



Mapping fine-scale distribution of the northern pika *Ochotona hyperborea* considering duality in microhabitat thermal conditions

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Abstract

Species distributions are frequently modeled using predictors that exceed the spatial scale experienced by the focal species. Incorporating fine-scale environmental conditions is therefore expected to lead to more realistic model predictions. However, the importance of the existing local heterogeneity on species distribution remains poorly assessed although species can effectively utilize multiple microhabitats for behavioral adaptation to withstand climate change impacts. Here, we developed a fine-resolution species distribution model based on ambient air conditions for the northern pika (*Ochotona hyperborea*), a small lagomorph found in rocky landforms, in Hokkaido, Japan, to first understand the improvement in the model performance from the conventional coarse-resolution model. We then assessed how model predictions alter by incorporating the rock-interstice microclimates that are found in their habitats for the baseline (1981–2010) and future periods (2041–2100). The fine-resolution model performed better and overall predicted lower habitat suitability across the study area than the coarse-resolution model. Incorporation of rock-interstice microclimate increased the habitat suitability markedly relative to predictions based on ambient thermal conditions, which resulted in predicting more suitable areas in lower (hotter) elevations and more areas remaining suitable into the future. This result suggests that the northern pika may withstand the negative impacts from rising ambient temperatures by effectively utilizing rock interstices via behavioral adaptation. Our findings highlight the importance of analyzing species distribution at fine scales and considering local environmental heterogeneity, which helps species mitigate the adverse impacts of climate change, for conservation under climate change.

Highlights

- Species use a wide variety of microhabitats and experience thermal conditions existing locally.
- In the northern pika (*Ochotona hyperborea*), the fine-resolution species distribution model performed better than the coarse-resolution model.
- Complex topographical features that locally buffer ambient thermal conditions were predicted to increase habitat suitability and enable species persistence in the future.
- Local environmental heterogeneity that helps species mitigate climate change impact will be important for conservation.

Keywords

Behavioral thermoregulation, climate change, microclimate, species distribution model, topography

Introduction

Climate change is having a profound influence on species distributions worldwide. Evidence from historical resurveys shows that species distribution limits are generally expanding at the leading edge and contracting at the trailing edge towards higher elevations and latitudes (Moritz et al. 2008; Lenoir et al. 2020). These range shifts are predicted to affect species extinction risks (Urban 2015), as well as ecosystem functions and services (Pecl et al. 2017). It is therefore important in contemporary biogeography to assess accurately how species will change their

spatial distribution in the future and identify conservation priority areas to mitigate those impacts. Species distribution models (SDMs) have become extremely useful in this role by relating species occurrence with environmental data and enabling forecasts of how suitable habitats and associated distribution ranges will change over time (Elith and Leathwick 2009). Yet, SDMs have been criticized for analyzing species' occurrence and environment relationships at spatial resolutions that are often too coarse relative to the actual scales at which species utilize those habitats. A review by Potter et al. (2013) showed that the grid lengths of the environmental data used in previous studies were approximately 10,000 times larger than the body length of the focal animal species and 1,000 times in plants, suggesting a strong spatial mismatch between the environmental data and the actual conditions experienced by species. While some researchers argue that species distribution models aim to model population-level rather than individual-level responses (Bennie et al. 2014), the issue of scale mismatch in distribution modelling is still recognized as important when considering the population dynamics for a wide range of taxa, such as small mammals, herpetofauna, and plants (Nadeau et al. 2017).

The spatial resolution of SDMs is of concern particularly in rugged terrains where coarse climate data cannot capture appropriately the variation in thermal conditions existing at fine spatial scales that are created by complex topographies (Austin and Van Niel 2011). This could lead to the coarse-resolution SDM overlooking potential refugial areas that can offer favorable thermal conditions for species that allow them to withstand the negative impacts from climate change, resulting in an overestimation of the predicted species range shifts (Luoto and Heikkinen 2008; Randin et al. 2009; Mosblech et al. 2011). Indeed, studies exploring range shifts in response to past climate change have suggested species persistence in small areas with suitable conditions while surrounded by unsuitable conditions (McLachlan et al. 2005), often referred to as microrefugia (Rull 2009; Ashcroft 2010). Thus, endeavors to develop SDMs that incorporate thermal conditions at biologically relevant scales are warranted for range shift assessments (Lembrechts et al. 2019).

A growing body of literature has explored the effect of spatial resolution on SDMs mainly by using downscaling techniques (Guisan et al. 2007; Randin et al. 2009; Gillingham et al. 2012; Franklin et al. 2013; Maclean and Early 2023; Moudry et al. 2023; Patiño et al. 2023). While downscaled climate data is considered to represent ambient conditions often driven by local elevation, recent SDM studies are further attempting to incorporate modeled microclimates that are created by various environmental features (e.g., forest canopies), by combining *in-situ* thermal sensor measurements (Stark and Fridley 2022; Haesen et al. 2023) and remote sensing techniques (Stickley and Fraterrigo 2023). These studies show that incorporation of downscaled climate and modeled microclimates can improve performance of SDMs and alter predictions of suitable areas, thus affecting the trajectory of potential range

shifts over time (e.g., Maclean and Early 2023). Therefore, relying solely on coarse-resolution models is problematic for conservation practice under climate change because it can lead to poor decisions that overlook suitable areas when designing protected areas and allocating resources for management. Further research is therefore required in this field because a wide variety of environmental features create distinct climates at various spatial scales (Morelli et al. 2017), and how species utilize and interact with them is system-specific (Shi et al. 2016).

One of the perspectives still unexplored in previous SDM studies, particularly for animals, is that a given species can experience various thermal conditions even within a single grid cell, set by the nominal resolution of the raster predictors used in the model, as vertical structures generate heterogeneous conditions (e.g., Scheffers et al. 2014). Most previous studies have only considered the environmental condition of a single vertical position, overlooking the fine-grain heterogeneity in environmental conditions that likely influences overall habitat suitability of a given location that an individual occupies. This is particularly important in the context of species adaptation to climate change since species may mitigate the negative impacts by altering their behavior effectively to exploit local heterogeneity in climatic conditions (Beever et al. 2016b), which may cascade to have broader implications for patterns in the overall distribution (Marske et al. 2023). Therefore, predicting habitat suitability considering the variety of environmental conditions existing at different vertical positions should improve the assessment of climate-induced species range shifts.

Pikas are small lagomorphs adapted to cold environments in montane ecosystems (Smith 2018). Various aspects of temperature, such as magnitude and variation, often act as strong drivers of their distribution (Beever et al. 2010; Rodhouse et al. 2017) and abundance (Moyer-Horner et al. 2016). Mounting evidence also suggest their vulnerability to recent climate change, with field observations reporting range contractions (Beever et al. 2016a; Billman et al. 2021), while other studies have predicted future range contractions (Schwalm et al. 2016; Bhattacharyya et al. 2019). Some pika species belonging to the *Pika* subgenus dwell in rocky landforms such as talus slopes, lava flows, and moraines (Smith 2018). In these habitats, pikas experience duality in thermal conditions as they utilize both the above-ground and sub-ground microhabitats (Millar et al. 2016; Smith et al. 2016). The above-ground space is used for moving, vocalizing, foraging and collecting winter diet (i.e. haypile), and pikas experience the local ambient air temperatures during these activities. In contrast, the sub-ground space in the rock interstices is used as the shelter (Gliwicz et al. 2005), which provide pikas with cool and stable microclimates buffered from the ambient air (Varner and Dearing 2014; Millar et al. 2016; Sakiyama et al. 2021). While both microhabitats are essential for pikas, observations show that pikas respond flexibly to avoid the heat stress from the ambient air by utilizing rock-interstice microclimates (Smith 1974; Smith et al. 2016). Therefore,

rock interstices are considered a key feature for their distribution by allowing the species to occur in counterintuitive, low-elevation areas and for them to persist under climate change (Smith 2020). However, despite occurring in complex terrain and utilizing its heterogeneous conditions for thermoregulation, previous studies modeling pika distribution have often used coarse-resolution data reflecting only the above-ground air temperatures (e.g., 1-km² scale in Bhattacharyya et al. (2019)), possibly introducing bias into the habitat suitability predictions and associated range shift estimates. Predicting the habitat suitability at fine-resolutions for both the above- and sub-ground space should thus facilitate a more accurate assessment of their vulnerability to climate change while also taking their adaptive capacity into account.

Herein, we establish a coarse-resolution SDM for the northern pika *Ochotona hyperborea* (subgenus *Pika*) in Hokkaido, Japan and compare this model with a fine-resolution SDM to determine improvements in model performance, suitable area prediction, and range shift forecasts. In particular, we use coarse temperature data (30 arcsecs) and downscaled temperature data (3 arcsecs) to build the coarse-resolution model and the fine-resolution model, respectively. While the fine-resolution model considers the effect of ambient air (i.e., above-ground) temperature, we further assessed the habitat suitability for the sub-ground space by incorporating rock-interstice microclimates into the predictions, which we modeled based on local thermal measurements (Sakiyama and García Molinos 2024). We then projected future range shifts for the species and compared the area of suitable habitat between ambient air and microclimate-based predictions. We hypothesized that (1) the fine-resolution model will have higher model performance than the coarse-resolution model; (2) the habitat suitability values will be higher in the prediction using rock-interstice microclimate than that using ambient air temperature; and (3) the rock-interstice microclimate will contribute to retaining suitable habitats in future predictions.

Materials and methods

Study area and species distribution data

We modeled the distribution of northern pika in central Hokkaido, Japan, because detailed habitat thermal measurements have been conducted in this area (Sakiyama et al. 2021; Sakiyama and García Molinos 2024). The northern pika in Hokkaido is located at the southern margin of its distribution and therefore its population is likely among the most vulnerable of the species to climate warming. Although northerly neighboring populations are found across the Sea of Japan in Sakhalin and Primorsky, the Hokkaido population is essentially a disjunct population. As such, the accessibility and availability of climate change refugia within Hokkaido is of significant importance for the Hokkaido population, while it is likely to respond to climate change by shifting their distribution ups-

lope or by utilizing cool microclimates. However, previous studies have not predicted its future distributions.

