







Lineage-level distribution models lead to more realistic climate change predictions for a threatened crayfish

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Abstract

Aim: As climate change presents a major threat to biodiversity in the next decades, it is critical to assess its impact on species habitat suitability to inform biodiversity conservation. Species distribution models (SDMs) are a widely used tool to assess climate change impacts on species' geographical distributions. As the name of these models suggests, the species level is the most commonly used taxonomic unit in SDMs. However, recently it has been demonstrated that SDMs considering taxonomic resolution below (or above) the species level can make more reliable predictions of biodiversity change when different populations exhibit local adaptation. Here, we tested this idea using the Japanese crayfish (*Cambaroides japonicus*), a threatened species encompassing two geographically structured and phylogenetically distinct genetic lineages.

Location: Northern Japan.

Methods: We first estimated niche differentiation between the two lineages of *C. japonicus* using *n*-dimensional hypervolumes and then made climate change predictions of habitat suitability using SDMs constructed at two phylogenetic levels: species and intraspecific lineage.

Results: Our results showed only intermediate niche overlap, demonstrating measurable niche differences between the two lineages. The species-level SDM made future predictions that predicted much broader and severe impacts of climate change. However, the lineage-level SDMs led to reduced climate change impacts overall and also suggested that the eastern lineage may be more resilient to climate change than the western one.

Main conclusions: The two lineages of *C. japonicus* occupy different niche spaces. Compared with lineage-level models, species-level models can overestimate climate change impacts. These results not only have important implications for designing future conservation strategies for this threatened species, but also highlight the need for incorporating genetic information into SDMs to obtain realistic predictions of biodiversity change.

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KEY WORDS

Cambaroides japonicus, evolutionarily significant unit, genetic lineage, habitat suitability, species distribution model, taxonomic unit

1 | INTRODUCTION

Amidst the current global climate emergency (Ripple et al., 2019), our planet is changing rapidly in an unpredictable manner. According to the latest assessment by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2019), climate change is one of the five most influential direct drivers of biodiversity decline, along with habitat loss, direct exploitation of organisms, pollution, and invasion of alien species. It has been demonstrated that climate change indiscriminately threatens species in virtually all ecosystems—terrestrial (Burrows et al., 2011; Pinsky et al., 2019), subterranean (Mammola, Cardoso, et al., 2019; Mammola, Piano, et al., 2019), freshwater (Woodward et al., 2010) and marine (Burrows et al., 2011; Pinsky et al., 2019). Climate change can affect species by altering physiological performance, phenology, geographical distribution and species interactions, among others (review by Hughes, 2000; Walther et al., 2002). For instance, there is mounting evidence that species are rapidly rearranging their distributions along elevational and/or latitudinal gradients in response to changing climates (Burrows et al., 2011; Lenoir et al., 2020). To better protect and manage biological resources in an era of climate change, it is therefore fundamental to gain a better understanding of how climate change will redefine the geography of life (Román-Palacios & Wiens, 2020).

Species distribution models (SDMs) are powerful tools in this regard, as they can estimate species' habitat suitability by determining statistical relationships between species' range data and environmental predictors, and can also be used to forecast how suitable areas may vary under different climate change scenarios (Araújo et al., 2019; Booth et al., 2014; Elith & Leathwick, 2009; Guisan et al., 2017). To date, SDMs have often been used to investigate the potential impacts of climate change on target species of conservation concern (Araújo et al., 2019; Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Zhang, Mammola, Liang, et al., 2020). For instance, Zhang, Mammola, Liang, et al. (2020) developed a SDM for the Critically Endangered Chinese giant salamander *Andrias davidianus* (Blanchard, 1871)—the world's largest extant amphibian—and found that this species might be extremely vulnerable to climate change and might lose more than two-thirds of its suitable habitat in the future.

As the term “species distribution model” suggests, the species level is the most commonly used taxonomic unit in SDMs (Qiao

et al., 2017; Smith et al., 2019). One basic assumption underlying species-level SDMs is “niche conservatism” (Guisan et al., 2017; Peterson et al., 1999), positing that species should exhibit uniform responses to climate and retain similar niche characteristics over space and time. However, recent studies have emphasized that taxonomic resolution below (or above) the species level should be considered in SDMs for some systems (e.g. Collart, Hedenäs, Broennimann, Guisan, & Vanderpoorten, in press; Guisan et al., 2017; Pearman et al., 2010; Serra-Varela et al., 2015; Smith et al., 2019). Different populations of the same species inhabiting geographically and ecologically distinct environments may experience local adaptation and thus have niches that are divergent to some extent (e.g. Zhang et al., 2020). For such systems, modeling habitat suitability below the species level should lead to more accurate range estimates and climate change projections (Collart et al., in press; Pearman et al., 2010; Smith et al., 2019). In threatened species conservation, for example, climate change responses of phylogeographic lineages have recently been considered for some taxonomic groups from terrestrial and marine systems (e.g. Cacciapaglia & van Woesik, 2018; Collart et al., in press; D'Amen et al., 2013; Lecocq et al., 2016), but such studies have rarely been conducted in freshwater systems (but see Zhao et al., 2020).

