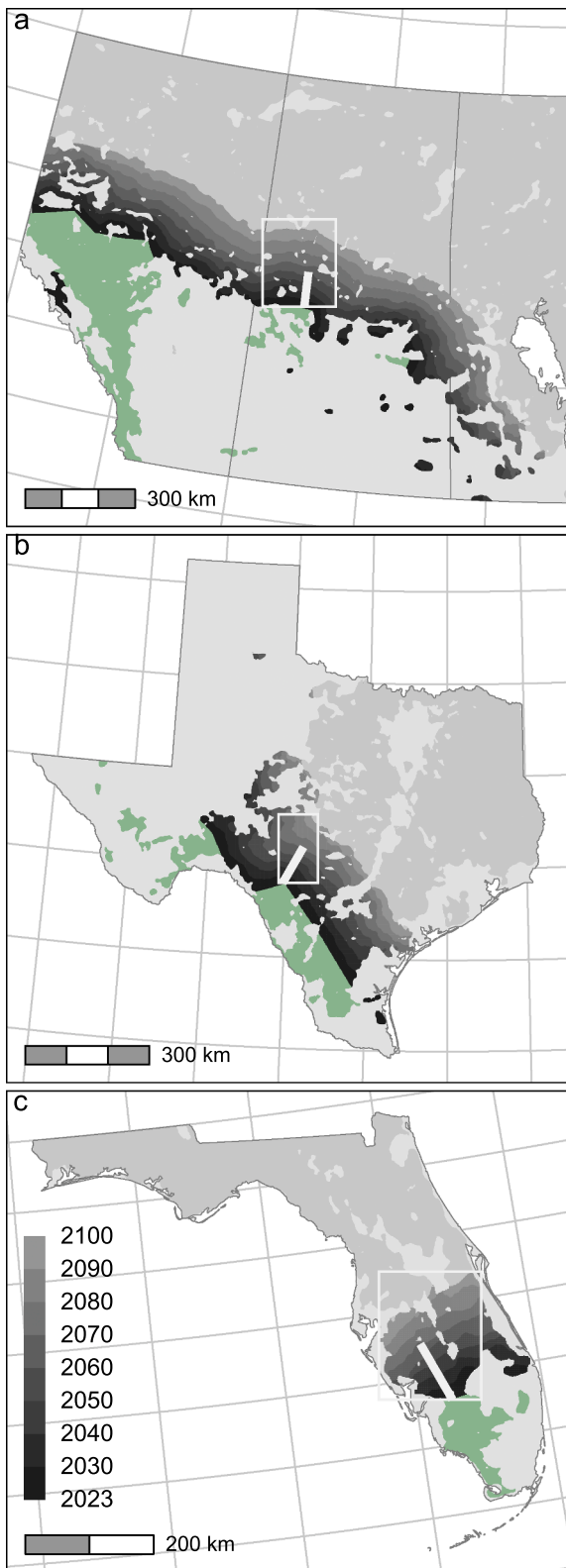
Fig. 4. Predicted range spread of cougars from 2023 to 2100 across Alberta, Saskatchewan, and Manitoba (a), Texas (b), and Florida (c). Green indicates current cougar range circa 2023 and light grey indicates suitable but unoccupied range. Note that current range in Alberta, based on Knopff et al. (2014), is circa 2010 and has likely shifted north and east since then; range expansion predictions likely lag accordingly. White boxes indicate regions within which range spread rates were calculated, and white bars (100 km long) are provided for comparative scale across panels.

females, we retained only animals with mortalities east of their starting location. We then calculated the per-simulation proportion of these individuals that established and reproduced, established but failed to reproduce, died by vehicle collision, died by harvest, died by natural causes, or died by nonharvest mortality, and bootstrapped the median 500 times across simulations.