To model the distribution of northern pikas, we compiled occurrence data in central Hokkaido from previous literature. Given almost all the compiled data comprised presence (but not absence) locations, we decided to apply a presence-only algorithm for distribution modeling (see Model development section). We only used presence locations reported on high resolution maps (i.e. 1/25,000 and 1/50,000 scale) for analysis since we were interested in modeling at fine scales and those surveyed between 1961–2010 to match the timeframe with the environmental data. Overall, a total of 305 presence points encompassing a wide elevational gradient (50–2,210 m) were obtained from the literature (Suppl. material 1: table S1, fig. S1). Survey years spanned between 1963 and 2009 (Suppl. material 1: fig. S1a, b). Detection signs of northern pika presence were clearly mentioned for almost all points (298 points, 97.7%), with the vocalization representing the main method enabling detection of 241 points (79.0%) while other methods were also used for detection: direct sightings (78 points, 25.6%), haypiles (47 points, 15.4%), feces (35 points, 11.5%), and eatmarks (9 points, 3.0%).

As calibration extent for this study, we considered the area corresponding to the known geographical range of the species comprising the continuous mountainous areas in central Hokkaido delimited by the flatlands (i.e., river valleys) as the extent borders. Specifically, we considered the Abira and Ishikari River systems as the western, the Teshio River system as the northwestern, the Okoppe River system and the Sea of Okhotsk as the northeastern, the Tokoro and the Tokachi River systems as the eastern, and the Pacific Ocean as the southern borders of the extent (Suppl. material 1: fig. S1a). Next, we removed irrelevant land cover types from within the study extent area such as urban land, agricultural fields, and aquatic area (e.g., lakes) since northern pikas require pristine montane conditions for inhabitation. The resulting filtered study extent area covered approximately 21,000 km² in central Hokkaido (Suppl. material 1: fig. S1a).

Model settings

To understand how differences in spatial resolutions of climate data affect model performances and predictions of species distribution, we constructed coarse-resolution and fine-resolution models (Fig. 1; Suppl. material 1: table S2). In the coarse-resolution model, we used environmental predictors at a resolution of 30 arcsecs, which converts to a grid cell of 691 m by 926 m (longitude × latitude) and size of 639,682 m². We consider this setting to be a coarse resolution for the northern pika because their home range is much smaller, typically within the range 1,822–11,530 m² ($n = 4$; Onoyama et al. 1991). We also note that the mountainous terrains of our study area are significantly smoothed at this resolution, with median and maximum elevational differences within one 30-arcsec grid

cell as large as 182 m and 770 m, respectively, when computed based on 10-times finer (3 arcsecs) elevation data (Suppl. material 1: fig. S2). Since species occurrence-environment relationships might be confounded by such a large degree of simplification, we developed the fine-resolution model using environmental data at 3 arcsecs, which converts to a grid cell of 69.1 m by 92.6 m and size of 6,397 m². We consider this setting to reflect the local ambient air conditions experienced by pika individuals. Based on the fine-resolution model, we then generated two habitat suitability predictions to account for the duality in thermal conditions experienced by the northern pika. The first corresponds to the raw predictions based on the fine-resolution model, which represents the above-ground habitat suitability considering the effect of local ambient air. The second prediction incorporates information on rock-interstice microclimates that are buffered from the ambient air, to further predict sub-ground habitat suitability.

Topographical and geological variables

We used the terrain slope angle as a topographical predictor in the SDMs because it has been shown to have a

positive relationship with the northern pika distribution (Sakiyama et al. 2021). We computed the slope angle raster in QGIS 3.34 (QGIS Development Team 2023) using the MERIT DEM (Yamazaki et al. 2017), a digital elevation model provided at a spatial resolution of 3 arcsecs. Slope angles for the coarse-resolution setting were calculated using a DEM aggregated to 30 arcsecs (Suppl. material 1: table S2). We also considered surface geology as a categorical binary predictor because 99% of the known distribution of the northern pika lies on igneous and metamorphic rocks and moraines (Kawabe 1992). To do so, we assigned whether any of these geological types occurred per grid cell within the study area based on the Seamless Digital Geological Map of Japan (1:200,000) V2 (Geological Survey of Japan, National Institute of Advanced Industrial Science and Technology 2017) (Suppl. material 1: table S2).

Bioclimatic variables

To model and predict the distribution of northern pikas, we computed the mean daily temperature and mean diurnal range over July and August to account for the effects of thermal magnitude and variation during the summer. We

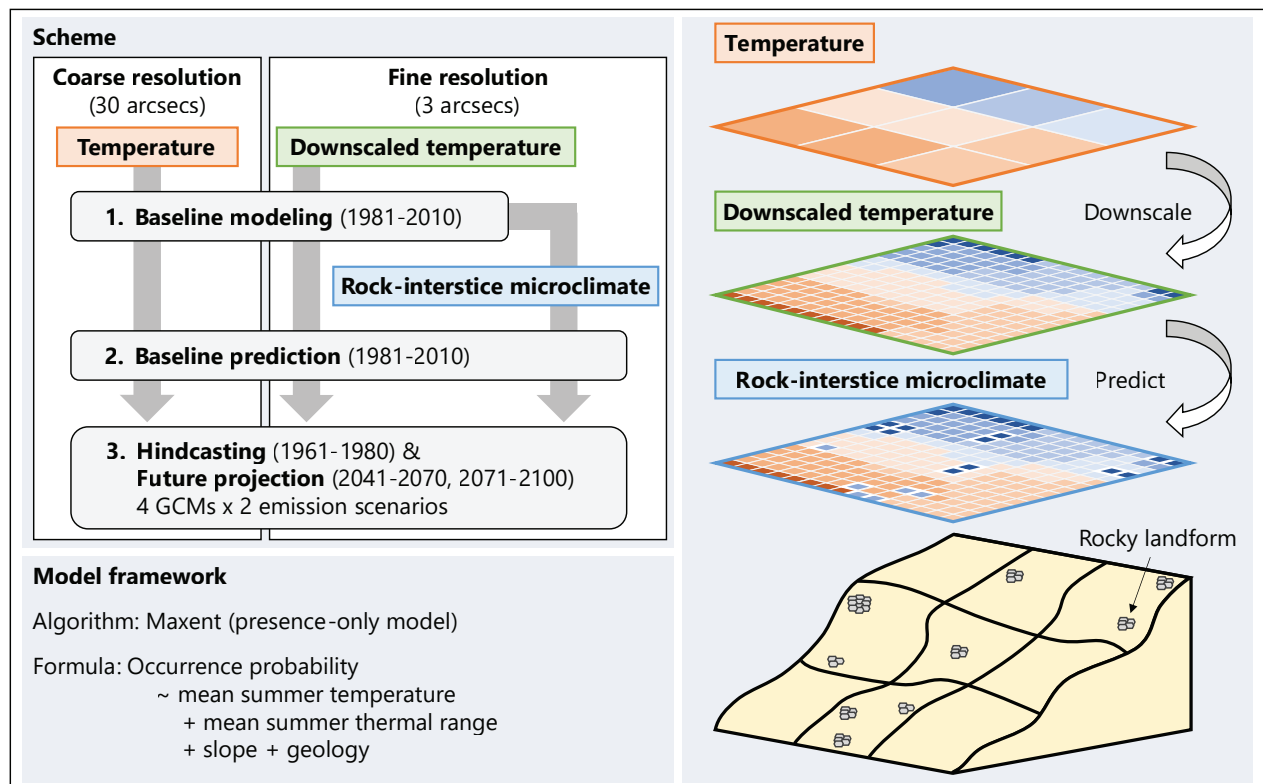


Figure 1. Schematic diagram describing the different model settings of the study. We considered two spatial resolutions for analyzing the northern pika distribution: coarse-resolution (30 arcsecs), representing conventional, temperature data; and fine-resolution (3 arcsecs), which is more adequate for the species due to their small home range size. We used widely available temperature data for developing the coarse-resolution model, while downscaled temperature data, which we considered to reflect the ambient air temperature, was used for the fine-resolution model. We further used the fine-resolution model to evaluate the habitat suitability in areas with rocky landforms (cells surrounded by thick white lines in the microclimate layer) by incorporating the rock-interstice microclimate, which is known to be buffered from the ambient air temperature. Finally, we conducted hindcasting and future projection analyses to predict distribution changes over time.

focused on summer conditions because the effects of climate change on cold-adapted species are likely to be particularly strong during this season. We used the average following previous studies exploring the effects of thermal conditions on the northern pika distribution (Sakiyama et al. 2021; Sakiyama and García Molinos 2024). Briefly (see Suppl. material 1: appendix S1 for a detailed explanation), we first obtained temperature data at 30 arcsecs using the *chelsa-cmip6* R package, which provides access to downscaled Global circulation model (GCM) projections (Karger et al. 2023). Four GCMs that are known to reproduce well the climatic conditions of our study area were selected (i.e. ACCESS-CM2, IPSL-CM6A-LR, MIROC6, and MRI-ESM2-0) (Shiogama et al. 2021). We used temperature data for 1981–2010 to model the baseline distribution. To create the bioclimatic variables, we adapted the computation formulas used in ANUCLIM, a software package used to build spatial climatic data (Xu and Hutchinson 2011, 2013), to the summer season, and calculated mean summer temperature and mean summer diurnal range. The resulting variables were then used in the coarse-resolution model (Suppl. material 1: table S2).

For the fine-resolution model, we downscaled the temperature data obtained at 30 arcsecs to 3 arcsecs through a kriging analysis using the *krigR* R package (Davy and Kusch 2021; Kusch and Davy 2022). This approach first models the relationship between temperature and elevation at a coarse resolution (30 arcsecs), which is then used to interpolate the temperature to the target resolution (3 arcsecs) using elevation data with the same resolution. We used the raw MERIT DEM (Yamazaki et al. 2017) dataset, provided at 3 arcsecs, as the elevation data for the interpolation and the aggregated version at 30 arcsecs to model the coarse-resolution relationship (Suppl. material 1: table S2).

