

Detecting the potential sympatric range and niche divergence between Asian endemic ungulates of *Procapra*

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Abstract Species distribution modeling (SDM) is increasingly used to reveal biogeographical relationships, for example the sympatric range for species coexistence, and fundamental questions about niche evolution between related species. We explored the sympatric ranges between three *Procapra* species (*Procapra przewalskii*, *Procapra picticaudata*, and *Procapra gutturosa*) via two methods of defining the study region (method 1, in which models were developed in a larger region including the whole geographic range of *Procapra*, and method 2 in which a smaller region surrounding focal species' localities was used and then projected to the larger region). We also quantified environmental niche divergence between gazelles across the whole range in *Procapra*. Models for gazelles generally performed well. Compared with method 2, method 1 led to larger predicted areas with high suitability and was less concentrated around known localities. Clamping, which deals with variables outside the training range, varied between gazelles and occurred primarily in regions unsuitable for respective species. For all gazelle pairs, models revealed an overlap zone where more than one species should occur, while the estimates varied between the two methods. Moreover, we found that the niche overlap was closely associated with geographic distance but not with phylogenetic distance among gazelles. Our findings indicate that SDM is a useful tool for testing whether related species tend to be in

sympatry at large scales, with method 1 leading to more realistic predictions for *Procapra*. This study provides evidence of a distinct niche divergence among related species and supports the theory that ecological speciation plays a significant role in lineage generation.

Keywords Gazelle · Maxent · Niche evolution · Species distribution modeling · Study region extent · Sympatric distribution

Introduction

Identifying and understanding the geographical patterns of species' ranges are a major focus of biogeography, evolutionary biology, and conservation biology (Doebeli and Dieckmann 2003; Lomolino et al. 2006). Both biological and physical environments shape the geographical range of a species which can be viewed as a spatial reflection of its niche (Lomolino et al. 2006). The fundamental niche of species, as defined by the intersection of necessary conditions on multiple environmental axes, determines its suitable regions. However, few species occupy the whole fundamental niche (Costa and Schlupp 2010; Guisan and Thuiller 2005). For example, a species' realized niche could be restricted by related species, since a substantial proportion of species share congeners with which they may compete to coexist. In fact, congeners are often found to occur in sympatry (Anderson et al. 2002; Martínez-Freiría et al. 2008).

The use of species distribution models (SDMs) combined with geographic information systems has led to a renaissance in addressing questions related to ecology, biogeography, evolutionary process, and species conservation (Guisan and Thuiller 2005; Hu et al. 2010a; Lawler et al. 2009; Peterson et al. 1999; Warren et al. 2008). SDMs are typically used for addressing ecological niche requirements

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of species and identifying potential areas with a high probability of presence for the focal species based on the environment attributes (Guisan and Thuiller 2005). Regions of predicted absence do not fulfill the focal niche requirements in the examined environmental dimensions. If sufficient niche dimensions are examined, regions of potential presence that lack species records may highlight instances where either historical causes or biotic interactions have played a role in restricting species' realized distributions (Anderson et al. 2002). In particular, we can use SDMs to assess biogeographical relationships between ecologically interacting species, such as potential competitors (Acevedo et al. 2010; Anderson et al. 2002), predators and their prey (Real et al. 2009), and hosts and their parasites (Araújo and Luoto 2007). For related species occurring along well-sampled environmental gradients, SDMs can be helpful in exploring the roles of competitive interactions and/or environmental characteristics in limiting and shaping their distributions and in predicting ranges where their coexistence can be expected, as well as in answering questions about niche evolution (Acevedo et al. 2010; Costa and Schlupp 2010; Martínez-Freiría et al. 2008; Warren et al. 2008).

It is a central and recurrent problem to identify an appropriate spatial scale (Wiens 2002), which is usually best expressed independently as resolution (grain size) and extent of the study region in SDMs (Guisan and Thuiller 2005). Compared with spatial resolution, which has attracted substantial attention (e.g., Braunschweig and Suchant 2010; Hu and Jiang 2010), the extent of the study region has until recently been ignored, or at least has not been considered explicitly in most studies (e.g., Costa and Schlupp 2010; but see Acevedo et al. 2012; Anderson and Raza 2010; Barve et al. 2011). Because patterns observed on one scale may not be apparent on another, it is essential to understand the theory and processes driving the observed distribution patterns in order to avoid a mismatch between the scale used for modeling and the one at which key processes occur (Guisan and Thuiller 2005).

