Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Shifting Boundaries: Climate-Driven Niche Limits in North American Felids — Insights from Variable Ecological Restriction Analysis

İdris Sarı

botanical24@gmail.com

Erzincan Binali Yıldırım University

Petr Papežík

Comenius University in Bratislava

Abid Ali

Chinese Academy of Sciences

Research Article

Keywords: climatic niche divergence, envelope-driven niche, Lynx canadensis, Lynx rufus, niche truncation, VERA

Posted Date: May 7th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-9460867/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Biodiversity and Conservation on November 6th, 2026. See the published version at https://doi.org/10.1007/s10531-026-03526-2.

Shifting Boundaries: Climate-Driven Niche Limits in North American Felids — Insights from Variable Ecological Restriction Analysis

İdris Sarı[1]*, Petr Papežík[2], Abid Ali[3]

[1]*botanical24@gmail.com; 0000-0003-2475-8759;

Department of Biology, Faculty of Science and Art, Erzincan Binali Yıldırım University, Erzincan, Türkiye

[2]petr.papezik.upol@gmail.com; 0000-0002-5295-4266;

Department of Zoology, Faculty of Natural Sciences, Comenius University in Bratislava, Bratislava, Slovakia

[3]abid.biosci@gmail.com; 0000-0002-7646-6304;

Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, China

*Corresponding author

Abstract

The Canada lynx (*Lynx canadensis*) and the bobcat (*Lynx rufus*) are congeneric felids whose climatic niches and distributional overlap are being reshaped by climate change. We integrated ensemble distribution models, Humboldt niche overlap analysis, and a novel centroid-distance diagnostic—Variable Ecological Restriction Analysis (VERA)—using 6,723 and 9,030 independent occurrence records and 36 climatic predictors to characterize their climatic relationship. Niche equivalency was rejected (p = 0.0099), and niche divergence was not explained by background climate differences (p = 0.0101; p = 0.0263), indicating active climatic segregation despite 62.83% analogous environmental space. This divergence was asymmetric: the Canada lynx exhibited an envelope-driven niche constrained by multiple climatic axes

(no single predictor exceeding 25.08% importance), whereas the bobcat exhibited a threshold-driven niche dominated by coldest-quarter potential evapotranspiration (45.83%). A regional diagnostic comparison between VERA and Multivariate Environmental Similarity Surfaces (MESS) across 95 jurisdictions showed higher spatial concordance for the bobcat (81% of jurisdictions; 64.6% by area) than for the Canada lynx (60%; 42.4%), with VERA demonstrating greater ecological alignment across 31.6% of the continent for the envelope-driven specialist. Mid-century projections (SSP1-2.6, SSP2-4.5) indicated asymmetric redistribution: highly suitable space for the Canada lynx is projected to contract >50%, whereas the bobcat is positioned for an approximately 50% net gain through substantial northward expansion. Potential Niche Truncation Index values (Canada lynx: 0.875; bobcat: 0.850) indicate that occupied niches already approach continental climatic boundaries, leaving limited capacity for compensatory redistribution under continued warming.

Keywords: climatic niche divergence, envelope-driven niche, *Lynx canadensis*, *Lynx rufus*, niche truncation, VERA

1. Introduction

North America is home to two congeneric wild cats: the bobcat (*Lynx rufus* (Schreber, 1777)) and the Canada lynx (*Lynx canadensis* Kerr, 1792) (Sunquist and Sunquist 2002; Peers et al. 2013; Lavoie et al. 2019). The bobcat, one of the continent's most widely distributed native felids, is a broadly tolerant generalist occupying diverse ecosystems from deserts and shrublands to forests and wetlands (Sunquist and Sunquist 2002; Popescu et al. 2021). In contrast, the Canada lynx is an obligate cold-adapted specialist of boreal and sub-boreal forests, with morphological traits—such as long legs and large, fur-covered feet—that enhance hunting efficiency in deep snow

(Buskirk et al. 2000; Lavoie et al. 2019). As a result, the long-term persistence of this specialized felid is tightly linked to narrow hydro-thermal regimes, making it highly vulnerable to ongoing climatic shifts (USFWS 2023; Singh et al. 2025).

Morphological divergence between the two species has historically contributed to spatial segregation along climatic gradients (Roemer et al. 2009; Lavoie et al. 2019). Across their ranges, niche displacement in sympatry is strongly mediated by snow conditions. Because bobcats lack deep-snow adaptations, their historical expansion into core boreal habitats has been constrained (Murray and Boutin 1991; Peers et al. 2013; Gooliaff et al. 2018). However, climate change is rapidly restructuring this dynamic. Declines in snowpack extent and duration are expected to reduce the area and connectivity of core Canada lynx habitat, while rising ambient temperatures impose increasing climatic stress on cold-adapted specialists (Hoving et al. 2005; Peers et al. 2014; USFWS 2023). As warming accelerates, the weakening of historical climatic barriers may facilitate northward bobcat expansion, increase peripheral overlap, and reshape the macroecological dynamics between the two felids (Peers et al. 2013; Koen et al. 2014; Litvaitis et al. 2015; Scully et al. 2018; Marrotte et al. 2020; Sirén et al. 2020; Singh et al. 2025).

Recent literature on Canada lynx range modeling has underscored the methodological sensitivity of correlative species distribution modeling when applied across broad spatial and temporal scales (Ivan et al. 2024; Thornton and Murray 2024). In particular, model outcomes can vary substantially depending on the spatial representativeness of training data, the degree of temporal extrapolation, and the ecological interpretation of occurrence records from range peripheries (Sillero et al. 2021). These considerations highlight the importance of careful model calibration and validation, particularly when distributional limits are shaped by climatic constraints that broad-

scale models may not fully capture. Despite the urgency of these dynamics, traditional correlative species distribution models generally summarize environmental constraints through global variable-importance metrics (Elith and Leathwick 2009). This can obscure the spatially explicit climatic boundaries operating at geographic margins (Gaston 2009), limiting inference on where specific thermal or moisture limitations actually restrict distributions. To address this gap, we combined ensemble distribution modeling with Variable Ecological Restriction Analysis (VERA), a centroid-distance diagnostic that identifies the most limiting climatic variable at each locality by quantifying the standardized departure from a species' climatic optimum. In contrast to range-based extrapolation diagnostics such as Multivariate Environmental Similarity Surfaces (MESS; Elith et al. 2010), which detect novelty outside calibration envelopes, VERA evaluates restriction intensity within nominally analogous environments. We then cross-validated VERA and MESS outputs against published ecological evidence across 95 administrative jurisdictions in North America, and applied the Humboldt niche comparison framework (Brown and Carnaval 2019) to test climatic niche equivalency and divergence in multidimensional environmental space.

Accordingly, our study had three primary objectives: (1) to model current and mid-century (2041–2060) climatic suitability for both species under SSP1-2.6 and SSP2-4.5 scenarios and to quantify the resulting asymmetry in projected range trajectories; (2) to quantify interspecific climatic niche divergence and Potential Niche Truncation Index values within the Humboldt framework; and (3) to cross-validate VERA and MESS diagnostic outputs against regional ecological evidence.

2. Materials and Methods

2.1. Occurrence data and climatic predictors

Occurrence data for the bobcat (*L. rufus*; *n* = 79,222) and the Canada lynx (*Lynx canadensis*; *n* = 70,900) were compiled from primary databases (GBIF.org 2026a, b, c; iNaturalist 2026). These records were supplemented with high-precision tracking, genetic, and field data (Whittington et al. 2015; Farrell et al. 2018; Morin et al. 2020; Prentice et al. 2020; Tattersall et al. 2020; Sirén et al. 2022; Szumski et al. 2023; Arnold et al. 2025a; Singh et al. 2025; U.S. Fish and Wildlife Service n.d.). To mitigate the effects of sampling bias and spatial autocorrelation, we applied outlier filtering and spatial thinning protocols to the initial records (Smith et al. 2023). Following these refinements, the final datasets consisted of 9,030 spatially independent records for the bobcat and 6,723 for the Canada lynx (Fig. 1).

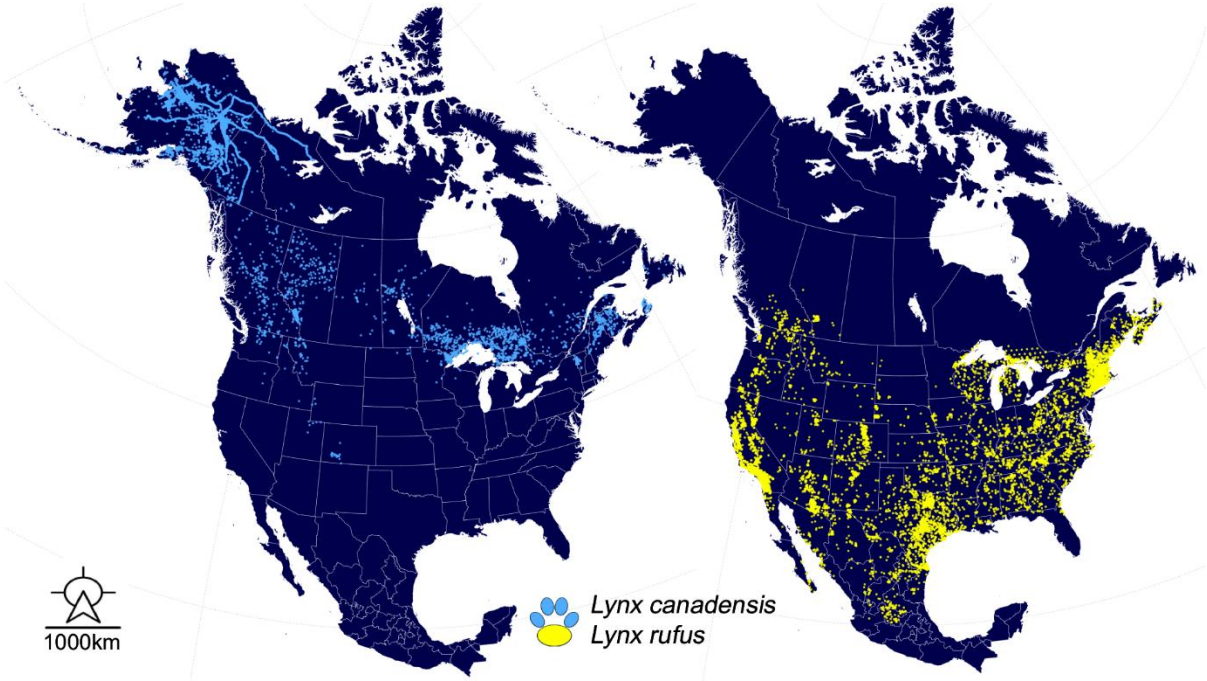


Fig. 1 Distribution of spatially thinned occurrence records for *L. canadensis* (left, blue points) and *L. rufus* (right, yellow points) across North America

We compiled 36 continuous climatic predictors at a 2.5 arc-minute resolution, integrating 19 bioclimatic variables from WorldClim v2.1 (Fick and Hijmans 2017) and

115 17 climate indices from Envirem (Title and Bemmels 2018) to capture a broad range
116 of climatic conditions.