Finally, we considered that northern pikas can utilize the rock-interstice microclimate in the sub-ground space, which are known to be buffered from ambient air temperature (Millar et al. 2016; Smith et al. 2016; Sakiyama and García Molinos 2024), in areas with rocky landforms. However, given the absence of sufficient spatial distribution information regarding rocky landforms throughout our study extent, we selected three representative regions where we had sufficient data, separated by elevational ranges: Biei (1,100–2,000 m), Shikaribetsu (600–1,250 m), and Oketo (400–800 m) (Fig. 3d). For Biei, we were able to map the rocky landforms directly using aerial images. For Shikaribetsu and Oketo, we referred to the mapped occurrence of rocky landforms in previous literature (Kojima 2004; Kurumada 2010). For these regions, we then used an empirical relationship between ambient and interstice temperatures previously derived from northern pika taluses in our study area (Sakiyama and García Molinos 2024) to convert downscaled temperature (i.e., ambient air) into rock-interstice temperature for each of the 3 arc second grid cells containing rocky landforms (Suppl. material 1: fig. S3, appendix S1). Since rocky landforms are patchily distributed within each region, our assumption was that northern pika in grid cells without rocky landforms experience only

ambient air temperatures, while those in grid cells with rocky landforms experience dual thermal conditions of ambient air and rock interstice temperatures. We validated our downscaling and microclimate incorporation approach by comparing thermal conditions measured in northern pika habitats with values of each bioclimatic variable in the grid cells where those observations had been made (see Suppl. material 1: appendix S2). Results confirmed that the fine-resolution data were moderately accurate in reflecting observed ambient temperature and that the microclimate data were highly accurate in reflecting observed rock interstice temperatures (Suppl. material 1: fig. S4; Fig. 5).

Model development

We performed the distribution modeling analysis of northern pikas in Hokkaido using maximum entropy (MaxEnt; Phillips et al. 2006). While model averaging is often used in SDM studies to remove potential bias in the predictions emerging from the algorithm used, we decided to use a single algorithm considering the overall methodological complexity and computation time. We chose MaxEnt because it has been shown to consistently rank among the best performing algorithms in comparative studies (Valavi et al. 2022). Models were developed separately for coarse- and fine-resolution settings considering years 1981–2010 as the baseline period using presence points obtained during this period for model fitting. Prior to model fitting, we reduced the effect of spatial sampling bias by thinning the presence data using the *spThin* R package (Aiello-Lammens et al. 2015) at a distance of 500 m as presence locations could be viewed as independent at this distance considering the complex mountainous terrain and the limited mobility of the northern pika. Considering that the diagonal distance of coarse grid cells is larger than this thinning distance and duplicate sampling thus could occur, we randomly selected a single point for each cell after thinning. This pre-selection process resulted in a total of 91 presence points remaining. We generated 10,000 background points throughout the study area, which are used in MaxEnt for characterizing the environmental conditions within the study area. To avoid multicollinearity issues, we computed the pairwise Pearson's correlation coefficients among the continuous predictors for both the coarse- and fine-resolution settings and confirmed that all pairs did not have a strong correlation ($|r| > 0.7$) (Dormann et al. 2013) (Suppl. material 1: fig. S6).

Since MaxEnt models with default settings can lead to overfitting (Anderson and Gonzalez 2011), we initially tuned the model hyperparameters to control the complexity while fitting well to the data. To do this, we used various hyperparameter combinations of feature classes, which determines the shape of the response curves, and regularization multipliers, which controls the model complexity (Phillips et al. 2006; Phillips and Dudík 2008), and selected the combination that resulted in the highest predictive accuracy. For the feature class, we considered linear (L), quadratic (Q), product (P), and/or hinge (H) characteristics,

and for the regularization multipliers, we used values ranging from 0.2 to 2.0 with intervals of 0.2. The predictive accuracy was assessed for each model by separating the presence data into training (80%) and test (20%) data and computing the area under the receiver operating characteristic curve (AUC), which indicates the accuracy condition on a range of 0 to 1 (Fielding and Bell 1997). All tuning processes were conducted using the `optimizeModel` function in the `SDMtune` R package (Vignali et al. 2020). After hyperparameter tuning, we evaluated the optimized model's predictive accuracy based on 5-fold cross validation using Continuous Boyce Index (CBI), which indicates whether the predicted habitat suitability is consistent with the distribution of presence points (Hirzel et al. 2006). CBI values range from -1 to 1, with positive values indicating an accurate prediction, values close to zero indicating inaccurate prediction (i.e., prediction is close to random), and negative values indicating counter predictions.

Comparing baseline predictions

For both coarse- and fine-resolution models, we predicted the habitat suitability for the baseline period across the study area and compared the predictions by computing the difference (Coarse – Fine). We also generated binarized maps of predicted species occurrence (i.e. presence or absence) based on the habitat suitability prediction across the whole study area. Since discriminant thresholds were likely to differ between the optimized models for coarse- and fine-resolutions and could be problematic for comparison, we instead used a sensitivity analysis approach by applying successive thresholds from 0 to 1 at 0.01 increments to discriminate presence or absence. Then, binary predictions were compared between coarse- and fine-resolution models by assessing the proportion of predicted species' range in the study area calculated as the total amount of cells predicted as present divided by the number of all cells. We used proportion instead of simply calculating the total area of presence because the total study area was subtly different between the scales due to processing procedures of environmental data.

We further predicted the habitat suitability for the sub-ground space for the three selected regions by replacing local ambient air temperatures with rock interstice microclimate using the fine-resolution model. The resultant prediction based on rock-interstice microclimate was mapped and compared with those based on the coarse-resolution model and fine-resolution model using ambient air temperature by considering the average habitat suitability at the region-wide scale and in areas with rocky landforms. In each region and prediction setting, the region-wide habitat suitability was assessed by sampling the predicted values using the cell centroids of the coarse-resolution data, while the rocky landform habitat suitability was evaluated by sampling the predicted values at random points generated within areas with rocky landforms. The habitat suitability values were then compared among the prediction

settings by conducting a beta regression analysis using the `betareg` R package (Cribari-Neto and Zeileis 2010) followed by a pairwise comparison between prediction settings using the Tukey method for p -value adjustments.

Hindcasting

We use a hindcasting approach to evaluate the transferability of the models to project distributions over time (see Nogués-Bravo 2009) by projecting the distribution of the species to the past and comparing it to known past presence points from the same past period for validation (Hodel et al. 2022). Although this approach is still rarely used in SDM studies (Yates et al. 2018), it allowed us to assess how confident we can be using the models to predict distributions for a time period different to that the model was calibrated for. We projected the distribution of northern pikas for the years 1961–1980, a period for which early presence records are available (Suppl. material 1: table S1, fig. S1). The same procedures as the baseline climate data were used for processing past data. We evaluated the model's predictive accuracy using the CBI (Hirzel et al. 2006).

Future projection

To project the future distribution of the northern pika, we obtained climate data for two future time periods, 2041–2070 and 2071–2100, considering two emission scenarios, SSP1-2.6 and SSP5-8.5, representing a globally sustainable and a fossil-fuel based development scenario, respectively. We predicted the future distribution for the whole study extent based on the coarse-resolution model and the fine-resolution model using ambient air temperature by applying future bioclimatic data, which were processed based on the same procedures for the baseline climate data (i.e., we assume that future topographical and geological variables will remain the same as present). We then binarized the suitability predictions to presence or absence by applying the same approach used for the baseline period to calculate the proportion of predicted species' range.

Moreover, we also projected the future distribution of the northern pika for the three selected regions to assess how rock-interstice microclimate contributes to retaining suitable conditions in the future. When processing the future microclimate data, we assumed that the buffering effect of the rock interstices (i.e., the empirical relationship between local ambient and rock-interstice temperatures) will remain invariable over time. We believe that this assumption is robust because the field thermal measurements from which this relationship was derived contained a large elevational gradient of 350–2200 m and the model residual was stable across the ambient temperature gradient (Sakiyama and Garcia Molinos 2024), although we note that some extrapolation did occur for some lower elevation areas where future conditions exceeded the

observed thermal gradient. We binarized the suitability predictions for both fine-resolution and microclimate using the maximum true skill statistic computed for the fine-resolution model (Santini et al. 2021). The consensus among the resulting binarized predictions from each of the four GCMs was then computed by considering a cell as present whenever that cell was predicted as present by two or more individual GCMs (i.e., $\geq 50\%$ consensus). The resultant prediction was compared between the fine-resolution prediction using ambient air temperature for each period and emission scenario.

Results

Model performance and variable importance

The optimized models for both the coarse- and fine-resolution yielded CBI values of 0.73 and 0.80, respectively (Table 1). Among the multiple variables used, mean

Table 1. Optimized hyperparameters and Continuous Boyce Index (CBI) values of the best coarse-resolution and fine-resolution models.

Model	Feature class	Regularization multiplier	CBI	Hindcast CBI
Coarse-resolution	LQP	2.0	0.73	0.82
Fine-resolution	LQP	2.0	0.80	0.96

summer temperature was the most important predictor explaining the northern pika distribution in both models with a permutation importance of 74.5% and 76.2% in the coarse- and fine-resolution models, respectively (Fig. 2). Mean summer temperature showed a negative effect on occurrence probability in both models, while the slope of the response curve was slightly steeper in the fine-resolution model (Fig. 2). In both models, surface geology was the second most important predictor with 20.5% and 17.8% of permutation importance, respectively, which exhibited a positive relationship with occurrence probability (Fig. 2). The contribution of daily thermal range and slope was less than 5% in both models (Fig. 2).