Procapra is a genus of ungulates endemic to Central Asia with three species: Mongolian gazelle *Procapra gutturosa*, Przewalski's gazelle *Procapra przewalskii*, and Tibetan gazelle *Procapra picticaudata*. Across the distributional ranges of *Procapra*, *P. gutturosa* and *P. picticaudata* display a typical allopatric distribution pattern at the regional scale, while sympatry occurs for the more distantly related pair in the phylogeny, *P. przewalskii* and *P. picticaudata*, with known sympatric location in the Upper Buha River, Qinghai, China (Jiang 2004; Li et al. 2010). Because sympatric ungulate species often show considerable overlap of habitat and nutritional niches, the potential competition between them may be intense (Jiang 2004; Putman 1996). Relationships between sympatric occurrence of *Procapra* species have been addressed only at local

scales (e.g., Li et al. 2008), which limits our ability for understanding the biogeographical relationships between the three related gazelles and clearing of speciation patterns in *Procapra* at large scales. Based on the identification of sympatry, and follow-up studies on the dietary overlap and group pattern (Li et al. 2008, 2010), we can detect the issues regarding biogeographical relationships between gazelles which show overlapping and/or disjunct distributions beyond local scales.

Here we identify environmental requirements of *Procapra* species and model their potential distributions using SDMs. Then, we detect potential overlapping areas that satisfy their common environmental requirements and generate habitat suitability maps. By implementing SDMs using two methods of defining the extent scale, we aim to test the hypothesis that the extent of the study region selection could affect the projected outputs. We also quantify the environmental niche differentiation between gazelles across the whole geographic range in *Procapra*. The results in this study will help with regional or national conservation and management plans (e.g., Hu et al. 2010a; Hu and Jiang 2010) and incite further research of niche evolution for *Procapra*.

Methods

Study taxa and distribution data

Procapra species inhabit Central Asia, including China, Mongolia, and Russia, where all large ungulates have experienced population declines (Mallon and Jiang 2009). Populations of *P. gutturosa* has declined significantly, to the point that it is now considered regionally endangered even if it is one of the few remaining abundant, wide-ranging grassland ungulates (Clark et al. 2006; Mallon 2008). *P. przewalskii* is now restricted to small areas in the vicinity of Qinghai Lake, China, and is arguably among the most endangered large mammals on the Earth (IUCN SSC Antelope Specialist Group 2008; Jiang 2004). Although *P. picticaudata* is one of the most geographically widespread ungulates on the Qinghai-Tibet Plateau, it resides in fragmented habitat patches (Schaller 1998), and its sharply declining numbers and distribution prompted its reclassification from "Least Concern" to "Near Threatened" (Mallon and Bhatnagar 2008).

Compared with *P. gutturosa*, the other two gazelles appear to move little (Jiang 2004; Schaller 1998). Therefore, we used two approaches to obtain distribution data. For *P. przewalskii* and *P. picticaudata*, we took presence records, 33 and 131 records in total, respectively, at the resolution of 8 × 8 km, from population censuses conducted between 2002 and 2008 and the literature (Jiang 2004; [!\[\]\(c50c8b7b2cc2cf9ff925edec0ee94c0d_img.jpg\) Springer](http://</p>
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www.baohu.org/csis_search/search1.php; Fig. 1). For *P. gutturosa*, in addition to the records from field work, we also used its digital range map (Mallon 2008), which was sampled to summarize the environmental data (see Lawler et al. 2009; Fig. 1) with 156 records (including 79 records from field surveys) at 8×8 km. This treatment was reasonable and essential due to the wide range of *P. gutturosa* and their long distance nomadic movements (Olson et al. 2010).

