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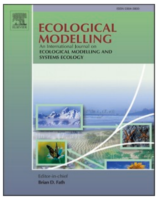

Incorporation of latitude-adjusted bioclimatic variables increases accuracy in species distribution models

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ABSTRACT

Latitudinal variations in species niche due to factors such as phenotypic plasticity and local adaptation pose fundamental problems for ecological niche modelling at large geographic scales. Species adaptation to varying climates across latitudes thus necessitates the latitudinal adjustment of climatic variables for incorporation into more accurate models of habitat suitability and species distribution. Previous studies have identified changes in species' elevational distributions across latitudes, however few studies incorporate latitude-adjusted variables into suitability or distribution models. In this study, we utilized generalized additive models (GAMs) to adjust bioclimatic variables by latitude in order to remove latitudinal variation in ecological niche models. We incorporated these latitude-adjusted variables into maximum entropy (MaxEnt) models of two species of toad, *Bufo sachalinensis* (previously *Bufo gargarizans*) and *Bufo stejnegeri*, in northeast Asia. We additionally identified thresholds in bioclimatic and terrain variables that delineate boundaries between the two *Bufo* species where their ranges overlap. We found that GAM adjustment of bioclimatic variables effectively removed latitudinal variation in said variables. MaxEnt models incorporating these latitude-adjusted variables had significantly improved model fit (AUC and TSS) for both *Bufo* species. We identified a potential sympatric area shared by the two species and delineated a geographic boundary thresholding the probable presence of one species over the other. This study shows a clear improvement for distribution models with the inclusion of latitude-adjusted bioclimatic variables for both narrow and wide-ranging species. This has implications for future distribution modelling practices, especially for geographically widespread species, and has potential for modelling species distributions in climate change scenarios. Further, the methodology for delimiting species thresholds has future use in modelling contact zones of related species.

1. Introduction

Species' ranges have been shown to be affected by environmental variables along a latitudinal gradient as a response to changing bioclimatic conditions along those gradients (Brock and Inman, 2006). Ecologically speaking, adaptation occurs when resource use changes to match availability (Dobzhansky, 1968). If there is a climatic gradient across latitudes, a species will exhibit some degree of adaptation to match that gradient, likely depending on how widespread it is. For instance, a relationship between latitude and distribution was found in the northeastern United States with *Catharus bicknelli* (Bicknell's Thrush), whose lower elevational limit has been observed to decrease by 81.63 m per degree of latitude (Lambert et al., 2005). In a study of *Gulo gulo* (wolverines) in Finland, Copeland et al. (2010) demonstrated that

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for average maximum August temperature across 14° of latitude, use of the bioclimatic variable by the species followed the average of availability, or the available range of the bioclimatic variable, at higher latitudes and diverged from the average at lower latitudes.

Due to a range of environmental conditions, including abiotic and biotic factors, a species is unlikely to occupy the full range of climatic conditions across its distribution, as evidenced by tree species which favour a "peaked suitability hypothesis" wherein species occupancy is proportional to the suitability index and peaks at the species' optimum (Boucher-Lalonde et al., 2012). Additionally, phenotypic plasticity specifies that a species can express different phenotypes in order to tolerate varying environmental conditions (Fox et al., 2019). Although phenotypic plasticity does not translate directly to adaptation (Schilthuizen and Kellermann, 2014), it can allow a species to colonize and endure conditions in novel habitats and is particularly advantageous to species at higher latitudes which experience greater climatic variation than those at lower latitudes. This positive correlation between phenotypic plasticity and latitude has been observed in an invasive plant *Taraxacum officinale* (Molina-Montenegro and Naya, 2012) and copepods (Pereira et al., 2017). In addition to phenotypic plasticity, species may also exhibit local adaptation corresponding to climate or latitude, as in *Panicum virgatum* (vascular plant; Casler et al., 2004), *Viola reichenbachiana* and *Aesculus hippocastanum* (vascular plants; Tryjanowski et al., 2006), and *Rana temporaria* (common brown frog; Liess et al., 2013).

According to Rapoport's rule, species found at higher latitudes will have a larger geographic range than those found at lower latitudes (Stevens, 1989). This is because higher latitudes have greater climatic variability, so an organism found at high latitudes will be adapted to and experience a wider range of climatic conditions than lower latitude species (Stevens, 1989). This pattern is found in many taxa, including reptiles and amphibians in North America (Conant, 1958; Stevens, 1989); and Rapoport's rule has been demonstrated more recently in snakes (Böhm et al., 2017) but is shown to be more regional than global for amphibians (Whitton et al., 2012).

Although adaptation and plasticity across latitudinal gradients are important for species physiology, few species distribution or habitat modelling techniques consider species' adaptability to new climates or geographic variation in climate tolerance within a species. That is, populations at higher latitudes will experience larger climatic fluctuations than those at lower latitudes (Bonebrake and Mastrandrea, 2010; De Frenne et al., 2013) and will therefore likely have different suitability requirements. Distribution and habitat use models incorporating latitude-adjusted elevation have been created for *G. gulo*, wolverines, in the United States (Carroll et al., 2020; Inman et al., 2012), phenology of bird species in western North America (Socolar et al., 2017), and woodboring beetle outbreak predictions (Ray et al., 2019). However, this method of incorporating latitude-adjusted elevation is limited to a single linear conversion of an indicator of climatic variation and remains untested against unadjusted corresponding variables. Other methods incorporating adaptation in distribution models largely rely on genetics (Hällfors et al., 2016; Kearney et al., 2009), which are not always readily available for many taxa of interest to modelling. Some methods allowing for geographic differences are trait-based (Benito Garzón et al., 2019), or mechanistic, which will not work for understudied species (Evans et al., 2015). Another type of latitudinal adjustment uses latitude in bias correction (Brown, 2014), however this is meant to correct for greater amounts of model background points at higher latitudes due to unequal cell size rather than accounting for potential adaptation of species to higher latitudes. To our knowledge no studies currently utilize latitude-adjusted bioclimatic factors as environmental predictor variables.