Habitat suitability for the baseline period

Mountainous areas were predicted as suitable areas for the northern pika, with higher elevations predicted as highly suitable areas while low elevations were predicted as areas with low to moderate suitability in both the coarse- and fine-resolution models (Fig. 3a, b). Comparing the predictions, the habitat suitability was generally higher in the coarse-resolution model than the fine-resolution model (Fig. 3c). Difference in habitat suitability was relatively large in mountainous areas, particularly in the slopes rather than the summits (Fig. 3c). The proportion of predicted species' range for both models exhibited similar inverse curves along the binarization

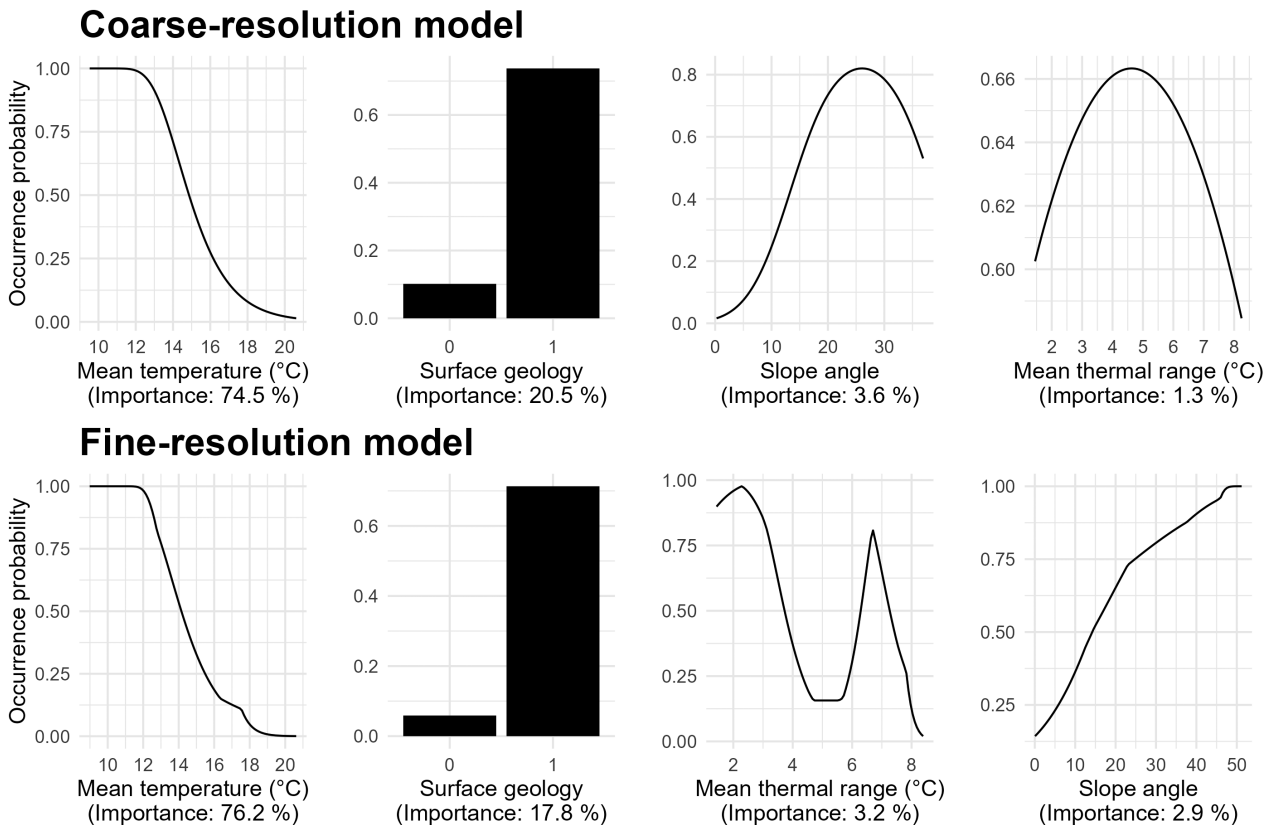


Figure 2. Response plots of the model predictors for the best-fit coarse-resolution (top) and fine-resolution (bottom) models. Permutation importance of the model predictors is provided below each variable name on the horizontal axis.

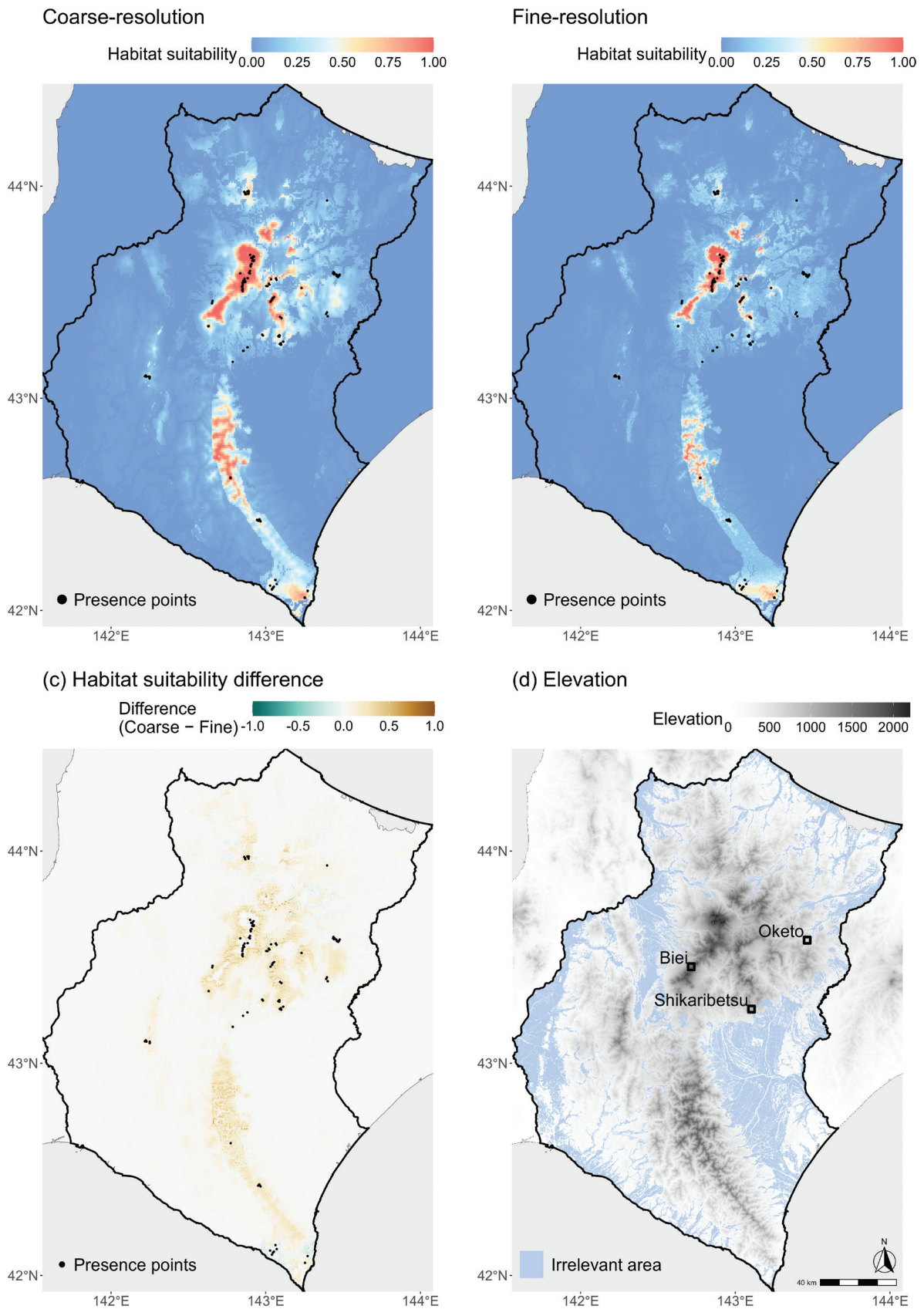


Figure 3. Predicted habitat suitability of the whole distribution of the northern pika in Hokkaido, Japan, for the baseline period (1981–2010), based on (a) coarse- and (b) fine-resolution models. In (c), the habitat suitability difference between these two predictions (coarse – fine) is provided. Black points represent presence locations used for the analysis. In (d), the elevation of central Hokkaido is shown in the background with locations of three regions used for the subsequent analysis depicted in squares. The black border line denotes the model’s calibration extent with light blue areas in (d) representing areas excluded from the analysis (see Methods for details).

threshold. However, the proportion was always higher in the coarse-resolution model than the fine-resolution model across the whole range of binarization threshold (Fig. 4a).

In the three selected regions, the regional habitat suitability based on both the coarse-resolution model and fine-resolution model using ambient air temperature was highest in Biei, followed by Shikaribetsu and Oketo, reflecting the regional elevational difference (Fig. 5). Within each region, the habitat suitability reflected the local elevational variation, with higher elevation areas predicted as more suitable (Fig. 5). In the fine-resolution model prediction, accounting for rock-interstice microclimate resulted in boosting the habitat suitability from that based on ambient air temperature in areas with rocky landforms in all regions (Fig. 5). Consequently, the habitat suitability in areas with rocky landforms was always significantly higher in the fine-resolution prediction based on rock-interstice microclimate than the coarse-resolution prediction and the fine-resolution prediction based on ambient air temperature (Fig. 5). However, the region-wide habitat suitability was not significantly different among the three prediction settings in two regions (Biei and Oketo), and it was only found to be different between the coarse-resolution prediction and the fine-resolution prediction based on ambient air temperature in Shikaribetsu (Fig. 5).

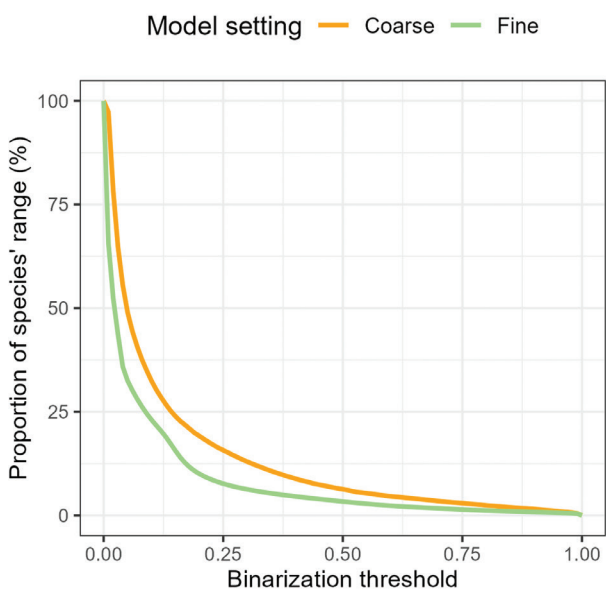
Hindcasting and future projection

Both coarse- and fine-resolution models were supported by high transferability to predict distributional changes

over time, as indicated by the positive CBI values in the hindcasting analysis (Table 1). This enabled projecting future distributions with confidence, in which both models indicated inverse curves in the proportion of predicted species' range (Fig. 4b). Compared to the baseline period, future range was predicted to decrease by more than 60% in both time periods and emission scenarios considered (Suppl. material 1: fig. S7). Between the two future time periods, the difference in the habitat decrease rate was relatively small under the SSP1-2.6 scenario, suggesting that the northern pika's range will shrink until 2041–2070 but will then remain relatively stable until 2071–2100. However, the habitat decrease was apparent under the SSP5-8.5 scenario, suggesting that suitable habitats will continue to decrease until 2071–2100. (Fig. 4b; Suppl. material 1: fig. S7).