Here, we examined how predictions of climate change responses can differ when taking into account intraspecific genetic heterogeneity for a threatened freshwater arthropod, the Japanese crayfish *Cambaroides japonicus* (De Haan 1841) (see Species description in Methods for details). Most freshwater crayfish have specialized habitats and limited mobility, which contribute to their vulnerability to climate change (Hossain et al., 2018). *Cambaroides japonicus* is largely sedentary and its intraspecific phylogeography has been resolved for its entire distribution. There are two distinct genetic lineages (eastern and western) in *C. japonicus* delineated by partial sequences of mitochondrial and nuclear DNA (Koizumi et al., 2012). On the basis of molecular phylogeographic analysis, Koizumi et al. (2012) inferred that the two genetic lineages have undergone distinct evolutionary histories over several million years in different geographical regions characterized by differential climatic factors and topography. Given these different histories over a substantial time-scale, it is likely that these lineages have experienced at least some local adaptation, which would lead to an expectation of differential responses to climate change. In this case, it is important to compare future range projections at the levels of species and lineage to assess the impacts

of climate change (Benito Garzón et al., 2019; Peterson et al., 2019; Smith et al., 2019).

In this study, we quantified realized niches (i.e. the portion of the fundamental niche currently used by the species; Guisan et al., 2017; Soberón & Nakamura, 2009), developed SDMs and made future predictions to examine how climate change might influence *C. japonicus* by constructing species-level versus genetic lineage-level models. We sought to address the following hypotheses: (1) there will be divergence in realized niches between the eastern and western lineages of *C. japonicus*, and (2) there will be considerable differences between the future projections of the SDMs at the species and lineage levels. Our results address the uncertainty in climate change predictions for species with high intraspecific variation in genetic diversity, as well as highlight the importance of developing SDMs below the species level. Moreover, our results should provide a useful guide for designing conservation strategies for *C. japonicus* lineages.

2 | MATERIALS AND METHODS

2.1 | Species description

Cambaroides japonicus is designated a threatened species (Category II; Vulnerable) in the Ministry of the Environment, Japan's Red List (Ministry of the Environment, Japan, 2020) and data-deficient but with a decreasing population trend in the IUCN Red List (IUCN, 2020). The species is the only crayfish species native to Japan, endemic to freshwater areas of Hokkaido and northern Honshu in northern Japan (Miyake, 1982). Natural populations of this species have declined substantially in recent decades. Multiple stressors including habitat loss, water quality degradation, and predation and competitive exclusion by invasive crayfish are thought to be major factors for the observed decline of *C. japonicus* (Kawai, 2003; Usio et al., 2001). *Cambaroides japonicus* is also a popular pet for ornamental aquariums and is distributed through Internet auctions and aquarium shops (Kawai, 2003; N. Usio, personal observation). Nevertheless, there is no environmental law to protect this species except for the southernmost population in Akita Prefecture which was designated a national monument (Miyake, 1982). In addition to current pressures, another important yet largely neglected threat to *C. japonicus* might be climate change, given that the distributions of other crayfish species were predicted to be driven by temperature and other climatic conditions (e.g. Capinha et al., 2013; Gallardo & Aldridge, 2013; Zhang, Capinha, Usio, et al., 2020).

2.2 | Study area and species distribution data

Considering the known distribution of *C. japonicus*, we selected northern Japan (138°E–146°E, 40°N–46°N) as our study extent and restricted the analysis to freshwater areas (Figure S1). We identified freshwater areas with MERIT Hydro (Yamazaki et al., 2019), a

global hydrography dataset at 3 arc-second resolution (~90 m at the equator), and then resampled this layer to the spatial resolution of our environmental predictors (30 arc-seconds; ~1 km at the equator).

We obtained occurrence data for *C. japonicus* from published literature (Koizumi et al., 2012), data collections by the Bihoro Museum, Hokkaido, Japan (2001–2019), and field surveys (N. Usio 2003, 2015, K. Tanaka 2007–2017, S. Niwa 2000–2019, and N. Ichijo 2003–2012). From these sources, we collected a total of 497 presence records. Based on the phylogenetic results of Koizumi et al. (2012), which determined a clear spatial partition between the two lineages, we divided the study extent into two regions by drawing a boundary of straight lines to assign presence data to either the western or eastern lineage (Figure S1). Note, however, that eight presence records at the boundary were unable to be assigned to any lineage due to an absence of phylogenetic information; these were excluded from lineage-level SDM analyses. Overall, we assigned 325 records to the western lineage and 164 records to the eastern lineage.