The basis of utilizing latitude-adjusted bioclimatic variables is that species use environmental factors relative to what is available to them, and so these adjusted variables will provide a baseline from which this relative use can be modelled and extrapolated. To address latitudinal variation as a factor in species distributions, we utilized a suite of ecological modelling methods including generalized linear models (GAMs), maximum entropy (MaxEnt) algorithm and thresholding. Our primary objective was to test the effect of incorporating latitude-adjusted bioclimatic variables on the model fit statistics for species distribution models of two example *Bufo* (toad) species from northeast Asia. As a secondary objective, we aimed to delineate a geographic boundary between the two *Bufo* species, which are geographically close but whose ecological requirements are effectively exclusive of each other. In doing so we present novel methods for delineating species thresholds in sympatric areas.

2. Materials and methods

2.1. Target species

To analyse effects of latitude on bioclimatic niche, we chose to focus on two species of toads, *Bufo sachalinensis* and *Bufo stejnegeri*, ranging across a similar geographic extent in northeast Asia. *Bufo sachalinensis* was recently split from *B. gargarizans*, and the species is widespread across northeast China, the Russian Primorye region and the Korean peninsula (Othman et al., 2022). The species is common and found in many types of landscapes (IUCN SSC Amphibian Specialist Group, 2019). It mainly inhabits lowland areas and is less common at higher elevations (Borzée et al., 2017; Zhan and Fu, 2011). Conversely to *B. sachalinensis, B. stejnegeri* has a more restricted range, occurring in the Korean peninsula and northeastern China (Borzée et al., 2021; IUCN SSC Amphibian Specialist Group 2020, 2020). The species is restricted to forests and wetlands and is mostly found at higher elevation streams in mountainous areas (Fong et al., 2020; Lee et al., 2010). While the two species are similar in appearance, their habitats differ such that they are not expected to be found living sympatrically (Messenger et al., 2020; Othman et al., 2022), and are only purported to do so in the southern Korean peninsula (Matsui, 1980). The inclusion of both species in this study allowed us to analyse the effect of latitude on both widespread and narrow ranging species and to delimit their ranges and contact zones.

2.2. Occurrence data and geographic range

To model distributions of our two focal species, we collected occurrence data from multiple sources including the literature (Matsui, 1980; Zhang et al., 2016; Zhao et al., 2008), governmental survey data (National Institute of Ecology Korea), open-source and citizen science data (GBIF doi:10.15468/dl.gnm233, inaturalist.org, naturing.net), and field observations from authors [dataset](Andersen et al., 2021). For the purpose of this study, we only included *B. sachalinensis* occurrence points following the definition of Othman et al. (2022) since the geographic range of the species overlaps with that of *B. stejnegeri*, it is deeply divergent from the clade *B. gargarizans*, and the species has specific ecological requirements (Borzée et al., 2017). In total, we used 695 occurrences of *B. sachalinensis* and 639 occurrences of *B. stejnegeri*. We also collected 976 absence points for *B. stejnegeri*, defined as a surveyed location where the species was not found for three visits to the site. For *B. sachalinensis*, we considered *B. stejnegeri* occurrences as absence points, and vice versa, since their habitats exclude each other (Kang and Yoon, 1975; Matsui, 1980).

Our total geographic range (34.0°N to 56.0°N and 116°E to 145°E; see Fig. 2) was approximately that of the easternmost *B. sachalinensis* clade (Borzée et al., 2017) expanded to the next whole decimal degree from occurrence points to include potential unknown areas of distribution. We excluded Japan and Jeju Island from the geographic range, as neither species is found on these islands.

2.3. Latitude adjustment for bioclimatic variables

To adjust for latitudinal gradient as to remove latitudinal variation of bioclimatic variables, we used a modified version of the method presented by Brock and Inman (2006), which was originally used to adjust treeline elevation across latitudes. While they suggest in their study that this method may not be suitable for bioclimatic variables, the purpose of the current study is to determine whether incorporation of such latitude-adjusted variables in modelling can lead to more accurate distribution models. Instead of using a linear model as in Brock and Inman (2006), we used a generalized additive model (GAM, 'gam' function in the 'mgcv' R package). GAMs, which describe nonparametric relationships between predictor and response variables (Hastie and Tibshirani, 1987), are largely used in ecology to ascertain relationships between environmental conditions and species presence probability (Leathwick et al., 2006; Yee and Mitchell, 1991; Zaniewski et al., 2002). These are useful in tackling the shortcomings of generalized linear models (GLMs) which assume a linear relationship between predictors and responses, as such responses in ecological studies can be much more complicated (Larsen, 2015), for example exhibiting bell-shaped responses instead of linear ones (Yee and Mitchell, 1991). Similarly, previously referenced studies which incorporate latitude-adjusted treeline elevation use both linear and quadratic terms (Ray et al., 2019; Socolar et al., 2017), demonstrating that such environmental responses across latitudinal gradients are more complex than simple linear models and such blanket assumptions cannot be made especially for multiple variables.

To utilize GAMs in our distribution models, we conducted latitude adjustment of bioclimatic variables with R version 3.6.1. We trained GAMs for each of 19 bioclimatic variables (from WorldClim version 2.0; Fick and Hijmans, 2017) from a dataset consisting of 20,000 random background points across the full extent of the study area (combined range of both species; 34°N to 56°N, 116°E to 145°E), and using latitude as our smoothing variable: gam(bio~s(latitude)) (Wood and Wood, 2015). We projected this model to a latitude raster covering our study area, then subtracted from this layer the expected value at 45° of latitude, or the mid latitude of our study area (Brock and Inman, 2006). This layer we then subtracted from the original raster for the bioclimatic variable. This equation, adapted from Brock and Inman (2006), is represented by:

$$V' = V - (V_{GAM} - V_{45})$$

Where:

$$V' = Latitude - adjustedvariable$$

$$V = Unadjustedvariable$$

$$V_{GAM} = VariablepredictedbyGAMmodel$$

$$V_{45} = Variablepredictedvalueat45^{\circ}latitude$$

2.4. MaxEnt distribution models

Our primary objective was to create a spatial model that best represented the species' distributions while incorporating latitudinal gradients corrected as described in this study, using the program MaxEnt (Phillips et al., 2017). We created and tested 36 models (see Table 1) for each *Bufo* species using different combinations of unadjusted and latitude-adjusted variable types, variable selection, and bias layers. We

Table 1

MaxEnt model types created with corresponding maximum true skill statistic (TSS), area under the curve (AUC), and percent omission at the 10 percent omission threshold for *Bufo sachalinensis* and *Bufo stejnegeri* in NE Asia. Percent contribution is abbreviated to CP while permutation importance is abbreviated to PI. Bolded values are the highest values for Max TSS and AUC, by species. Asterisks denote the final selected MaxEnt models.