117 **2.2. Species distribution modeling and climate-change projections**

118 To mitigate multicollinearity, we screened the initial predictors using Variance Inflation
119 Factor analysis (the *usdm* R package; Naimi et al. 2014), retaining the most
120 informative variables based on preliminary importance scores. We modeled the
121 potential climatic suitability of both species using an ensemble forecasting framework
122 in the *biomod2* R package (Thuiller et al. 2009; Guéguen et al. 2025). This framework
123 integrated five complementary statistical and machine-learning algorithms:
124 Generalized Linear Models (GLM; McCullagh and Nelder 1989), Flexible Discriminant
125 Analysis (FDA; Hastie et al. 1994), Random Forest (RF; Breiman 2001), Maximum
126 Entropy (MAXNET; Phillips et al. 2017), and Generalized Boosted Regression Models
127 (GBM; Friedman 2001).

128 Following the Biotic-Abiotic-Mobility (BAM) framework (Soberón 2007), we defined the
129 accessible area (M) for each species using administrative boundary layers covering
130 North America. To minimize spatial bias, we generated 10,000 pseudo-absence points
131 per species (Barve et al. 2011; Barbet-Massin et al. 2012). Models were calibrated
132 using repeated random cross-validation (80/20 split with two repetitions) with the
133 bigboss tuning profile, which provides optimized default hyperparameters for each
134 algorithm (Guéguen et al. 2025). Predictive performance was evaluated via the Area
135 Under the Receiver Operating Characteristic Curve (AUC) and the True Skill Statistic
136 (TSS), retaining only models with TSS > 0.8 (Leroy et al. 2018) to construct final
137 weighted-mean ensemble forecasts (Marmion et al. 2009).

Future habitat suitability was projected for the mid-century (2041–2060) under Shared Socioeconomic Pathways SSP1-2.6 and SSP2-4.5 (Meinshausen et al. 2020; Tebaldi et al. 2021). To ensure robust projections, we used the ensemble mean of three CMIP6 Global Climate Models (GCMs): EC-Earth3-Veg (Döscher et al. 2022), which dynamically integrates vegetation feedbacks; MPI-ESM1-2-HR (Müller et al. 2018), for its high-resolution ocean–atmosphere coupling; and MRI-ESM2-0 (Yukimoto et al. 2019), to increase institutional diversity and reduce systematic biases in the ensemble mean. Spatial extents of future suitability were quantified using the *terra* R package (Hijmans et al. 2026).

2.3. Ecological niche comparison in environmental space

We conducted a niche comparison to determine whether these felids maintain distinct climatic niches despite their broad geographic co-occurrence. This comparison used the 10 climatic variables retained by the species-specific species distribution models (SDMs) after multicollinearity screening (six per species, of which two were shared). We utilized the *Humboldt* R package (Brown and Carnaval 2019) to quantify niche similarity within a two-dimensional environmental space while robustly accounting for the spatial structure of available environments and species mobility. Climatic niche overlap was quantified using Schoener's *D* (Schoener 1968; Warren et al. 2008), ranging from 0 (no overlap) to 1 (complete overlap), to characterize the degree of niche convergence or divergence.

Following the BAM framework and its niche hierarchy (Fundamental Niche [FN], Existing Fundamental Niche [EFN], Potential Niche [PN], Occupied Niche [ON], and Invadable Niche [IN]; sensu Brown and Carnaval 2019), we characterized the climatic niche dimensions of each species across both geographic (G-space) and environmental (E-space) spaces (Broennimann et al. 2012). To account for spatial

biases in available background climates, we corrected for the proportional availability of environments in E-space. This ensures that the Niche Overlap Test (NOT) and Niche Divergence Test (NDT) reflect true ecological selection rather than mere geographic availability.

To assess whether these species are operating at or near their absolute climatic limits, we calculated the Potential Niche Truncation Index (PNTI). The PNTI expresses how closely the outer abiotic boundaries of the ON approach the limits of the EFN, indicating the degree to which the niche is truncated by the available environmental space (Brown and Carnaval 2019). A PNTI value exceeding 0.30 signifies that a species is operating against the extreme climatic limits of the studied geography. This index quantifies whether a species retains climatically suitable buffer space or is already constrained against the limits of the available climatic gradient.

2.4. Multivariate Environmental Similarity Surfaces (MESS) and Variable Ecological Restriction Analysis (VERA)

To assess climatic extrapolation and environmental novelty, we computed Multivariate Environmental Similarity Surfaces (MESS; Elith et al. 2010) using the *predicts* R package (Hijmans 2026). MESS quantifies the similarity of each projection pixel to the calibration environment, where negative values delineate regions of strict extrapolation and high novelty (Barbosa et al. 2009; Mesgaran et al. 2014). Crucially for spatial diagnostics, MESS identifies the Most Dissimilar variable (MoD) driving this novelty at each locality. While more recent metrics (e.g., MOP, ExDet, Shape; Owens et al. 2013; Mesgaran et al. 2014; Velazco et al. 2024) provide advanced capabilities such as Type 2 novelty detection, we utilized MESS specifically to contrast its established range-based logic (MoD) with the centroid-distance approach of our novel diagnostic tool, Variable Ecological Restriction Analysis (VERA).

While MESS effectively highlights environmental novelty relative to the calibration range, its range-based logic does not quantify climatic restriction intensity relative to a species' climatic optimum. Traditional limiting-factor methods generally rely on linear, gradient-based normalization (typically scaled 0 to 1; Malczewski 2000), which assumes monotonic species responses. However, such formulations often fail to capture the unimodal response structure typical of specialized species (Hirzel et al. 2002; Austin 2007; Yáñez-Arenas et al. 2012) and can over-predict climatic restriction within core habitats (Jiménez-Valverde et al. 2008; Kearney and Porter 2009).

2.4.1. Mathematical formulation of VERA

To resolve this limitation, which we term the "gradient trap," we developed VERA. VERA shifts the analytical framework from absolute gradient normalization to a centroid-distance metric, quantifying environmental restriction as the standardized multidimensional departure from the species' climatic optimum (Hirzel et al. 2002; Austin 2007; Yáñez-Arenas et al. 2012; Martínez-Meyer et al. 2013). This approach is conceptually aligned with Ecological-Niche Factor Analysis (ENFA; Hirzel et al. 2002) and distance-to-centroid modeling, where the centroid represents the species' climatic optimum in environmental space (Yáñez-Arenas et al. 2012; Martínez-Meyer et al. 2013).

Following standard ecological distance-normalization principles (Legendre and Legendre 2012), VERA defines the species' climatic optimum and tolerance breadth by calculating the arithmetic mean (μ_i) and standard deviation (σ_i) for each environmental variable i based on N presence records (Hirzel et al. 2002; Yáñez-Arenas et al. 2012; Martínez-Meyer et al. 2013):

$$\mu_i = \left(\frac{1}{N}\right)\sum_{k=1}^{N} V_{ik} \quad (1a)$$

$$\sigma_i = \sqrt{\left(\frac{1}{N-1}\right)\sum_{k=1}^{N}(V_{ik} - \mu_i)^2} \quad (1b)$$

where V_{ik} is the observed value of environmental variable *i* at presence location *k*. The climatic restriction intensity (*Z*-score) at pixel *x* is then quantified as the squared standardized departure from the climatic optimum (Yáñez-Arenas et al. 2012):

$$Z_{ix} = \left(\frac{(V_{ix} - \mu_i)}{\sigma_i}\right)^2 \quad (2)$$

where Z_{ix} denotes the climatic restriction intensity imposed by variable *i* at pixel *x*. The application of *Z*-standardization (mean = 0, variance = 1) ensures that variables measured in different units (e.g., °C and mm) are commensurable and prevents analytical bias arising from scale differences (Legendre and Legendre 2012). The squared term ensures that both positive and negative departures from the centroid are coded as absolute increases in climatic restriction, consistent with Shelford's Law of Tolerance, which posits that an organism's performance decreases from either side of an optimum along any environmental gradient (Shelford 1931; Austin 2007). argmax

2.4.2. Identification of the Most Limiting Variable (MLV)

In the final diagnostic step, VERA identifies the single environmental driver most responsible for local spatial exclusion. The environmental variable *i* yielding the maximum *Z_ix* at pixel *x* is identified as the Most Limiting Variable (*MLV*), representing the primary climatic constraint at that specific geographic location — the factor pushing

231 the species furthest from its climatic centroid (Hirzel et al. 2002; Yáñez-Arenas et al.
232 2012):

233 $$MLV_x = \text{argmax}i(Z_{ix}) \quad (3)$$

234 This diagnostic criterion is grounded in Liebig's Law of the Minimum (von Liebig 1840;
235 Austin 2007), which posits that an organism's performance is determined by the single
236 most restrictive factor among a suite of environmental variables. However, unlike
237 MESS's MoD, which identifies the variable most dissimilar to the training data range,
238 VERA's MLV identifies the variable imposing the greatest departure from the species'
239 climatic optimum. This distinction is fundamental: MESS operates on a range-based
240 logic (is this value outside the calibration envelope?), whereas VERA operates on a
241 centroid-distance logic (how far is this value from the species' optimal environmental
242 conditions?). Consequently, VERA can detect climatically restrictive conditions even
243 within the calibration range where MESS would report positive (i.e., analogous) values.