Patterns of distributional change based on the fine-resolution model largely differed among the three selected regions between predictions based on ambient air temperature and rock-interstice microclimate. Based on ambient air temperature, the northern pika presence was predicted in Biei in both future time periods and scenarios and in Shikaribetsu under the SSP1-2.6 scenario, while the whole region was predicted to be absent in Oketo under all future settings (Fig. 6). Conversely, the northern pika presence was predicted in almost all regions in all future settings when accounting for rock-interstice microclimate, except in Oketo for the far future under the SSP5-8.5 scenario (Fig. 6). Discrepancies between predictions based on ambient air temperature and rock-interstice microclimate were high towards the lower elevations (Shikaribetsu and Oketo) and under the higher carbon emission scenario (SSP5-8.5).

(a) Baseline



(b) Future

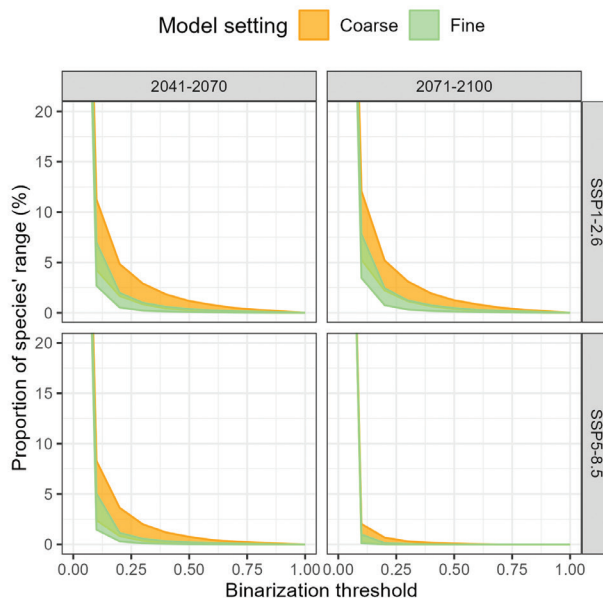


Figure 4. Proportion of predicted species' range along the successive binarization threshold applied at 0.01 increments (see Methods for details) for the (a) baseline and (b) future periods. The lines and shade colors represent model settings (orange = coarse-resolution, green = fine-resolution). The future panels are divided by time period (2041–2070 and 2071–2100) and emission scenario (SSP1-2.6 and SSP5-8.5), while the filled envelopes represent the range of proportions based on four Global circulation models.

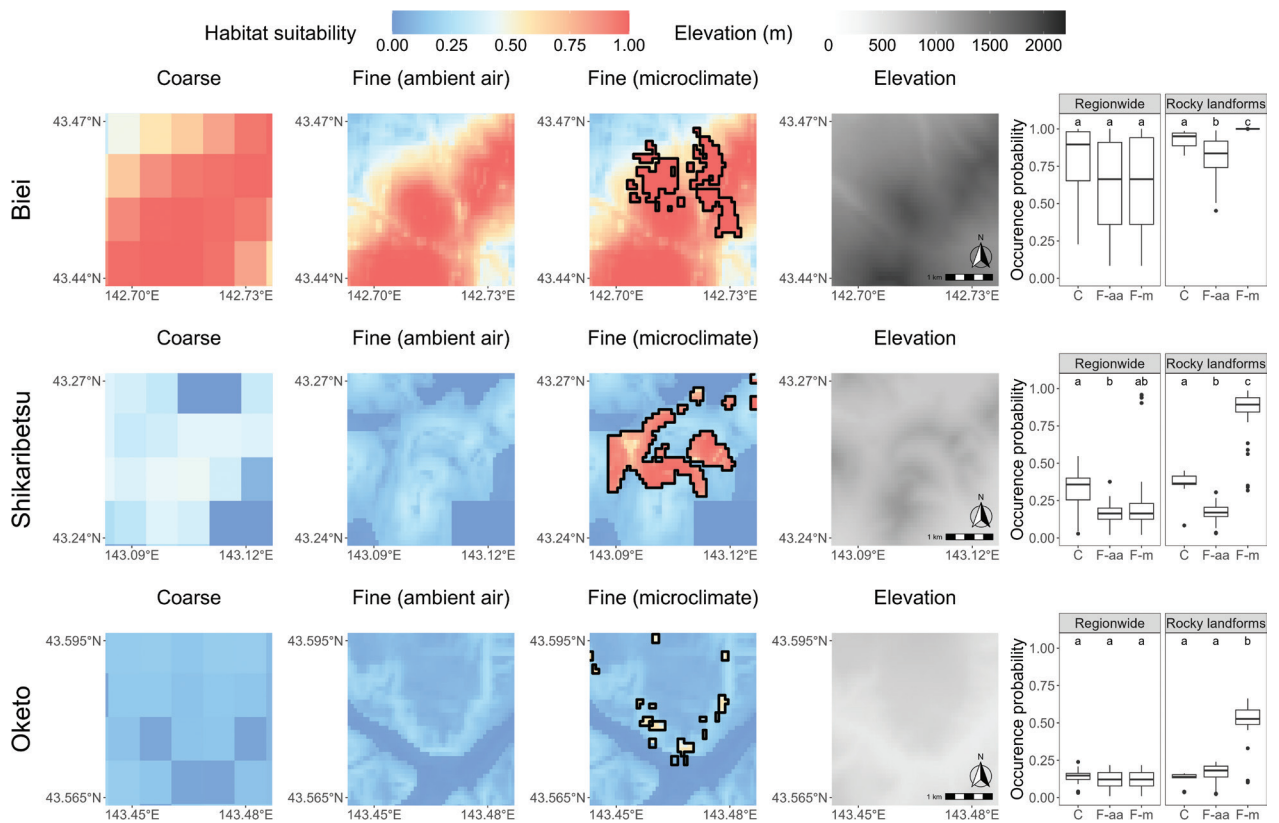


Figure 5. Predicted habitat suitability of the northern pika in (starting from top row) the Biei, Shikaribetsu, and Oketo regions for the baseline period (1981–2010), based on (starting from left column) the coarse-resolution model, fine-resolution model using ambient air (downscaled temperature), and fine-resolution model using rock-interstice microclimate. Areas with rocky landforms are depicted by black lines in the microclimate panels. The elevation for each region is shown in the fourth column. The last column shows boxplots comparing the predicted habitat suitability among the settings at the regionwide-scale (left) and within rocky landforms (right). The abbreviations on the x-axis correspond to: C = coarse-resolution model; F-aa = fine-resolution model using ambient air; and F-m = fine-resolution model using rock-interstice microclimate.

Discussion

We developed distribution models for the northern pika to assess how varying spatial resolution, and the further incorporation of duality in microhabitat thermal conditions into the fine-resolution model, affected performance and habitat suitability predictions. Our results show that the fine-scale model incorporating the rock-interstice microclimate found in the sub-ground space of rocky landforms generated predictions with markedly higher habitat suitability compared to those of the models based on ambient air temperature in all regions analyzed. This demonstrates that a single location (grid cell) can exhibit dual habitat suitability due to the existence of diverse thermal conditions in complex topographies. Interestingly, this led to detecting potential habitats that are overlooked in predictions based solely on ambient air conditions, especially in the lower elevations (Fig. 5), and to predicting a larger number of remnant habitats in the future under warming conditions (Fig. 6). Although microrefugia are often cryptic (Provan and Bennett 2008), we believe that our approach can be used effectively for identifying such areas, which can provide valuable information for conservation prioritization.

The duality in habitat suitability of fine-resolution predictions could be interpreted by categorizing them into three combinations, considering predicted values based on ambient air temperature and rock-interstice microclimate conditions: high-high, low-high, and low-low. Here, the combination of high-low suitability was not observed because habitat suitability was negatively related to temperature (Fig. 2) and rock interstices were generally cooler than the local ambient air (Suppl. material 1: fig. S3), hence more suitable. Northern pikas are expected to be present in areas with high-high suitability, and absent from areas with low-low suitability. However, whether areas with low-high suitability, such as in Shikaribetsu (mid-elevation) and Oketo (low-elevation), serve as functional habitats for northern pikas will likely depend on the extent to which the rock-interstice microclimate mitigates the negative impact of ambient air temperatures, which should be strongly linked to the capacity of northern pikas to adapt their thermoregulation behavior. Previous studies have indicated that northern pikas utilize above-ground space during the cooler times of the day (Onoyama 1991); a behavior also observed in American pika studies (Smith 1974; Smith et al. 2016). Additionally, American pika studies show that it regulates body temperature by reducing above-ground activities and