			Bufo sachalinensis			*Bufo stejnegeri*		
Variables	Selection	Bias level	Max TSS	AUC	Omission	Max TSS	AUC	Omission
Unadjusted	Full	None	0.5857	0.8615	0.1185	0.8651	0.9678	0.1163
Unadjusted	Full	Weak	0.5903	0.8519	0.1231	0.8652	0.9779	0.1085
Unadjusted	Full	Moderate	0.6024	0.8609	0.1291	0.8607	0.9786	0.1101
Unadjusted	Full	Strong	0.5772	0.8509	0.1428	0.8613	0.9766	0.1101
Unadjusted	CP	None	0.5283	0.8243	0.1018	0.8517	0.9644	0.1069
Unadjusted	CP	Weak	0.5012	0.8104	0.1078	0.8601	0.9738	0.1022
Unadjusted	CP	Moderate	0.5335	0.8359	0.1140	0.8629	0.9768	0.1038
Unadjusted	CP	Strong	0.5167	0.8312	0.1231	0.8589	0.9759	0.1038
Unadjusted	PI	None	0.5215	0.8238	0.1018	0.8612	0.9668	0.1053
Unadjusted	PI	Weak	0.5632	0.8394	0.1109	0.8591	0.9767	0.1006
Unadjusted	PI	Moderate	0.5737	0.8483	0.1139	0.8567	0.9769	0.1038
Unadjusted	PI	Strong	0.5546	0.8421	0.1124	0.8565	0.9753	0.1085
Latitude-Adjusted	Full	None	0.6329	0.8887	0.1155	0.8429	0.9625	0.1133
Latitude-Adjusted	Full	Weak	0.6291	0.8907	0.1231	0.8450	0.9669	0.1148
Latitude-Adjusted	Full	Moderate	0.6487	**0.8965**	0.1200	0.8475	0.9697	0.1195
Latitude-Adjusted	Full	Strong	**0.6532***	0.8921	0.1216	0.8539	0.9725	0.1195
Latitude-Adjusted	CP	None	0.6021	0.8751	0.1201	0.8302	0.9563	0.1069
Latitude-Adjusted	CP	Weak	0.5786	0.8713	0.1200	0.8147	0.949	0.1054
Latitude-Adjusted	CP	Moderate	0.5990	0.8795	0.1292	0.8212	0.9545	0.1022
Latitude-Adjusted	CP	Strong	0.5951	0.8742	0.1216	0.8304	0.9597	0.1085
Latitude-Adjusted	PI	None	0.6173	0.8719	0.1003	0.8302	0.9563	0.1054
Latitude-Adjusted	PI	Weak	0.5917	0.8758	0.1216	0.8410	0.9609	0.1053
Latitude-Adjusted	PI	Moderate	0.6103	0.8807	0.1292	0.8398	0.9637	0.1069
Latitude-Adjusted	PI	Strong	0.5868	0.8742	0.1171	0.8555	0.9692	0.1038
Both	Full	None	0.6158	0.8725	0.1155	0.8842	0.9757	0.1132
Both	Full	Weak	0.6043	0.8671	0.1306	0.8871	**0.9822**	0.1117
Both	Full	Moderate	0.6307	0.8773	0.1398	**0.8882***	0.9818	0.1211
Both	Full	Strong	0.6211	0.8671	0.1353	0.8823	0.9797	0.1196
Both	CP	None	0.6010	0.8604	0.1125	0.8808	0.9739	0.1085
Both	CP	Weak	0.5475	0.8469	0.1273	0.8847	0.9796	0.1007
Both	CP	Moderate	0.5824	0.8614	0.1268	0.8772	0.9777	0.1054
Both	CP	Strong	0.5632	0.85	0.1261	0.8728	0.976	0.1085
Both	PI	None	0.5769	0.8567	0.1124	0.8737	0.9702	0.1053
Both	PI	Weak	0.5658	0.8534	0.1200	0.8780	0.98	0.0991
Both	PI	Moderate	0.5702	0.8603	0.1215	0.8781	0.9795	0.1054
Both	PI	Strong	0.5524	0.8483	0.1337	0.8820	0.9783	0.1069

created models using latitude-adjusted variables only, unadjusted variables only, and both unadjusted and latitude-adjusted variables combined. By combining unadjusted and latitude-adjusted variables, we were able to apply both strict climatic limitation (unadjusted) and variability with latitude (latitude-adjusted). We also used unadjusted elevation (USGS), slope, slope', and slope''. Slope was derived using the Slope tool in ArcMap 10.6 (ESRI Redlands, CA, USA). Both slope' and slope'' were derived through the Focal Statistics tool in ArcMap 10.6 (ESRI Redlands, CA, USA), creating averaged raster values within a neighbourhood of 3 and 10 raster cells, representing average slope in degrees within a ~5.44 km^2 area and ~60.5 km^2 area, respectively. Landscape variables were not used in model training as occurrence points were taken from the years 1890–2020 (of 1585 total observations, 92 were taken before 1970 and 396 were taken after 2000), and landscape variables are subject to change over time due to human activities and yearly variations, especially on the Korean peninsula (Lee and Miller-Rushing, 2014; Park et al., 2014). We then ran models containing the full set of variable types (unadjusted, latitude-adjusted, or both), then used model selection to reduce model complexity (Warren and Seifert, 2011) by selecting amongst correlated variables ($r < 0.8$) based on percent contribution and permutation importance, separately. Since bias in the current study was largely driven by sampling effort within countries, we created three bias layers (input in the MaxEnt platform) representing the number of occurrence points per country, number of presence and absence points for *B. sachalinensis*, and number of presence and absence points for *B. stejnegeri*. We therefore created four model sets corrected for no bias (model run without bias layer correction), weak bias (occurrence points per country), moderate bias (presence and absence points for *B. sachalinensis*), and strong bias (presence and absence points for *B. stejnegeri*) based on the number of occurrence points represented, the lowest number being weak bias and highest number being strong bias.

