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Environmental Drivers of Geographic Isolation in Three Pika Species in Northeast Asia

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ABSTRACT

Geographic segregation among closely related species may arise from divergent environmental preferences or constraints of interspecific interactions. For these three congeneric pika species in northeastern Asia, the relative contributions of these mechanisms remain poorly understood. This study investigates three congeneric species: *Ochotona coreana*, *Ochotona mantchurica*, and *Ochotona hyperborea*, to identify how environmental gradients and interspecific niche relationships jointly shape their spatial segregation. We combined public records with field survey to build species distribution models and reduced sampling bias through regional mammal density to optimize environmental variables and background points. We quantified each species' potential distribution, identified key environmental drivers, and evaluated ecological niche overlap to assess whether isolation reflects potential competition or habitat divergence. The three species showed distinct distribution patterns and environmental associations. *O. coreana* had the smallest potential range, restricted to high-elevation forests and tundra of the Changbai Mountains in China and DPR Korea. *O. hyperborea* ranged from northeastern China to the Russian Far East, with suitability driven by precipitation seasonality, isothermality, and forest composition. *O. mantchurica* distribution across Hulunbuir and eastern Mongolian grasslands mainly associated with precipitation seasonality and slope. Niche overlap was high between *O. mantchurica* and *O. hyperborea*, but low for *O. coreana* and the other species. Limited sympatry between the two wide-ranging species suggests potential niche segregation. The three species are isolated by distinct environmental drivers and potential competitive interactions. Our findings clarify the environmental and ecological drivers shaping species boundaries in these closely related pika species and provide a framework for evaluating distributional dynamics in data-limited small mammals.

1 | Introduction

Geographic isolation is an ecological phenomenon that influences species distribution, genetic structure, and evolutionary trajectories (Wang and Bradburd 2014). It occurs when physical barriers, such as rivers, mountains, or oceans, separate populations of the same or closely related species, thereby impeding gene flow (Etherington 2015). Such isolated fragments form discon-

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tinuous habitats, preventing interbreeding between segregated populations and restricting genetic exchange. Consequently, geographic isolation limits species dispersal and expansion into disconnected but suitable habitats, ultimately shaping patterns of diversification and speciation (Hellberg 2009). In contrast, spatial segregation can also arise without absolute physical barriers, driven either by environmental filtering across divergent habitats or by biotic interactions like potential competition (Danielson 1992; Pizzolotto 2009).

Pikas (genus *Ochotona*) are small alpine and steppe-dwelling lagomorph that have adapted to cold, high-elevation, and high-latitude environments. They play a vital role in maintaining the structure and function of alpine and grassland ecosystems (Gliwicz et al. 2006). The distribution patterns, ecological adaptations, and responses to climate change of these alpine specialists are generally well understood, driven by numerous drivers of isolation. For instance, for *Ochotona curzoniae* on the Qinghai–Tibetan Plateau, topographic barriers are the key drivers of geographic isolation (Song et al. 2025). Alternatively, for six pika species across the Himalayas, habitat variation is related to ecological niche differentiation (Dahal et al. 2023). Similarly, glacial oscillations and geographic barriers played pivotal roles in the divergence of three North American pika subspecies (Klingler et al. 2021), providing further evidence for the influence of geological processes on population genetic structure.

Despite these insights, the exact drivers of spatial segregation among these three pika species in northeastern Asia remain poorly understood. Three closely related pika species in this region: the Northern pika (*Ochotona hyperborea*), which exhibits the widest distribution, the Manchurian pika (*Ochotona mantchurica*), which has a much smaller range, and the Korean pika (*Ochotona coreana*), which occupies the smallest range. *O. hyperborea* and *O. mantchurica* occur in adjacent regions along the border between northeastern China and eastern Mongolia, where their distribution boundary is delineated by the Amur River (Lissovsky et al. 2008). Further south, the mountains north of the Changbai Mountain range separate *O. hyperborea* and *O. coreana*. However, it remains unclear whether this segregation is driven by physical barriers, environmental divergence, or competition.

This study focuses on the patterns and driving mechanisms of geographical isolation among *O. coreana*, *O. mantchurica*, and *O. hyperborea* in northeastern Asia, building on the solid background generated by Lissovsky et al. (2024) for some of our focal species. Using species distribution models (SDMs), we predicted the suitable habitats for the three focal species, and by combining differentiated ecological niche, we aimed to provide an explanation as to why realized niches do not overlap with suitable habitat. We hypothesize that patterns of niche overlap may reflect environmental filtering, but acknowledge that alternative mechanisms, such as historical constraints, dispersal limitation, and geographic barriers, cannot be distinguished with the current data. Through this comparative biogeographic interpretation, the methodological framework developed here can be applied to other small mammal species with narrow distributions and high sensitivity to climate change.

2 | Material and Methods

2.1 | Study Area and Focal Species

The study area extends from 30°N to 80°N and 50°E to 180°E, encompassing a total area of approximately 29 million km^2. It covers the central and northeastern regions of Asia, including China, Mongolia, central and Far Eastern Russia, the Korean Peninsula, and northern Japan. This region encompasses the ranges of the three focal pika species: *O. coreana*, *O. mantchurica*, and *O. hyperborea* (Figure 1). We defined this unified extent to fully encompass the IUCN ranges of all three species and provide a standardized baseline for our comparative niche analyses, rather than defining species-specific areas (Figure 2).