In accordance with standard practices for SDMs, we cleaned and spatially thinned the presence records using a 5 km thinning distance to avoid spatial sampling bias (Kramer-Schadt et al., 2013) (see Supporting Information for Presence data processing). After processing the presence data, we retained 113 records for the species-level SDM, 47 records for the eastern lineage SDM, and 60 records for the western lineage SDM (Figure S1).

2.3 | Predictor variables

For modelling realized niches and potential distributions for *C. japonicus*, we initially considered 14 environmental predictor variables with a spatial resolution of 30 arc-seconds: eight bioclimatic predictors from CHELSA (Karger et al., 2017), three land use and land cover predictors (Li et al., 2016), and three topographic predictors (Amatulli et al., 2018; Hengl, 2018) (see Table 1 for details). We chose these variables based on our expert opinion that bioclimatic extremes, seasonality, and means likely influence the species' physiological performance; land use and land cover can have strong relationships with its habitat preferences; and water velocity and rain infiltration are closely related to topography and can affect habitat quality. The Japanese crayfish is typically found in small streams, ponds or mesic areas (where groundwater emerges) in broadleaf forests (Kawai, 2003; Usio, 2007). Therefore, we also generated a broadleaf forest variable using the EarthEnv dataset (Tuanmu & Jetz, 2014) by summing the layers for evergreen broadleaf trees, deciduous broadleaf trees and mixed/other trees (Table 1). We checked for collinearity among 15 predictors by calculating the pairwise Pearson's correlation coefficient (r) and retained one predictor when two or more were highly correlated (i.e. $|r| > .70$) (Zhang, Capinha, Karger, et al., 2020; Zhang et al., 2020). Given biological importance, collinearity analysis results, and data availability under present-day and future scenarios, we selected the following eight predictors for modelling: maximum temperature of warmest month, minimum

TABLE 1 The 15 environmental predictor variables considered in this study, marked with ✓ if used in model development and × if not used

Description	Reference	Used (✓) or not (×)
Annual mean temperature	Karger et al. (2017)	×
Temperature seasonality	Karger et al. (2017)	×
Maximum temperature of warmest month	Karger et al. (2017)	✓
Minimum temperature of coldest month	Karger et al. (2017)	✓
Annual precipitation	Karger et al. (2017)	×
Precipitation of wettest month	Karger et al. (2017)	✓
Precipitation of driest month	Karger et al. (2017)	✓
Precipitation seasonality	Karger et al. (2017)	×
Fraction of water in each grid cell	Li et al. (2016)	✓
Fraction of wetland in each grid cell	Li et al. (2016)	✓
Fraction of forest in each grid cell	Li et al. (2016)	✓
Fraction of broadleaf forest in each grid cell	Tuanmu and Jetz (2014)	×
Slope	Amatulli et al. (2018)	✓
Elevation	Amatulli et al. (2018)	×
Topographic wetness index	Hengl (2018)	×

Note: Future projections for slope, elevation and topographic wetness index are not available.

temperature of coldest month, precipitation of wettest month, precipitation of driest month, slope, and percent cover of forest, water, and wetland (Figure S2).

We considered two future time periods (2050s: average of 2041–2060; 2070s: average of 2061–2080) under two representative concentration pathway (RCP) scenarios (RCP 4.5 and RCP 8.5). We addressed the inherent uncertainty in future climate projections by considering four different global circulation models (CESM1-BGC, CMCC-CM, MIROC5, MPI-ESM-MR) (Karger et al., 2017) and obtained future projections for land use and land cover from Li et al. (2016). We assumed that slope would remain unchanged in the future.

2.4 | Niche comparisons

We used n -dimensional hypervolumes to quantify the realized niche space for the eastern and western lineages. In brief, we performed a principal component analysis on the eight selected predictors and used the first four principal components to describe species niches as they accounted for more than 75% of the total variance (Figure S3). We used the R package *hypervolume* (Blonder, 2019) to

construct hypervolumes for the two lineages. We used the volume of each hypervolume as a measure of the size of the realized niche in multidimensional space (note that the volume of a hypervolume is a unitless measure). We then used the R package *BAT* (Cardoso et al., 2020) to evaluate niche overlap between the two lineages. In particular, we expressed differentiation between hypervolumes as the sum of two components: niche shifts (i.e. replacement of space between hypervolumes) and niche contraction/expansion (i.e. net difference between hypervolumes) (Carvalho & Cardoso, 2020; Mammola & Cardoso, 2020). Niche differentiation varies from 0 (complete overlap between hypervolumes) to 1 (complete separation between hypervolumes).

