Climate change increases the distribution of reservoirs of the Raccoon Rabies Virus in Quebec

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Abstract: Zoonoses often emerge in environments where human-animal interactions intensify. In Québec, climate change and land use alterations are suspected drivers in the shifts of the potential distribution of urban-adapted hosts such as raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*), which serve as reservoirs for Raccoon Rabies Virus (RRV; a variant of Lyssavirus rabies). We used species distribution modeling (SDM) to predict current and project future potential habitats for *P. lotor* and *M. mephitis* under three climate change scenarios (SSP126, SSP370, SSP585) from 2021 to 2100. Our model predicts significant northward expansions of potential habitats for both species, with *P. lotor* exhibiting faster and broader shifts compared to *M. mephitis*. High-emission scenarios further amplify these shifts, proportionally favoring the apparition of favorable habitats for *P. lotor*. Potential habitats for these reservoirs are projected to overlap with areas that currently lack robust infrastructure for surveillance and vaccination, highlighting potential public health vulnerabilities. Using a technique from interpretable machine learning, we provide a more mechanistic understanding of why the response of both reservoirs to climate change is decoupled. This study underscores the need for proactive monitoring of ecological and epidemiological shifts in Québec as climate change alters the potential distribution of key wildlife reservoirs.

Keywords: zoonosis, rabies raccoon virus, climate change, species distribution modeling

Introduction

Biodiversity loss under climate change creates new risks of zoonotic spillovers and increases challenges for public health [1]. The spillover of zoonotic viruses often takes place in environments where novel human-animal interactions are taking place, such as areas of intensive agricultural practices and increasing urbanization [2]; these new interactions result in the potential sharing of novel viruses [3], leading to increased spillover events [4]. Loss of natural habitats and ecological stress may push wildlife into habitats occupied by humans, thus increasing the risk of zoonotic pathogen transmission [5–7]. The extensive exposure of the terrestrial biosphere to novel ecological conditions [8] underscores the urgent need to address the interconnected risks of biodiversity redistribution and zoonotic disease spillovers. Understanding the drivers of ecological novelty is critical for developing proactive strategies that mitigate public health risks and promote biosphere stewardship.

Disease transmission at regional scales

While climatic phenomena are global in scope, their impacts manifest differently in specific regions due to local variations in species presence, climate, geography, and ecosystem structure. In Québec, for instance, the interaction between climate change and biodiversity is shaped by the province's northern latitude and distinct ecological characteristics, such as its extensive boreal forest, freshwater ecosystems, and fragmented habitats caused by human activities. Climate change and habitat fragmentation can alter Québec's biodiversity in unique ways compared to other regions of the world, as intensifying wildfire activity and warming temperatures threaten the resilience of insect like black spruce (*Picea mariana*), leading to shifts toward alternative forest states with cascading effects on carbon storage, ecosystem flammability, and biodiversity [9]. Québec experiences faster warming than the global average [10], which accelerates changes in species distributions and alters ecosystem dynamics [11]. This regional variation can influence the transmission dynamics of infectious diseases by creating favorable conditions for reservoirs to expand their range and interact with new species. For instance, in northern Québec, warmer temperatures have helped extend the range of ticks *Ixodes scapularis*, a vector of *Borrelia burgdorferi*, the causal agent of Lyme disease [12]. Until recently, Lyme disease was rarely observed in the province, but in the past decade, reported cases have increased dramatically in the Estrie and Laurentides regions and other parts of southern Québec [13]. This example underscores the need to evaluate the complex links between biodiversity, climate change, and zoonotic diseases at regional scales.

Although biodiversity is understood as a driver of zoonotic disease transmission [14], specific biodiversity-related processes that act on disease transmission often need to be evaluated locally, and for specific reservoirs-disease system [1]. Host diversity can either mitigate or amplify the transmission of pathogens depending on the local ecological context. For example, the "dilution effect" suggests that higher biodiversity can reduce disease risk by diluting the pool of competent hosts [15], whereas the "spillover effect" highlights how habitat fragmentation may concentrate interactions among wildlife, livestock, and humans, increasing the risk of emerging zoonoses [16]. These mechanisms, too, are likely to be expressed differently according to the regional context. Climate-driven changes to biodiversity may alter these dynamics by reshaping species distributions and interspecies interactions, creating novel ecological contexts that challenge established disease control strategies. For example, shifts in host species ranges due to warming temperatures and habitat fragmentation can facilitate the emergence of new zoonotic hotspots, where changes in host diversity or density amplify the likelihood of pathogen transmission if these reservoirs meet human populations [16]. These complex interactions between biodiversity, climate, and health, underscore the importance of integrating biodiversity and climate change considerations into public health frameworks to better anticipate and mitigate zoonotic risks.

Raccoons rabies virus in Québec, Canada

Rabies, caused by Lyssavirus rabies, is in addition to Chiroptera, well-documented in skunks (*Mephitis mephitis*) and raccoons (*Procyon lotor*). Lyssavirus is a genus of viruses in the family Rhabdoviridae that primarily infect mammals and are known for their neurotropic effects [17]. Variants within the species are often associated with specific hosts, such as bats (Chiroptera) and terrestrial mammals like foxes (*Vulpes vulpes*) and raccoons [18,19]. Unlike bat-related rabies variants, raccoon rabies virus (RRV) circulates predominantly in terrestrial mammals, with distinct transmission dynamics [20]. Surveillance and control efforts in the United States have tracked the geographic expansion of RRV [21], which led to the detection of a case of raccoon rabies in Québec in December 2024. This marked the first such occurrence since 2015, when a case was identified in the southwest of the Montérégie region of Québec, despite extensive control operations carried out in both Québec and Vermont. By January 2025, additional cases were reported in Estrie and Montérégie, highlighting an increasing risk of a Northern expansion of RRV in the region.

Raccoons and skunks, as main reservoirs of RRV [22], are already well-established in the South of the province, emphasizing the need to document how their distribution may shift under different climate change scenarios. These species are particularly sensitive to environmental changes that influence resource availability, habitat structure [23], and species interactions [24,25]. Climate change can alter their geographic ranges by modifying key factors such as temperature thresholds (the minimum or maximum temperatures species can tolerate), snow cover duration, and the distribution of prey and shelter. For instance, milder winters can increase survival rates and extend the breeding seasons of raccoons and skunks, leading to population growth and expanded territories [26,27]. Surveillance and vaccination strategies may not remain effective if these shifts alter the geographic range of these hosts [28,29], in particular by allowing them to expand outside the area that is currently monitored. For example, oral rabies vaccination campaigns depend on accurate predictions of reservoir population distributions to ensure efficient bait deployment. If raccoons and skunks migrate to previously unaffected areas or experience changes in population density, existing control strategies may require recalibration. Understanding how environmental changes in Québec may transform the risk of zoonotic disease transmission dynamics is critical for predicting future areas of high risk for human populations. By focusing on raccoons and skunks—species highly adaptable to urban and peri-urban environments [30], we explore how climate change-induced shifts in the habitable area of the two main reservoirs of RRV could influence the dynamics of zoonotic disease transmission.