The taxonomic history of the widespread *O. hyperborea* dates back more than two centuries (Gusev and Tiunov 2023), reflecting the gradual refinement of scientific understanding of East Asian pika lineages. *O. coreana* was originally described as a distinct species by Allen and Andrews (1913) but was later treated as a synonym of *O. hyperborea*. Similarly, *O. mantchurica* was first designated as a subspecies of *O. hyperborea* by Thomas (1909), until Lissovsky et al. (2008) elevated it to full species rank based on morphological and genetic evidence. Since the formal recognition of *O. mantchurica* as an independent species (Lissovsky et al. 2008), most studies have accepted the three taxa as distinct species (Lissovsky 2014; Zhao et al. 2020). Nevertheless, existing research has largely focused on single-species characteristics, including the cytogenetics of *O. hyperborea* (Lissovsky et al. 2021), morphological differentiation in *O. mantchurica* (Lissovsky 2015), and mitochondrial genome analyses of *O. coreana* (Zhang et al. 2021). Knowledge about the mechanisms of geographic isolation among the three species remains limited.

2.2 | Occurrence and Environmental Data

2.2.1 | Occurrence Data

Occurrence records for the three pika species were obtained from both field surveys and public available datasets. Public data sources included digitized occurrence points extracted from published distribution maps (Formozov and Baklushinskaya 2011; Korolev 2018; Lissovsky 2015; Lissovsky et al. 2008; Popova et al. 2022; Rybakova et al. 2003; Zhang 2021). To minimize uncertainty from map-derived localities, these maps were carefully georeferenced using GIS, and all records were subsequently standardized into a unified format (species name, longitude, and latitude) under a consistent WGS 1984 coordinate system. To compensate for the limited online records of *O. coreana*, additional field surveys were conducted in and around the Changbai Mountain area in Jilin Province, China. These surveys were carried out by reserve staff along fixed transects to record direct sightings, vocalizations, and indirect signs. The presence of the species was primarily confirmed through direct sightings and diagnostic vocalizations, supported by indirect evidence such as distinct pellet morphology and characteristic rock-dwelling signs. This identification was further strengthened by the absence of any other sympatric pika species in the region. In total, 700

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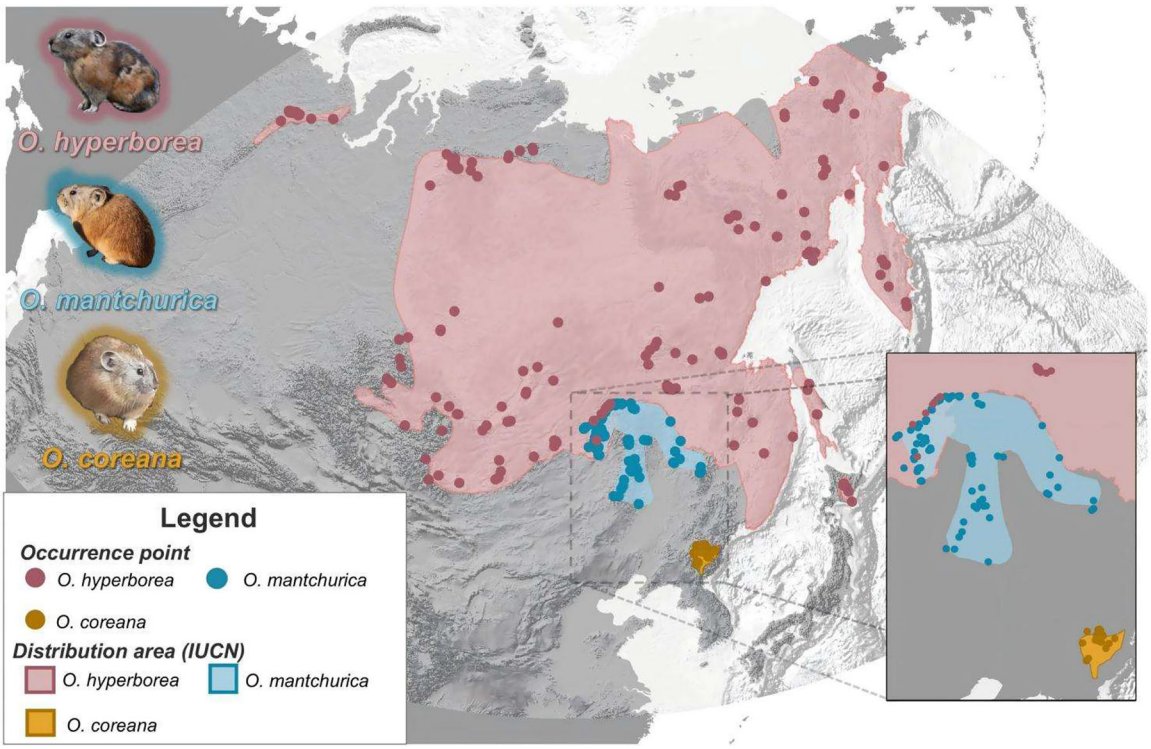


FIGURE 1 | Distribution of the three focal pika species. Colors represent *O. hyperborea* (red), *O. mantchurica* (blue), and *O. coreana* (orange). Range maps originating from IUCN Red List update (Smith and Lissovsky 2016a, 2016b; Smith and Jo 2016). Additionally, species photos from GBIF (Table S1). This map was generated using ArcMap 10.8.

occurrence records were compiled for the three pika species, including 48 records for *O. coreana*, 35 for *O. mantchurica*, and 617 for *O. hyperborea*. The data records adopted are primarily from 2010 to 2020, as this time range matches the research data.