2.5 | Species distribution modelling

We performed an extensive SDM analysis incorporating explorations of model complexity, evaluations of model transferability, and multiple post hoc procedures to better understand model behaviour, in line with current best practices for SDMs (Araújo et al., 2019). We developed SDMs for *C. japonicus* with Maxent 3.4.1, a machine learning presence-background algorithm used extensively to model species' ranges (Phillips et al., 2017). Machine learning algorithms like Maxent can produce overfitted models if run with default settings (Radosavljevic & Anderson, 2014), and thus a tuning process is advocated wherein different combinations of model settings are evaluated (Araújo et al., 2019; Merow et al., 2013). We first tuned Maxent with different combinations of feature classes, which govern the complexity of the model response [linear (L), quadratic (Q) and/or hinge (H)] and regularization multipliers, which penalize complexity (ranging from 0.5 to 4.0 at an interval of 0.5) using a version of the R package *ENMeval* under expansion (1.9.0) (<https://github.com/jamiemkass/ENMeval>; Muscarella et al., 2014). We evaluated each model using spatial block cross-validation, which is recommended for assessing model transferability, or how well models extrapolate to new environments (Roberts et al., 2017). We used the “block” partition option to divide the study region into four regions containing an equal number of presences: three blocks were used for model training and the withheld block for model validation, and this process was repeated until all blocks were withheld. Using new partitioning options in *ENMeval* 1.9.0, we specified spatial block partitions with different orientations for each occurrence dataset to best ensure each block represented discrete and contiguous areas: longitudinally for the eastern lineage, latitudinally for the western lineage and a combination of both for the species level (Figure S7). We chose optimal settings from among the candidate models by applying sequential criteria on performance metrics (Kass, Anderson, et al., 2020; Radosavljevic & Anderson, 2014). We first selected models with the minimum average 10% omission rate, or the proportion of validation occurrences with suitability predictions below that of the 0.1 quantile of training predictions. When multiple models had the minimum omission rate, we selected the model with the highest average validation AUC, or area under the receiver operating

characteristic curve for validation data. The AUC value ranges from 0 to 1, with higher values indicating better model discrimination—this metric is problematic for determining the absolute performance ability of presence-background SDMs, though it is acceptable to use for relative comparisons across models with the same data (Lobo et al., 2008).

We additionally performed post hoc procedures on the selected models via tuning to assess performance with different methods, determine variable importance and marginal response curves, and visualize the extent of extrapolation across spatial blocks. We first assessed the predictive abilities of the selected models using the continuous Boyce index calculated on the full dataset, which unlike AUC can be used for absolute evaluations of presence-background SDMs (Hirzel et al., 2006). The continuous Boyce index varies from -1 to 1 , whereby values above 0 indicate model predictions consistent with distribution data, values of 0 indicate performance no better than random, and values below zero refer to incorrect model predictions (Hirzel et al., 2006). We then ran a series of null model simulations ($n = 100$) using the complexity settings of each selected model to determine if the empirical models predicted validation data better than models built with random occurrences (results for simulations with 1000 iterations, which do not change our conclusions, are available in Figure S9). To do so, we used a recently described null model approach for SDMs available in *ENMeval* 1.9.0 that evaluates null model performance against the same validation data as the empirical model, making the null and empirical results directly comparable (Bohl et al., 2019; Kass, Anderson, et al., 2020). Next, we examined the permutation importance calculated by Maxent

and marginal response curves for the variables of each selected model. Finally, we calculated multivariate environmental similarity surface (MESS) values (Elith et al., 2010) using the *rmaxent* package (Baumgartner & Wilson, 2020) to determine how environmentally similar training data was to validation data for each spatial block. We plotted histograms to visualize the extent of extrapolation that occurred during cross-validation for each model.

We used the selected models and environmental variables to predict current and future habitat suitability. We made predictions using Maxent's cloglog transformation (bounded by 0 and 1) (Phillips et al., 2017) and additionally made binary range maps by thresholding the continuous predictions by the 10% omission values. All analyses were performed in R (R Core Team, 2020).

3 | RESULTS

3.1 | Comparison of realized niches

The volume of the four-dimensional hypervolume for the western lineage (1,971.14) was larger than that of the eastern lineage (1,848.67), and niche overlap between the two lineages was intermediate (0.50) (Figure 1). Niche differentiation was mainly due to contraction/expansion ($>90\%$), while niche shifts only contributed marginally ($<10\%$). Niche differentiation between the two lineages was mostly observable along PC2 (mainly explained by precipitation of driest month, minimum temperature of coldest month, and maximum temperature of warmest month) (Figures 1 and S3).