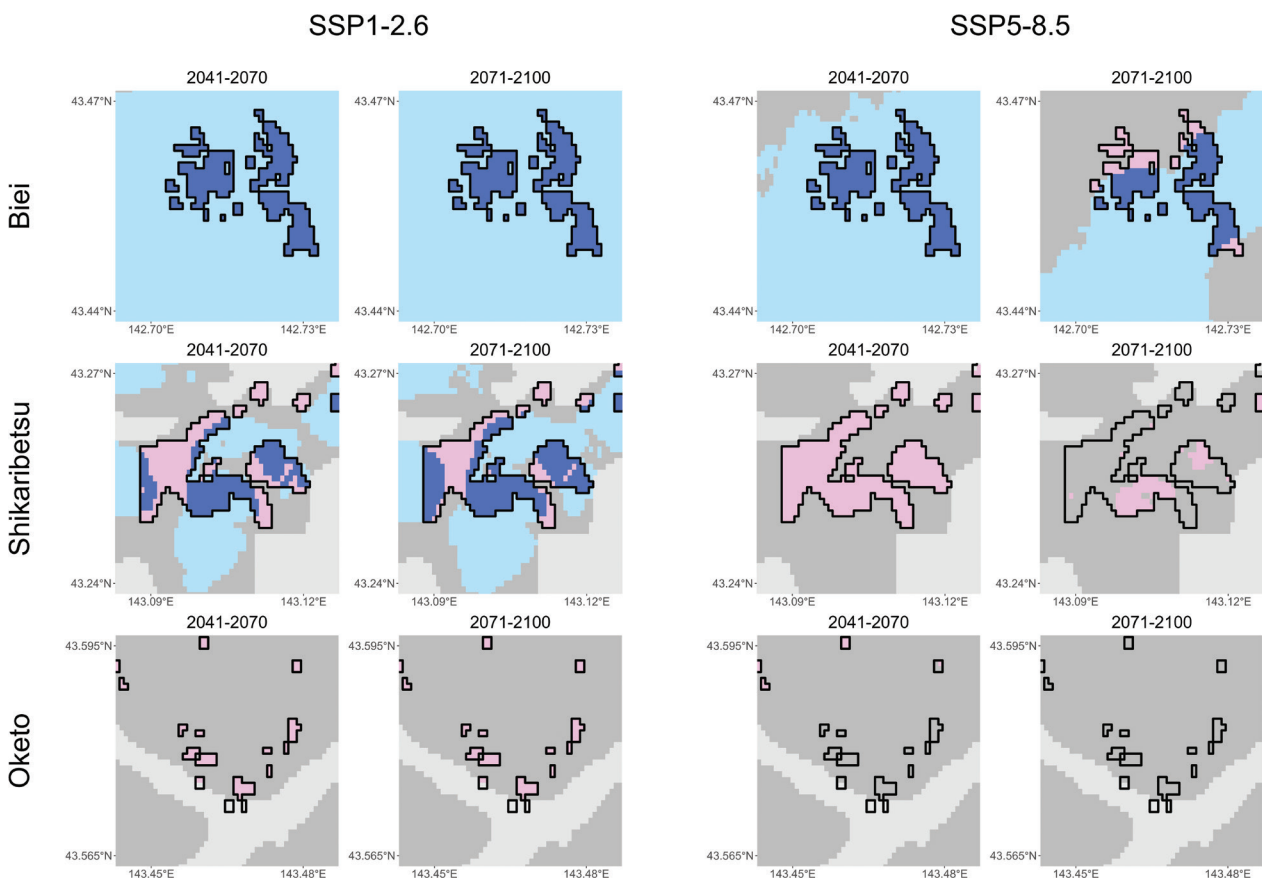


Figure 6. Predicted future distribution of the northern pika considering microclimates in (starting from top row) the Biei, Shikaribetsu, and Oketo regions based on the consensus approach. The 1st and 2nd columns are predictions for the 2041–2070 and 2071–2100 under the SSP1-2.6 scenario, and the 3rd and 4th those under the SSP5-8.5 scenario. Dark gray areas represent where suitable habitat is lost in the future, while light gray areas represent unsuitable areas at the baseline period. Areas with rocky landforms are depicted by black lines. The light blue areas represent suitable habitats supported by ambient air outside rocky landforms. Within rocky landforms, the dark blue areas represent suitable habitats supported by both ambient air and rock-interstice microclimate, whereas the pink areas represent those supported only by microclimate.

retreating into rock interstices (MacArthur and Wang 1974; Smith 1974). Thus, the northern pika may exhibit high behavioral flexibility to mitigate heat stress from rising ambient air temperatures, allowing them to occupy areas with low-high suitability, which aligns with their wide elevational range despite their adaptation to colder climates.

Over half of the suitable habitats in the future predictions based on the coarse-resolution model and the fine-resolution model using ambient air temperature were predicted to disappear by mid-century (Fig. 4): a pattern in line with other pika species (Beever et al. 2011; Bhattacharyya et al. 2019; but see Smith 2020). However, predictions using rock-interstice microclimate showed some localities in lower elevations remaining as suitable habitats despite prevailing ambient air temperatures becoming unsuitable (i.e., low-high suitability pattern; Fig. 6). This demonstrates the significance of rock-interstice microclimate for the persistence of northern pika, but it will be important to validate this projection through monitoring surveys over time. A study by Maclean and Early (2023) exemplifies this, demonstrating that fine-resolution predictions reduced the number of species at extinction risk and were in agreement

with the actual observed patterns, while coarse-resolution predictions estimated several species to become extinct. Importantly, the predicted change in species distribution depended strongly on the future period and emission scenario (Figs 4, 6). This result stresses the need to enforce effective policies for greenhouse gas emission mitigation and to guide effective conservation of the species by protecting areas that will account for the effect of climate change and maintain its distribution in the future.

Comparing the coarse-resolution and fine-resolution models, there are two possible reasons that likely contributed to the higher predictive accuracy in the fine-resolution model (Table 1). First, model response curves showed an important difference. While mean temperature had a dominant negative effect on the distribution in both models (Fig. 2), the response curve was steeper in the fine-resolution model. This indicates that the model fitted towards cooler conditions, which may be reflecting the response of the northern pika more accurately than the coarse-resolution model. Interestingly, as presence points in higher elevations were located in areas higher than its surroundings, they had cooler conditions in the fine-resolution model than

the coarse-resolution model (Suppl. material 1: fig. S8). However, it remains unclear whether this bias is due to a potential sampling bias in convex topographies such as ridgelines and mountain tops. We believe that assessing species distribution at fine-resolutions could introduce its scale-dependent issues, which requires attention as more fine-resolution SDMs are developed (Mitchell et al. 2017). Second, the accuracy of the predictors may have also had an effect on model performance. Even when coarse- and fine-resolution models exhibit the same relationship between occurrence and environment, the validated accuracy is likely to decrease if predictors are smoothed at coarse-resolutions. Instead, fine-resolution predictors are more likely to represent true environmental conditions, which could have resulted in higher predictive accuracy by resolving better local complex topographies, which has also been shown in previous studies (Trivedi et al. 2008; Randin et al. 2009; Meineri and Hylander 2017). Thus, the overall increase in accuracy of the fine-resolution model can be attributed to these small refinements in the modeled relationship and predictors. In general, our results are in agreement with recent studies finding higher performance in SDMs incorporating fine-resolution climates (Stark and Fridley 2022; Haesen et al. 2023).

Our results also showed a decrease of suitable areas in the fine-resolution prediction using ambient air temperatures when compared to the coarse-resolution prediction, under both the baseline and future condition (Fig. 4). This is likely due to differences in the modeled response to mean summer temperature, where the fine-resolution model fitted towards cooler temperatures relative to the coarse-resolution model, resulting in lower habitat suitability at certain temperatures and leading to a greater area of species' range in the coarse-resolution prediction. Previous studies have also commonly shown that fine-resolution models predict smaller suitable areas for the baseline period than coarse models (Franklin et al. 2013; Haesen et al. 2023; Stickley and Fraterrigo 2023), while there are mixed results of both smaller (Franklin et al. 2013) and greater (Stickley and Fraterrigo 2023) areas for future conditions. Therefore, the difference in the predicted habitat between coarse- and fine-resolution models may be specific to each study system and the scale-dependent relationship between the occurrence records and environmental predictors used in the model (Franklin et al. 2013).

One of the limitations of our study is that, despite using the downscaled climate data, we still rely on a simplified representation of time and space to develop the fine-resolution models. Rocky landforms exhibit high heterogeneity, with ambient air and rock interstice temperatures varying depending on height and depth, respectively, and changing across seasons (Millar et al. 2016; Benedict et al. 2020; Smith 2020). In this regard, our study may still be considered as a coarse representation of reality. Moreover, our study only considers effects of thermal conditions on the northern pika, while other climatic factors, such as precipitation and snow cover, could have influenced habitat suitability (e.g., Erb et al. 2011; Bhattacharyya et al.

2019). Furthermore, while we used only a single algorithm for modeling the northern pika distribution considering computation time and methodological complexity, using multiple algorithms to generate ensemble predictions may limit bias and uncertainty arising from the single algorithm approach (Araujo and New 2007). Finally, the current lack of an extensive dataset reporting presence of rocky landforms in high spatial resolutions limited identifying potential habitats supported by rock-interstice microclimates across our study extent. While our approach of microclimate incorporation was restricted to three regions and was implemented at the phase of prediction using a model trained by ambient air temperature, extensive dataset of rock-interstice microclimate would have enabled a more straightforward modeling approach by including it as a predictor to assess its influence on the distribution. Therefore, further refinements in geospatial data, for instance using remote sensing techniques (Pu et al. 2021), are warranted for predicting potential microrefugia.

In conclusion, the development of fine-resolution SDM and incorporation of thermal variation at biologically relevant scales into predictions yielded contrasting results from the conventional, coarse-resolution prediction. While future distribution was predicted to decrease when considering only ambient air conditions, our results imply that accounting for duality in fine-scale thermal conditions could alter future trajectories of species distribution, which is an essential information for the conservation of northern pikas in Hokkaido, as previous studies have not assessed such impacts. Nevertheless, it is crucial to better understand whether the seemingly adaptive behavioral responses of pikas to fine-scale thermal conditions are linked to maintenance of populations and scale up to influence species distributions (Marske et al. 2023). Based on these results, we advocate for the identification of rocky landforms to effectively integrate microclimates in conservation efforts.

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Author contributions

TS contributed to conceptualization and design of methodology, data analysis, funding acquisition, and writing the original draft; TS and JGM contributed to discussion of results, writing the final manuscript and gave final approval for publication.

Declaration of competing interest

The authors have no competing interests to declare.

Data accessibility statement

Data will be made available on request.