Finally, to further explore constraints on recolonization and evaluate the potential influence of interventive measures, we ran two additional sets of 50 forecasting simulations representing hypothetical management scenarios. In the first, we eliminated hunting in North Dakota, South Dakota, and Nebraska. In the second, we simulated wildlife crossing structures in midwestern jurisdictions and Florida (Fig. S2.1). To do this, we extracted roadkill mortality locations of the eastward-moving females described above and identified the road segment for the eight Midwestern jurisdictions with the most vehicle collisions (in the case of ties, we retained the easternmost segment). We used the same approach for Florida, except we started with all female mortality and restricted possible road segments to those north of current range. We note that this approach may underestimate structures' facilitation of successful crossing since it excludes any associated fencing, which is commonly recommended to promote crossing structure efficacy (Rytwinski et al., 2016; Shilling et al., 2023). For each scenario, we then calculated the probability of establishment, by decade, for currently unoccupied jurisdictions, as described above, and used overlap between bootstrapped 95 % confidence intervals to evaluate significant change from "status quo" simulations.

3. Results

3.1. Hindcasting midwestern recolonization

The model accurately hindcasted the broad pattern of midwestern recolonization timing and locations; actual recolonization dates fell within the 95 % interquartile range of simulated values for all populations except Pine Ridge (Fig. 1; Table 1). Hindcasted timing was generally earlier and less variable for habitat patches that are closer to current range and/or larger (e.g., Black Hills and Missouri Breaks), and later with more variation for farther and smaller patches (e.g., NW Saskatchewan and Niobrara River Valley). For more detailed results and discussion of hindcasting simulations see Appendix S1 Sections 1.4 and 1.5.

3.2. Predicting continued range expansion

The model predicted continued range expansion in Midwestern jurisdictions and Florida via both matrix (Fig. 3; Midwest only) and contiguous spread (Fig. 4). Predicted rate of expansion, however, was modest, and eastward expansion never reached farther than central Minnesota (93.8°W) by 2100, nor did northward expansion in Florida extend beyond Orlando (28.4°N). Median area of historical range reclaimed by cougars was 137,975 km^2 (95 % bootstrapped confidence interval: 136,300–139,132 km^2), most of which was in boreal Canada; i. e., 2.1 % of currently unoccupied potential breeding habitat.

Of currently unoccupied jurisdictions, Manitoba alone received universal support across simulations for recolonization by 2100 (Fig. 2). There, 70 % and 95 % of simulations yielded at least one litter born in the province during the decades ending in 2050 and 2070, respectively. The next likeliest jurisdictions for recolonization were Oklahoma and Minnesota (both 30 % probability of at least one litter between 2090 and 2100), the currently unoccupied portion of Nebraska (25 % probability), followed by Kansas (11 %) and Iowa (2 %). No other currently unoccupied jurisdictions were predicted to host reproducing cougars by 2100.

Successful female dispersal to currently unoccupied jurisdictions was dominated by movement into Manitoba from Saskatchewan (mean individuals per 77-year simulation = 110.5), North Dakota (mean = 13.5),

and Montana (mean = 1.6; Table 2; Fig. 3). After Manitoba, Minnesota and Oklahoma received the most female dispersers (3.7 and 3.8 individuals per simulation, respectively), originating predominately in North Dakota and New Mexico, respectively. Apart from movement into Manitoba from Saskatchewan, North Dakota contributed the most overall female dispersers to colonizing currently unoccupied jurisdictions, followed by New Mexico and Nebraska.

Range expansion in contiguous habitat varied from 2.01 km·yr^{-1} in Florida (95 % bootstrapped confidence interval: 1.90–2.08 km·yr^{-1}) to 2.37 km·yr^{-1} in Texas (2.29–2.44 km·yr^{-1}), and 2.92 km·yr^{-1} in Saskatchewan (2.83–3.00 km·yr^{-1}; Fig. 4).

Of eastward-moving female cougars, 8.8 % survived to reproduce in currently unoccupied breeding habitat whereas 2.9 % successfully established territories but failed to find mates (Table 3). The plurality (35.4 %) were harvested prior to leaving current cougar range, and nearly as many were killed by vehicles during dispersal (29.7 %). However, neither eliminating Midwest hunting nor simulating the construction of one overpass per Midwestern jurisdiction significantly altered probability of recolonization for currently unoccupied jurisdictions, although 1/50 "no Midwest hunting" simulations yielded breeding females in Missouri during the decade 2080–2090, whereas no "status quo" simulations did (Fig. S2.2).