Environmental variables

We selected 10 environmental variables, which are grouped into four types of macroenvironmental factors (Table 1). Bioclimatic data were obtained from WorldClim 1.4 (Hijmans et al. 2005). These variables, based on monthly temperature and precipitation data produced from weather-station data, are more relevant biologically. Because bioclimatic variables are often highly correlated and environmental variables need to be as proximal as possible, we performed Pearson's correlation tests across all pair-wise combinations of the initial 19 bioclimatic variables for the whole range of *Procapra* to reduce the initial variable set. We considered variable pairs highly correlated if $r \geq |0.8|$ and retained for modeling only the variable that was more relevant to the life history of *Procapra*. These resulted in a set of seven largely independent variables including annual mean temperature (T_{anu}), mean monthly temperature range (T_{ran}), isothermality (T_{iso}), temperature seasonality (T_{sea}), annual precipitation (Prec_{anu}), precipitation of the driest month (Prec_{dry}), and precipitation seasonality (Prec_{sea}). The land cover data were obtained from the Global Land Cover 2000 database (GLC 2003). We also used the human influence index (HII), which is an estimate of human influence based on human settlement, land transformation, accessibility, and

infrastructure data (Sanderson et al. 2002). Additionally, we obtained the compound topographic index (CTI, commonly referred to as the wetness index) that was representative of the topography variable from the USGS's Hydro1K dataset (USGS 2009). Land cover, HII, and CTI data did not have strong correlation with each other and with the selected bioclimatic variables from the correlation tests.

To strike a balance between the spatial resolution of environmental variables and occurrence data, and also to consider the effects of reduced resolution on predicted outputs (Braunisch and Suchant 2010; Hu and Jiang 2010), we resampled all variables with an initial grid cell of 1×1 km to 8×8 km using ArcGIS 9.2 (ESRI, Redland, USA).

Model building

Maxent is a recently developed presence-background technique (Phillips et al. 2006; Phillips and Dudík 2008) that has been performed well in recent comparative studies with good statistical performance (Elith et al. 2006). For estimating the target distribution, Maxent satisfies a set of constraints representing the incomplete information on the distribution and, subject to those constraints, maximizes the entropy of the probability distribution (Phillips et al. 2006). We implemented Maxent 3.3.3 k for 10 cross-validated replicates with default settings (Phillips et al. 2006) while partitioning the presence records between training and test samples (80 and 20 %, respectively). The default settings have been shown to achieve good performance (Phillips and Dudík 2008). Selection of the feature's classes (functions of environmental variables) for a species was carried out automatically. These include linear,

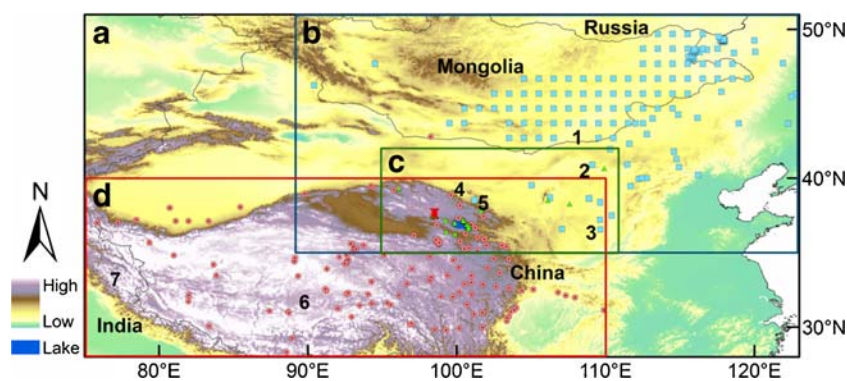


Fig. 1 Spatial occurrence records used and the two methods for defining the study region when modeling the potential distributions of *Procapra*: *P. gutturosa* (squares, a, b), *P. przewalskii* (triangles, a, c), and *P. picticaudata* (circles, a, d). In method 1, each species' potential distribution was calibrated in a large study region including the whole range of *Procapra* (a). In method 2, the model for each gazelle was calibrated in a smaller study region encompassing its known localities (b–d); then, this model was applied to the larger

region used for calibration in method 1, indicating environmental suitability for the species throughout the whole larger region. The pushpin represents the known sympatric location for the pair *P. przewalskii*–*P. picticaudata* in the Upper Buha River, Qinghai, China. The Arabic numerals indicate locations of the significant toponymies mentioned in this study: 1, Mongolian Plateau; 2, Hetao Ordos middle high plain; 3, Loess Plateau; 4, Qilian Mountains; 5, Shandan County; 6, Qinghai-Tibet Plateau; 7, Ladakh region

Table 1 Explanatory environmental variables used in species distribution models for *Procapra* species