References

- Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 38: 541–545. <https://doi.org/10.1111/ecog.01132>
- Anderson RP, Gonzalez I (2011) Species-specific tuning increases robustness to sampling bias in models of species distributions: An implementation with Maxent. *Ecological Modelling* 222: 2796–2811. <https://doi.org/10.1016/j.ecolmodel.2011.04.011>
- Araujo M, New M (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution* 22: 42–47. <https://doi.org/10.1016/j.tree.2006.09.010>
- Ashcroft MB (2010) Identifying refugia from climate change. *Journal of Biogeography* 37: 1407–1413. <https://doi.org/10.1111/j.1365-2699.2010.02300.x>
- Austin MP, Van Niel KP (2011) Improving species distribution models for climate change studies: variable selection and scale. *Journal of Biogeography* 38: 1–8. <https://doi.org/10.1111/j.1365-2699.2010.02416.x>
- Beever EA, Ray C, Mote PW, Wilkening JL (2010) Testing alternative models of climate-mediated extirpations. *Ecological Applications* 20: 164–178. <https://doi.org/10.1890/08-1011.1>
- Beever EA, Ray C, Wilkening JL, Brussard PF, Mote PW (2011) Contemporary climate change alters the pace and drivers of extinction. *Global Change Biology* 17: 2054–2070. <https://doi.org/10.1111/j.1365-2486.2010.02389.x>
- Beever EA, Perrine JD, Rickman T, Flores M, Clark JP, Waters C, Weber SS, Yardley B, Thoma D, Chesley-Preston T, Goehring KE, Magnuson M, Nordensten N, Nelson M, Collins GH (2016a) Pika (*Ochotona princeps*) losses from two isolated regions reflect temperature and water balance, but reflect habitat area in a mainland region. *Journal of Mammalogy* 97: 1495–1511. <https://doi.org/10.1093/jmammal/gyw128>
- Beever EA, O’Leary J, Mengelt C, West JM, Julius S, Green N, Magness D, Petes L, Stein B, Nicotra AB, Hellmann JJ, Robertson AL, Staudinger MD, Rosenberg AA, Babij E, Brennan J, Schuurman GW, Hofmann GE (2016b) Improving conservation outcomes with a new paradigm for understanding species’ fundamental and realized adaptive capacity: a new paradigm for defining adaptive capacity. *Conservation Letters* 9: 131–137. <https://doi.org/10.1111/conl.12190>
- Benedict LM, Wiebe M, Plichta M, Batts H, Johnson J, Monk E, Ray C (2020) Microclimate and summer surface activity in the american pika (*Ochotona princeps*). *Western North American Naturalist* 80: 316–329. <https://doi.org/10.3398/064.080.0303>
- Bennie J, Wilson RJ, Maclean IMD, Suggitt AJ (2014) Seeing the woods for the trees – when is microclimate important in species distribution models? *Global Change Biology* 20: 2699–2700. <https://doi.org/10.1111/gcb.12525>
- Bhattacharyya S, Mungi NA, Kawamichi T, Rawat GS, Adhikari BS, Wilkening JL (2019) Insights from present distribution of an alpine mammal Royle’s pika (*Ochotona roylei*) to predict future climate change impacts in the Himalaya. *Regional Environmental Change* 19: 2423–2435. <https://doi.org/10.1007/s10113-019-01556-x>
- Billman PD, Beever EA, McWethy DB, Thurman LL, Wilson KC (2021) Factors influencing distributional shifts and abundance at the range core of a climate-sensitive mammal. *Global Change Biology* 27: 4498–4515. <https://doi.org/10.1111/gcb.15793>
- Cribari-Neto F, Zeileis A (2010) Beta Regression in R. *Journal of Statistical Software* 34: 1–24. <https://doi.org/10.18637/jss.v034.i02>
- Davy R, Kusch E (2021) Reconciling high resolution climate datasets using KrigR. *Environmental Research Letters* 16: 124040. <https://doi.org/10.1088/1748-9326/ac39bf>
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36: 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40: 677–697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>
- Erb LP, Ray C, Guralnick R (2011) On the generality of a climate-mediated shift in the distribution of the American pika (*Ochotona princeps*). *Ecology* 92: 1730–1735. <https://doi.org/10.1890/11-0175.1>
- Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24: 38–49. <https://doi.org/10.1017/S0376892997000088>
- Franklin J, Davis FW, Ikegami M, Syphard AD, Flint LE, Flint AL, Hannah L (2013) Modeling plant species distributions under future climates: how fine scale do climate projections need to be? *Global Change Biology* 19: 473–483. <https://doi.org/10.1111/gcb.12051>
- Geological Survey of Japan, National Institute of Advanced Industrial Science and Technology (2017) Seamless Digital Geological Map of Japan V2 1: 200,000. <https://gbank.gsj.jp/seamless/>
- Gillingham PK, Huntley B, Kunin WE, Thomas CD (2012) The effect of spatial resolution on projected responses to climate warming. *Diversity and Distributions* 18: 990–1000. <https://doi.org/10.1111/j.1472-4642.2012.00933.x>
- Gliwicz J, Witczuk J, Pagacz S (2005) Spatial behaviour of the rock-dwelling pika (*Ochotona hyperborea*). *Journal of Zoology* 267: 113–120. <https://doi.org/10.1017/S0952836905007211>
- Guisan A, Graham CH, Elith J, Huettmann F, the NCEAS Species Distribution Modelling Group (2007) Sensitivity of predictive species distribution models to change in grain size. *Diversity and Distributions* 13: 332–340. <https://doi.org/10.1111/j.1472-4642.2007.00342.x>
- Haesen S, Lenoir J, Gril E, De Frenne P, Lembrechts JJ, Kopecký M, Macek M, Man M, Wild J, Van Meerbeek K (2023) Microclimate reveals the true thermal niche of forest plant species. *Ecology Letters* 26: 2043–2055. <https://doi.org/10.1111/ele.14312>
- Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 199: 142–152. <https://doi.org/10.1016/j.ecolmodel.2006.05.017>
- Hodel RGJ, Soltis DE, Soltis PS (2022) Hindcast-validated species distribution models reveal future vulnerabilities of mangroves and salt marsh species. *Ecology and Evolution* 12: e9252. <https://doi.org/10.1002/ece3.9252>

- Karger DN, Chauvier Y, Zimmermann NE (2023) chelsa-cmip6 1.0: a python package to create high resolution bioclimatic variables based on CHELSA ver. 2.1 and CMIP6 data. *Ecography*: e06535. <https://doi.org/10.1111/ecog.06535>
- Kawabe M (1992) Geological factor of distribution of Northern Pika *Ochotona hyperborea* in Hokkaido. *Bulletin of the Higashi Taisei-su Museum of Natural History* 14: 103–106.
- Kojima N (2004) Conservation biology of the Japanese pika *Ochotona hyperborea yesoensis* [Unpublished doctoral dissertation]. Iwate University.
- Kurumada T (2010) The habitat patches distribution and utilization of the northern pika in Mt. Nakayama, Hokkaido. *Report of Hokkaido Institute of Environmental Sciences* 36: 65–69.
- Kusch E, Davy R (2022) KrigR—a tool for downloading and statistically downscaling climate reanalysis data. *Environmental Research Letters* 17: 024005. <https://doi.org/10.1088/1748-9326/ac48b3>
- Lembrechts JJ, Nijs I, Lenoir J (2019) Incorporating microclimate into species distribution models. *Ecography* 42: 1267–1279. <https://doi.org/10.1111/ecog.03947>
- Lenoir J, Bertrand R, Comte L, Bourgeaud L, Hattab T, Murienne J, Grenouillet G (2020) Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution* 4: 1044–1059. <https://doi.org/10.1038/s41559-020-1198-2>
- Luoto M, Heikkinen RK (2008) Disregarding topographical heterogeneity biases species turnover assessments based on bioclimatic models. *Global Change Biology* 14: 483–494. <https://doi.org/10.1111/j.1365-2486.2007.01527.x>
- MacArthur RA, Wang LCH (1974) Behavioral thermoregulation in the pika *Ochotona princeps*: a field study using radiotelemetry. *Canadian Journal of Zoology* 52: 353–358. <https://doi.org/10.1139/z74-042>
- Macleán IMD, Early R (2023) Macroclimate data overestimate range shifts of plants in response to climate change. *Nature Climate Change* 13: 484–490. <https://doi.org/10.1038/s41558-023-01650-3>
- Marske KA, Lanier HC, Siler CD, Rowe AH, Stein LR (2023) Integrating biogeography and behavioral ecology to rapidly address biodiversity loss. *Proceedings of the National Academy of Sciences* 120: e2110866120. <https://doi.org/10.1073/pnas.2110866120>
- McLachlan JS, Clark JS, Manos PS (2005) Molecular indicators of tree migration capacity under rapid climate change. *Ecology* 86: 2088–2098. <https://doi.org/10.1890/04-1036>
- Meineri E, Hylander K (2017) Fine-grain, large-domain climate models based on climate station and comprehensive topographic information improve microrefugia detection. *Ecography* 40: 1003–1013. <https://doi.org/10.1111/ecog.02494>
- Millar CI, Westfall RD, Delany DL (2016) Thermal components of American pika habitat—how does a small lagomorph encounter climate? *Arctic, Antarctic, and Alpine Research* 48: 327–343. <https://doi.org/10.1657/AAAR0015-046>
- Mitchell PJ, Monk J, Laurenson L (2017) Sensitivity of fine-scale species distribution models to locational uncertainty in occurrence data across multiple sample sizes. *Chisholm R (Ed.). Methods in Ecology and Evolution* 8: 12–21. <https://doi.org/10.1111/2041-210X.12645>
- Morelli TL, Maher SP, Lim MCW, Kastely C, Eastman LM, Flint LE, Flint AL, Beissinger SR, Moritz C (2017) Climate change refugia and habitat connectivity promote species persistence. *Climate Change Responses* 4: 8. <https://doi.org/10.1186/s40665-017-0036-5>
- Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322: 261–264. <https://doi.org/10.1126/science.1163428>
- Mosblech NAS, Bush MB, van Woesik R (2011) On metapopulations and microrefugia: palaeoecological insights: Metapopulations and microrefugia. *Journal of Biogeography* 38: 419–429. <https://doi.org/10.1111/j.1365-2699.2010.02436.x>
- Moudrý V, Keil P, Gábor L, Lecours V, Zarzo-Arias A, Barták V, Malavasi M, Rocchini D, Torresani M, Gdulová K, Grattarola F, Leroy F, Marchetto E, Thouverai E, Prošek J, Wild J, Šimová P (2023) Scale mismatches between predictor and response variables in species distribution modelling: A review of practices for appropriate grain selection. *Progress in Physical Geography: Earth and Environment* 47: 467–482. <https://doi.org/10.1177/03091333231156362>
- Moyer-Horner L, Beever EA, Johnson DH, Biel M, Belt J (2016) Predictors of current and longer-term patterns of abundance of American pikas (*Ochotona princeps*) across a leading-edge protected area. Russo D (Ed.). *PLOS ONE* 11: e0167051. <https://doi.org/10.1371/journal.pone.0167051>
- Nadeau CP, Urban MC, Bridle JR (2017) Coarse climate change projections for species living in a fine-scaled world. *Global Change Biology* 23: 12–24. <https://doi.org/10.1111/gcb.13475>
- Nogués-Bravo D (2009) Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography* 18: 521–531. <https://doi.org/10.1111/j.1466-8238.2009.00476.x>
- Onoyama K (1991) Diurnal behaviors. In: Hokkaido Government (Ed.) *Survey Report of Wildlife Distribution: Pika Ecology*, 56–65.
- Onoyama K, Kurumada T, Ohmija S (1991) Home range. In: Hokkaido Government (Ed.) *Survey Report of Wildlife Distribution: Pika Ecology*, 66–94.
- Patiño J, Collart F, Vanderpoorten A, Martin-Esquivel JL, Naranjo-Cigala A, Mirolo S, Karger DN (2023) Spatial resolution impacts projected plant responses to climate change on topographically complex islands. *Diversity and Distributions* 29: 1245–1262. <https://doi.org/10.1111/ddi.13757>
- Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen I-C, Clark TD, Colwell RK, Danielsen F, Evengård B, Falconi L, Ferrier S, Frusher S, Garcia RA, Griffis RB, Hobday AJ, Janion-Scheepers C, Jarzyna MA, Jennings S, Lenoir J, Linnetved HI, Martin VY, McCormack PC, McDonald J, Mitchell NJ, Mustonen T, Pandolfi JM, Pettorelli N, Popova E, Robinson SA, Scheffers BR, Shaw JD, Sorte CJB, Strugnell JM, Sunday JM, Tuanmu M-N, Vergés A, Villanueva C, Wernberg T, Wapstra E, Williams SE (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* 355: eaai9214. <https://doi.org/10.1126/science.aai9214>
- Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31: 161–175. <https://doi.org/10.1111/j.0906-7590.2008.5203.x>
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Potter KA, Arthur Woods H, Pincebourde S (2013) Microclimatic challenges in global change biology. *Global Change Biology* 19: 2932–2939. <https://doi.org/10.1111/gcb.12257>
- Pu J, Zhao X, Dong P, Wang Q, Yue Q (2021) Extracting information on rocky desertification from satellite images: A comparative study. *Remote Sensing* 13: 2497. <https://doi.org/10.3390/rs13132497>
- QGIS Development Team (2023) QGIS Geographic Information System. <http://www.qgis.org>