2.2.2 | Environmental Data and Process

The environmental variables used in this study encompassed four major categories: terrain, climate, natural, and anthropogenic factors. The terrain factors included elevation, slope, and aspect. Elevation data were obtained from the SRTM elevation dataset (Jarvis et al. 2008), while slope and aspect were derived from the elevation data using ArcMap 10.5. Aspect values were subsequently reclassified into five categories: level areas (−1° to 0°), north-facing (315°–360° and 0°–45°), east-facing (45°–135°), south-facing (135°–225°), and west-facing slopes (225°–315°). Climate factors consisted of 19 bioclimatic parameters (Bio1–Bio19) sourced from the WorldClim database (https://www.worldclim.org/) with a spatial resolution of 30 arc seconds, representing long-term temperature and precipitation characteristics. Natural factors included vegetation type, Temperature Vegetation Dryness Index (TDVI), soil carbon density, soil depth, distance to rivers, distance to representative water bodies, and mammal richness. Vegetation data were derived from the GLC_FCS30 Global Land-Cover 30 m dataset and reclassified into nine vegetation categories: (1) evergreen broadleaf forest, (2) deciduous broadleaf forest, (3) evergreen coniferous forest, (4) deciduous coniferous forest, (5) mixed forest, (6) shrubland, (7) grassland, (8) moss and lichen tundra, and (9) unvegetated areas. TDVI and soil carbon density data were obtained from the National Earth System Science Data Center (https://www.geodata.cn/data/), whereas soil depth data were extracted from the Harmonized World Soil Database (HWSD) (https://www.fao.org/). The distances to rivers and to representative water bodies were calculated using the Euclidean Distance tool in ArcMap 10.8 based on hydrographic data from OpenStreetMap (OSM), with the distance to lakes measured from the closest bank of the lake. Additionally, the mammal richness layer was derived by overlapping the geographic range maps of terrestrial mammals sourced from the IUCN Red List. This specific layer was incorporated into the models as a broad biodiversity and habitat productivity proxy. Anthropogenic factors included distance to cropland, distance to construction, and population density. Distance layers were derived from the cropland and construction land categories of the GLC_FCS30 dataset and computed using the Euclidean Distance tool in ArcMap. Population density data were obtained from the WorldPop database (https://www.worldpop.org/) with a spatial resolution of 1 km. To ensure spatial consistency across datasets, all environmental variables were resampled to a uniform resolution of 1 km and projected to the WGS 1984 coordinate system, which is intended to capture macro-scale biogeographic patterns rather than fine-scale microhabitats.

2.3 | Model Preparation

2.3.1 | Occurrence Data Thinning and Background Point Selection

To minimize spatial clustering effects in model predictions, all occurrence records were spatially filtered using the R package

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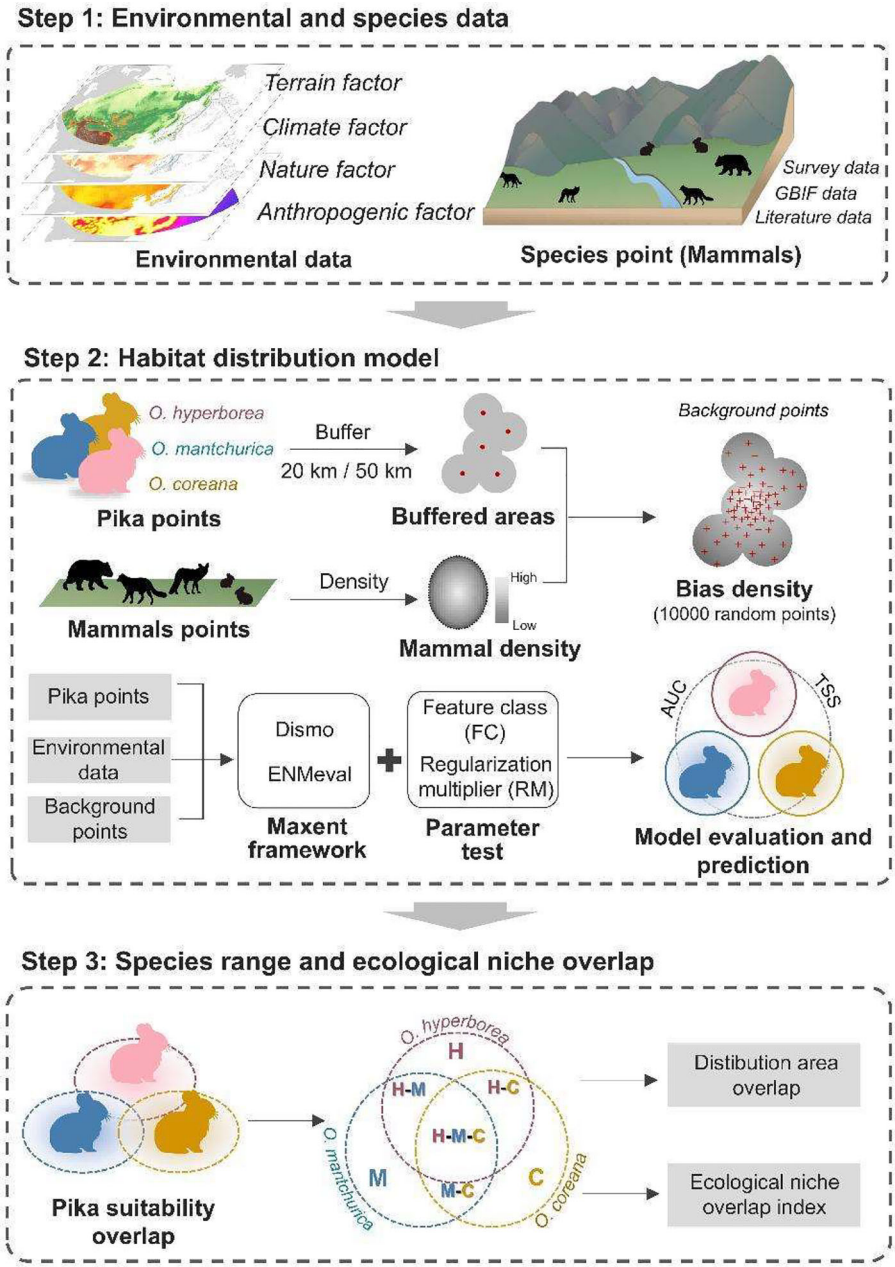