Objectives

This study aims to assess potential spatial and temporal redistribution of the two main reservoirs of RRV in Québec. We analyze the current and future habitats of *Mephitis mephitis* and *Procyon lotor* under various climate change scenarios. We hypothesize that the reservoir's range will shift northward, initially affecting regions near the United States and Ontario border in the short term, and later extending to the Laurentians, as warming conditions create more favorable environments [31]. Deforestation and urbanization are leading to habitat fragmentation, pushing hosts species to adapt to new environments, often in urban areas. These changes create new opportunities for zoonotic pathogens to spread.

To address this, we develop machine-learning based species distribution models, and rely on explanatory techniques to identify drivers of projected range shift of the two species. Results indicate that climate change drives northward range expansions of both species, with *P. lotor* demonstrating faster and broader range shifts compared to *M. mephitis*, particularly under high-emission scenarios, amplifying the risk of zoonotic spillover in northern and peri-urban areas. Under the more optimistic climate change scenarios, the expansion of the range of either species is predicted to be limited (or reversed) as early as 2070, while all other scenarios result in ongoing or accelerating range shift.

Methods

This study utilized species distribution modeling (SDM) trained on a large corpus of observations of *Procyon lotor* and *Mephitis mephitis*, which are then projected under multiple climate scenarios. Cross-validation serves to assess the predictive performance of these models under contemporary climatic conditions. Future habitat projections were made under various Shared Socioeconomic Pathways (SSPs) and a range of Global Circulation Models (GCMs), which explore different emission and societal scenarios for the years 2021–2100 [32]. These projections provide insights into the potential impact of climate change on zoonotic disease transmission dynamics in Québec. All analyses were conducted using Julia [33] v1.11, with the code and data publicly available on GitHub (PoisotLab/RRVReservoirsDistribution). The *SpeciesDistributionToolkit.jl* [34] package was used for data acquisition, cleaning, analysis and visualization.

Data on reservoirs occurrences

Data source on reservoir distribution was retrieved from the Global Biodiversity Information Facility (GBIF), which compiles georeferenced observational data for a wide range of species. The exact data downloaded for this project have been archived to ensure long-term reproducibility [35]. These data are observational, and therefore often concentrated in urban and peri-urban areas or near roads [36,37], potentially underrepresenting rural and remote regions [38]. However, the large volume of observations in North America allows the model to capture realistic trends in species distributions, which spans a gradient from warmer southern regions (near the Gulf of Mexico) to colder northern areas, providing a robust foundation for interpretation [39,40]. Differences in bioclimatic conditions between the Southern and the Northern edges of the range of both species are strong enough to compensate for local biases in sampling. GBIF data was chosen for its comprehensive global coverage and accessibility, which facilitates the identification of high-risk zones for zoonotic transmission.

Data cleaning

Data cleaning involved filtering duplicate records, and removing entries with geospatial issues that cannot be easily corrected. We therefore focus on high-confidence records to minimize noise. This process included verifying geographic coordinates to ensure they were within the expected range for the species and cross-referencing species names to avoid misidentified entries. All sub-species of *P. lotor* were considered as a single species. Additionally, records with incomplete or inconsistent data fields, such as missing dates or implausible locations (e.g., occurrences recorded far outside the known range of *Mephitis mephitis*), were excluded. By retaining only validated data points, we aimed to enhance the reliability of subsequent analyses. To avoid over-representing areas that were more sampled due to the sampling biases previously mentioned, we conducted spatial thinning of occurrences [41–43], by merging all occurrences within a grid cell of the rasterized climatic data into a single occurrence, located at the center of the grid cell. This essentially communicates that the habitat is occupiable by the species, without reflecting differential sampling effort.

Pseudo-absences generation

Pseudo-absences for the model were generated by applying a distance-based sampling approach to refine the selection of absence data in relation to known presence locations. This technique involves defining areas where pseudo-absences are more ecologically realistic, avoiding regions that are either too close or too far from observed occurrences. By restricting the sampling of pseudo-absences to these plausible zones, we ensure that the absences better reflect the environmental conditions that are relevant for the species' potential distribution [44]. We drew pseudo-absences randomly, according to the inverse of the distance to known presences of the species, at most 500 km away from a presence, and no closer than 20 km away. This method (known as "background thickening") is particularly valuable for balancing the dataset, addressing the issue of spatial bias, and improving the accuracy and predictive power of species distribution models [45]. We generated three pseudo-absences for each grid cell containing one observation, to avoid the issues of learning from severely class-imbalanced data that would be introduced by using lower prevalences [46].

Climatic variables

Climatic variables were obtained from the suite of BioClim data [47] according to the WorldClim v2.1 database [48,49]. These variables were downloaded at a resolution of 2.5 arcminutes (approximately 20 km^2 at the equator). These bioclimatic variables are derived from long-term temporal series, aggregated across a target temporal range of 1970–2000, using data from between 9 000 and 60 000 weather stations [48]. For this reason, some variables may display edges in space, notably BIO5, representing maximum temperature of the warmest month [50]. We have visually inspected all model outputs, including maps of model explanations, to ensure that this did not create artifacts in our reconstructed distributions.

Variables, such as temperature and precipitation, are essential for understanding how environmental conditions influence the distribution of rabies reservoirs. Indeed, the breeding season, den site selection, and access to resources are examples of factors that depend on climatic variables such as harsher winters, long periods of drought, or a mild climate throughout the year [25,26]. If the variables change, these factors may also change, potentially altering the habitat suitable for the establishment of reservoirs. The selection of these variables was justified by their relevance to species ecology and their ability to capture critical aspects of habitat suitability under current and future climatic conditions. This dataset formed the foundation for mapping both present and projected habitat distributions, as the potential habitat of skunks and raccoons partly depends on environmental conditions at a given time.