244 **2.4.3. Ecological evaluation of VERA and MESS**

245 To evaluate the ecological interpretability of VERA outputs, we compared its primary
246 limiting variables with those identified by MESS across 95 administrative jurisdictions
247 in North America. Although the two methods employ different algorithmic logic, we first
248 assessed the overall spatial concordance between their outputs before focusing on
249 regions of divergence.

250 A 75% spatial agreement threshold was applied to distinguish robust methodological
251 consensus from meaningful divergence. Jurisdictions exceeding this threshold were
252 not subjected to further diagnostic review. The detailed evaluation therefore targeted
253 the discordant jurisdictions falling below this threshold: 49 for *L. canadensis* and 20
254 for *L. rufus*.

For each discordant jurisdiction, we evaluated whether each method's statistically dominant variable functioned as an ecologically interpretable proxy for documented regional constraints, based on published field evidence. Jurisdictions were assigned to one of four diagnostic classes: (1) VERA-supported, where VERA provided the more plausible ecological signal; (2) MESS-supported, where MESS variables aligned better with field evidence; (3) Ambiguous, where both methods showed weak or conflicting signals; and (4) Co-supported, where both frameworks identified valid, co-limiting mechanisms despite initial spatial discordance.

2.5. Standardized niche density profiles

To visually diagnose and compare the climatic niche breadth of each species, we constructed standardized niche density profiles (SNDPs) derived from species occurrence records and their associated climatic values. For each species, climatic values were extracted at all spatially independent occurrence points for the core climatic predictors retained in the respective SDM. Because these predictors operate on vastly different measurement scales, all extracted values were subjected to *z*-score standardization (mean = 0, variance = 1; Legendre and Legendre 2012), centering each variable's distribution at the species' mean occurrence value. The resulting probability densities were visualized as ridgeline plots using the *ggridges* and *ggplot2* packages in R (Wickham 2016; Wilke 2026).

Interpretation is guided by three graphical attributes. First, peak height and kurtosis: leptokurtic distributions indicate narrow climatic specialization (Wiens et al. 2010), whereas platykurtic distributions reflect broad tolerance (Sexton et al. 2009). Second, peak displacement from the zero-centroid reveals asymmetric niche occupation (Austin 2007). Third, abrupt tail truncation implies that the species has reached the

limit of the available climatic gradient, indicating limited scope for further range shifts (Owens et al. 2013).

To ensure full transparency and the strict reproducibility of our analytical framework, all methodological protocols and foundational datasets are provided in Supplementary material 1. This comprehensive package includes the complete, spatially independent occurrence records for both *L. canadensis* and *L. rufus*, environmental data configurations, and the step-by-step analytical workflows required to fully replicate our SDMs and diagnostic assessments.

3. Results

3.1. Model performance

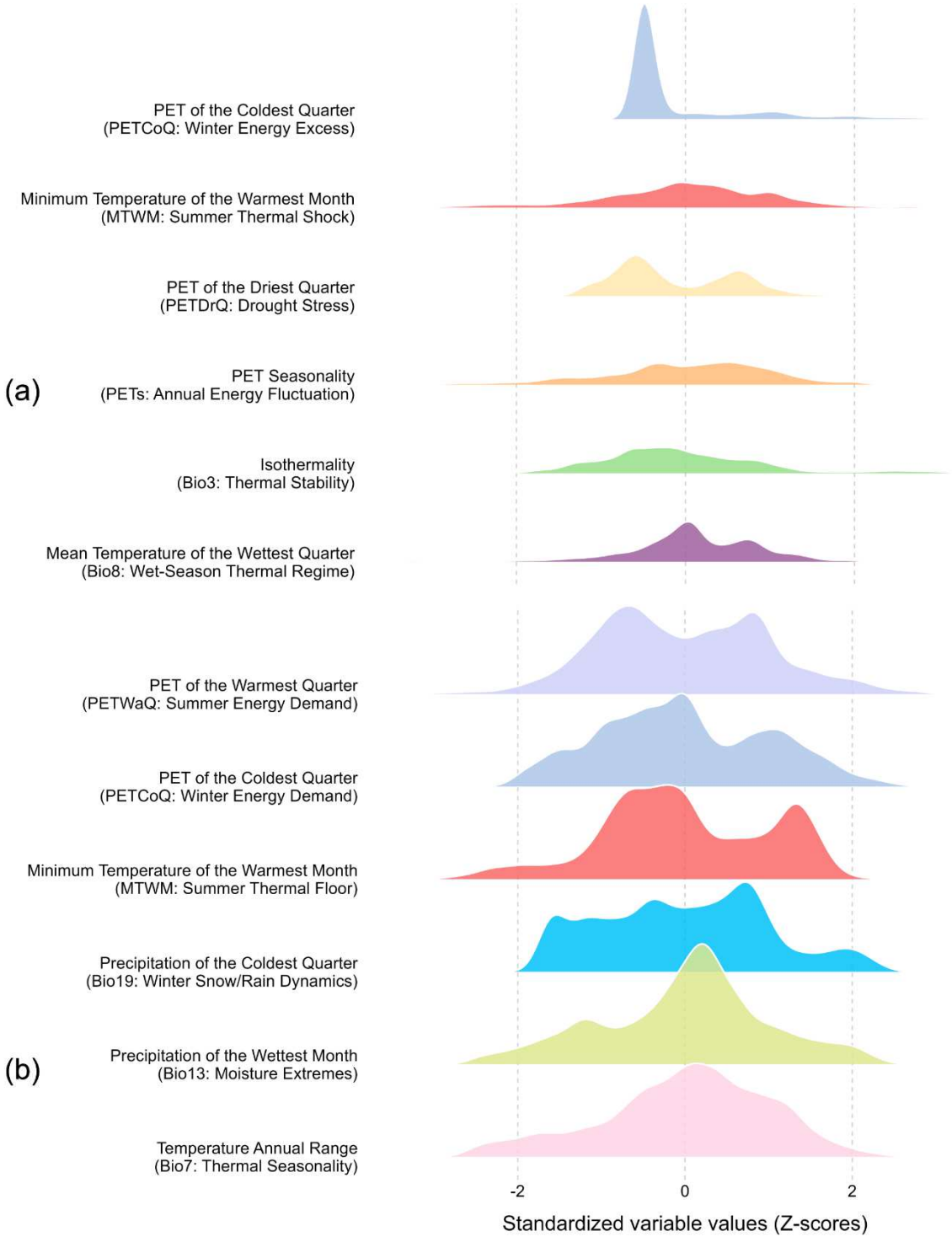
The ensemble models for both species demonstrated high predictive performance across all evaluation metrics. For the Canada lynx, the model achieved a TSS of 0.958 and an AUC of 0.999, with a sensitivity of 98.96% and a specificity of 96.81%. The ensemble model for the bobcat achieved a TSS of 1.00 and an AUC of 1.00, with a sensitivity of 100% and a specificity of 99.99%, reflecting the broad climatic envelope and large sample size available for this widely distributed species.

3.2. Variable importance and standardized niche density profiles (SDNPs)

The SDNPs of the Canada lynx and the bobcat reveal contrasting patterns of climatic specialization. For the Canada lynx, the ensemble model identified potential evapotranspiration (PET) of the coldest quarter (PETCoQ) as the primary driver of habitat suitability (variable importance = 25.08%). This was followed by isothermality (Bio3; 20.99%), PET seasonality (PETs; 15.20%), minimum temperature of the warmest month (MTWM; 14.36%), PET of the driest quarter (PETDrQ; 12.74%), and mean temperature of the wettest quarter (Bio8; 11.63%). This relatively even

distribution of importance scores—with no single predictor exceeding 25.08%—indicates that the occupied niche of the Canada lynx is shaped by a multivariate climatic constraint rather than a single dominant axis. The density profiles reflect this multivariate structure: PETCoQ is distinguished by a sharp, high-amplitude peak below the standardized mean, indicating a highly concentrated utilization of low winter energy environments and narrow tolerance for the core population. In contrast, the other bioclimatic variables (PETs, Bio3, MTWM, and Bio8) display noticeably lower and broader peaks. Furthermore, the extended tails (skewness) observed across the distributions reflect the existence of marginal populations occupying more extreme, peripheral climatic conditions (Fig. 2a).

In contrast, the bobcat ensemble model is strongly dominated by a single predictor: PETCoQ accounts for 45.83% of the variable importance. The remaining five predictors—MTWM (11.55%), PET of the warmest quarter (PETWaQ; 11.50%), precipitation of the coldest quarter (Bio19; 11.23%), temperature annual range (Bio7; 10.89%), and precipitation of the wettest month (Bio13; 9.00%)—contribute at considerably lower magnitudes, functioning as secondary constraints on a niche primarily defined by winter energy availability. The bobcat SDNPs corroborate this structure. The PETCoQ distribution is remarkably broad and extends well into positive z-score territory, contrasting sharply with the narrow, low-energy concentration observed for the Canada lynx. Furthermore, PETWaQ, MTWM, and the precipitation variables also exhibit wide, centered distributions, perfectly reflecting the bobcat's generalist nature and its capacity for broad climatic tolerance (Fig. 2b).



325

326 **Fig. 2** SNDPs of *L. canadensis* (a) and *L. rufus* (b) across standardized environmental
327 gradients (z-scores). Colored lines represent the top twelve climatic predictors.
328 Interpretation attributes: (1) narrow, high-amplitude peaks indicate specialization,
329 whereas broad distributions reflect wide tolerance; (2) peak displacement from zero

reveals asymmetric niche occupation; and (3) extended tails indicate marginal populations occupying extreme climatic boundaries

3.3. Spatial diagnostics of climatic limits: MESS extrapolation and VERA constraints

Across the low-agreement jurisdictions, the two species showed markedly different diagnostic patterns (Fig. 6; Supplementary materials 2 and 3).