FIGURE 2 | Workflow of the habitat suitability modeling and niche overlap analysis for the three focal pika species. The figure illustrates the process of data collection, model construction, and niche overlap analysis.

spThin, with a minimum nearest-neighbor distance threshold of 1 km (Brown 2014). For background point selection, we adopted a differentiated strategy based on the potential dispersal capacity of each species. First, species-specific buffer zones were constructed based on overall range size to represent the biologically accessible area for each taxon. Since field-derived dispersal rates are largely unavailable for these species, range size serves as a biogeographical proxy for biologically accessible areas, consistent with the BAM framework (Barve et al. 2011; Anderson and Raza 2010). A 50-km radius buffer was applied to the wide-ranging *O. hyperborea* to reflect the broader regional landscape it occupies. In contrast, 20-km radius buffers were used for the more range-restricted *O. coreana* and *O. mantchurica* to ensure the background captures the complete local altitudinal gradient while preventing the inclusion of irrelevant, distant macroclimates (Lobo et al. 2008). These species-specific buffers were chosen to approximate the IUCN range for each taxon and to avoid inflating the background environmental space in subsequent modeling. Second, within each buffer zone, mammalian density raster layers were generated using the megaSDM package in R. These rasters were derived from mammalian occurrence records obtained from the Global Biodiversity Information Facility (GBIF; https://doi.org/10.15468/dl.udyjjs; https://doi.org/10.15468/dl.jarjea; and https://doi.org/10.15468/dl.kuk82z) within each pika species' buffer area and were used to represent the relative density of mammal records. Finally, the mammal density rasters within each buffer zone were converted into probability surfaces for background point generation. Weighted random sampling was then conducted using the MASS package in R to extract 10 000 background points from these probability surfaces.

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This approach ensured that the spatial distribution of background points corresponded to the spatial heterogeneity of the target region, mitigating the sampling bias that arises from uneven research efforts across countries and the inaccessibility of remote pika habitat to enhance model robustness (Brown 2014; Syfert et al. 2013).

2.3.2 | Environmental Data Selection

To select environmental variables for constructing the habitat suitability models of the three pika species, we employed a systematic procedure designed to balance model complexity with ecological interpretability. First, a default model was built to eliminate variables with low contributions and high collinearity. Using the ENMeval package (Muscarella et al. 2017) in R, we initially constructed species-specific default models for each of the three pikas. Variables with a percentage contribution ≤1% were removed to exclude predictors with minimal influence on model performance. Subsequently, highly correlated variables were excluded based on Spearman's correlation coefficient ($|r| > 0.8$) to reduce redundancy and multicollinearity effects among predictors. Second, based on the preliminary screening, additional ecological considerations were incorporated to retain key environmental variables that are known to exert strong constraints on each species' distribution. For example, the Korean pika (*O. coreana*), which primarily inhabits the Changbai Mountain region, is highly sensitive to fine-scale microhabitat conditions. Therefore, the variable "Distance to representative water bodies" was retained to constrain the model's prediction of high-suitability areas within the core range of the Changbai Mountain.

2.3.3 | Model Parameter Testing and Selection

For parameter optimization, we employed a random 10-fold cross-validation approach to systematically evaluate model performance across 72 parameter combinations, derived from six feature classes (L, Q, H, LQ, LQH, and LQHP) and 12 regularization multiplier values ranging from 0.5 to 6.0 at 0.5 intervals. A sequential selection strategy was used to assess and compare model performance metrics. Parameter sets yielding the lowest AUCDIFF or the lowest 10% training omission rate were retained as candidate models. Among these candidates, we selected the final optimal parameter combinations for each pika species based on two criteria: (1) broad consistency with known distribution patterns, using IUCN maps only as a coarse reference. Overlap was informative for *O. hyperborea*, where the IUCN range is relatively reliable, but was treated cautiously for *O. coreana* and *O. mantchurica* due to greater uncertainty in their mapped ranges; and (2) a model performance threshold of AUC > 0.6. These selections were applied consistently across all three species. For each species, we identified the variable set that satisfied both criteria as its optimal model configuration. Based on the optimized models, we further calculated the potential habitat overlap indices among the three species. All model construction, parameter testing, and optimization procedures were implemented in R using the ENMeval package (Kass et al. 2021; Phillips et al. 2017).

2.4 | Habitat Suitability and Processing

Based on the optimal parameter combinations for each species, habitat suitability models for the three species were run using the MaxEnt algorithm implemented in the dismo package (4.5.1) in R (Hijmans et al. 2017). Model predictions were compared with the existing IUCN distribution ranges of each species to evaluate the spatial predictive accuracy. To classify habitat suitability, we applied the maximum test sensitivity plus specificity threshold to the continuous MaxEnt outputs. Areas with predicted suitability values below the threshold were classified as unsuitable habitats, while areas with values equal to or above the threshold were identified as suitable habitats. This thresholding method ensured an objective delineation of suitable areas and allowed for consistent comparison among species.