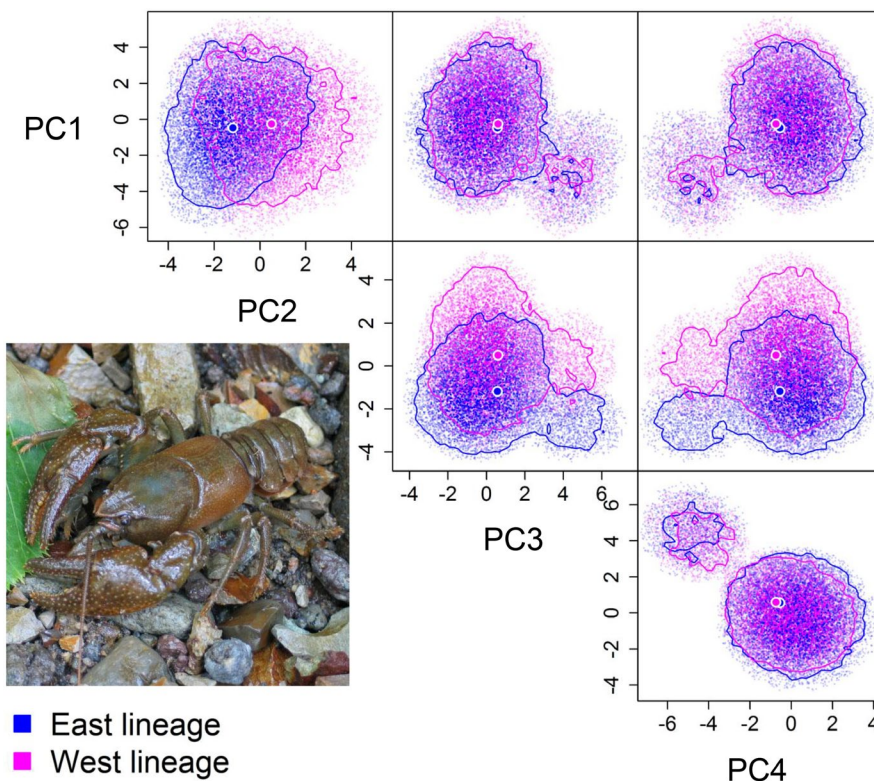


FIGURE 1 The four-dimensional hypervolumes for western and eastern lineages of Japanese crayfish. To visualize the shape and boundary of the hypervolumes in two dimensions, a random selection of 10,000 stochastic points for each hypervolume was used

TABLE 2 Optimal complexity settings, evaluation statistics and threshold values used to create binary maps for Maxent models for Japanese crayfish at the lineage and species levels

SDM	Feature ^a	RM ^b	Validation AUC	10% omission rate (%)	Threshold ^c	CBI ^d	No. of non-zero model coefficients
Western lineage	L	1.5	0.61	3.33	0.48	0.65	6
Eastern lineage	L	0.5	0.66	17.23	0.33	0.66	7
Species	LQH	3.0	0.65	8.74	0.46	0.92	12

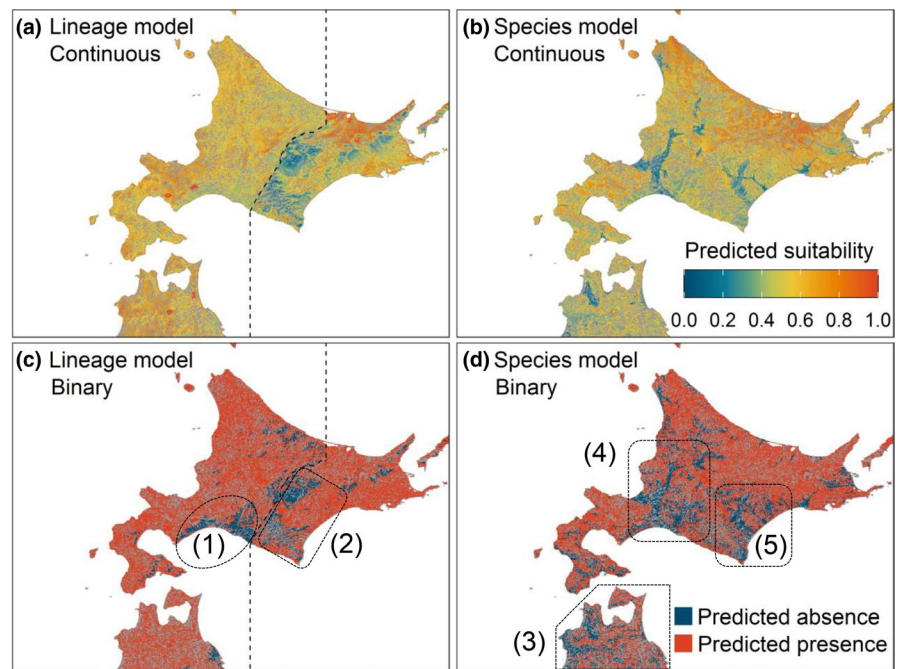
^aL: linear; Q: quadratic; and H: hinge.

^bRegularization multiplier.

^c10% omission suitability threshold.

^dContinuous Boyce Index. Calculated on full dataset.