For *L. canadensis*, 49 evaluated jurisdictions covered 15,420,724 km² in total. By jurisdiction count, MESS was the most frequent outcome (28 of 49; 57.14%), followed by VERA (19; 38.78%) and Ambiguous (2; 4.08%). However, the area-weighted pattern was reversed: VERA-supported jurisdictions accounted for 10,180,855 km² (66.02% of the total assessed area), compared with 4,138,568 km² for MESS (26.84%) and 1,101,301 km² for Ambiguous (7.14%). This divergence reflects the fact that the largest jurisdictions—spanning the boreal core, subarctic, and western montane regions—were more consistently interpretable through VERA, whereas MESS was favored predominantly across smaller warm-temperate and Mid-Atlantic jurisdictions where warm-season thermal stress (MTWM) emerged as the dominant exclusion signal. Among the 19 VERA-supported jurisdictions, the most frequently identified limiting variables were PETs in high-latitude boreal and subarctic systems, PETDrQ along the Pacific corridor and arid western landscapes, and Bio3 in montane Rocky Mountain environments. Among the 28 MESS-supported jurisdictions, 24 shared a common diagnostic pattern in which VERA identified PETCoQ while MESS identified MTWM, with warm-season thermal limitation consistently judged as the more ecologically interpretable exclusion mechanism for this boreal specialist.

For *L. rufus*, 20 evaluated jurisdictions covered 6,831,143 km² and produced a more heterogeneous outcome structure. By jurisdiction count, the most common result was concordance between methods (7 of 20; 35.00%), followed by VERA-supported and Ambiguous (5 each; 25.00%) and MESS-supported (3; 15.00%). The area-weighted distribution was dominated by ambiguous outcomes, which covered 3,676,288 km² (53.82% of the total assessed area), followed by MESS-supported jurisdictions (1,608,215 km²; 23.54%), VERA-supported jurisdictions (1,092,526 km²; 15.99%), and concordant jurisdictions (454,114 km²; 6.65%). This pattern indicates that for a broadly tolerant generalist, neither diagnostic method achieved consistent interpretive advantage across large spatial extents, and the largest jurisdictions (Alaska, Québec, Texas) were predominantly classified as ambiguous.

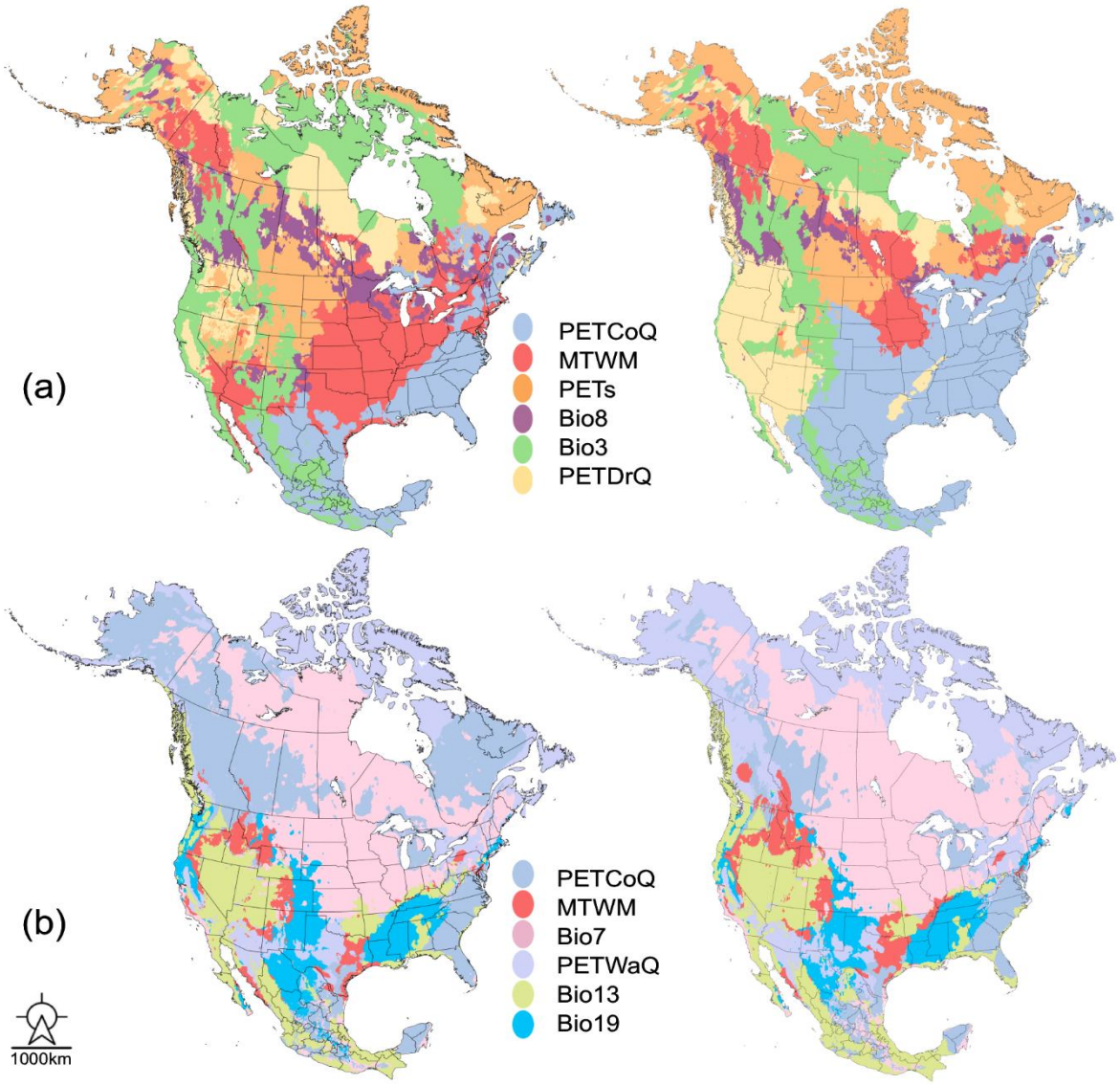


Fig. 3 Comparative spatial diagnostics of climatic constraints for *L. canadensis* (a) and *L. rufus* (b). Left panels: distribution of the most dissimilar variables (MoD) driving extrapolation. Right panels: primary climatic constraints (MLV) identified through VERA

3.3.2. Contrasting restrictions in sympatric zones

The comparative diagnostic power of VERA was most evident in regions of potential geographic overlap, where the two species were restricted by distinct climatic thresholds. For example, in the northern Rocky Mountains, the Canada lynx was constrained by Bio3, whereas the bobcat was limited by Bio7. Similarly, in British

Columbia, the species were restricted by different climatic axes, confirming that even within shared territories the two felids are constrained by different climatic mechanisms.

3.4. Climatic segregation and potential niche truncation

The environmental niche analysis conducted within the two-dimensional E-space revealed distinct climatic boundaries and high truncation for both species. Despite sharing a substantial proportion of available environmental space (62.83%) across the study area, the observed climatic niche overlap between the species was moderate (Schoener's D = 0.599). The Niche Overlap Test (NOT) rejected niche equivalency (p = 0.0099), and Niche Divergence Tests (NDT) were significant in both directions (Canada lynx to bobcat: p = 0.0101; bobcat to Canada lynx: p = 0.0263), indicating that this divergence was not explained solely by differences in available background climates.

PNTI values were high for both species (Canada lynx: 0.875; bobcat: 0.850), substantially exceeding the 0.30 threshold. This indicates that the occupied niches are heavily constrained by the extreme boundaries of the available continental climatic space. The Canada lynx occupied a narrow niche concentrated toward the cold extreme, whereas the bobcat occupied a broader climatic envelope spanning more diverse conditions.

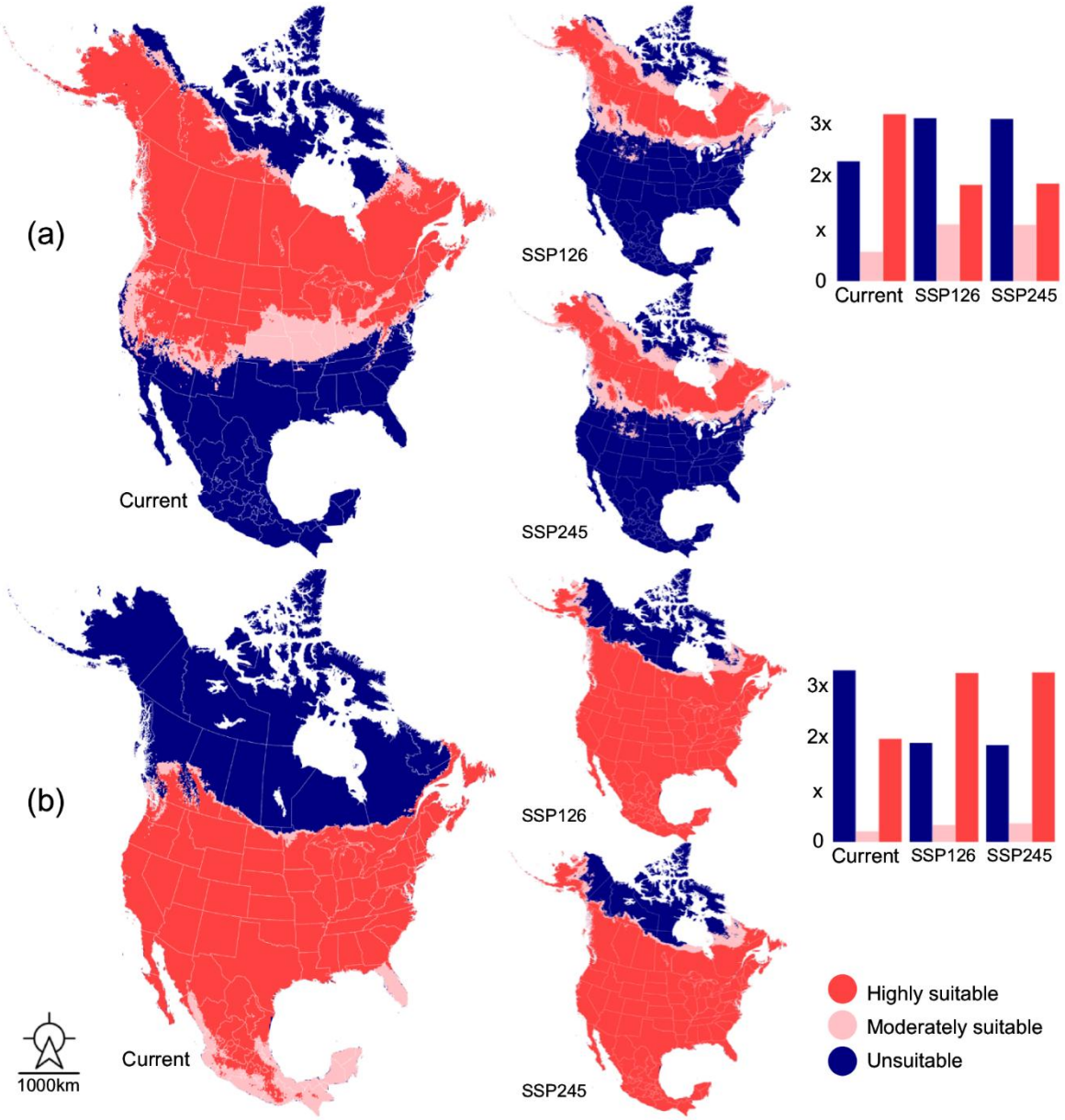
3.5. Current and projected future distributions of the Canada lynx and the bobcat