2.5 | Overlap Analyses

Ecological niche overlaps among the three pika species reflect their potential geographic isolation and potential interspecific competition. To evaluate the degree of habitat overlap between species pairs, we conducted pairwise comparisons of their modeled ecological niches, using Schoener's D and Hellinger's I as indices of quantitative measures of niche overlap. Schoener's D index assesses the similarity in suitable habitat across environmental space, reflecting the extent of environmental niche overlap, while Hellinger's I index, derived from Hellinger distance, quantifies the similarity between normalized probability distributions. All niche overlap analyses were performed using the corresponding functions in the ENMeval package in R (Kass et al. 2021).

3 | Results

3.1 | Species Distribution Model of pikas

Model accuracy evaluation indicated varying levels of discriminatory performance among the three pika species (AUC > 0.6; TSS ranging from 0.50 to 0.75). Specifically, the models achieved the following metrics: *O. coreana* (AUC = 0.615, TSS = 0.745), *O. mantchurica* (AUC = 0.616, TSS = 0.66), and *O. hyperborea* (AUC = 0.766, TSS = 0.498).

Analysis of environmental variable importance revealed both similarities and differences in the ecological requirements of the three species (Table 1). Climatic factors and anthropogenic disturbance variables were critical for all species, whereas the importance of soil-related and topographic factors varied among them. Precipitation seasonality (Bio15) and distance to cropland contributed substantially to the models for all three pikas, accounting for 9.1%–19.2% and 6.3%–16.1% of model contributions, respectively. Variables with high contributions shared by *O. hyperborea* and *O. mantchurica* included slope, isothermality (Bio3), and distance to construction land, contributing 10.1%–12.2%, 6.1%–14%, and 3.6%–14.4%, respectively. Vegetation type was a shared influential variable for *O. hyperborea* and *O. coreana*, contributing 5.1%–25.6%. Fewer common variables were

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TABLE 1 | Environmental variables and their percentage contributions to the pika distribution models. The percentage contribution of environmental variables greater than 3% is marked in bold and with an asterisk (*).

Environmental variables	Environmental variables percentage contribution (%)		
	O. hyperborea	*O. mantchurica*	*O. coreana*
Altitude	**5.4%***	——	——
Aspect	0.4%	**17.7%***	——
Slope	**10.1%***	**12.2%***	0%
Bio1	**6.6%***	0.5%	——
Bio2	——	——	0%
Bio3	14%	6.1%	0.2%
Bio5	5.7%	——	——
Bio6	0.9%	——	——
Bio12	0.2%	——	0%
Bio13	0.8%	——	——
Bio15	**18.5%***	**19.2%***	**9.1%***
Bio17	——	——	**42.3%***
Vegetation	**5.1%***	——	**25.6%***
TDVI	——	**4.7%***	——
Soil carbon density	——	**8.7%***	0%
Mammal richness	**20.2%***	0.4%	——
Soil depth	2.3%	——	**3%***
Distance to representative water bodies	——	——	**6.2%***
Distance to cropland	**6.3%***	**16.1%***	**11.3%***
Distance to construction	**3.6%***	**14.4%***	——

identified between *O. coreana* and *O. mantchurica*; aside from the highly contributing precipitation seasonality and distance to cropland, only mean diurnal temperature range overlapped as an influential variable.

Further analysis showed distinct response patterns among the three pika species to the key environmental variables highlighted above. For precipitation seasonality (Bio15), habitat suitability for *O. hyperborea* and *O. mantchurica* decreased with increasing seasonality, with suitability values > 0.8 corresponding approximately to Bio15 values <40 and <100. In contrast, suitability for *O. coreana* increased with precipitation seasonality, and high-suitability areas (> 0.8) associated with Bio15 values > 105. Regarding distance to cropland, habitat suitability for *O. hyperborea* and *O. mantchurica* increased with greater distance, with high-suitability thresholds approximately > 50 and > 85 km, respectively. Conversely, *O. coreana* exhibited higher suitability in closer proximity to croplands, with most high-suitability areas located near agricultural lands (Figure 3).

3.2 | Pika Habitat and Ecological Niche Overlap

Spatially, the high-suitability habitat for *O. coreana* was highly concentrated in the border region between China and DPR Korea, primarily encompassing the main peak of the Changbai Mountains and the surrounding alpine tundra zone, forming a distinct core area. The suitable habitat for *O. mantchurica* was mainly distributed in the southern part of the Heilongjiang River basin, including the Greater and Lesser Khingan Mountains and the Songnen Plain, characterized by relatively contiguous yet internally patchy distribution. Small areas of suitable habitat are also found in adjacent regions of Mongolia, although these are very limited in extent. In contrast, the suitable habitat for *O. hyperborea* was widespread across the plains and low hill regions of the study area, representing the most extensive coverage. The areas of highest habitat suitability for *O. hyperborea* were primarily located in the North Siberian Lowland, the Kolyma Lowland, the Lena River Basin, and the Ural Mountains region, in Russia (Figure 4).