FIGURE 2 Present-day habitat suitability of Japanese crayfish projected by lineage (a, c) and species (b, d) Maxent models. Continuous projections (a, b) were converted into binary results (c, d) using 10% presence thresholds. Dashed lines in (a) and (c) represent the boundary between eastern and western lineages. Numbers in parentheses represent region locations for reference: (1) coastal areas of south-central Hokkaido (Iburi and Hidaka Subprefectures), (2) east-central Hokkaido (Tokachi and Hidaka Subprefectures), (3) northern Honshu (Aomori and Akita Prefectures), (4) central Hokkaido (Ishikari, Sorachi and Iburi Subprefectures), and (5) eastern Hokkaido (Tokachi Subprefecture)



3.2 | Best-performing SDMs and variable importance

The three Maxent models we selected had different settings that resulted in different levels of complexity. The western and eastern lineage models were relatively simple (L1.5 with six non-zero coefficients and L0.5 with seven non-zero coefficients, respectively), while the species-level model was more complex (LQH3.0 with 12 non-zero coefficients) (Table 2 and Figure S4). All three models had continuous Boyce index values well above 0 (western: 0.65, eastern: 0.66, species: 0.92), indicating that each had predictions consistent with the distribution of presence data (Hirzel et al., 2006) (Table 2). For both 10% omission rate and validation AUC, the western lineage (both $p < .05$) and species-level (both $p < .01$) models performed significantly better than null models, and effect sizes for the species-level model were larger for both metrics (Table S1 and Figure S5). However, although the selected eastern lineage model performed

the best on withheld spatial blocks compared to other candidate models, its cross-validation performance was not significantly better than null models ($p = .094$ for AUC and $p = .933$ for omission rate; Table S1 and Figure S5). Thus, there is evidence that the transferability of the eastern lineage model may be poorer than that of the other models, resulting in higher uncertainty for its future projections. The environmental variables with the highest permutation importance differed among models: precipitation of wettest month was shared by all, while precipitation of driest month was shared by the lineage-level models, slope was shared by the western lineage and species models, and others were particular to each model (eastern: minimum temperature of coldest month, species: forest) (Table S2). For most environmental variables, the marginal response curves were either positive or relatively neutral, though precipitation of the wettest month was negative for all models (Figure S6). Regarding the MESS analysis, the eastern lineage model showed considerable extrapolation across spatial blocks, whereas

TABLE 3 Range size change (%) of Japanese crayfish *Cambaroides japonicus* under future climate conditions

GCM	East lineage				West lineage			
	RCP4.5 2050s	RCP8.5 2050s	RCP4.5 2070s	RCP8.5 2070s	RCP4.5 2050s	RCP8.5 2050s	RCP4.5 2070s	RCP8.5 2070s
CESM1-BGC	16.5 (-1.6) ^a	2.2 (-47.3)	16.4 (-8.4)	3.6 (-53.9)	5.5 (-10.6)	-6.4 (-63.5)	0.3 (-23.2)	-6.9 (-60.1)
CMCC-CM	8.1 (-28.2)	17.7 (-12.5)	5.3 (-33.4)	17.6 (-45.2)	-8.0 (-29.5)	1.8 (-22.1)	-6.0 (-41.4)	0.0 (-50.9)
MIROC5	7.5 (-38.4)	16.7 (-16.9)	14.2 (-33.8)	15.0 (-38.8)	-2.8 (-54.1)	3.3 (-32.9)	1.3 (-56.1)	0.9 (-56.4)
MPI-ESM-MR	10.2 (1.2)	8.9 (-16.0)	14.6 (-10.2)	17.2 (-23.1)	-3.1 (-9.8)	-9.2 (-32.4)	2.6 (-15.5)	0.6 (-43.2)

Abbreviation: GCM, global circulation model.

^aValues in parentheses represent range size change obtained from species-level Maxent model.