Under current climatic conditions, the ensemble SDM projects a broad, contiguous area of highly suitable climatic space for the Canada lynx across the boreal zone, from British Columbia and the Yukon through Quebec and the Maritime provinces,

extending into central Alaska. A transitional fringe of moderate suitability borders the southern margin across the northern contiguous United States.

Mid-century projections (2041–2060) under both SSP1-2.6 and SSP2-4.5 indicate a marked contraction: the total area of highly suitable climatic space is projected to decrease by more than 50%, with the most pronounced losses along the southern trailing edge (including the transition from aspen parkland to prairie in Alberta and Saskatchewan, the Pacific Northwest, and the northern United States). Core areas in western and southern Alaska also show substantial reductions. Concurrently, the spatial extent of moderately suitable areas is projected to nearly double, indicating widespread climatic degradation rather than a simple geographic range shift. Notably, neither scenario projects substantial northward expansion into Arctic regions to offset these southern losses (Fig. 4a).

M



412

413 **Fig. 4** Current and projected mid-century (2041–2060) climatic suitability for *L.*
414 *canadensis* (a) and *L. rufus* (b) across North America under SSP1-2.6 and SSP2-4.5
415 scenarios. Inset bar charts summarize the relative area of each suitability class across
416 the two time periods

417 **4. Discussion**

418 **4.1. Climatic niche divergence and asymmetric specialization**

The Humboldt niche analysis indicated that the felids occupy statistically distinct climatic niches, with divergence not driven solely by background climate differences. Following Brown and Carnaval (2019), this supports active climatic segregation despite substantial analogous environmental space (62.83%), aligning with documented competitive asymmetries and range-boundary dynamics (Peers et al. 2013; Litvaitis et al. 2015; Nakamoto et al. 2024; Singh et al. 2025).

Crucially, the structure of this divergence is highly asymmetric. The Canada lynx exhibited an envelope-driven, multivariate niche where no single predictor exceeded 25.08% of the ensemble variable importance. Its narrow, leptokurtic density profiles are consistent with a cold-adapted specialist constrained by multiple interacting climatic axes (Wiens et al. 2010; Olson et al. 2021). In contrast, the bobcat niche was threshold-driven and heavily dominated by a single winter energy predictor (PETCoQ; 45.83%). Its broad, platykurtic density profiles suggest a climatic generalist exhibiting wide environmental tolerance once minimum winter energy requirements are met (Sexton et al. 2009; Gooliaff et al. 2018). Under this framework, threshold-driven niches (bobcat) may remain relatively stable while the critical limiting axis stays within tolerance, whereas envelope-driven niches (Canada lynx) are highly vulnerable to perturbation along any constituent axis (Peers et al. 2014).

Furthermore, density profiles exhibit abrupt truncations at the extremes of the standardized gradient (Fig. 2), mirroring the high Potential Niche Truncation Index (PNTI) values reported for both species (Section 3.4). This indicates that neither felid possesses climatically suitable buffer space; rather, their occupied niches have nearly converged with the absolute abiotic limits of the continental Existing Fundamental Niche (the A-component in the BAM framework, illustrated by the yellow domain in Fig. 5) (Owens et al. 2013; Brown and Carnaval 2019). Taken together, their climatic

segregation is not a static spatial partitioning, but a dynamic asymmetry bounded by hard continental limits. Lacking room for compensatory redistribution, the threshold-driven generalist appears positioned to expand under warming conditions, while the envelope-driven specialist faces progressive geographic contraction.

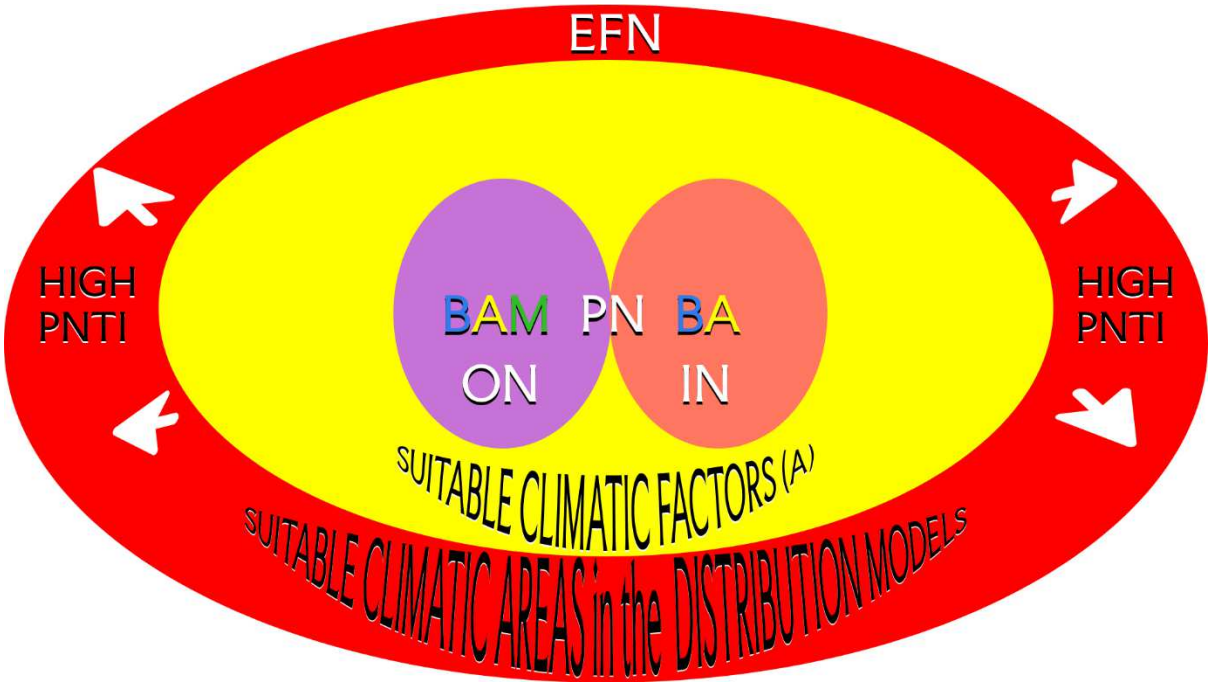


Fig. 5 Conceptual diagram illustrating the relationship between niche truncation and continental climatic constraints for the Canada lynx and the bobcat. The yellow domain represents the Existing Fundamental Niche (EFN), defined as the intersection of each species' fundamental niche with the available North American climate space. The Potential Niche (PN) encompasses climatically suitable conditions, within which the Occupied Niche (ON) and the Invadable Niche (IN) are embedded, following the BAM framework (sensu Brown and Carnaval 2019). White arrows indicate high PNTI values, showing that both species' climatic niches approach the extreme boundaries of the EFN

4.2. Region-specific climatic barriers and the complementary roles of VERA and MESS

Our continent-wide cross-validation suggests that VERA and MESS capture complementary dimensions of climatic limitation. Across most of the study area, the two methods produced concordant spatial predictions, reinforcing the view that their underlying algorithmic logics converge on similar ecological conclusions when applied to well-characterized climatic space. However, in the jurisdictions where the methods diverged, the diagnostic clarity of each varied markedly between the two species, in a manner consistent with differences in their niche architecture.

For the Canada lynx, VERA exhibited substantially higher diagnostic clarity across the evaluated low-agreement jurisdictions, with VERA-supported areas accounting for approximately 66% of the total assessed area, compared with 27% for MESS and only 7% for ambiguous outcomes. This spatial pattern indicates that the larger northern and western jurisdictions—where the species' core boreal and montane populations occur—were more consistently interpretable through VERA's distance-to-optimum framework. In these systems, VERA more often identified climatic signals that are ecologically coherent at the range margin, including seasonal energy dynamics (PETs) across the boreal core, evaporative demand (PETDrQ) along the Pacific corridor, and montane thermal structure (Bio3) in the Rocky Mountain region (Squires et al. 2013; Vanbianchi et al. 2017). For species with comparatively constrained macroclimatic limits, distance-to-optimum approaches may therefore provide a more informative representation of climatic stress than distance-to-range-edge metrics alone (Koen et al. 2014; Peers et al. 2014).

By contrast, the bobcat produced a fundamentally different diagnostic pattern. Here, the dominant outcome was ecological ambiguity, which accounted for approximately 54% of the total assessed area, followed by MESS (24%), VERA (16%), and concordant outcomes (7%). No single climatic mechanism—and no single diagnostic

485 method—consistently explained distribution limits across this species' heterogeneous
486 range. This pervasive ambiguity is better interpreted not as algorithmic failure, but as
487 evidence of ecological co-limitation by multiple interacting constraints, consistent with
488 the eurytopic character of the bobcat (Roberts and Crimmins 2010; Thornton et al.
489 2004; Litvaitis et al. 2015).