The total predicted suitable area for each species was estimated as follows: *O. coreana*, 5.5 million km^2; *O. mantchurica*, 15 million km^2; and *O. hyperborea*, 8.2 million km^2. It is important to note that these values represent the predicted potential suitable area from the MaxEnt model, which estimates the fundamental niche rather than the realized distribution (Elith and Leathwick 2009; Peterson et al. 2011). Although the predicted suitable area for *O. mantchurica* (15 million km^2) exceeded that of *O. hyperborea* (8.2 million km^2), this reflects its more contiguous grassland habitat in environmental space rather than a broader actual geographic range. The actual distribution of *O. hyperborea* spans

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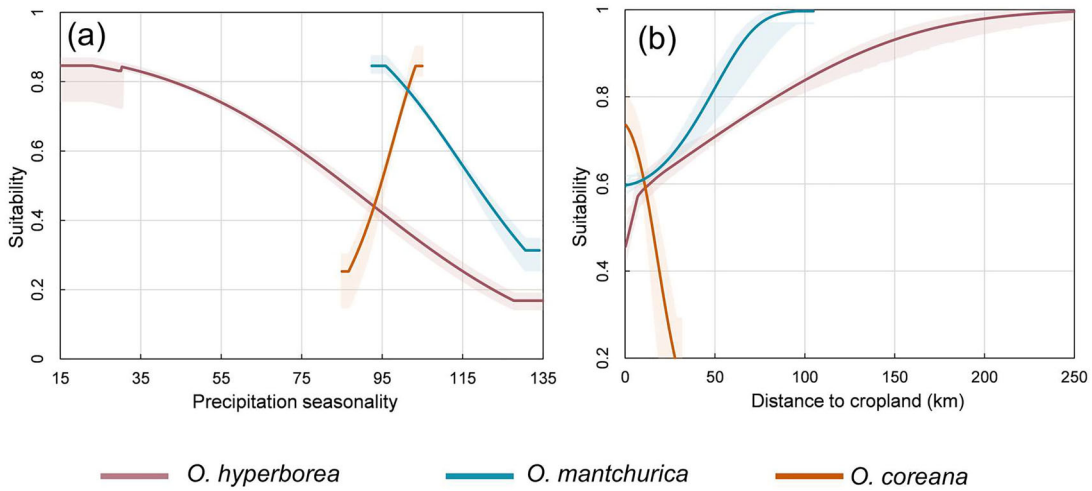


FIGURE 3 | Shared and highly influential environmental variables for the three focal pika species. This figure highlights the response curves of three species of pikas to two environmental variables: (a) Bio15 (precipitation seasonality) and (b) distance to cropland.

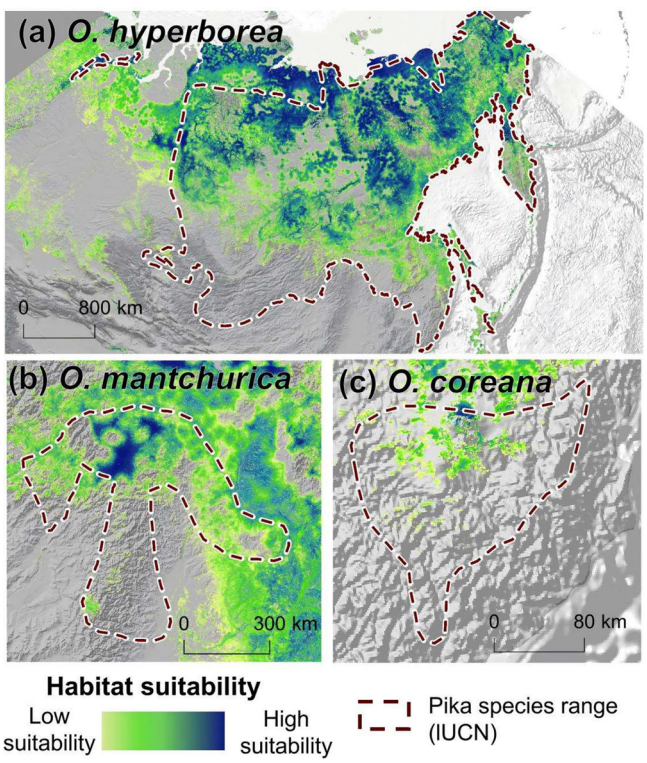


FIGURE 4 | Habitat suitability predictions for the three pika species. The color gradient represents suitability levels from low (light green) to high (dark blue), and red dashed lines indicate the current IUCN ranges for geographical comparison. (a) *O. hyperborea*; (b) *O. mantchurica*; (c) *O. coreana*. This figure was drawn using ArcMap 10.8 software.

a far larger latitudinal and longitudinal extent across Siberia and the Russian Far East (Lissovsky et al. 2008). Distributional and niche overlap analyses revealed pronounced niche differentiation among the three pika species. *O. hyperborea* and *O. mantchurica* exhibited the highest niche similarity, whereas *O. hyperborea* and *O. coreana* showed the lowest. The niche overlap indices were quantified as follows: Schoener's $D = 0.39$ and Hellinger's $I = 0.73$ for *O. mantchurica* versus *O. coreana*; $D = 0.29$ and $I = 0.62$ for *O. coreana* versus *O. hyperborea*; and $D = 0.74$ and $I = 0.94$ for *O. mantchurica* versus *O. hyperborea* (Figure 5).