When running MaxEnt, we used environmental layers (Table A.1) with a 0.0083 decimal degree (dd) (~778 m) resolution, the coarsest resolution of all layers. For model replication, we used the cross-validate run type option with five replicates (5 k-fold). We set background points at 20,000 (Hill et al., 2012; Sidder et al., 2016; Jenkins et al., 2020; Muscatello et al., 2021) and removed duplicate presence points within the same cell of the environmental layers (0.0083 dd). We set background points at 20,000 rather than the default 10,000 because increasing the number of background points can improve model accuracy (Phillips and Dudík, 2008; Barbet-Massin et al., 2012) and because the larger number of points allowed more thorough sampling of environmental factors across our large study area. All other parameters were unchanged from MaxEnt's base settings (Phillips et al., 2017). The easternmost *Bufo sachalinensis* clade is found in lower elevations with upper elevation limits ranging from 800 m (Borzée et al., 2017) to 1600 m (Zhan and Fu, 2011). We therefore used 1400 m as an upper elevation cutoff in geographical representation of our selected model for the species, as it was the maximum elevation value of our occurrence points. For *B. stejnegeri*, we removed unsuitable landscape classes (agriculture, bare, grassland, urban; Lee et al., 2010; source: MDAUS Basevue 2013 World Land Cover layer with 30 m resolution) from suitable area in our selected model for the species.

To test our distribution models, we opted to test presence with known absence locations from our dataset, rather than using the background points created in MaxEnt, as those points can only be considered pseudo-absences and may represent locations where the species is actually present. For testing *B. sachalinensis*, we added 1000 random points >0.0083 dd away (resolution of environmental layers) from occurrence of both *B. sachalinensis* and *B. stejnegeri*, to cover the full geographic range of the *B. sachalinensis*. From the model values at our presence and absence points, we calculated area under the curve (AUC) of the receiver operating characteristic (ROC) and maximum true skill statistic (TSS; Allouche et al., 2006) of presence-absence by predicted values. To test for overfitting, we additionally calculated the test omission rate at the 10 percent omission threshold. We selected the best model for each species based on maximum TSS (sensitivity + specificity – 1; Allouche et al., 2006) of actual by predicted values at the maximum test sensitivity plus specificity threshold, since this statistic best maximizes the true positive and negative rates while minimizing the false positive and negative rates. Sensitivity is defined as "the proportion of correctly predicted presences" and specificity as "the proportion of correctly predicted absences" (Allouche et al., 2006). To determine which combinations of variable types, variable selections, and biases significantly affected model fit, we ran analysis of variance and TukeyHSD tests on AUC and TSS using variable types, variable selections, and biases as factor covariates. These analyses were conducted with R version 3.6.1.

2.5. *Species boundary*

Our secondary objective was to delineate a geographic boundary between the two *Bufo* species. To do this, we calculated environmental variable thresholds at which one species could be reliably found over the other by applying the sensitivity and specificity concepts (Allouche et al., 2006). By equating sensitivity and specificity for a binary where *B. sachalinensis* = 1 and *B. stejnegeri* = 0, we were able to find the threshold at which one species could be found over the other. In this analysis, we calculated equal sensitivity and specificity thresholds for unadjusted and latitude-adjusted bioclimatic variables, elevation, and three slope variables (slope, slope', and slope'') by using the extracted values of each environmental variable at observation points. These analyses were conducted with R version 3.6.1. For geographical representation we created a weighted average of the 20 thresholded layers with the highest TSS values (sensitivity + specificity – 1; Allouche et al., 2006), weighted by their corresponding TSS values (Marmion et al., 2009). We then overlaid the weighted average over the overlapping area of our selected MaxEnt models that were thresholded using the maximum TSS threshold approach. The average width of these overlap areas (collectively referred to as "ribbon") was calculated from the generic equation to find the width of a rectangle with the same perimeter and width of the irregular polygon, using the quadratic equation:

$$width = \frac{Perimeter - \sqrt{Perimeter^2 - 16 * Area}}{4}$$

All areas were calculated after projecting our models to the Behrmann (world) equal area projection (ESRI: 54,017).

3. Results

3.1. *Latitude adjustment for bioclimatic variables*

GAMs of bioclimatic variables using a smoothed latitude coefficient described between 11.7% and 87.5% of variation ($\mu = 53.5\% \pm 25.1\%$) for the 19 bioclimatic variables tested. These models showed that the smoothed latitude coefficient was significant for all bioclimatic variables. After applying the formula for latitude adjustment, the adjusted R^2 was 0 and the p-value was 1 for all variables, effectively removing latitudinal variation (Fig. 1).

3.2. *MaxEnt distribution models*

Our MaxEnt models had AUC values ranging between 0.8104 and 0.8965 for *B. sachalinensis* and between 0.9490 and 0.9822 for *B. stejnegeri*, and maximum TSS ranging between 0.5012 and 0.6532 for *B. sachalinensis* and between 0.8147 and 0.8882 for *B. stejnegeri*. For *B. sachalinensis*, the selected model (Fig. 2) with the highest TSS of 0.6532 (AUC = 0.8921) was the model using latitude-adjusted variables only without variable selection, and the strong bias layer (Table 1). The full area of minimum suitability for the *B. sachalinensis* model was 2356,241 km^2 (~73.8% of total study area), with the area above the