Species Distribution Models

We used Species distribution modelling (SDM) to predict the geographical distribution of the two reservoirs. This method uses environmental data to construct models that predict the current and future habitat suitability for these species [51,52]. The SDM approach was selected due to its utility in guiding conservation and management actions, especially in areas where observation data alone is insufficient [53]. While SDMs are closely linked to the concept of the ecological niche, it is important to distinguish between SDMs and Ecological Niche Models (ENMs). SDMs often focus on predicting spatial distributions by incorporating environmental, biotic, or accessibility predictors, whereas ENMs [54] aim to approximate the ecological niche, which includes both fundamental and realized components. This distinction reflects different modelling priorities and assumptions. In this study, we are primarily interested in the spatial distribution of species, rather than their ecological niches per se, to better identify areas that may become occupiable by the species under various scenarios.

For both species, we followed the same modeling approach. We built an SDM based on a logistic regression, optimized through the gradient descent algorithm with L1 regularization (to avoid over-inflating the importance of variables), which is appropriate for our data. Indeed, logistic regression is particularly suitable for binary outcomes such as presence-absence predictions [55], making it an ideal tool for evaluating the suitability of habitats for skunks and raccoons' distribution. It also returns a score that is a true probability of the habitat being occupiable, which is more informative than presence/absence outputs [56], and does not mandate the use of post-hoc calibration of the model to be interpretable [57]. Given that our data involves the classification of environmental conditions into suitable and unsuitable habitats for RRV reservoirs, logistic regression offers the simplicity of interpretation, statistical efficiency, and the ability to model the relationship between environmental variables and habitat suitability [55]. For both models, we have confirmed that there is no overfitting by first investigating the traces of the L1-adjusted cross-entropy loss function on the training and testing data over all training epochs, in addition to performing post-training cross-validation as outlined in the next section. To ensure parsimonious models, we incorporated variable selection into the modelling process. We specifically relied on forward variable selection, in which predictors were added to the model one at a time untill the model performance (according to the cross-validation scheme described below) stopped improving.

Model validation

To assess model performance, we used cross-validation. Cross-validation is a critical method for evaluating the accuracy of species distribution models and addressing the issue of overfitting [58], particularly when working with presence-absence data [59]. In this process, the data is divided into training and testing subsets multiple times, allowing the model to be trained on different sets and evaluated on others. This procedure ensures that the model is robust and generalizable, thus providing more reliable predictions. We used k-fold cross-validation, stratified so that the class imbalance (proportion of presences in the training and validation sets) was constant and equal, with 10 folds.

To assess the performance of the models (and decide when to include a variable during variable selection), we used Matthews correlation coefficient (MCC) as a performance metric [60,61]. MCC summarizes the confusion matrix (true positives, true negatives, false positives, and false negatives) into a single score, offering a more balanced and reliable assessment than metrics like accuracy, F_β scores, or balanced accuracy. Unlike these methods or the diagnostic odds ratio (DOR), MCC provides superior trustworthiness and consistency, particularly in cases of class imbalance or discordant outcomes [62], making it highly suitable for ecological models with both presence-absence data and environmental noise.

To fully capture the behavior (and biases) of the models, we measured performance on a range of metrics, including Positive Predictive Value (PPV), Negative Predictive Value (NPV), Positive Likelihood Ratio (PLR), and Negative Likelihood Ratio (NLR), as summarized in Table 1. PPV quantifies the proportion of true positives among all positive predictions, while NPV assesses the proportion of true negatives among all negative predictions.

PLR and NLR are measures coming from biomedical research, and identify the reliability of predictive and negative outcomes. PLR represents how much more likely a positive result is in true positive cases than in negative ones, and NLR indicates how much more likely a negative result is in negative cases than in positives ones. Note that the likelihood ratios are not on a linear scale, are on a log scale. In clinical trials, value of PLR above 10 and values of the NLR below 0.1 are considered "strong evidence" [63].

Model explanations

To assess the relative importance of various climatic variables on the habitat distribution of *M. mephitis* and *P. lotor* and explain predictions, we conducted a Shapley value analysis. The Shapley value, originally developed in cooperative game theory, is a method for fairly allocating the contribution of individual variables to an overall outcome [64]. In simple terms,

Table 1: Measures of model performance averaged over ten splits of k-fold cross validation, reported for the training and validation set for the model of both species. The models for both species exhibit comparable performances, with good positive predictive values, and excellent negative predictive values, suggesting that the models would predict comparatively fewer false positive predictions. Note that for all species, the values for the validation and training data are equivalent, suggesting that there was no overfitting during the model training process.

	P. lotor		*M. mephitis*	
Measure	Validation	Training	Validation	Training
MCC	0.765	0.768	0.740	0.743
PPV	0.765	0.768	0.831	0.834
NPV	0.921	0.922	0.915	0.916
TSS	0.770	0.776	0.734	0.737
PLR	8.856	8.977	11.236	11.368
NLR	0.145	0.142	0.208	0.206

it quantifies how much each variable contributes to the predictions made by a model by comparing scenarios with and without the variable, ensuring fairness in attributing influence.

In ecological modeling, Shapley values are particularly useful for understanding the role of predictor variables in complex models with intricate interactions and non-linear relationships [65]. The method is built on theoretical axioms—efficiency, which ensures that the total contribution matches the difference between the actual prediction and the average prediction; symmetry, ensuring equal attribution for variables with identical contributions; dummy, which assigns no influence on irrelevant variables; and additivity, which allows combining results from submodels. These axioms enhance the reliability of Shapley value-based analyses [66].

While the method has notable strengths, including the ability to provide contrastive explanations by comparing specific subsets of data, its high computational cost often necessitates approximation techniques [66]. In this study, we used a Monte Carlo sampling approach to approximate Shapley values, balancing computational feasibility with analytical rigor [67]. Shapley values were computed to analyze the contributions of variables such as temperature and precipitation under current climate conditions. Although this approach could be extended to future predictions, care must be taken to address covariate shifts caused by ecological novelty under climate change [52]. These shifts occur when future predictor variables fall outside the range of the training data, potentially destabilizing Shapley value interpretations [65]. For this reason, we only report the Shapley values for the historical climatic data, i.e., corresponding to the climate at the time when species occurrences were sampled.

This analysis identified key drivers of habitat distribution for both species and quantified their relative contributions. The most important variable for each reservoir at each grid cell was determined by calculating the largest absolute value of all Shapley values for a single prediction, argmax(abs(S)), where S represents the Shapley values associated to each environmental variable at this location. This approach identifies the variable with the highest absolute contribution, indicating its dominant influence on the model's predictions. By comparing the magnitude of Shapley values, we can pinpoint which environmental factor has the strongest impact on the habitat suitability predictions. This method ensures that we focus on the most influential variables, providing a clearer understanding of the ecological drivers of species distribution [65].