Spatial overlay characteristics further elucidated these relationships. The overlap between *O. hyperborea* and *O. mantchurica* (H–M; Figure 5) was widespread across northeastern Asia, with substantial overlap, particularly observed east of the Stanovoy Range and Lake Baikal, primarily within the temperate mixed coniferous-broadleaf forest zone. This pattern indicates high niche similarity and suggests potential niche differentiation. In contrast, the overlap between *O. hyperborea* and *O. coreana* (H–C; Figure 5) was confined to northern parts of the Korean Peninsula and the eastern mountainous regions of Jilin Province. The overlap between *O. mantchurica* and *O. coreana* (M–C; Figure 5) was evident in the northern Korean Peninsula, the Changbai Mountains, and their extensions. This zone, characterized by both coniferous forests and mountain tundra, constitutes a niche ecotone. The moderate overlap amplitude, especially in the Changbai Mountains–northern Peninsula area, shows lower overlap amplitude compared to the H–M pair. Spatially, the overlap area between *O. hyperborea* and *O. mantchurica* was the largest among the three pairwise comparisons, extending across northeastern Asia. The overlap between *O. coreana* and the other two species was confined to the northern Korean Peninsula and Changbai Mountains. Collectively, these patterns demonstrate a spatial succession gradient from north to south, with localized overlap occurring primarily in marginal zones (Figure 5).

4 | Discussion

This study presents the first macro-scale assessment in Northeast Asia that simultaneously delineates the potential habitats of the pika species *O. coreana*, *O. mantchurica*, and *O. hyperborea* and quantifies their ecological niche overlaps. Our results for *O. mantchurica* and *O. hyperborea* align with the literature in terms of suitable habitat (Lissovsky et al. 2024) and match existing evidence that both species are typically associated with temperate mixed forests and alpine tundra zones (Lissovsky

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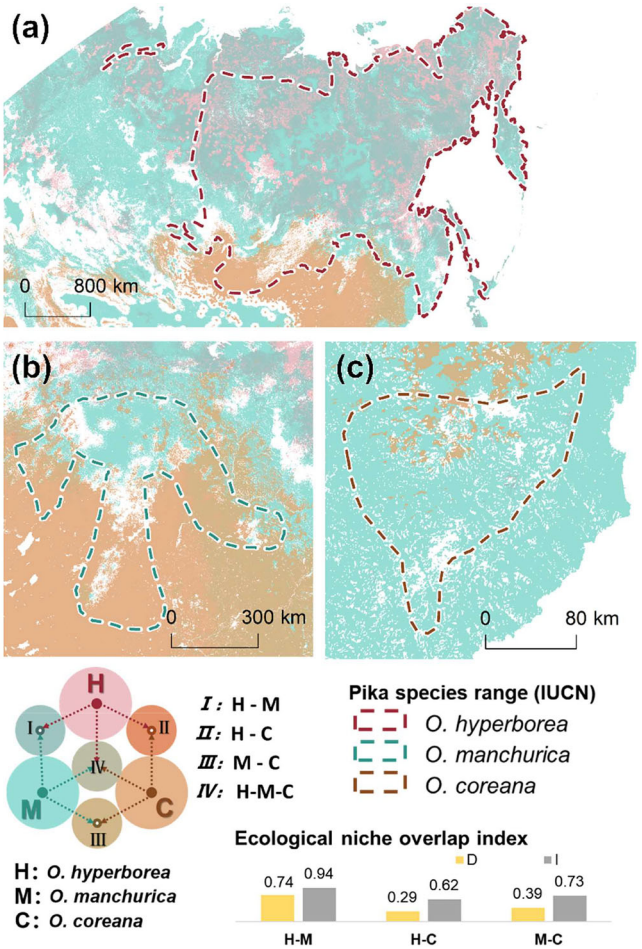


FIGURE 5 | Geographic range and ecological niche overlap among three pika species. (a) *O. hyperborea* (red); (b) *O. mantchurica* (green); (c) *O. coreana* (brown). The ecological niche overlap index (Schoener's *D* and Hellinger's *I*) is presented for each species pair. This figure was drawn using ArcMap 10.8 software.

2014), environments that are widespread across northeastern Asia. In addition, our results show restricted suitable habitat for *O. coreana* at the border between China and DPR Korea, and the absence of niche overlap with the two other *Ochotona* focal species.

O. hyperborea had the most extensive suitable habitat, with highly suitable areas primarily concentrated in the Siberian lowlands and the margins of the Far Eastern mountainous regions, reflecting a generalized adaptation to similar habitats. In contrast, *O. coreana*, despite having the smallest habitat area, exhibited a sky island distribution pattern, indicating a highly specialized niche rather than broad expansion. *O. mantchurica* occupied an intermediate position, with a distinctly patchy habitat distribution, suggesting it might be in a dynamic equilibrium of niche expansion or contraction. Habitat area in small mammals does not directly equate to niche breadth as a species' niche is defined by multiple environmental dimensions (Polechová and Storch 2008). This distinction between habitat extent and niche breadth is highlighted by our results: *O. hyperborea* occupies the broadest spatial range but shares a high degree of niche similarity with *O. mantchurica*, whereas *O. coreana* shows a much narrower spatial distribution yet occupies a distinct ecological niche with minimal overlap with the other two species.

Studies utilizing SDMs and niche dynamics simulations further suggest that widespread species may possess broad niche amplitudes, yet their highly suitable areas are often concentrated within specific environmental gradients (Kearney and Porter 2009; Thuiller et al. 2005). Our results mirror these expectations for *O. hyperborea*, which shows both the widest geographic extent and the broadest ecological niche among the three focal species, while still exhibiting its highest suitability within specific environmental gradients. In contrast, *O. mantchurica* displays an intermediate pattern, with a moderately broad distribution and niche that overlap substantially with those of *O. hyperborea*. *O. coreana*, however, departs markedly from these patterns, exhibiting both a restricted spatial distribution and a narrow, highly specialized niche with minimal overlap with the other two species.