Variable type	Code	Description	Source
Climate	T_{anu}	Annual mean temperature (°C)	http://www.worldclim.org , WorldClim 2004
	T_{ran}	Mean monthly temperature range (°C)	http://www.worldclim.org , WorldClim 2004
	T_{iso}	Isothermality (mean monthly temperature range/temperature annual range) ($\times 100$)	http://www.worldclim.org , WorldClim 2004
	T_{sea}	Temperature seasonality (standard deviation $\times 100$)	http://www.worldclim.org , WorldClim 2004
	Prec _{anu}	Annual precipitation (mm)	http://www.worldclim.org , WorldClim 2004
	Prec _{dry}	Precipitation (mm) of the driest month	http://www.worldclim.org , WorldClim 2004
	Prec _{sea}	Precipitation seasonality (coefficient of variation)	http://www.worldclim.org , WorldClim 2004
Habitat	Landcov	Land cover type (31 categories)	http://gem.jrc.ec.europa.eu/products/glc2000/glc2000.php , GLC 2003
Human impact	HII	Human influence index value (0–64)	http://www.ciesin.columbia.edu/wild_areas/ , Last of the Wild Data Version 2, 2005
Topography	CTI	Compound topographic index	http://edcdaac.usgs.gov/gtopo30/hydro/ , USGS 2009

quadratic, product, threshold, and hinge features, depending on the number of presence records. We selected logistic output format due to its easier interpretability (Phillips and Dudík 2008). We ensured only one occurrence per grid cell while running models. Additionally, we tested autocorrelation for the presence data which have been removed duplicates using the average nearest neighbor index in spatial statistics tools of ArcGIS 9.2 (ESRI, Redland, USA). Calculations using the Manhattan distance revealed that there was no statistical significance of spatial clustering for each *Procapra* species. The nearest neighbor index was 1.242 ($p < 0.001$, toward dispersion) for *P. gutturosa*, 0.859 ($p = 0.116$) for *P. przewalskii*, and 1.041 ($p = 0.373$) for *P. picticaudata*, respectively. We also carried out the jackknife analysis to identify the variable importance based on the regularized gain with training data of variables used in isolation and show values that are averages over replicate runs.

Defining the study region

To examine how changes in the extent of the study region affect the results of SDMs, we applied two methods to define the study region extent (Anderson and Raza 2010). In method 1, we modeled each species' distribution in a large study region that included the whole range of *Procapra* (28–51° N and 75–123° E; Fig. 1(a)). In method 2, we calibrated the models in a smaller study region immediately surrounding gazelles' known localities (*P. gutturosa*: 35–51° N, 89–123° E; *P. przewalskii*: 35–42° N, 95–111° E; *P. picticaudata*: 28–40° N, 75–110° E; Fig. 1(b–d)). Then, we projected the respective model for method 2 to the larger

study region applied in method 1. Disadvantages are considered to exist in both methods of defining the extent in SDMs (Anderson and Raza 2010). The models may be prone to overfitting to environmental conditions present in the region where the species is known to occur in method 1; concurrently, the values for one or more environmental variables in some pixels of the larger study region may be uncovered by the model when projecting in method 2.

There is a problem of novel climate conditions when projecting; the environmental variables may take on values outside the range seen during model training. Maxent currently resolves this issue via a more conservative assumption that is termed “clamping”, which treats variables outside the training range as if they were at the limit of the training range (Phillips et al. 2006). A map is provided by Maxent to alert the user to such possibilities and to show the degree of clamping (if any) that was employed in each pixel when making a prediction into the larger study region. Without assessing the effect of clamping, no prediction should be reasonably interpreted. Hence, Maxent predictions in areas with large clamping should be discarded.

Model evaluation, comparison, and interpredictivity assessment

We tested model performance using the area under the receiver operating curve (AUC) statistic, which gives a measure of ability to discriminate between observed presences and absences, and has been widely applied (Acevedo et al. 2010; Anderson and Raza 2010; Phillips et al. 2006; but see Lobo et al. 2008). It ranges from 0 to 1, with a score of 1 representing perfect discrimination and a score of 0.5

representing a model that performs no better than random chance. Data here are presented as mean±standard deviation based on multi-replicates.