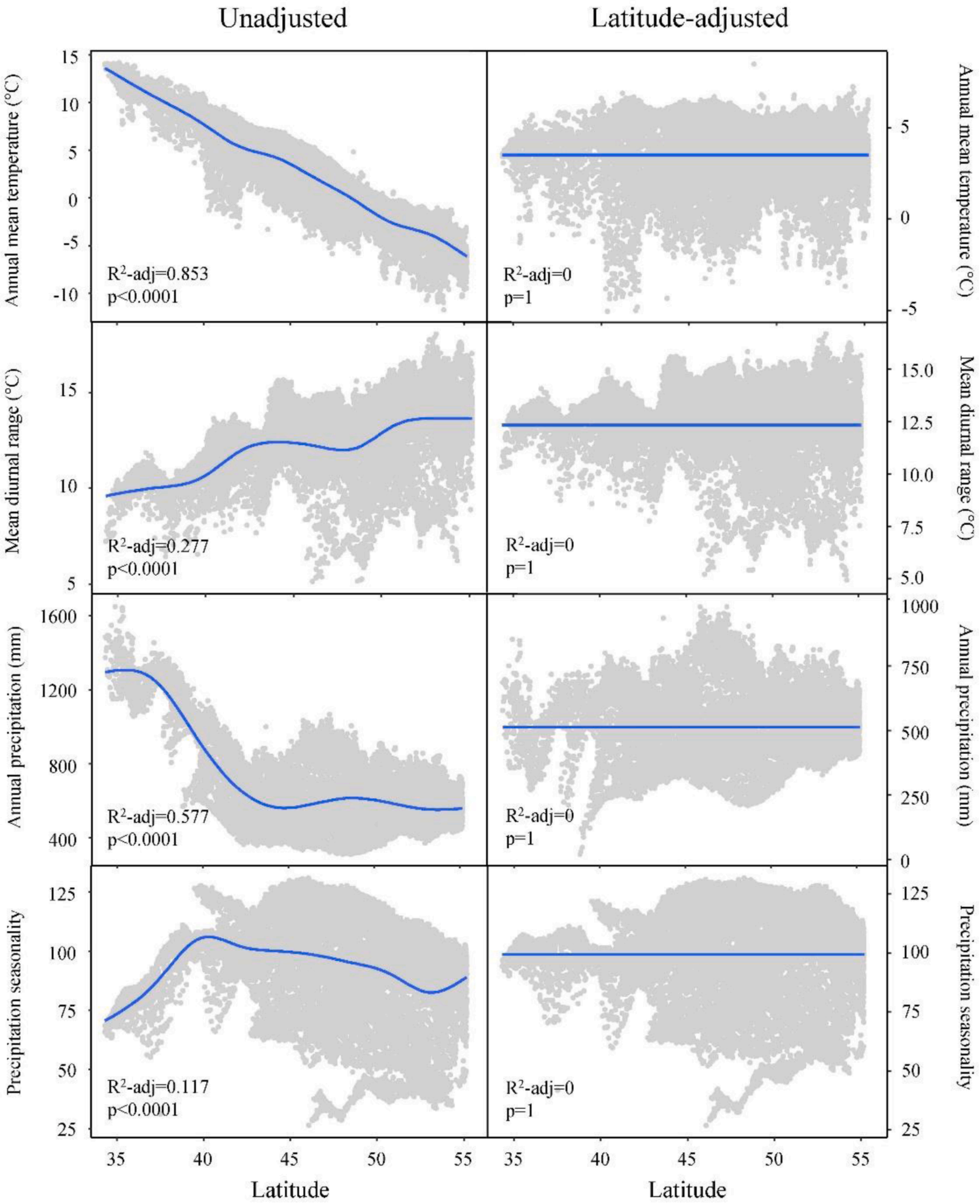

Fig. 1. Exampled unadjusted and latitude-adjusted bioclimatic variables (bio1, bio2, bio12, bio15) using generalized additive model (GAM) smoothing for 20,000 background points across northeast Asia. Example variables were chosen based on a range of adjusted R^2 values of the unadjusted bioclimatic variable correlation with latitude to demonstrate the capability of the GAM adjustment in removing latitudinal variation.

maximum TSS of 642,470 km^2 (~20.1% of total study area). For *B. stejnegeri*, the selected model (Fig. 3) with the highest TSS of 0.8882 (AUC = 0.9818) was the model using all variable types (unadjusted and latitude-adjusted) without variable selection, and the medium bias layer (Table 1). The full area of minimum suitability for this model was 375,590 km^2 (~11.8% of total study area), with the area above the maximum TSS of 144,666 km^2 (~4.5% of total study area). For details of variables used in each model, see Appendix A.3.

Analysis of variance for effect of model covariates on AUC and TSS revealed that for *B. sachalinensis*, variable type (unadjusted vs. latitude-adjusted vs. both) had the greatest influence on AUC ($F_{3,28} = 140.9$, $p < 0.0001$) and TSS ($F_{3,28} = 47.8$, $p < 0.0001$), followed by selection (full vs. percent contribution vs. permutation importance; AUC: $F_{2,28} = 42.9$, $p < 0.0001$; TSS: $F_{2,28} = 45.1$, $p < 0.0001$) and bias (AUC: $F_{3,28} = 5.084$, $p = 0.0062$; TSS: $F_{3,28} = 3.153$, $p = 0.0404$). The Tukey HSD test found that latitude-adjusted variables with the exclusion of unadjusted variables had the highest of both statistics, followed by all variable types, followed by unadjusted variables only ($p < 0.0001$ for all pairs). The full model had higher AUC and TSS than models reduced by selection based on percent contribution and permutation importance ($p < 00{,}001$ for both pairs), where the latter two were not significantly different ($p = 0.1692$). Significant differences were found between models incorporating medium and weak bias layers (AUC: $p = 0.0047$; TSS: $p = 0.0341$), and for AUC between models incorporating strong and medium bias layers ($p = 0.0432$).