490 The contrast between these profiles is itself informative. For the Canada lynx, VERA
491 achieved clear area-weighted diagnostic clarity with ambiguity confined to a small
492 fraction of the landscape. For the bobcat, ambiguity dominated the spatial pattern and
493 neither method achieved consistent interpretive advantage. This asymmetry suggests
494 that the relative utility of extrapolation diagnostics is contingent on the niche
495 architecture of the focal species—a finding with practical implications for how
496 diagnostic outputs are evaluated in species distribution modeling.

497 The ecological value of this discordance became clearer when variable-level outputs
498 were compared against regional field evidence. Along the Pacific Coast corridor, VERA
499 identified warm-season moisture deficit (PETDrQ) as the dominant limiting signal for
500 the Canada lynx, a result more consistent with field-based evidence than the
501 alternative MESS signal of isothermality (Vanbianchi et al. 2017). Across the boreal
502 core, VERA highlighted seasonal energy dynamics (PETs) in a manner that aligns with
503 hare–lynx population synchrony (Stenseth et al. 1997; Krebs et al. 2001). In the warm-
504 temperate exclusion zone spanning the southern Great Plains and Mid-Atlantic states,
505 MESS frequently identified warm-season thermal stress (MTWM) as the dominant
506 exclusion signal, broadly consistent with evidence that increasing temperatures
507 contribute to southern range constraints (Hoving et al. 2005). For the bobcat, MESS
508 identified cold-season energy limitation (PETCoQ) at the northern range margin in
509 British Columbia and Yukon, consistent with documented winter-severity constraints

(Marrotte et al. 2020; Dyck et al. 2021), whereas VERA captured an additional warm-season signal (PETWaQ) that may reflect reduced prey productivity in boreal environments. In topographically complex regions such as Arizona and Durango, localized discordance further suggests that bobcat responses are shaped by multiple overlapping constraints rather than a single dominant climatic barrier.

Taken together, these patterns indicate that extrapolation diagnostics should not be treated as interchangeable or strictly competitive. Given the high degree of spatial concordance observed across vast portions of both species' ranges, MESS and VERA are best viewed as complementary frameworks. While MESS remains highly effective for delineating absolute multivariate novelty beyond calibration envelopes, VERA provides enhanced diagnostic clarity for isolating the specific climatic dimensions associated with range limitation, particularly for species with relatively narrow niche architectures. The continental-scale realism check employed here—linking variable-level outputs to regional ecological evidence across approximately 95 jurisdictions—provides a replicable validation framework that could be extended to other taxa and geographic contexts.

Beyond its present diagnostic use, VERA's centroid-distance structure may provide a basis for further methodological development. Because it quantifies the magnitude of climatic departure from an inferred species-level optimum, it could potentially be extended to represent variation in climatic resistance across space, helping identify dispersal bottlenecks, climatic corridors, and connectivity pathways. When combined with projected climate scenarios, VERA-derived resistance gradients may contribute to spatially explicit conservation planning for species undergoing range reorganization (Fig. 6) (McRae et al. 2008; Koen et al. 2014; USFWS 2023).

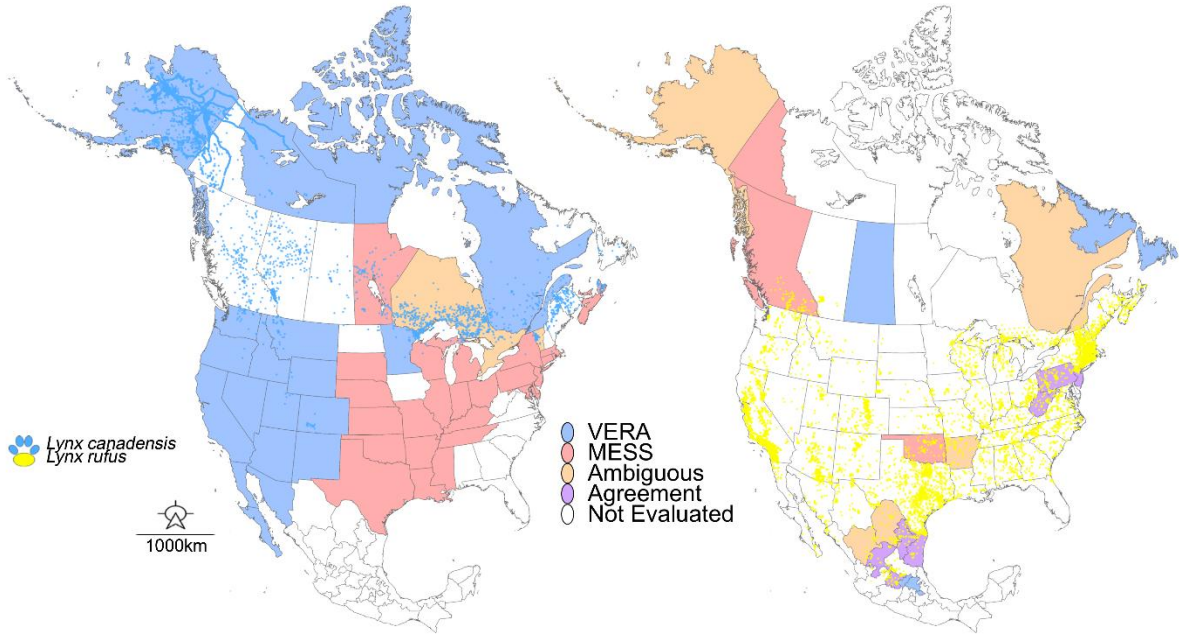


Fig. 6 Regional concordance between VERA (MLV) and MESS (MoD) across 95 administrative jurisdictions for *L. canadensis* (left) and *L. rufus* (right). Purple: both methods identified the same dominant limiting variable (Agreement). Blue: VERA was better supported by regional ecological evidence. Pink: MESS was better supported. Peach: neither method was clearly superior (Ambiguous). Blue and yellow points indicate species occurrence records overlaid for geographic reference

4.3. Methodological considerations and limitations

This study used exclusively climatic predictors, following the premise that climate acts as the primary broad-scale filter on species distributions, defining the abiotic template within which finer-scale factors (e.g., land cover, prey availability, biotic interactions) operate (Pearson and Dawson 2003; Peers et al. 2013; Loidi et al. 2022). Consequently, model outputs should be interpreted as climatic suitability diagnostics rather than full realized-habitat models.

Within this broad-scale climatic framework, although regional cross-validation provided empirical support for VERA's diagnostic realism, it remains a novel analytical tool requiring broader independent validation. Its current architecture does not explicitly parse the direction of environmental stress (e.g., differentiating between the excess or deficiency of a variable). Furthermore, its performance should be tested in highly mobile generalists, rare endemics with limited occurrence data, and taxa with strongly non-Gaussian environmental responses to fully establish its generalizability.

The accuracy of any correlative SDM—and by extension, any centroid-based diagnostic such as VERA—depends on the spatial representativeness of the underlying occurrence dataset. Recent assessments of Canada lynx range modeling emphasize that models calibrated primarily from southern range margins risk mischaracterizing the climatic optimum (Thornton and Murray 2024; Ivan et al. 2024). We compiled records spanning the full extent of both species' ranges to ensure that VERA's climatic centroid reflects the realized niche across the entire occupied geography. Nevertheless, future studies should prioritize the continued enrichment of Canada lynx occurrence records, especially from core boreal and undersampled edge populations, to further refine the calibration of both SDMs and spatially explicit diagnostic tools.

Beyond the spatial analyses presented here, temporal and projection uncertainties warrant further refinement. While the use of three CMIP6 GCMs provides a defensible baseline, incorporating wider model ensembles through tools such as the *GCMcompareR* R package (Fajardo et al. 2020) would better characterize the diverse precipitation and temperature trajectories inherent in climate modeling. Furthermore, moving beyond traditional 30-year averages by utilizing emerging tools like the *fastbioclim* package (Pinilla-Buitrago and Osorio-Olvera 2026) would allow for the

generation of custom-time variables that capture seasonal dynamics and recent environmental shifts more accurately, ensuring a tighter alignment between occurrence records and environmental data (Arnold et al. 2025b).

Although our models project a severe habitat contraction for the Canada lynx, the analytical framework presented here serves as a reproducible baseline rather than a definitive forecast. By combining centroid-based and range-based diagnostics, this integrated approach provides a transferable method for assessing environmental vulnerability in other specialist-generalist pairs. Ultimately, we view these projections as testable hypotheses. Future research incorporating expanded datasets and broader climate models will be essential to determine if the Canada lynx possesses greater intrinsic resilience than current correlative models can capture.

Data Availability

All data and code necessary to reproduce the analyses presented in this study are available in the Supplementary Information repository. This repository includes raw and spatially independent occurrence records, ensemble SDM outputs, the VERA protocol, Humboldt E-space tests, and the R scripts used to identify Most Limiting Variables (MLVs) and Most Dissimilar Variables (MoDs). Additional materials, including methodological proofs and variable-specific restriction profiles, are also provided to support transparency and reproducibility.

Funding

The authors did not receive support from any organization for the submitted work. No funding was received to assist with the preparation of this manuscript.