4. Discussion

The return of carnivores to their historic range is hailed as a potential mechanism of ecosystem reconfiguration, revitalization, and restoration (Hobbs et al., 2024; Perino et al., 2019; Sandom et al., 2013). Many carnivores regulate prey populations and lower trophic levels, including via trophic cascade. Cougars in particular have been identified as ecological brokers for their broad role in shaping the ecosystems they inhabit (LaBarge et al., 2022). For instance, cougar recolonization would likely increase carrion provisioning to small scavengers but may also increase mortality risk among mesopredators (LaBarge et al., 2022). Similarly, cougar restoration is expected to reduce ungulate-vehicle collisions (Gilbert et al., 2017), but may be met with resistance among livestock producers and hunters (Landon et al., 2019).

Our model, which was validated by hindcasting recolonization of existing Midwestern populations, predicted a high probability of cougar recolonization, defined as the occurrence of at least one reproduction event, in Manitoba by 2100 via both contiguous and matrix expansion. Further, our model predicted a moderate probability of recolonization in currently unoccupied midwestern jurisdictions via matrix expansion. Predicted recolonization of Manitoba is consistent with abundant sightings in the province (Watkins, 2005). Our model did not predict reproducing cougars east of central Minnesota or north of Orlando in Florida by 2100, suggesting that the peak of natural recolonization may

Table 3

Outcomes for eastward-moving female cougars originating in current range. Percentages represent medians across simulations (95 % interquantile range).

Outcome	
Harvest	35.4 % (35.1–35.5 %)
Roadkill	29.7 % (29.5–29.9 %)
Non-harvest mortality[a]	11.9 % (11.8–12.1 %)
Natural mortality	11.1 % (11–11.4 %)
Established and reproduced	8.8 % (8.7–8.9 %)
Established without mate	2.9 % (2.8–3 %)

[a] Represents all human-caused mortality excluding legal harvest and roadkill.

have passed. Although harvest in source populations and roadkill were leading sources of mortality among eastward dispersing females, simulations of interventive measures (i.e., constructing nine overpasses and eliminating Midwestern U.S. hunting) did not significantly change recolonization probability.

Our results fit well into ecological theory of species expansion (Bocedi et al., 2014; Crone et al., 2019). Cougars spreading via matrix expansion across Midwestern nonhabitat incurred sufficiently high mortality rates, predominantly from vehicle strikes, to constrain recolonization. These rates increased as cougars moved east and encountered denser road networks (Fig. 3c), allowing historical recolonization of areas with relatively few roads (e.g., Black Hills, Badlands; Fig. 3a), but largely impeding continued eastward expansion (Fig. 3b). This mortality prevented cougars from reaching the most proximate high-quality eastern habitat (e.g., eastern Kansas or NE Minnesota) in roughly 70 % of simulations (Figs. 2 and 4). Although wildlife crossing structures are commonly considered to be effective in promoting connectivity (Pimm et al., 2021), results from our "overpass" scenario suggest that more crossing structures or a different configuration (e.g., many overpasses along a single corridor) may be required to produce an appreciable difference in recolonization timing.

Meanwhile, contiguous cougar range in boreal Canada, Texas, and Florida expanded at rates determined predominately by demographic parameters but mediated by local mortality risk. Modeled rates of spread in these regions (roughly 2–3 km·yr^{-1}) are similar to those observed among recolonizing carnivores elsewhere (Eisaguirre et al., 2021; Hody and Kays, 2018; Baklid, 2022; Pyare et al., 2004). For instance, brown bears (*Ursus arctos*) recolonized Slovenia from 1945 to 1995 at a rate of 1.6–1.9 km·yr^{-1} (Jerina and Adamič, 2008), and even coyotes (*Canis latrans*), highly adaptable to human development, required over a century to expand approximately 700–1000 km from the Midwest to the East Coast of the USA (Hody and Kays, 2018).

Our model predicted a low-to-moderate probability of continued

Table 2

Predicted number of female cougars establishing territories in currently unoccupied states by state of origin, 2023–2100. Numbers represent mean across simulations.