Qantification of differences in environmental suitability

Understanding the differential suitability of an habitat is critical for studying habitat selection and spatial dynamics. To quantify the level of ecological polarization between the predicted suitability for *P. lotor* and *M. mephitis*, we define an ecological polarization index, defined by the following equation:

$$P = \frac{\widehat{p_P} - \widehat{p_M}}{\widehat{p_P} + \widehat{p_M}} \tag{1}$$

This index is a normalized difference index of the predicted probability that the grid cell is usable by *P. lotor* ($\widehat{p_P}$) and *M. mephitis* ($\widehat{p_M}$). When positive, it represents a strong bias in favor of *P. lotor*; when negative, a strong bias in favor of *M. mephitis*. The absolute value of the index is expressed in relation to the overall habitat suitability for both species.

Projection of bioclimatic variables

Shared Socioeconomic Pathways are socioeconomic scenarios developed by the Intergovernmental Panel on Climate Change (IPCC) to explore how global development pathways might interact with climate change [68]. SSPs offer a framework for examining how societal and environmental changes influence health and ecological outcomes. They are particularly valuable for assessing the risks of zoonotic and vector-borne diseases, which are closely tied to biodiversity and climate. By integrating biodiversity, land use, and climate considerations, SSPs help explore how development pathways shape zoonotic spillover risks and inform interventions to mitigate these threats (Gibb et al., 2025).

Future habitat projections for *Mephitis mephitis* and *Procyon lotor* were generated using SSPs and climate projections from nine GCMs participating in CMIP6. Global Climate Models (GCMs) are sophisticated numerical tools that simulate the Earth's climate system by representing interactions between the atmosphere, oceans, land surface, and ice. They are essential for understanding and projecting future climatic conditions under various socioeconomic scenarios [3]. Each SSP represents a distinct trajectory for societal, economic, and technological changes, paired with a corresponding level of radiative forcing (measured in W/m^2) expected by 2100. Radiative forcing measures the energy imbalance between incoming solar radiation and the energy re-emitted back into space. The first part of the name (e.g., SSP1) describes the socioeconomic narrative, while the second part (e.g., 1.9) specifies the level of radiative forcing associated with greenhouse gas emissions [69,70].

We used the following scenarios: SSP1-RCP1.9 (Sustainability - Taking the Green Road): A sustainable development pathway with low challenges to mitigation and adaptation, aiming for global temperature rise limited to 1.5°C. This corresponds to very low emissions and a radiative forcing of 1.9 W/m^2. SSP2-RCP4.5 (Middle of the Road): A scenario with moderate challenges to mitigation and adaptation, leading to a moderate warming by 2100 (around 3°C). This reflects moderate emissions and a radiative forcing of 4.5 W/m^2. SSP3-RCP7.0 (Regional Rivalry - A Rocky Road): A pathway with high challenges to both mitigation and adaptation, leading to higher emissions and a substantial temperature rise (around 4°C). This corresponds to a radiative forcing of 7.0 W/m². SSP5-RCP8.5 (Fossil-fueled Development - Taking the Highway): A high-emission scenario driven by rapid economic growth and fossil fuel use, leading to the highest level of warming (around 4.3°C). This reflects extremely high emissions and a radiative forcing of 8.5 W/m².

To account for model uncertainty, projections were derived from the median of nine GCMs: BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, GFDL-ESM4, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, and MRI-ESM2-0, with the MIROC6 model showing a lower sensitivity of 2.6 K, while the CanESM5 model exhibits a higher sensitivity of 5.6 K. This contrasts with the broader range of 1.8–5.6 K observed across the 27 models in the CMIP6 ensemble, reflecting the variability in how different models simulate climate response to greenhouse gas emissions. Using the median of these projections ensure robust predictions by mitigating the variability between individual models, while not being as sensitive to biases as the average.

These projections are part of the Scenario Model Intercomparison Project (ScenarioMIP), a key activity within CMIP6, which provides multi-model climate projections based on alternative scenarios of future emissions and land-use changes produced with integrated assessment models [32]. ScenarioMIP aims to address various science and policy questions related to climate change and the impact of specific forcings like land use and aerosols, contributing to the evidence base for future IPCC assessments. Projections span from the present day to 2100, providing a broad temporal perspective on potential climatic changes, with the following time intervals: 2021–2040, 2041–2060, 2061–2080 and 2081–2100. In the text, these time intervals are refered to by their midpoints (2030, 2050, 2070, 2090).

This comprehensive approach allows for the exploration of a range of socioeconomic and emission scenarios, capturing both optimistic and pessimistic outcomes. The choice to include all SSPs was made to provide a nuanced understanding of possible future trajectories and to better inform adaptive management strategies. By examining range shifts under climatic change, mitigation and reduction, these projections emphasize the importance of proactive measures to address potential zoonotic disease risks.

Results & discussion

Both *Procyon lotor* and *Mephitis mephitis* are expected to expand their suitable habitats northward, with varying rates of expansion depending on the SSP scenarios. In addition, the timing and intensity of this expansion differ, with SSP126 showing significant arrivals as early as 2030, while SSP585 predicts a delayed and more intense arrival by 2070. Nevertheless, our results under SSP126 suggest that habitat expansion can be more gradual and potentially mitigated by effective management practices. Taken together, these results show that climate change will open up northern areas as newly habitable by both species. The extent of this area open for potential movement will be heavily influenced by the emission scenarios affecting regional climatic factors, leading to the need for adaptive management policies.

Climatic Variables Have Differential Effects on Rabies Reservoirs

Procyon lotor and *Mephitis mephitis* show different responses to the bioclimatic variables considered for inclusion in the model, as measured by the Shapley values. These results are presented in Figure 1, and Table S1. For both species, the maximal temperature of the warmest month is the variable with both the largest relative importance and the largest spatial cover. Despite this, the two species have different responses to this variable: this explains why spatial responses are likely to be decoupled over time, something that was supported in our simulations (Figure 3).

Mean Temperature of Coldest Quarter is the second most influential variable for *P. lotor*, particularly in the middle of Québec's latitude. Meanwhile, temperature-related measures of the firest months and quarter are the most important ones, particularly along the St. Lawrence River, with other variables being locally more important. The distribution of *Mephitis mephitis* is shaped by different bioclimatic factors. Precipitation emerges as the most critical variable, particularly variables related to the warmest and wettest quarters, as well as precipitation over the driest month. By contrast with *P. lotor*, the spatial effect of the less determinant variables is not concentrated around the St-Lawrence river. Previous data on habitat use at small scales also highlighted that *M. mephitis* responded differently from other mesopredators [71].