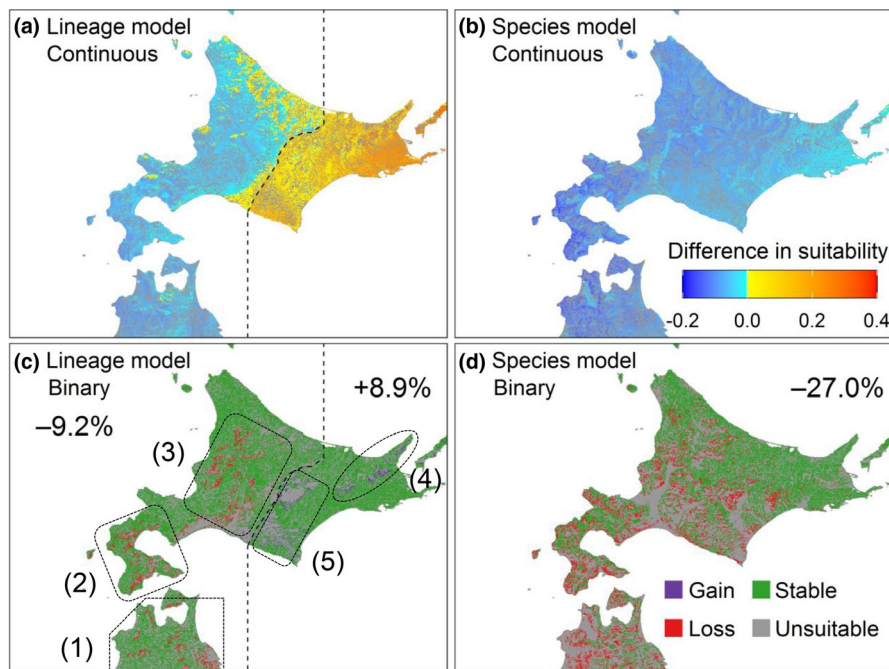


FIGURE 3 Changes in future habitat suitability of Japanese crayfish projected by lineage (a, c) and species (b, d) Maxent models. Continuous differences (a, b) expressed as difference between future and present-day habitat suitability. (c) and (d) indicate range size change based on binary results. Gain: area unsuitable at present but becomes suitable in future; stable: area suitable at present and in future; loss: area suitable at present but becomes unsuitable in future; and unsuitable: land area and freshwater area unsuitable at present and in future. Dashed lines in (a) and (c) represent boundary between eastern and western lineages. Numbers in parentheses represent region locations for easy reference: (1) northern Honshu (Aomori and Iwate Prefectures), (2) southern Hokkaido (Shiribeshi, Hiyama and Oshima Subprefectures), (3) north-central Hokkaido (Rumoi, Sorachi, Kamikawa, Ishikari and Iburi Subprefectures), (4) eastern Hokkaido (Okhotsk, Kushiro and Nemuro Subprefectures), and (5) east-central Hokkaido (Tokachi and Hidaka Subprefectures). We presented suitability projections of MPI-ESM-MR for RCP 8.5 in the 2050s as an example

extrapolation for the other models was proportionally quite smaller (Figures S7 and S8).

3.3 | SDM projections

Lineage and species SDMs resulted in different suitability projections for *C. japonicus* under current environmental conditions, though all predicted a majority of the study region to be suitable (Figure 2). The lineage-level models predicted broader suitable areas

than the species-level model for both the eastern (lineage: 84.1%, species: 78.4%) and western (lineage: 90.9%, species: 74.0%) regions. According to the lineage-level model binary range maps, there is some overlap but distinct differences exist between areas with predicted absence for each region: for the west, predicted absence occurs in the coastal areas of south-central Hokkaido, and for the east in more eastern coastal and inland areas (Figure 2). For the species model binary map, predicted absence has a much broader distribution, encompassing a majority of northern Honshu, central Hokkaido, and eastern Hokkaido (Figure 2).

The lineage-level and species-level SDMs resulted in largely different projections for future conditions, with reasonable agreement between GCMs (Table 3 and Figure 3). Taking the MPI-ESM-MR for RCP 8.5 in the 2050s as an example, according to the lineage-level model predictions, the western lineage is predicted to experience range restrictions (9.2% decrease overall) in north-central Hokkaido, southern Hokkaido and northeast Honshu, while the eastern lineage is predicted to slightly expand its range (8.9% increase overall) in two distant areas in east-central Hokkaido and eastern Hokkaido. According to the species-level model, large areas in Hokkaido and northern Honshu are predicted to become unsuitable (27.0% decrease overall, 16.0% decrease in east, 32.4% decrease in west) (Figure 3 and Table 3).

4 | DISCUSSION

In this study, we quantified realized niches for two genetic lineages of *C. japonicus* and used SDMs calibrated at species and lineage levels to investigate potential impacts of climate change on the species' range. We found intermediate niche overlap between the two lineages driven mainly by niche contraction/expansion processes, indicating that the two lineages occupy different niche spaces and that the niche conservatism assumption is not likely for this species. Our results also showed that species- and lineage-level SDMs projected largely different impacts of climate change: the species-level model predicted widespread range reductions, while the lineage-level models predicted contraction or little change for the western lineage but expansion for the eastern lineage. If there is indeed local adaptation in these two distinct lineages, which is probable given the known phylogenetic history and our niche overlap results, the lineage-level models are likely to make more realistic future predictions of habitat suitability than the species-level models, and our results show that the eastern lineage may be more resilient to climate change and may experience range expansion. Our findings demonstrate the importance of developing SDMs below the species level to obtain different predictions of biodiversity change that account for intraspecific variation, which has important implications for designing conservation and management strategies.

4.1 | Intraspecific variation in SDMs

Species distribution models have been frequently used in biodiversity assessments with the most common application being to estimate habitat suitability at the species level (e.g. Araújo et al., 2019; Collart et al., in press; Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Guisan et al., 2017). The species-level SDM relies on the "niche conservatism" assumption and does not take into account intraspecific phylogenetic or functional heterogeneity. Recently, however, many studies have demonstrated that local adaptation and intraspecific variation are important to account for in SDM exercises (e.g. Benito Garzón et al., 2019; Ikeda et al., 2017; Mammola et al., 2019; Oney et al., 2013).