The same analysis for *B. stejnegeri* also revealed that variable type had the greatest influence on both AUC ($F_{3,28} = 66.4$; $p < 0.0001$) and TSS ($F_{3,28} = 119.4$; $p < 0.0001$). Bias had a stronger effect ($F_{3,28} = 8.926$,

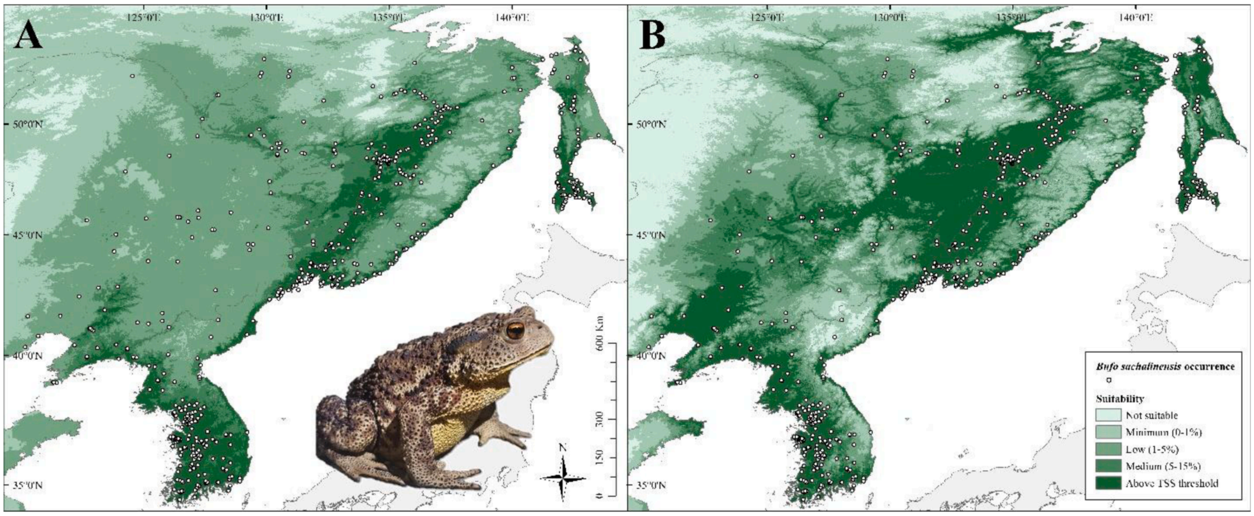

Fig. 2. Species distribution model of *Bufo sachalinensis* in northeast Asia from unadjusted (A) and adjusted (B) selected MaxEnt model incorporating latitude-adjusted bioclimatic variables without removal of variables by model selection and adjusting for a strong bias. Elevations above 1400 m are removed from the suitable range as the northeast Asian *Bufo sachalinensis* clade is not found above that elevation.

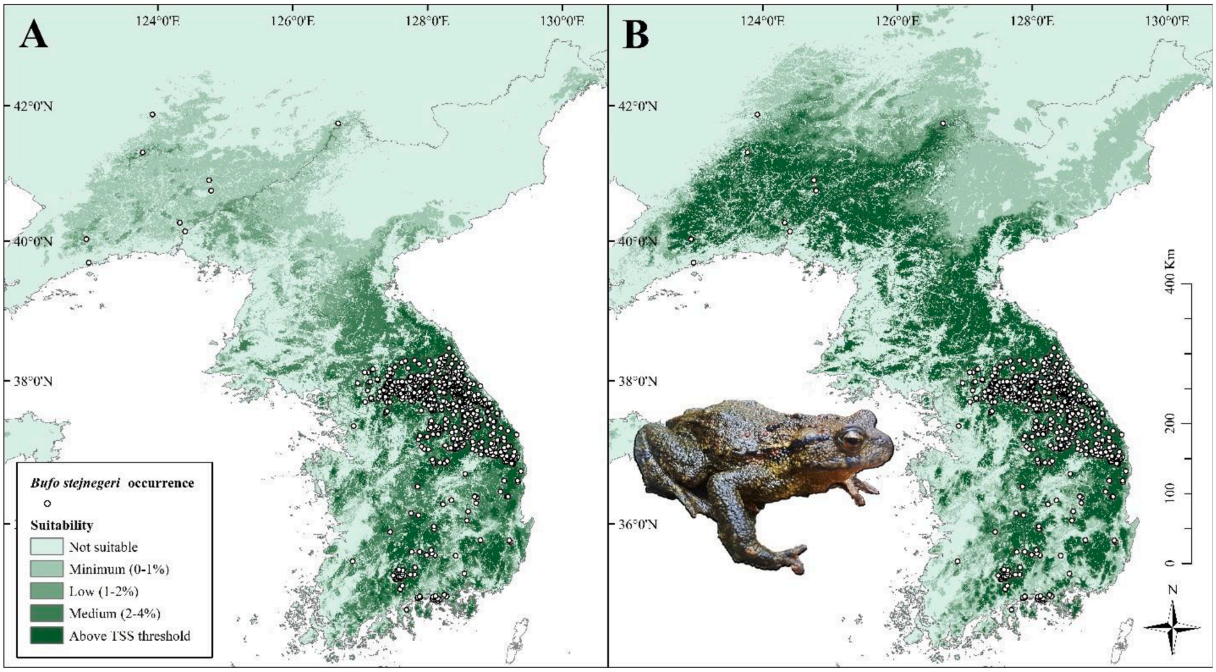

Fig. 3. Species distribution model of *Bufo stejnegeri* in China and on the Korean peninsula from unadjusted (A) and adjusted (B) selected MaxEnt model incorporating latitude-adjusted and non-adjusted bioclimatic variables without removal of variables by model selection and adjusting for an intermediate bias. Unsuitable habitat classes (agriculture, bare, grassland and urban from MDAUS Basevue 2013 World Land Cover layer) are removed from the suitable range as the suitable habitat type (forested, shrubland) is known for the species.

$p = 0.0003$) than selection ($F_{2,28} = 9.006$, $p = 0.0010$) for AUC but was not significant for TSS ($F_{3,28} = 0.458$, $p = 0.7136$) while selection was significant ($F_{2,28} = 8.514$, $p = 0.0013$). In this species, the models incorporating all variable types had the highest AUC and TSS, followed by unadjusted variables only, then latitude-adjusted variables only ($p < 0.05$ for all pairs; Table 1). The full model had significantly higher statistics than the models with variables selected by percent contribution (AUC: $p = 0.0006$; TSS: $p = 0.0009$), with no significance between full and permutation importance selection (AUC: $p = 0.0930$; TSS: $p = 0.0987$), and between selection by permutation importance selection and selection by percent contribution selection (AUC: $p = 0.1151$; TSS: $p = 0.1361$). Incorporation of all bias layers had significantly higher AUC values than the model without bias ($p < 0.05$), but incorporation of bias layer was not significant for TSS ($p > 0.05$).