The assignment of most important variables lines up with our understanding of the biology of both species. For *P. lotor*, the dominance of temperature related variables indicates its

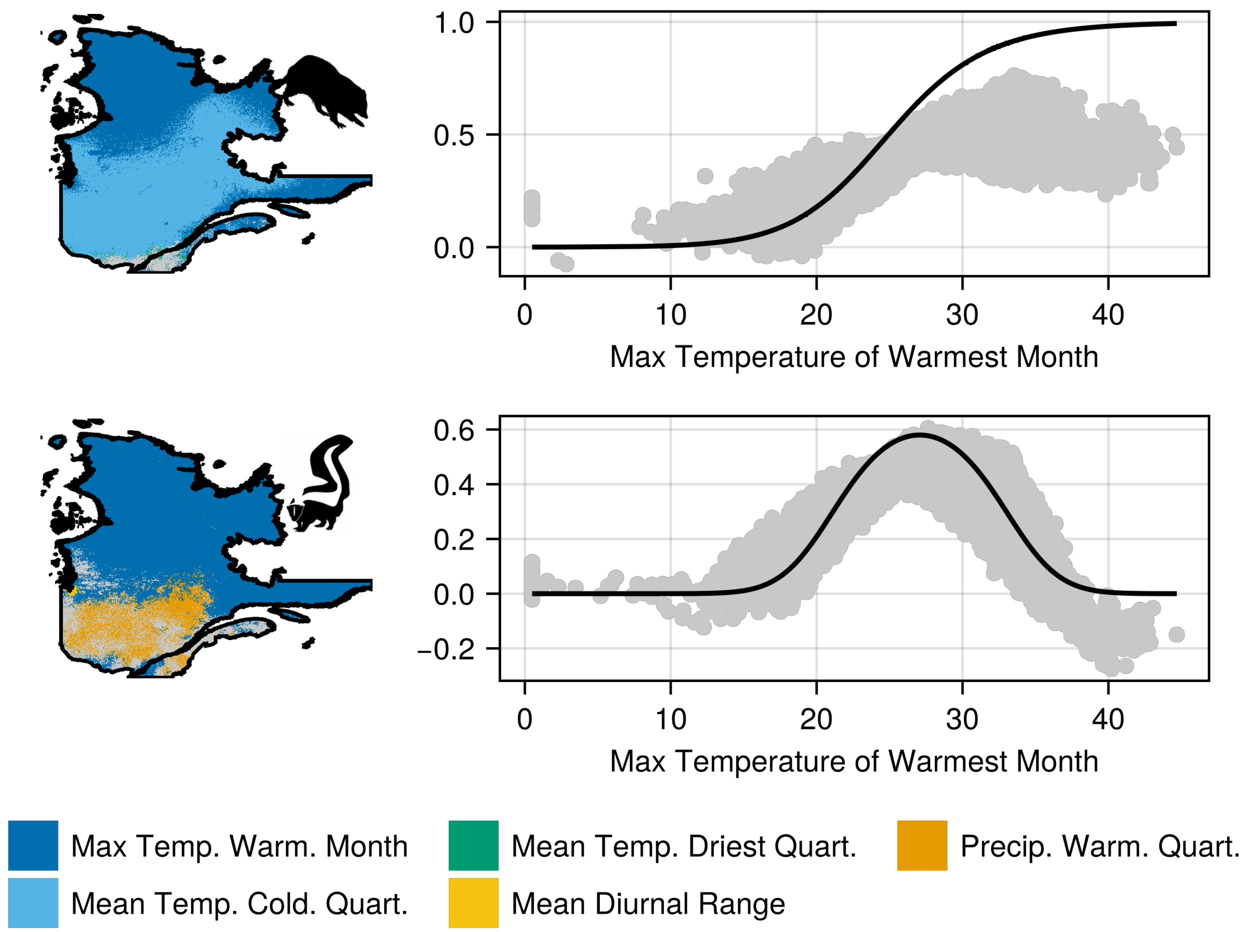

Figure 1: Map of the spatial coverage of the five most important variables (according to Shapley values) for *P. lotor* (top) and *M. mephitis* (bottom). Note that the areas covered by other variables are shown in grey, but represent a small fraction of the landscape. The full list of variables selected for each model, alongside their relative importance and spatial coverage, is given in Table S1. On thr right column, the Shapley values (added to the average prediction) for the entire training dtaaset are in light grey, with the partial response of the model as a black line. The two species have different responses to the most important variable. Note that the Shapley values and the partial response do not perfectly overlap because Shapley values account for the values of all variables at the scale of each point, ratherthan for their marginalized effects across the entire model.

adaptability to broader thermal ranges and fragmented landscapes, which enables its rapid colonization of both peri-urban and natural habitats [72]. Conversely, the stronger response of *M. mephitis* to precipitation-related variables, such as precipitation seasonality and variables linking precipitation to temperature, reflects its reliance on stable and consistent conditions. Changes in precipitation can significantly impact wetland availability, a key factor for the regulation of *M. mephitis* abundance. Since the density of skunks correlates positively with cultivated lands and habitats near wetlands, which provide essential resources like food and denning sites [73], fluctuations in precipitation could directly affect their habitat quality and distribution. Additionally, winter minimum temperatures play a critical role in shaping the behavior and distribution of *M. mephitis*. Striped skunks enter a state of torpor during the winter, and are generally more negatively affected by winter conditions [74], with body temperatures dropping to as low as 25.8°C. Changes in ambient winter temperatures due to climate change could alter their hibernation behaviors, affecting their survival and range dynamics [75]. The focus on variables that captures complex temperature-precipitation relationship can help assess how much intra-annual variation in risk is expected within years [76].

These factors highlight the necessity of incorporating both global and regional climatic data in predictive models. Specifically, studies in Europe have identified the minimum temperature of the coldest month as the most important bioclimatic variable for habitat suitability models of both *P. lotor* and *M. mephitis*, explaining the observed differences in their projected range distributions [77]. Differences in the importance of these climatic variables reflect the distinct ecological niches of the two species. While *P. lotor* thrives in a wide array of environments, *M. mephitis* faces constraints in areas with extreme climatic variability, suggesting a narrower ecological tolerance. These distinctions suggest that their responses to climate change will vary, making it crucial to examine how future climatic scenarios under different SSP trajectories may shape their respective distributions.

Northward Expansion of Suitable Habitat is Expected

Temporal maps in Figure 2 highlight the northward expansion of either species. The timing of their arrival differs based on SSP scenarios. In SSP126, the most substantial arrival occurs around 2030. In contrast, higher-emission scenario (SSP585) sees peak arrivals shifting to 2070, accompanied by increased intensity. There appears to be an expansion of both species toward areas near Ontario, despite the region's effective management efforts [78].