Incorporating local adaptation and intraspecific variation into SDMs stems from the recognition that populations of species inhabiting largely different habitats over significant time-scales will often show adaptations to their respective local conditions, resulting in intraspecific niche variation (Collart et al., in press; Smith et al., 2019). While these local adaptations are known to result in clear morphological differences among populations in some organisms (e.g. DeWoody et al., 2015), crayfish are known to exhibit a wide range of body shape and colour differences among intraspecific populations, at least in part due to abiotic habitat characteristics (including light availability and water chemistry) and food resources therein (Holdich, 2012; Thacker et al., 1993). In crayfish, local adaptations to climate may be rather represented by intraspecific genetic differences that are only discernible via phylogenetic analysis, as in our study species (Koizumi et al., 2012). We now have ample evidence on intraspecific genetic divergence (Avice, 2000, 2009), as well as local adaptation (Hereford, 2009; Savolainen et al., 2013). Unsurprisingly, many researchers have recently stressed the benefits of taking genetic data into account when employing SDMs (e.g. Peterson et al., 2019; Razgour et al., 2019; Smith et al., 2019). However, incorporating genetic diversity into SDMs is still not routinely done for threatened or endangered species (but see Zhao et al., 2020 for an example of the Chinese giant salamander).

Our results showed that niche overlap between the eastern and western lineages of *C. japonicus* was only intermediate, indicating that there are real niche differences warranting consideration of lineage-level SDMs for this species. All of our models achieved high predictive performance on spatial blocks indicating good model transferability (compared to all other candidate models), but the species-level model predicted more range contractions due to climate change than the lineage-level models. It must be noted that the predictions for the eastern lineage model should be treated with higher uncertainty as this model did not perform better than null models evaluated on the same spatial blocks, likely because predicting to withheld blocks required more extrapolation for this model than for the other models. As genetic lineage-level SDMs incorporate possible local adaptations, they can give quite different predictions of climate change impacts, and our climate change projections were indeed less pessimistic for the lineage-level models. This finding is consistent with previous studies, which suggest that intraspecific variation may buffer species against climate change (e.g. Ikeda et al., 2017; Oney et al., 2013; Pearman et al., 2010; Razgour et al., 2019).

4.2 | Conservation implications

Our findings have important implications for designing conservation strategies for *C. japonicus*. With the purpose of preserving genetic diversity for conservation efforts, the concept of the Evolutionarily Significant Unit, also termed "Unified Species Concept" (De Queiroz, 2007), was developed to define separately evolving

lineages below the species level as the only reasonable conservation unit (Ryder, 1986). Although both lineages of *C. japonicus* are of conservation importance and should be preserved carefully, in the current state of limited conservation resources, our results indicate that the western lineage is likely to be more vulnerable to climate change, signalling that western Hokkaido and northern Honshu should be identified as priority conservation areas.

Given our findings and the multiple threats faced by *C. japonicus*, we propose several management guidelines applicable to both lineages. First of all, despite being designated as a threatened species, *C. japonicus* is still reported in Japan to be captured and traded as an aquarium pet; thus far, as is the case of several commercialized invertebrates (Fukushima et al., 2020), there are no specific laws enforced to protect this species from harvesting or distributing. Some prefectural governments in Japan are making efforts to protect specific threatened species through regulations under the Act on Conservation of Endangered Species of Wild Fauna and Flora (Act No. 75 of June 5, 1992). However, such species of special conservation concern are usually limited to a portion of critically endangered or endangered species (Category I). Because *C. japonicus* is designated a vulnerable species (Category II), it does not receive attention for protection by the current Regulations or Act in Japan. We think a wider range of taxonomic groups in the Red List, including vulnerable and near-threatened species, should be protected by the Regulation or Act. Second, to keep track of long-term changes in population dynamics, various populations of this species should be subject to continuous monitoring, which can be done effectively with advanced passive sampling techniques using environmental DNA (Ikeda et al., 2016). Long-term population data can also help validate our SDM projections, which should be treated as hypotheses in need of testing.

In conclusion, this study represents a first attempt to explore climate change impacts on *C. japonicus*, which to date have remained largely unexplored for this species. As multiple nuances exist, further studies are required to test whether intraspecific variation in environmental requirements between the two lineages reflects different adaptation at the physiological levels. Future experimental studies and monitoring programmes would be needed to explore these possibilities.

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CONFLICT OF INTEREST

The authors declare there are no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Presence records of the Japanese crayfish *Cambaroides japonicus* are presented in Figure S1. Environmental predictors can be retrieved from online databases (see details in Table 1). R scripts used for Maxent tuning are publicly available in Dryad (<https://doi.org/10.5061/dryad.z612jm6b7>).

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BIOSKETCH

Zhixin Zhang mainly focuses on biogeography and climate change, in particular exploring potential impacts of climate change on habitat suitability of both invasive and endangered species using species distribution modelling.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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