State of origin	State of establishment						Total
	Manitoba	Iowa	Kansas	Minnesota	Oklahoma	Missouri	
Alberta	0.1						0.1
Colorado		<0.1	0.3	<0.1	0.8		1.1
Kansas					<0.1	<0.1	<0.1
Manitoba				0.6			0.6
Minnesota	0.3						0.3
Montana	1.6	<0.1	<0.1	0.4	<0.1		2.0
Nebraska	<0.1	0.6	0.7	0.5	0.2	<0.1	2.1
New Mexico		<0.1	0.4	<0.1	2.6		3.1
North Dakota	13.5	<0.1	<0.1	1.6			15.2
Oklahoma			<0.1				<0.1
Saskatchewan	110.5	<0.1		<0.1			110.6
South Dakota	0.1	<0.1	0.1	0.3	<0.1	<0.1	0.6
Texas					<0.1		<0.1
Wyoming	0.1	0.2	0.3	0.3	0.1	<0.1	1.1
Total	126.4	1.0	1.9	3.7	3.8	<0.1	136.9

expansion in Midwestern states by the end of the century, whereas Larue and Nielsen (2016) predicted full recolonization. We suspect that this difference arises from how dispersal is simulated in each study. Whereas Larue and Nielsen (2016) used a fixed dispersal kernel, parameterized from observed female dispersal events but otherwise disregarding the processes governing dispersal distance, our model used a bottom-up approach to simulate movement and mortality during dispersal, which produced dispersal distances that we validated against an empirical kernel. Our approach therefore accounts, for example, for increasing mortality risk during road crossings as cougars encounter denser roads moving east, whereas Larue and Nielsen's (2016) did not. Given the evidence from our analyses that road traffic both deters and kills cougars in accordance with its volume, we expect that explicitly accounting for such processes in our model more accurately predicts expansion across Midwestern non-habitat.

Although we are confident in the broad recolonization patterns predicted by our model, it incorporates several nontrivial assumptions that could shift predictions.

First, our method for defining suitable breeding habitat based on GPS locations of western cougars (O'Malley et al., 2024) predicts more habitat in the East and Midwest than most other published estimates, which are based on Expert Opinion (EO; e.g., Glick, 2014; Larue and Nielsen, 2011; Laundré, 2013; Winkel et al., 2022; Yovovich et al., 2023). We chose O'Malley et al.'s (2024) approach because EO approaches have so far excluded Canada, and because EO approaches are typically limited to large contiguous parcels capable of supporting genetically healthy populations, excluding stepping stones. We note that less breeding habitat, as in EO approaches, would require longer dispersals between patches, which in turn would increase mortality risk during dispersal (Bocedi et al., 2014) and likely reduce recolonization probability even further.

Second, our approach uses road attributes (number of lanes and speed limit) to predict roadkill probability, but discounts other variables of potential importance (e.g., time of day, weather, roadway-adjacent vegetative cover, and sex). Additionally, our model does not account for existing over- and underpasses, including bridges over rivers, which likely improve permeability, particularly for cougars using rivers as travel corridors. It is unclear whether the cumulative effect of these variables would yield higher or lower roadkill rates, but Midwestern hindcasting validation offers assurance that roadkill mortality is well represented in our model. Further work investigating the full suite of factors influencing roadkill risk would be worthwhile to better understand its role in limiting recolonization.

Third, information about source populations varies regionally and we made several assumptions that may have influenced local recolonization predictions. This is most likely in the boreal transition zone of Saskatchewan and Manitoba, where we designated habitat according to the IUCN range map and a recent Saskatchewan Wildlife Management Report (Saskatchewan Ministry of Environment, 2018). We were unable to find information regarding population sizes for any of those areas, however, and we are therefore unsure whether they host breeding populations or only transients. This uncertainty could affect local recolonization patterns if, for example, some populations we designated "sources" (e.g., Beaver Hills) are not currently occupied, as may be the case. To quantify the influence of this uncertainty on model predictions, we evaluated simulated source-destination dynamics of colonizing females in the region. Details of this supplemental analysis are in Appendix S3. In short, the most pronounced change in predicted recolonization if these source populations are not occupied would be to northern Saskatchewan and west-central Manitoba; other currently unoccupied habitat in the region would likely still be colonized on similar timelines by females from, for example, the Badlands and Missouri Breaks (Appendix S3).