Under SSP126, characterized by sustainable development and climate stabilization, range expansions occur more gradually, with extreme distributional shifts being mitigated.The expansion of territories predicted to be favorable to the establishment of both species can be significantly slowed as early as 2030, with no significant gain predicted to occur in 2080-2100.

The border between Québec and Ontario is where a lot of range expansion takes place. This phenomenon could be attributed to warmer microclimates near the border that could enhance habitat suitability, potentially facilitating their northward expansion. It is important to note, however, that the expansion of favorable habitats does not necessarily equate to the spread of individuals carrying RRV. Effective management in areas where the RRV is currently endemic - *e.g.*, Hamilton, including the Niagara region, Brant County, and the Halton and Haldimand–Norfolk regions [79] - may limit the prevalence of infected individuals, even as the species

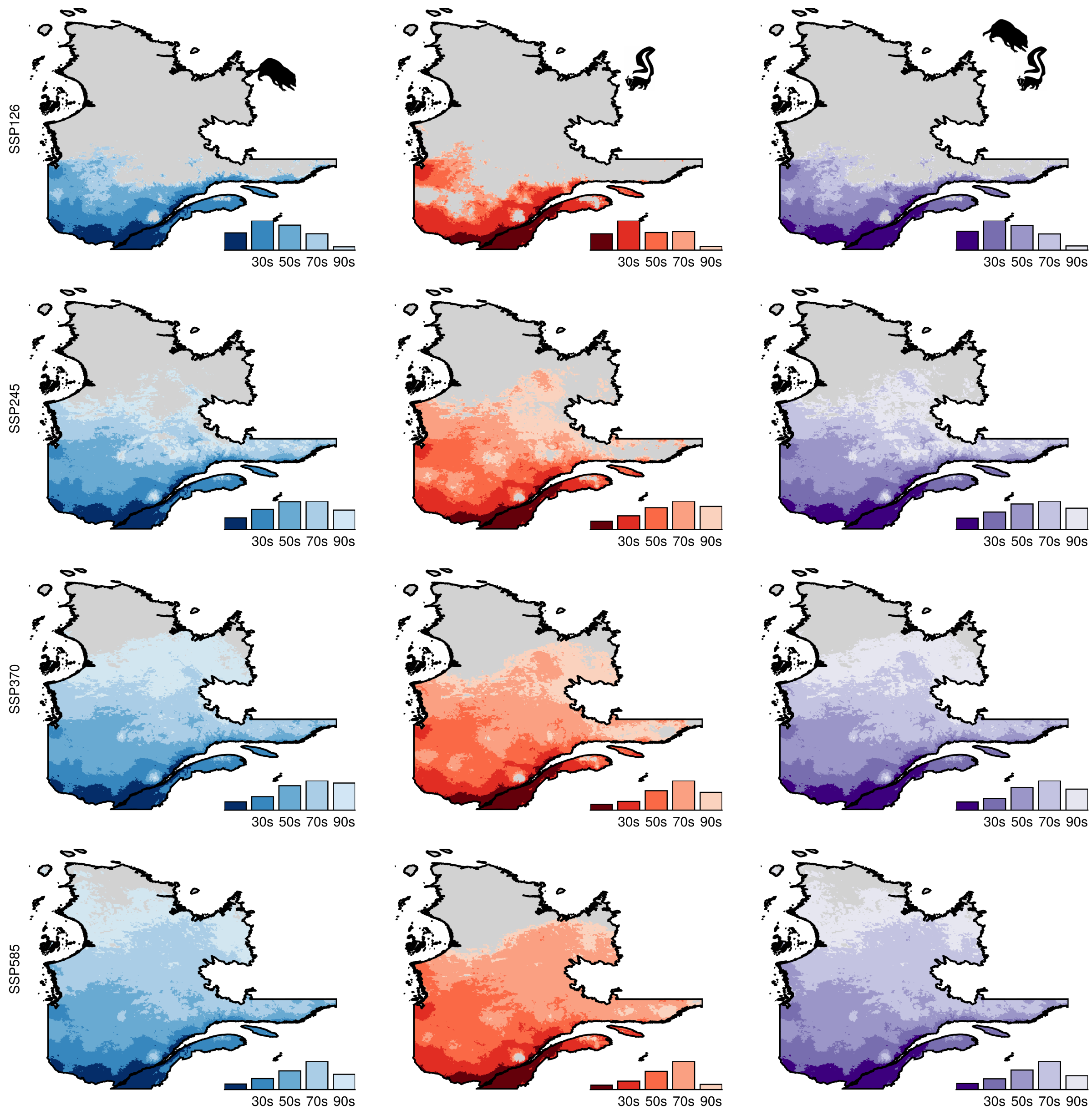

Figure 2: Temporal change of the predicted range of *P. lotor* (leftmost column), *M. mephitis* (central column), and either species (rightmost column). The color for each map represents bins of 20 years according to the climate change projections, where the heoght of each bar indicates the proportion of habitat gained by the end of the period. No habitat is predicted to be lost in this area. The darker color band always represents the current predicted range of the species. Each row in the figure corresponds to a climate change scenario.

themselves disperse both across the border and northwards. This nuance underscores the importance of integrated cross-border strategies to address both ecological and health-related concerns.

Pessimistic Scenarios Provide an Increasing Advantage to *Procyon lotor*

When habitat conditions are only marginally favorable, *M. mephitis* predominates Figure 3. When conditions are favorable, no species takes advantage of the other. Conversely, in SSP585 scenario, favorable conditions become increasingly restricted over time, leading to a decline in *M. mephitis* occupancy and a potential advantage for *P. lotor* in these regions. Under SSP126 and SSP245 overlap increases in marginally suitable areas, suggesting potential stability in these zones. However, towards the later periods of more pessimistic scenarios (SSP370 and SSP585), *P. lotor* sees consequential increases in habitat suitability, notably at higher latitudes. Therefore, all scenarios are potential associated with different outcomes for which of the two reservoirs may be dominant in different regions.

The advantage of *P. lotor* in high-emission scenarios may have cascading effects on local biodiversity. The displacement of *M. mephitis* could disrupt trophic interactions and alter ecosystem dynamics, necessitating further research into the long-term ecological implications of these shifts. An increase in mesopredator numbers may lead to local extinctions of prey species. For instance, *P. lotor* has been shown to suppress the reproductive success of songbirds, waterfowl, and turtles [80]. The co-occurrence of species in shared resting sites further increases the risk of rabies transmission, particularly in urban and wild areas, underscoring the need for vigilance in managing these species to prevent disease spread [81].