- Randin CF, Engler R, Normand S, Zappa M, Zimmermann NE, Pearson PB, Vittoz P, Thuiller W, Guisan A (2009) Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology* 15: 1557–1569. <https://doi.org/10.1111/j.1365-2486.2008.01766.x>
- Rodhouse TJ, Hovland M, Jeffress MR (2017) Variation in subsurface thermal characteristics of microrefuges used by range core and peripheral populations of the American pika (*Ochotona princeps*). *Ecology and Evolution* 7: 1514–1526. <https://doi.org/10.1002/ece3.2763>
- Rull V (2009) Microrefugia. *Journal of Biogeography* 36: 481–484. <https://doi.org/10.1111/j.1365-2699.2008.02023.x>
- Sakiyama T, García Molinos J (2024) Northern pikas experience reduced occupancy due to surrounding human land use despite the occurrence of suitable microclimates. *Journal of Biogeography* 51: 1199–1212. <https://doi.org/10.1111/jbi.14815>
- Sakiyama T, Morimoto J, Watanabe O, Watanabe N, Nakamura F (2021) Occurrence of favorable local habitat conditions in an atypical landscape: Evidence of Japanese pika microrefugia. *Global Ecology and Conservation* 27: e01509. <https://doi.org/10.1016/j.gecco.2021.e01509>
- Scheffers BR, Evans TA, Williams SE, Edwards DP (2014) Microhabitats in the tropics buffer temperature in a globally coherent manner. *Biology Letters* 10: 20140819. <https://doi.org/10.1098/rsbl.2014.0819>
- Schwalm D, Epps CW, Rodhouse TJ, Monahan WB, Castillo JA, Ray C, Jeffress MR (2016) Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. *Global Change Biology* 22: 1572–1584. <https://doi.org/10.1111/gcb.13189>
- Shi H, Wen Z, Paull D, Guo M (2016) A framework for quantifying the thermal buffering effect of microhabitats. *Biological Conservation* 204: 175–180. <https://doi.org/10.1016/j.biocon.2016.11.006>
- Shiogama H, Ishizaki NN, Hanasaki N, Takahashi K, Emori S, Ito R, Nakaegawa T, Takayabu I, Hijioka Y, Takayabu YN, Shibuya R (2021) Selecting CMIP6-based future climate scenarios for impact and adaptation studies. *SOLA* 17: 57–62. <https://doi.org/10.2151/sola.2021-009>
- Smith AT (1974) The distribution and dispersal of pikas: influences of behavior and climate. *Ecology* 55: 1368–1376. <https://doi.org/10.2307/1935464>
- Smith AT (2018) *Ochotona hyperborea*. In: *Lagomorphs: pikas, rabbits, and hares of the world*.
- Smith AT (2020) Conservation status of American pikas (*Ochotona princeps*). Ruedas LA (Ed.). *Journal of Mammalogy* 101: 1466–1488. <https://doi.org/10.1093/jmammal/gyaa110>
- Smith AT, Nagy JD, Millar CI (2016) Behavioral ecology of american pikas (*Ochotona princeps*) at Mono Craters, California: living on the edge. *Western North American Naturalist* 76: 459. <https://doi.org/10.3398/064.076.0408>
- Stark JR, Fridley JD (2022) Microclimate-based species distribution models in complex forested terrain indicate widespread cryptic refugia under climate change. *Global Ecology and Biogeography* 31: 562–575. <https://doi.org/10.1111/geb.13447>
- Stickley SF, Fraterrigo JM (2023) Microclimate species distribution models estimate lower levels of climate-related habitat loss for salamanders. *Journal for Nature Conservation* 72: 126333. <https://doi.org/10.1016/j.jnc.2023.126333>
- Trivedi MR, Berry PM, Morecroft MD, Dawson TP (2008) Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. *Global Change Biology* 14: 1089–1103. <https://doi.org/10.1111/j.1365-2486.2008.01553.x>
- Urban MC (2015) Accelerating extinction risk from climate change. *Science* 348: 571–573. <https://doi.org/10.1126/science.aaa4984>
- Valavi R, Guillera-Arroita G, Lahoz-Monfort JJ, Elith J (2022) Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. *Ecological Monographs* 92. <https://doi.org/10.1002/ecm.1486>
- Varner J, Dearing MD (2014) The importance of biologically relevant microclimates in habitat suitability assessments. Moreau CS (Ed.). *PLOS ONE* 9: e104648. <https://doi.org/10.1371/journal.pone.0104648>
- Vignali S, Barras AG, Arlettaz R, Braunisch V (2020) SDMtune: An R package to tune and evaluate species distribution models. *Ecology and Evolution* 10: 11488–11506. <https://doi.org/10.1002/ece3.6786>
- Xu T, Hutchinson MF (2011) ANUCLIM Version 6.1 User Guide.
- Xu T, Hutchinson MF (2013) New developments and applications in the ANUCLIM spatial climatic and bioclimatic modelling package. *Environmental Modelling & Software* 40: 267–279. <https://doi.org/10.1016/j.envsoft.2012.10.003>
- Yamazaki D, Ikeshima D, Tawatari R, Yamaguchi T, O’Loughlin F, Neal JC, Sampson CC, Kanae S, Bates PD (2017) A high-accuracy map of global terrain elevations. *Geophysical Research Letters* 44: 5844–5853. <https://doi.org/10.1002/2017GL072874>
- Yates KL, Bouchet PJ, Caley MJ, Mengersen K, Randin CF, Parnell S, Fielding AH, Bamford AJ, Ban S, Barbosa AM, Dormann CF, Elith J, Embling CB, Ervin GN, Fisher R, Gould S, Graf RF, Gregr EJ, Halpin PN, Heikkinen RK, Heinänen S, Jones AR, Krishnakumar PK, Lauria V, Lozano-Montes H, Mannocci L, Mellin C, Mesgaran MB, Moreno-Amat E, Mormede S, Novaczek E, Opiel S, Ortuño Crespo G, Peterson AT, Rapacciuolo G, Roberts JJ, Ross RE, Scales KL, Schoeman D, Snelgrove P, Sundblad G, Thuiller W, Torres LG, Verbruggen H, Wang L, Wenger S, Whittingham MJ, Zharikov Y, Zurell D, Sequeira AMM (2018) Outstanding challenges in the transferability of ecological models. *Trends in Ecology & Evolution* 33: 790–802. <https://doi.org/10.1016/j.tree.2018.08.001>

Supplementary materials

Supplementary material 1

The following materials are available as part of the online article at <https://escholarship.org/uc/fb>. **appendix S1. Derivation of the bioclimatic variables.** **appendix S2. Validation of the bioclimatic variables.** **table S1. List of previous literature reporting the northern pika distribution in Hokkaido.** **table S2. Procedures for generating the environmental variables.** **fig. S1. Geographical map of the presence points used in this study.** **fig. S2. A histogram indicating the elevational difference within coarse-resolution grid cells.** **fig. S3. The modeled relationship between mean ambient and rock interstice temperatures.** **fig. S4. Scatterplots used for validating the bioclimatic variables.** **fig. S5. Validation plots of the bioclimatic variables used in the study.** **fig. S6. Result of the correlation analysis.** **fig. S7. Percentage of change in species’ range from the baseline period to future.** **fig. S8. Elevational difference between the coarse-resolution and fine-resolution cells at the presence points. (.docx)**
 Link: <https://doi.org/10.21425/fob.18.131541.suppl1>