3.3. Species comparison

TSS of thresholds equating sensitivity and specificity ranged from 0.0061 to 0.7106, with slope” having the highest TSS followed by elevation, slope’, and latitude-adjusted Bio1 (or annual mean temperature; see Table A.2 for all thresholds). From the maximum TSS thresholded MaxEnt models, the two species have an overlap of predicted presence over 39,984 km^2. The average width of the overlap ribbon was 5.58 ± 3.36 km for overlap areas >10 km^2 (97.5% of total overlap area), 11.78 ± 4.43 km for the largest overlap areas comprising 90% of total overlap, and 16.83 ± 3.46 km for the 4 largest overlap areas comprising 80% of total overlap. When the weighted threshold layer was overlaid onto this overlap (Fig. 4), *B. sachalinensis* was more likely in 74.1% of this range and *B. stejnegeri* was more likely in 25.9%.

4. Discussion

4.1. Latitude-adjusted variables in maxent distribution models

An important finding of this research was that inclusion of latitude-adjusted bioclimatic variables was the most significant contributor to improved model accuracy in the form of AUC and TSS statistics for species with both wide and narrow ranges. This held true despite the suggestion of Brock and Inman (2006) that such latitude-adjusted bioclimatic variables may not be suitable for inclusion in ecological models. Also, although TSS was higher for *B. stejnegeri* models that only used unadjusted variables compared to latitude-adjusted variables, TSS was also higher for models incorporating both unadjusted and latitude-adjusted variables than models only using unadjusted variables. The caveat is that models incorporating these variables must be tested against those that do not incorporate latitude-adjusted variables. This inclusion was more important than either variable selection or correction of bias through use of a bias layer, although the use of a bias layer also significantly improved model accuracy. While current modelling techniques without the use of latitude-adjusted variables can and do produce accurate models, we believe that incorporation of such variables can improve on existing models and even provide a solution where model fit is inadequate without strong model effects of unadjusted variable. To exemplify the use of latitude-adjusted bioclimatic variables as a solution to models that do not accurately represent the species range, our models improve on previous models of *B. sachalinensis* distribution, which have not predicted suitability in the species northern range (Garcia-Porta et al., 2012), possibly due to the previous lack of consideration for the species' ability to adapt to climates at higher latitudes.

Our findings that inclusion of latitude-adjusted variables improves distribution models are in line with previous research. For example, latitude-adjusted treeline elevation provided highly accurate models for detecting habitat patches for *C. bicknelli* (Bicknell's thrush) in the northeastern United States (Lambert et al., 2005) and for *Gulo gulo* (wolverines) in Greater Yellowstone, USA (Inman et al., 2012). Based on our results, these methods of latitude adjustment can be taken a step further and applied to bioclimatic variables in complex distribution