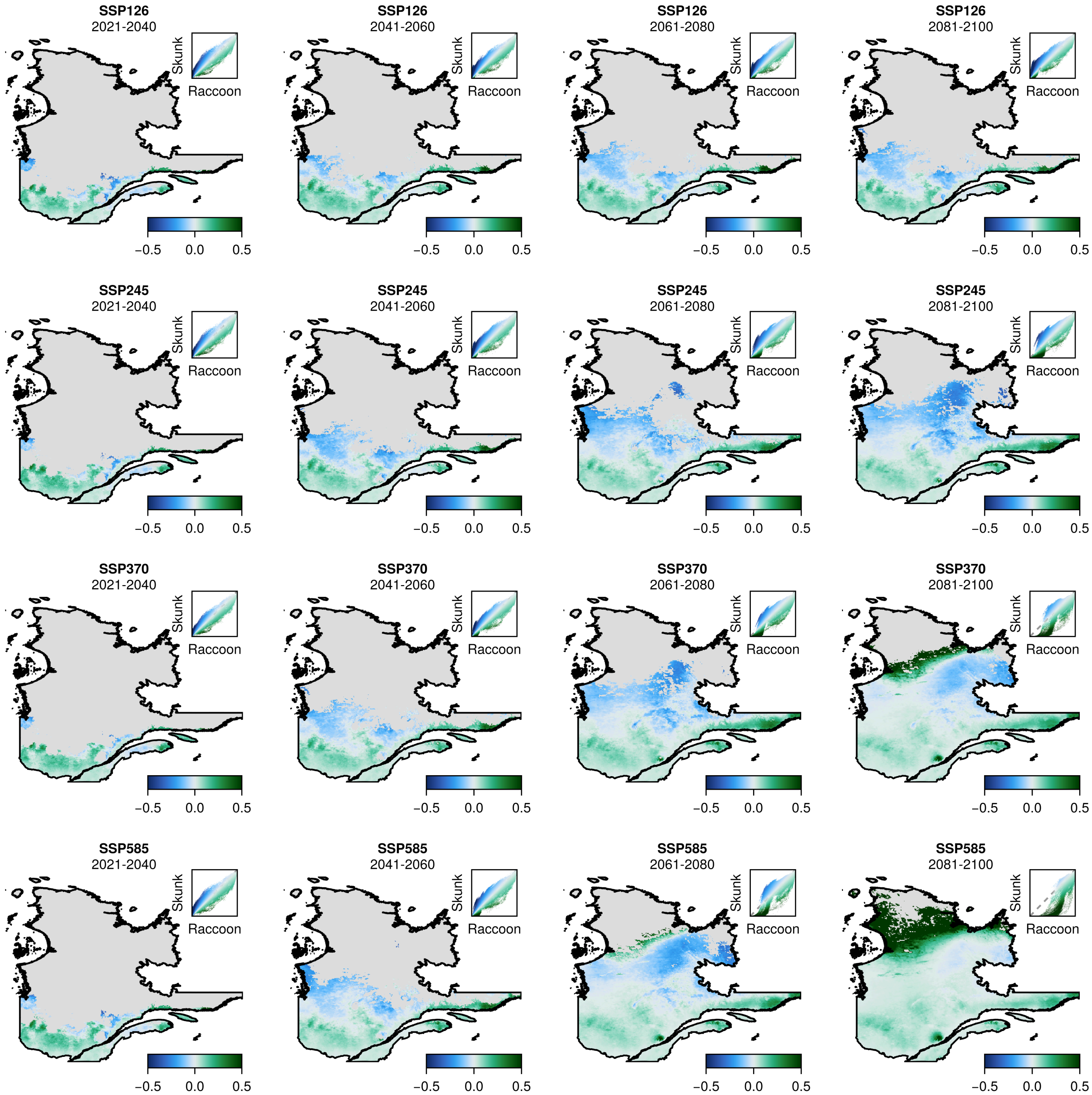

Figure 3: Measure of ecological polarization (Equation 1) across the timescales and scenarios considered. Values leaning towards blue (negative) indicate the the habitat is more suitable to *M. mephitis*, while value leaning towards green (positive) indicate an advantage to *P. lotor*. As time progresses (left to right) and climate change worsens (top to bottom), P. climatic conditions become increasingly favorable to *P. lotor*. Insets for each map represent the pairwise plot of suitability values for all pixels; point clustered along the 1:1 line indicate equitable relative habitat suitabilities.

Conclusion

The projected redistribution of *Procyon lotor* and *Mephitis mephitis* under various SSP scenarios highlights the intricate interplay between climate change, the displacement of species potential habitats, and spatial zoonotic disease risk. For SSP370 and SSP585, mitigating habitat fragmentation, enhancing monitoring systems, and implementing oral rabies vaccination (ORV) programs remain critical strategies [82]. Collaborative cross-border efforts between provincial and federal agencies are essential to address the shared challenges of wildlife movements, particularly given the interconnected nature of populations near the U.S.-Canada border and recent cases in Estrie. While some advocate for population reduction or fertility control to curb pathogen spread in wildlife, these methods are controversial and may prove ineffective in complex ecosystems where social structures and contact patterns are significant factors [22]. These results highlight how Québec could, through the increased range of generalist reservoirs, become more ammenable to disease under climate change [83].

In SSP126, strategies focusing on biodiversity conservation and habitat restoration provide an opportunity to slow the expansion of zoonotic hosts while strengthening ecological resilience. Promoting sustainable practices can reduce the public health risks associated with wildlife range shifts, particularly in northern Québec, where limited infrastructure presents challenges for surveillance and vaccination campaigns [84]. Urban sprawl under high-emission scenarios exacerbates habitat fragmentation, intensifying human-wildlife interactions and increasing the risk of zoonotic spillover. This underscores the importance of integrating ecological conservation with proactive public health measures to mitigate risks in peri-urban areas where *P. lotor* thrives, more of which are at risk of being in the range of either, or both, species as time passes and climate change worsens.

Despite these strategies, a limitation of this study lies in its reliance on climatic variables derived from SSPs. While these models offer valuable insights, incorporating land cover data could significantly enhance predictive accuracy. Land cover factors, such as urbanization, forest distribution, and wetland availability, have been shown to play a critical role in species range shifts, often surpassing climatic variables in importance [85]. Future research should prioritize integrating these elements into habitat suitability models to provide a more nuanced understanding of species distributions and inform management strategies, and when appropriate, couple species distribution models with techniques like agent-based models that may more reliably capture the dynamics of individuals and populations (rather than species) while accounting for infectious status. As the distribution of species is epxected to change rapidly and with a low predictibility, techniques that can simulate the dynamics of wildlife diseases over real landscapes are emerging as a key priority in both disease surveillance and public health.