References

598 Arnold DA, Breed GA, Laufenberg JS, Berg ND, Bertram MR, Scotton BD, Kielland K
599 (2025a) Cyclic functional connectivity of Canada lynx (Lynx canadensis) populations
600 across North American boreal landscapes. J Anim Ecol 94:1569–1586.
601 https://doi.org/10.1111/1365-2656.70080

602 Arnold DA, Breed GA, Laufenberg JS, Berg ND, Bertram MR, Scotton BD, Kielland K
603 (2025b) Seasonal patterns of habitat use by a mesopredator in boreal forest
604 landscapes fragmented by fire. Ecosphere 16:e70357.
605 https://doi.org/10.1002/ecs2.70357

606 Austin M (2007) Species distribution models and ecological theory: a critical
607 assessment and some possible new approaches. Ecol Model 200:1–19.
608 https://doi.org/10.1016/j.ecolmodel.2006.07.005

609 Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences
610 for species distribution models: how, where and how many? Methods Ecol Evol 3:743–
611 751. https://doi.org/10.1111/j.2041-210X.2011.00172.x

612 Barbosa AM, Real R, Muñoz AR, Brown JA (2009) New measures for assessing model
613 equilibrium and prediction mismatch in species distribution models. Divers Distrib
614 15:504–518. https://doi.org/10.1111/j.1472-4642.2009.00562.x

615 Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher SP, Peterson AT,
616 Soberón J, Villalobos F (2011) The crucial role of the accessible area in ecological
617 niche modeling and species distribution modeling. Ecol Model 222:1810–1819.
618 https://doi.org/10.1016/j.ecolmodel.2011.02.011

619 Breiman L (2001) Random forests. Mach Learn 45:5–32

620 Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG,
621 Thuiller W, Fortin M-J, Randin C, Zimmermann NE, Graham CH, Guisan A (2012)

622 Measuring ecological niche overlap from occurrence and spatial environmental data.
623 Glob Ecol Biogeogr 21:481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x

624 Brown JL, Carnaval AC (2019) A tale of two niches: methods, concepts, and evolution.
625 Front Biogeogr 11:e44158. https://doi.org/10.21425/F5FBG44158

626 Buskirk SW, Ruggiero LF, Krebs CJ (2000) Habitat fragmentation and interspecific
627 competition: implications for lynx conservation. In: Ruggiero LF, Aubry KB, Buskirk SW,
628 Koehler GM, Krebs CJ, McKelvey KS, Squires JR (eds) Ecology and conservation of
629 lynx in the United States. University Press of Colorado, Boulder, pp 83–100

630 Döscher R, Acosta M, Alessandri A et al (2022) The EC-Earth3 Earth system model
631 for the Climate Model Intercomparison Project 6. Geosci Model Dev 15:2973–3020.
632 https://doi.org/10.5194/gmd-15-2973-2022

633 Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and
634 prediction across space and time. Annu Rev Ecol Evol Syst 40:677–697.
635 https://doi.org/10.1146/annurev.ecolsys.110308.120159

636 Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species.
637 Methods Ecol Evol 1:330–342. https://doi.org/10.1111/j.2041-210x.2010.00036.x

638 Fajardo J, Corcoran D, Roehrdanz PR, Hannah L, Marquet PA (2020) GCMcompareR:
639 a web application to assess differences and assist in the selection of general
640 circulation models for climate change research. Methods Ecol Evol 11:656–663.
641 https://doi.org/10.1111/2041-210X.13360

642 Farrell LE, Levy DM, Donovan T, Mickey R, Howard A, Vashon J, Freeman M, Royar
643 K, Kilpatrick CW (2018) Landscape connectivity for bobcat (Lynx rufus) and lynx (Lynx
644 canadensis) in the northeastern United States. PLoS ONE 13:e0194243.
645 https://doi.org/10.1371/journal.pone.0194243

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315. https://doi.org/10.1002/joc.5086

Friedman JH (2001) Greedy function approximation: a gradient boosting machine. Ann Stat 29:1189–1232

Gaston KJ (2009) Geographic range limits: achieving synthesis. Proc R Soc B 276:1395–1406. https://doi.org/10.1098/rspb.2008.1480

GBIF.org (2026a) GBIF occurrence download. https://doi.org/10.15468/dl.hkz4bw. Accessed 19 Feb 2026

GBIF.org (2026b) GBIF occurrence download. https://doi.org/10.15468/dl.qn387t. Accessed 21 Feb 2026

GBIF.org (2026c) GBIF occurrence download. https://doi.org/10.15468/dl.vu564q. Accessed 19 Mar 2026

Gooliaff T, Weir RD, Hodges KE (2018) Estimating bobcat and Canada lynx distributions in British Columbia. J Wildl Manag 82:810–820. https://doi.org/10.1002/jwmg.21437

Guéguen M, Blancheteau H, Thuiller W (2025) biomod2: ensemble platform for species distribution modeling. R package version 4.3-4. https://github.com/biomodhub/biomod2

Hastie T, Tibshirani R, Buja A (1994) Flexible discriminant analysis by optimal scoring. J Am Stat Assoc 89:1255–1270

Hijmans RJ (2026) predicts: spatial prediction tools. R package version 0.1-17. https://github.com/rspatial/predicts

668 Hijmans RJ, Bivand R, Forner K, Ooms J, Pebesma E, Sumner MD (2026) terra:
669 spatial data analysis. R package. https://CRAN.R-project.org/package=terra

670 Hirzel AH, Hausser J, Chessel D, Perrin N (2002) Ecological-niche factor analysis:
671 how to compute habitat-suitability maps without absence data? Ecology 83:2027–
672 2036. https://doi.org/10.2307/3071784

673 Hoving CL, Harrison DJ, Krohn WB, Joseph RA, O'Brien M (2005) Broad-scale
674 predictors of Canada lynx occurrence in eastern North America. J Wildl Manag
675 69:739–751. https://doi.org/10.2193/0022-541X(2005)069[0739:BPOCLO]2.0.CO;2

676 iNaturalist (2026) Occurrence data export. https://www.inaturalist.ca. Accessed 18 Mar
677 2026

678 Ivan JS, Hodges KE, Holbrook JD, Moen RA, Olson LE, Squires JR, Vashon JH (2024)
679 Reply to Thornton and Murray: models for Canada lynx conservation planning require
680 nuance. Biol Conserv 299:110836. https://doi.org/10.1016/j.biocon.2024.110836

681 Jiménez-Valverde A, Lobo JM, Hortal J (2008) Not as good as they seem: the
682 importance of concepts in species distribution modelling. Divers Distrib 14:885–890.
683 https://doi.org/10.1111/j.1472-4642.2008.00496.x

684 Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological
685 and spatial data to predict species' ranges. Ecol Lett 12:334–350.
686 https://doi.org/10.1111/j.1461-0248.2008.01277.x

687 Koen EL, Bowman J, Murray DL, Wilson PJ (2014) Climate change reduces genetic
688 diversity of Canada lynx at the trailing range edge. Ecography 37:754–762.
689 https://doi.org/10.1111/j.1600-0587.2013.00629.x

690 Krebs CJ, Boonstra R, Boutin S, Sinclair ARE (2001) What drives the 10-year cycle of
691 snowshoe hares? BioScience 51:25–35. https://doi.org/10.1641/0006-
692 3568(2001)051[0025:WDTYCO]2.0.CO;2

693 Lavoie M, Renard A, Larivière S (2019) Lynx canadensis (Carnivora: Felidae). Mamm
694 Species 51:136–154. https://doi.org/10.1093/mspecies/sez019

695 Legendre P, Legendre LFJ (2012) Numerical ecology, 3rd English edn. Elsevier,
696 Amsterdam

697 Leroy B, Delsol R, Hugueny B, Meynard CN, Barhoumi C, Barbet-Massin M, Bellard
698 C (2018) Without quality presence–absence data, discrimination metrics such as TSS
699 can be misleading measures of model performance. J Biogeogr 45:1994–2002.
700 https://doi.org/10.1111/jbi.13402

701 Litvaitis JA, Johnson B, Jakubas W, Morris K (2015) Distribution and habitat of Canada
702 lynx in the contiguous United States: an update. Cat News 62:32–35

703 Loidi J, Navarro-Sánchez G, Vynokurov D (2022) Climatic definitions of the world's
704 terrestrial biomes. Veg Classif Surv 3:231–271. https://doi.org/10.3897/VCS.86102

705 Malczewski J (2000) On the use of weighted linear combination method in GIS:
706 common and best practice approaches. Trans GIS 4:5–22.
707 https://doi.org/10.1111/1467-9671.00035

708 Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W (2009) Evaluation of
709 consensus methods in predictive species distribution modelling. Divers Distrib 15:59–
710 69. https://doi.org/10.1111/j.1472-4642.2008.00491.x

711

712 Marrotte RR, Bowman J, Morin SJ (2020) Spatial segregation and habitat partitioning
713 of bobcat and Canada lynx. FACETS 5:503–522. https://doi.org/10.1139/facets-2019-
714 0019

715 Martínez-Meyer E, Díaz-Porras D, Peterson AT, Yáñez-Arenas C (2013) Ecological
716 niche structure and rangewide abundance patterns of species. Biol Lett 9:20120637.
717 https://doi.org/10.1098/rsbl.2012.0637

718 McCullagh P, Nelder JA (1989) Generalized linear models, 2nd edn. Chapman &
719 Hall/CRC, London

720 McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model
721 connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724.
722 https://doi.org/10.1890/07-1861.1

723 Meinshausen M, Nicholls ZR, Lewis J et al (2020) The shared socio-economic
724 pathway (SSP) greenhouse gas concentrations and their extensions to 2500. Geosci
725 Model Dev 13:3571–3605. https://doi.org/10.5194/gmd-13-3571-2020

726 Mesgaran MB, Cousens RD, Webber BL (2014) Here be dragons: a tool for quantifying
727 novelty due to covariate range and correlation change when projecting species
728 distribution models. Divers Distrib 20:1147–1159. https://doi.org/10.1111/ddi.12209

729 Morin SJ, Bowman J, Marrotte RR, Fortin M-J (2020) Fine-scale habitat selection by
730 sympatric Canada lynx and bobcat. Ecol Evol 10:9396–9409.
731 https://doi.org/10.1002/ece3.6626

732 Müller WA, Jungclaus JH, Mauritsen T et al (2018) A higher-resolution version of the
733 Max Planck Institute Earth System Model (MPI-ESM1.2-HR). J Adv Model Earth Syst
734 10:1383–1413. https://doi.org/10.1029/2017MS001217

735 Murray DL, Boutin S (1991) The influence of snow on lynx and coyote movements:
736 does morphology affect behavior? Oecologia 88:463–469.
737 https://doi.org/10.1007/BF00317707

738 Naimi B, Hamm NA, Groen TA, Skidmore AK, Toxopeus AG (2014) Where is positional
739 uncertainty a problem for species distribution modelling? Ecography 37:191–203.
740 https://doi.org/10.1111/j.1600-0587.2013.00205.x

741 Nakamoto BJ, Forbes G, Bursey C, Cormier J, O'Sullivan A, Hayden B (2024) Niche
742 partitioning of bobcat and Canada lynx near their distribution contact zone. FACETS
743 9:1–11. https://doi.org/10.1139/facets-2023-0023