In addition to uncertain source populations in the boreal transition zone, we note that our assignment of "current range" in Alberta derives from Knopff et al. (2014), the most recent published estimate of which

we are aware, and is therefore 14 years old (i.e., circa 2010). As such, our range spread predictions (e.g., Fig. 4a) likely lag behind reality by roughly the same offset. Finally, the paucity of information about cougars in Texas, and particularly our inability to validate human-caused mortality rates, warrants caution for interpreting our model's prediction of range spread in that region.

Fourth, we assume no hunting in newly-established populations, since hunting pressure in jurisdictions hosting existing populations varies widely (e.g., unlimited public take in Texas vs. no legal hunting in California) and any assignment of harvest pressure would therefore be subjective. Some existing recolonized populations are hunted, however, so this assumption is not always valid (e.g., Nebraska and Saskatchewan). Hunting following recolonization will reduce available dispersers and likely slow further establishment/recolonization.

Finally, our model assumes no landscape change between now and 2100, disregarding ongoing climate change and human development. While the impacts of such changes to cougars are difficult to predict, we expect that expansion of high-traffic road networks and increasing human population density would further decrease recolonization probability, whereas increasing white-tailed deer (*Odocoileus virginianus*) populations may facilitate recolonization, as has been suggested in boreal Canada (Knopff et al., 2014).

These caveats notwithstanding, we believe that our study represents a robust approach to understanding and predicting wildlife range expansion and yields information pertinent to natural resource management. Our results suggest that managers in Manitoba and Saskatchewan should anticipate arrival and expansion, respectively, of cougar populations in coming decades, and that those in Minnesota, Oklahoma, eastern Nebraska, Iowa, and Kansas may also see breeding populations of cougars by the century's end. Indeed, a recent report of reproduction in northeastern Nebraska, released after completing our literature search for such events, supports this (Nebraska Game and Parks Commission, 2023). Cougar recolonization of these areas will likely yield diverse ecological and socioeconomic impacts, which are increasingly recognized as positive under a rewilding framework (Sandom et al., 2013). Jurisdictions interested in promoting local recolonization in eastern North America may consider working with agencies to their west and/or Florida to relocate reproductive age animals, improve connectivity, and/or reduce source population mortality. Without such measures, our model suggests that jurisdictions east of the Mississippi River (excluding Florida) are unlikely to host breeding cougar populations before 2100.

5. Conclusions

This project provides a tractable framework for generating and validating continent-scale range expansion predictions for wide-ranging carnivores. We have demonstrated how diverse sources of empirical data can be integrated to build a process-based model yielding high-fidelity simulations of recolonization and actionable predictions for conservation practitioners. In doing so, we have offered a thorough investigation of a much-speculated topic in the field of North American conservation: the return of cougars to eastern North America.

CRediT authorship contribution statement

Thomas W. Glass: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Richard A. Beausoleil:** Writing – review & editing, Investigation, Funding acquisition, Data curation, Conceptualization. **L. Mark Elbroch:** Writing – review & editing, Investigation, Funding acquisition, Data curation, Conceptualization. **Brian N. Kertson:** Writing – review & editing, Investigation, Funding acquisition, Data curation, Conceptualization. **Benjamin T. Maletzke:** Writing – review & editing, Investigation, Funding acquisition, Data curation, Conceptualization. **Quinton**

Martins: Writing – review & editing, Funding acquisition, Data curation, Conceptualization. **Marc R. Matchett:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization. **T. Winston Vickers:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization. **Christopher C. Wilmers:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization. **Heiko U. Wittmer:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization. **Hugh Robinson:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare no conflicts of interest.

Data availability

Model code and datasets are available on Figshare: doi:https://doi.org/10.6084/m9.figshare.c.7119631.v1.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110756.

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