Addressing these challenges requires a balanced approach that combines adaptive conservation practices with robust public health strategies. By focusing on sustainable development and collaborative cross-border efforts [86], it is possible to manage the ecological and health-related implications of shifting wildlife distributions. This proactive, interdisciplinary approach is essential to mitigating zoonotic risks while preserving ecological integrity amid ongoing climate transformations. Previous studies highlighted that meoscarnivores are likely to benefit from climate change through range expansion [87]; out results suggests that this effect can lead to adverse health outcomes when meoscarnivores are reservoirs of zoonotic pathogens.

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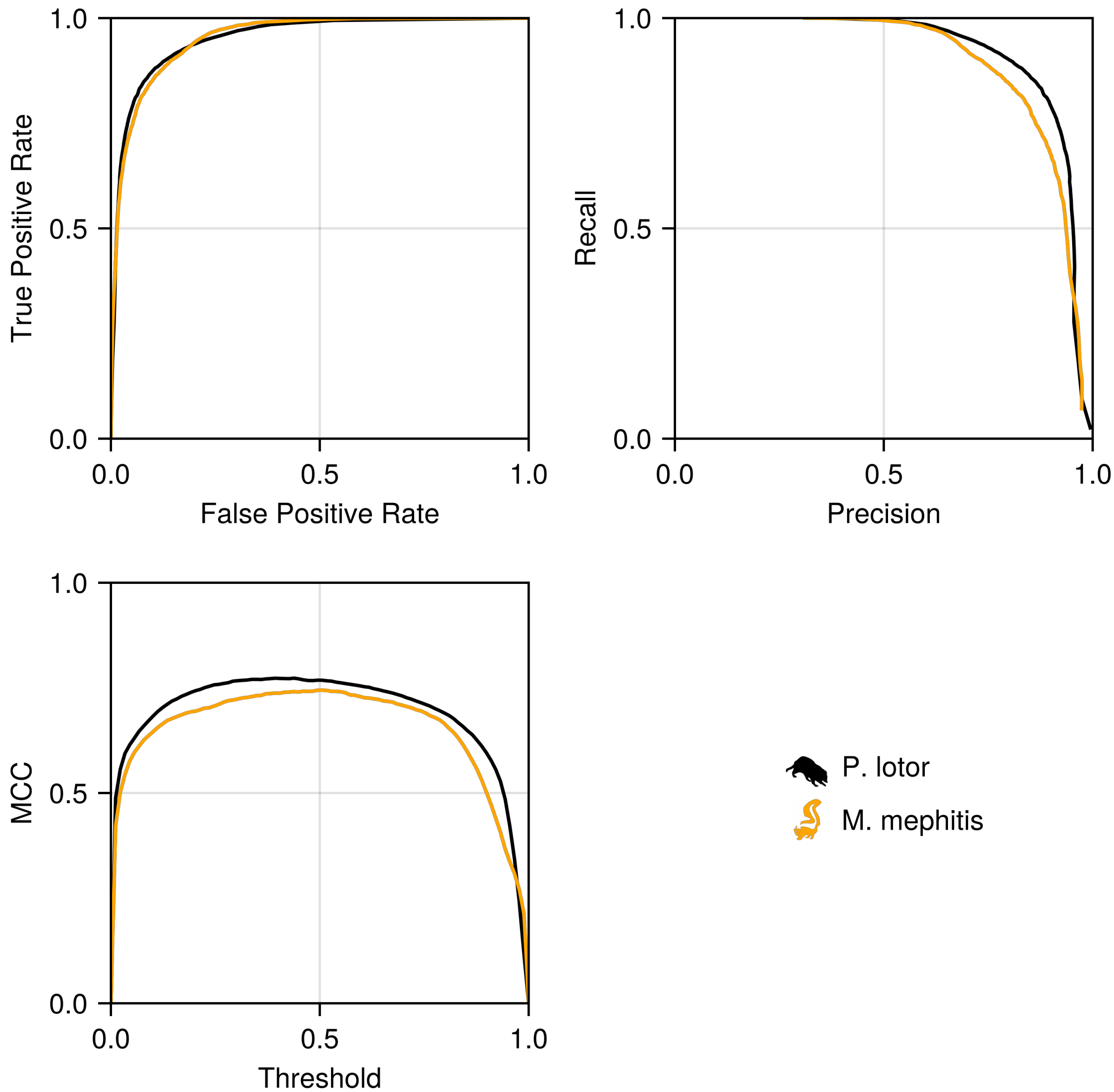

Figure S1: ROC curve (top-left) and PR curve (top-right) for *P. lotor* and *M. mephitis*. Both models show good, and similar, performances in both spaces, suggesting that they achieve adequate performance without different bias. The learning curve (bottom-left) for both models show that the response of the MCC around the optimal threshold is relatively flat; this suggests that the model is robust to choices of the exact threshold value. Averages over all training data splits are presented in this figure.

Table S1: Relative importance (according to Shapley values for each species' training set) for each variable selected for the model of either reservoir. Coverage is measured in thousands of kilometers squared, and represent the surface area of the prediction domain for which this variable is the most important, (*i.e.* has the largest absolute Shapley value) for each species. Variables are ordered by total spatial cover.

	P. lotor		*M. mephitis*	
Variable	Rel. imp.	Cover	Rel. imp.	Cover
Max Temp. of Warmest Month	0.29	649.27	0.3	1044.88
Mean Temp. of Coldest Quarter	0.28	786.67		
Precip. of Warmest Quarter	0.02		0.08	200.41
Precip. of Wettest Quarter			0.07	125.01
Precip. of Driest Month	0.06	55.51	0.06	79.75
Temp. Seasonality			0.06	42.05
Mean Temp. of Driest Quarter	0.11	13.21		
Isothermality	0.02	0.31	0.06	10.39
Mean Diurnal Range	0.09	0.95	0.12	6.48
Precip. Seasonality	0.03	7.22		
Mean Temp. of Warmest Quarter			0.07	1.82
Min Temp. of Coldest Month			0.06	2.0
Temp. Annual Range			0.03	0.13
Mean Temp. of Wettest Quarter	0.04		0.02	
Annual Precip.	0.04		0.03	0.01
Precip. of Wettest Month			0.02	
Precip. of Coldest Quarter	0.02		0.02	0.01