As an ecological implication of these current spatial patterns, we hypothesize that the three species may exhibit markedly different responses to ongoing climate change. The highly suitable areas for *O. coreana* are predominantly confined to the alpine tundra zone of the Changbai Mountains. If climate warming causes the tree line to ascend (Harsch et al. 2009), its habitat could undergo rapid vertical contraction, posing a risk of extinction. Conversely, while *O. hyperborea* is widely distributed, its high-suitability regions are largely located in the frigid tundra with minimal human activity. Although our study focuses on current environmental conditions rather than future climate projections, based on the modeled spatial pattern of its current cold-adapted niche and inferring from behavioral studies on other pika clades under climate warming scenarios (Hafner and Sullivan 1995; Smith 2020), we hypothesize that *O. hyperborea* might potentially expand northwards in the short term. This suggests a behavioral process where the species tracks cooler regions to mitigate warming pressures. Therefore, future conservation priorities should consider both the current spatial concentration of high-quality habitats and their susceptibility to future environmental changes.

Niche overlap analysis further supports this pattern of differentiation, showing a clear pattern where *O. mantchurica* and *O. hyperborea* share nearly identical niches whereas *O. coreana* exhibits significant niche isolation. This modeled spatial overlap aligns with existing morphological and genetic evidence (Tang et al. 2022), suggesting a relatively recent divergence between *O. mantchurica* and *O. hyperborea*, potentially with ongoing gene flow, while *O. coreana* has been isolated in the alpine ecosystem for an extended period, developing unique adaptive traits (Lissovsky et al. 2008). The overlap zone between *O. mantchurica* and *O. hyperborea* is primarily located on the southern slopes of the Greater Khingan Mountains, an area rich in resources and high in heterogeneity. While the high degree of theoretical niche overlap suggests that coexistence might be possible due to abundant resources, the actual overlap in this region is limited. This pattern is consistent with potential niche partitioning, where two species with similar ecological niches may engage in competitive processes, although alternative mechanisms cannot be ruled out (Hardin 1960). In contrast, the pattern of low overlap of *O. coreana* is consistent with its long-term isolation within a unique and highly specialized alpine ecosystem on the

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Changbai Mountains, which previous studies have demonstrated to be ecologically sensitive and extremely fragile under climate warming (Jin et al. 2019). Changes in this environment could not only lead to rapid contraction of its core niche but also disrupt the stability of this distinct ecosystem, thereby exacerbating local extinction risks.

Previous studies have generally considered geographic isolation, where physical barriers such as mountains and rivers disrupt gene flow (Sobel et al. 2010), as the decisive factor in speciation. However, the niche divergence observed in our results suggests that the process of environmental filtering also plays a role. For instance, the influence of Bio15 (precipitation seasonality) exhibited a clear gradient response among the three pikas, with *O. coreana* preferring high seasonality and the other two species preferring the opposite. Furthermore, the impact of human activities showed a divergent pattern: *O. coreana* surprisingly demonstrated higher suitability closer to croplands. Without independent field evidence, we caution against interpreting this as an adaptive or behavioral preference. This spatial correlation likely reflects the specific landscape configuration in the Changbai Mountain region, where the restricted geographic extent of the species inherently coincides with local elevation gradients and human settlement patterns. In contrast, both *O. hyperborea* and *O. mantchurica* exhibited a tendency to avoid croplands, reflecting their high sensitivity to anthropogenic disturbance. This suggests that the traditional concept of geographic isolation is being reshaped by the interplay between anthropogenic barriers and environmental gradients, highlighting the need for greater emphasis on the indirect regulatory mechanisms of human activities on species distribution boundaries and niche structure in the future.

Although this study is the first comparative biogeographic framework for understanding the ecological drivers isolating these three pika species in Northeast Asia, certain limitations remain. First, we acknowledge that SDM-based niche overlap alone cannot definitively distinguish competition from alternative mechanisms such as historical constraints or dispersal limitation (Broennimann et al. 2012). This limitation is inherent to comparative biogeographic studies relying on correlative data; independent evidence from field observations or genomic analyses would strengthen causal inference and represent a valuable direction for future research. Second, our study includes a sampling bias: the sample size for *O. hyperborea* far exceeds that for *O. coreana* and *O. mantchurica*. This imbalance may influence model stability and the interpretation of variable importance and niche breadth comparisons across species. Third, the 1 km resolution of the climate data might be insufficient to capture the fine-scale microclimatic dependencies of pikas. Additionally, the model performance for *O. hyperborea* in Mongolia was suboptimal, primarily due to the region's complex and unique climate, along with its complex geography gradients, which increased model uncertainty. Future research could integrate high-throughput genomic sequencing with spatial modeling to investigate the adaptive genetic basis of the three pika species and their response thresholds to climate change. Given the ongoing threats posed by climate change, especially for species with narrow habitat ranges like *O. coreana*, addressing these threats through targeted conservation efforts is critical. As temperatures rise and habitats shift, identifying species' adaptive capacities and thresholds for change will be essential for developing strategies to mitigate the risks of extinction.

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Data Availability Statement

The GIS analysis code, SDM results, and niche-overlap files for the three pika species (*O. coreana*, *O. mantchurica*, and *O. hyperborea*) are available at GitLab: https://gitlab.com/ochotona-research/three-ochotona.git. The repository contains R scripts and compressed raw/processed data that readers can clone or download directly.

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