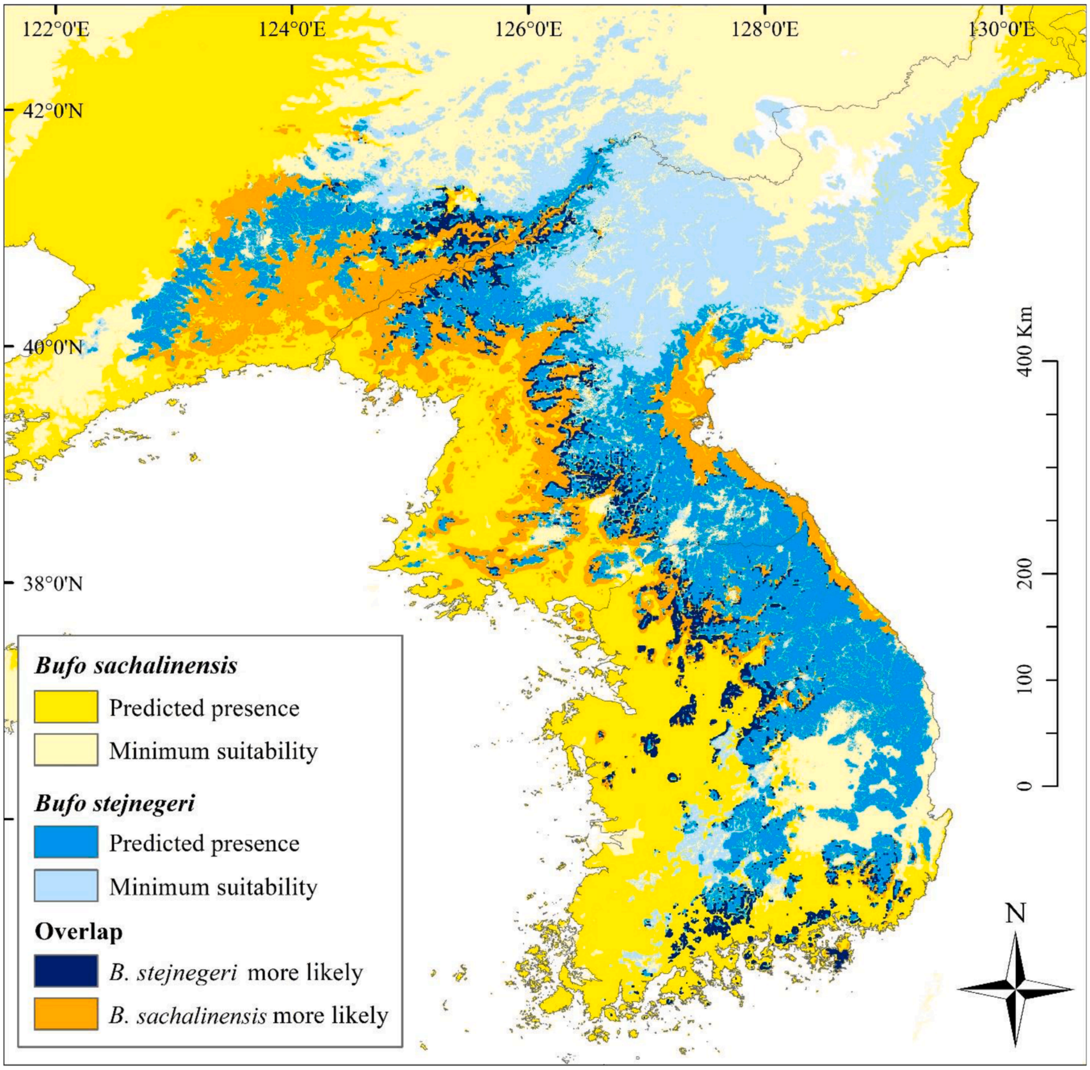

Fig. 4. Comparison of *Bufo sachalinensis* and *Bufo stejnegeri* within overlapping areas of each species' predicted presence for selected suitability models. Thresholded suitability models, thresholded at maximum true scale statistic (TSS), for *B. sachalinensis* and *B. stejnegeri* are overlaid with species threshold derived from weighted average of environmental thresholds. Minimum suitability is also overlaid with this species threshold. Note that habitat is minimally suitable for *B. sachalinensis* throughout the shown extent, except for elevations above 1400 m.

models to significantly improve model accuracy for species with both narrow and wide ranges. Although the incorporation of latitude-adjusted bioclimatic variables improves model accuracy from use of only unadjusted variables, there is a possibility for overextension of suitable area at higher latitudes, at which point physiological traits, if available, may be used to create a bounding climatic envelope. We also recommend that these methods be compared to those incorporating trait-based adaptive ability (Benito Garzón et al., 2019). If these methods yielded similar results, latitudinal adjustment methods could be used in lieu of fitness related traits for understudied species, which applies to many species which are endangered or rare and thus have restrictions on collection and experimentation (Doremus, 2001; Garmestani et al., 2008; Runge, 2011).

In addition to improve predictive accuracy of species distribution, we suggest that this methodology to adjust climate to latitude could be applied to projections under climate change. Such application would likely create significantly different projections from current practices and would better inform predictions of future suitability when used in conjunction with traditional methods. For instance, in a study of latitudinal patterns of climate change impacts, Bonebrake and Mastrandrea (2010) predicted greater impacts on tropical species compared to higher latitude species due to narrower climatic tolerance. For incorporation of these variables, we suggest applying the initial adjustment equation to future climates without training a new GAM to the future climatic conditions. This would adjust for latitude as well as incorporate extent of divergence from current climate. We expect the result to be a reduced vulnerability to climate change, similar to what has been previously demonstrated by incorporation of adaptation in such models (Bush et al., 2016). As a concrete example, Borzée et al. (2019a) projected the range of *Karsenia koreana* to expand by 9156 km^2 in 2050 and 28,245 km^2 in 2070 under an intermediate climate change scenario (RCP 4.5) with most expansion occurring to the north of the current range. However, using the methods developed in the current paper may have resulted in limited northward suitability expansion instead.

It has been predicted in terrestrial insects that species at higher latitudes will be less affected by climate change since they are adapted to a wider range of climatic conditions, and climate is expected to warm to the species optimum (Deutsch et al., 2008). In amphibians however, even though occurring at high latitude, temperate species have high margins of thermal tolerance and they are expected to be highly vulnerable to climatic change based on physiological (CTMax) tests and MaxEnt models (Gerick et al., 2014). Based on the conflicting results of these studies, we cannot make an accurate prediction of the effect of climate change on our example species, but from our use-availability and distribution results, we expect that *B. sachalinensis* will be less affected because of its wide range and therefore greater overall tolerance of a wide range of climatic conditions, whereas the narrow-ranging high elevation *B. stejnegeri* may find its range greatly reduced.

4.2. Multi-species range and contact zone delimitation

Our results for delineating a contact zone and boundary between the two focal species highlight the usefulness of our methodology for identifying such areas between other related species, such as cryptic species, or multiple species that are classified as one due to morphological similarities (Pfenninger and Schwenk, 2007). This can then be a useful tool for conservation if one or more of these species are threatened. Previous studies using genetics of geolocated samples can further be enhanced using distribution models representing contact zones. For instance, a study of a *Hynobius* species complex in the Republic of Korea delineated general contact boundaries between morphologically similar *Hynobius* species in the southern part of the country (Borzée et al., 2019b; Borzée and Min, 2021), but the zones of sympatry and boundaries between ranges could be further enhanced using the methods described in the current study. However, such an application at a finer scale would require inclusion of landscape variables and consideration of interspecies competition.

5. Conclusions

Our results show that consideration of latitude greatly improves species distribution model accuracy. We therefore posit that this aspect has been greatly overlooked in the field up to this point and that the inclusion of latitude-adjusted bioclimatic variables in model building is necessary to model more accurate species distributions and suitability. The methodology presented here also has the benefit of deconstructing influences of latitude into parameters that are likely more closely linked to mechanisms determining species distributions than the single parameter estimate of treeline elevation described by Brock and Inman (2006). Further, our methodologies and results have implications for indicating species' adaptive abilities, species distributions under climate change, and delimiting contact zones of related species. Additionally, GAM latitude adjustment successfully removed latitudinal climatic variation similar to Brock and Inman (2006), providing support for GAMs to be more widely used in modelling responses across environmental gradients.

CRediT authorship contribution statement

Desiree Andersen: Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Spartak N. Litvinchuk:** Data curation, Writing – review & editing. **Hoan Jin Jang:** Data curation, Writing – review & editing. **Jianping Jiang:** Data curation, Writing – review & editing. **Kyo Soung Koo:** Data curation, Writing – review & editing. **Irina Maslova:** Data curation, Writing – review & editing. **Daemin Kim:** Data curation, Writing – review & editing. **Yikweon Jang:** Funding acquisition, Writing – review & editing. **Amaël Borzée:** Conceptualization, Data curation, Formal analysis, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2022.109986.

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