744 Olson LE, Bjornlie N, Hanvey G, Holbrook JD, Ivan JS, Jackson S, Kertson B, King T,
745 Lucid M, Murray D, Naney R, Rohrer J, Scully A, Thornton D, Walker Z, Squires JR
746 (2021) Improved prediction of Canada lynx distribution through regional model
747 transferability and data efficiency. Ecol Evol 11:1667–1690.
748 https://doi.org/10.1002/ece3.7157

749 Owens HL, Campbell LP, Dornak LL, Saupe EE, Barve N, Soberón J, Ingenloff K, Lira-
750 Noriega A, Hensz CM, Myers CE, Peterson AT (2013) Constraints on interpretation of
751 ecological niche models by limited environmental ranges on calibration areas. Ecol
752 Model 263:10–18. https://doi.org/10.1016/j.ecolmodel.2013.04.011

753 Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the
754 distribution of species: are bioclimate envelope models useful? Glob Ecol Biogeogr
755 12:361–371. https://doi.org/10.1046/j.1466-822X.2003.00042.x

756 Peers MJL, Thornton DH, Murray DL (2013) Evidence for large-scale effects of
757 competition: niche displacement in Canada lynx and bobcat. Proc R Soc B
758 280:20132495. https://doi.org/10.1098/rspb.2013.2495

759 Peers MJL, Wehtje M, Thornton DH, Murray DL (2014) Prey switching as a means of
760 enhancing persistence in predators at the trailing southern edge. Glob Chang Biol
761 20:1126–1135. https://doi.org/10.1111/gcb.12403

762 Phillips SJ, Anderson RP, Dudík M, Schapire RE, Blair ME (2017) Opening the black
763 box: an open-source release of Maxent. Ecography 40:887–893.
764 https://doi.org/10.1111/ecog.03049

765 Pinilla-Buitrago GE, Osorio-Olvera L (2026) fastbioclim: an R package for creating
766 custom-time bioclimatic and derived environmental summary variables. Methods Ecol
767 Evol 00:1–10. https://doi.org/10.1111/2041-210x.70291

768 Popescu VD, Kenyon M, Brown RK, Dyck MA, Prange S, Peterman WE, Dennison C
769 (2021) Habitat connectivity and resource selection in an expanding bobcat (Lynx rufus)
770 population. PeerJ 9:e12460. https://doi.org/10.7717/peerj.12460

771 Prentice MB, Bowman J, Murray DL, Khidas K, Wilson PJ (2020) Spatial and
772 environmental influences on selection in a clock gene coding trinucleotide repeat in
773 Canada lynx (Lynx canadensis). Mol Ecol 29:4637–4652.
774 https://doi.org/10.1111/mec.15652

775 Roberts NM, Crimmins SM (2010) Bobcat population status and management in North
776 America: evidence of large-scale population increase. J Fish Wildl Manag 1:169–174.
777 https://doi.org/10.3996/122009-JFWM-026

778

779 Roemer GW, Gompper ME, Van Valkenburgh B (2009) The ecological role of the
780 mammalian mesocarnivore. BioScience 59:165–173.
781 https://doi.org/10.1525/bio.2009.59.2.9

782 Schoener TW (1968) The Anolis lizards of Bimini: resource partitioning in a complex
783 fauna. Ecology 49:704–726. https://doi.org/10.2307/1935534

784 Scully AE, Fisher S, Miller DA, Thornton DH (2018) Influence of biotic interactions on
785 the distribution of Canada lynx (Lynx canadensis) at the southern edge of their range.
786 J Mammal 99:760–772. https://doi.org/10.1093/jmammal/gyy053

787 Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and ecology of species
788 range limits. Annu Rev Ecol Evol Syst 40:415–436.
789 https://doi.org/10.1146/annurev.ecolsys.110308.120317

790 Shelford VE (1931) Some concepts of bioecology. Ecology 12:455–467.
791 https://doi.org/10.2307/1928991

792 Sillero N, Arenas-Castro S, Enriquez-Urzelai U, Vale CG, Sousa-Guedes D, Martínez-
793 Freiría F, Real R, Barbosa A (2021) Want to model a species niche? A step-by-step
794 guideline on correlative ecological niche modelling. Ecol Model 456:109671.
795 https://doi.org/10.1016/j.ecolmodel.2021.109671

796 Singh S, Thornton D, Welfelt L (2025) Temperature driven density gradients of two
797 congeneric felids reveal contrasting responses to climate change at a range margin.
798 Sci Rep 15:45498. https://doi.org/10.1038/s41598-025-29375-7

799 Sirén AP, Morelli TL (2020) Interactive range-limit theory (iRLT): an extension for
800 predicting range shifts. J Anim Ecol 89:940–954. https://doi.org/10.1111/1365-
801 2656.13150

802 Sirén AP, Sutherland CS, Karmalkar AV, Duveneck MJ, Morelli TL (2022) Forecasting
803 species distributions: correlation does not equal causation. Divers Distrib 28:756–769.
804 https://doi.org/10.1111/ddi.13480

805 Smith AB, Murphy SJ, Henderson D, Erickson KD (2023) Including imprecisely
806 georeferenced specimens improves accuracy of species distribution models and
807 estimates of niche breadth. Glob Ecol Biogeogr 32:342–355.
808 https://doi.org/10.1111/geb.13628

809 Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of
810 species. Ecol Lett 10:1115–1123. https://doi.org/10.1111/j.1461-0248.2007.01107.x

811 Stenseth NC, Falck W, Bjørnstad ON, Krebs CJ (1997) Population regulation in
812 snowshoe hare and Canadian lynx: asymmetric food web configurations between hare
813 and lynx. Proc Natl Acad Sci USA 94:5147–5152.
814 https://doi.org/10.1073/pnas.94.10.5147

815 Sunquist M, Sunquist F (2002) Wild cats of the world. University of Chicago Press,
816 Chicago

817 Squires JR, DeCesare NJ, Olson LE, Kolbe JA, Hebblewhite M, Parks SA (2013)
818 Combining resource selection and movement behavior to predict corridors for Canada
819 lynx at their southern range periphery. Biol Conserv 157:187–195.
820 https://doi.org/10.1016/j.biocon.2012.07.018

821 Szumski CM, Roth JD, Murray DL (2023) Canada lynx foraging strategies: facultative
822 specialists become obligate generalists toward the distribution edge. Ecosphere
823 14:e4629. https://doi.org/10.1002/ecs2.4629

824 Tattersall ER, Burgar JM, Fisher JT, Burton AC (2020) Boreal predator co-occurrences
825 reveal shared use of seismic lines in a working landscape. Ecol Evol 10:1678–1691.
826 https://doi.org/10.1002/ece3.6028

827 Tebaldi C, Debeire K, Eyring V et al (2021) Climate model projections from the
828 Scenario Model Intercomparison Project (ScenarioMIP) of CMIP6. Earth Syst Dyn
829 12:253–293. https://doi.org/10.5194/esd-12-253-2021

830 Thornton DH, Murray DL (2024) Modeling range dynamics through time to inform
831 conservation planning: Canada lynx in the contiguous United States. Biol Conserv
832 292:110541. https://doi.org/10.1016/j.biocon.2024.110541

833 Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD: a platform for
834 ensemble forecasting of species distributions. Ecography 32:369–373.
835 https://doi.org/10.1111/j.1600-0587.2008.05742.x

836 Title PO, Bemmels JB (2018) Envirem: an expanded set of bioclimatic and topographic
837 variables increases flexibility and improves performance of ecological niche modeling.
838 Ecography 41:291–307. https://doi.org/10.1111/ecog.02880

839 U.S. Fish and Wildlife Service (n.d.) Northwest boreal forest lynx project.
840 https://www.fws.gov/project/northwest-boreal-forest-lynx-project

841 USFWS (2023) Species status assessment addendum for the Canada lynx (Lynx
842 canadensis) contiguous United States distinct population segment. U.S. Fish and
843 Wildlife Service, Lakewood

844 Vanbianchi C, Gaines WL, Murphy MA, Pither J, Hodges KE (2017) Habitat selection
845 by Canada lynx: making do in heavily fragmented landscapes. Biodivers Conserv
846 26:3343–3361. https://doi.org/10.1007/s10531-017-1409-4

847 Velazco SJE, Rose MB, De Marco P Jr, Regan HM, Franklin J (2024) How far can I
848 extrapolate my species distribution model? Exploring Shape, a novel method.
849 Ecography 2024:e06992. https://doi.org/10.1111/ecog.06992

von Liebig J (1840) Die organische Chemie in ihrer Anwendung auf Agricultur und Physiologie. Friedrich Vieweg und Sohn, Braunschweig

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x

Whittington J, Heuer K, Hunt B, Hebblewhite M, Lukacs PM (2015) Estimating occupancy using spatially and temporally replicated snow surveys. Anim Conserv 18:92–101. https://doi.org/10.1111/acv.12140

Wickham H (2016) ggplot2: elegant graphics for data analysis, 2nd edn. Springer, New York

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Davies TJ, Grytnes J-A, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010) Niche conservatism as an emerging principle in ecology and conservation biology. Ecol Lett 13:1310–1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x

Wilke CO (2026) ggridges: ridgeline plots in ggplot2. R package version 0.5.6. https://CRAN.R-project.org/package=ggridges

Yáñez-Arenas C, Martínez-Meyer E, Mandujano S, Rojas-Soto O (2012) Modelling geographic patterns of population density of the white-tailed deer in central Mexico by implementing ecological niche theory. Oikos 121:2081–2089. https://doi.org/10.1111/j.1600-0706.2012.20350.x

Yukimoto S, Kawai H, Koshiro T, Oshima N, Yoshida K, Urakawa S, Tsujino H, Deushi M, Tanaka T, Hosaka M, Yabu S, Yoshimura H, Shindo E, Mizuta R, Obata A, Adachi Y, Ishii M (2019) The Meteorological Research Institute Earth System Model version

873 2.0, MRI-ESM2.0: description and basic evaluation of the physical component. J
874 Meteorol Soc Jpn 97:931–965. https://doi.org/10.2151/jmsj.2019-051

875

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryMaterial1.zip
- SupplementaryMaterial2.pdf
- SupplementaryMaterial3.pdf