We used the ensemble-forecasting approach to reach a consensus scenario (Araújo and New 2007) and obtained one final predicted distribution from the average output of the 10 cross-validated replicates for each species. We used the 10th percentile training presence threshold, which is considered as a highly conservative estimate of a species' tolerance to each environmental variable and can therefore provide more ecologically significant results (Svenning et al. 2008). The continuous logistic output was then converted into a binary map of potential suitable environmental conditions. We conducted these analyses for models developed using both method 1 and method 2. To assess the potential sympatric range between gazelles, we superimposed the binary outputs in ArcGIS 9.2 (ESRI, Redland, USA).

To identify any artefactual differences that derive from discrepancies between the two methods of defining the extent, we assessed interpredictivity using two approaches (Anderson and Raza 2010). First, cross-species omission rates (a threshold-dependent measure indicating how well the models of each gazelle species predict localities of the other two gazelle species) were calculated. Using the binary prediction obtained above, we calculated the cross-species omission rates by determining the proportion of localities of other gazelles falling outside of (omitted from) areas predicted suitable for the focal gazelle. Then, based on the overlapped distribution maps obtained above, we examined the effect that the two methods of defining the extent had on the degree of geographic overlap between gazelles' distributions. We estimated the proportion of geographic overlap by dividing the number of pixels predicted suitable for more than one gazelle by either (1) the total number of pixels with data, or (2) the total number of pixels predicted suitable for each gazelle alone, or (3) the total number of pixels predicted suitable for either gazelle.

Testing niche identity

We used a niche identity test to explore if SDMs of the three *Procapra* species are distributed in identical environmental space for method 1 (Warren et al. 2008). To test the niche overlap, we first calculated two indices, i.e., Schoener's D and Warren et al.'s (2008) I , that summarize the similarity of projected suitability scores for each grid cell of the study area and range from 0 (no niche overlap) to 1 (identical niches). D and I are both niche similarity metrics and are obtained by comparing the estimates of habitat suitability from SDMs generated by Maxent for each grid cell of the study area after normalizing each SDM (Warren et al. 2008). We then generated 100 replicates, which pool empirical occurrence points and randomize their identities to produce

two new samples with the same number of observations as the empirical data, to calculate a pseudoreplicated null distribution via the niche identity test. The observed measures of niche overlap values were compared with this null distribution to determine whether gazelles are more different than would be expected by chance. The null hypothesis of niche identity is rejected when the empirically observed value for D or I is significantly different from the pseudoreplicated data sets. We calculated D and I using the program ENM-Tools (version 1.3; Warren et al. 2008). Significance was tested using independent samples t tests in SPSS 16.0 (SPSS Inc, Chicago, IL, USA).

Results

Potential distribution of *Procapra*

The models of *Procapra* generally performed well. In method 1, the training and testing AUC were, respectively, 0.935 ± 0.001 and 0.911 ± 0.016 for *P. gutturosa*, 0.996 ± 0.001 and 0.989 ± 0.017 for *P. przewalskii*, and 0.932 ± 0.004 and 0.888 ± 0.046 for *P. picticaudata*. In method 2, both the corresponding training and testing AUC were lower than those in method 1, with 0.877 ± 0.004 and 0.833 ± 0.037 for *P. gutturosa*, 0.978 ± 0.003 and 0.945 ± 0.066 for *P. przewalskii*, and 0.851 ± 0.004 and 0.746 ± 0.037 for *P. picticaudata*, respectively.

Jackknife analysis showed the importance of environmental variables and revealed that the variable contribution was affected by the extent selection in SDMs for gazelles (Fig. 2). For method 1, the variables that had the most useful information by themselves (i.e., the highest gain when used in isolation) were T_{sea} and T_{anu} for *P. gutturosa*, T_{iso} and Prec_{dry} for *P. przewalskii*, and T_{sea} and T_{iso} for *P. picticaudata*. Using method 2, those variables with the highest gain were T_{anu} and T_{sea} for *P. gutturosa*, T_{anu} and T_{iso} for *P. przewalskii*, and T_{sea} and T_{anu} for *P. picticaudata*.

Model outputs indicated sensible and intuitive projections of the distribution for *Procapra*, showing continuous predictions of relative suitability (Fig. 3). For *P. gutturosa*, the prediction revealed the highest suitability in eastern Mongolia and adjacent areas of Inner Mongolia of China and Russia (Fig. 3a, b). In contrast, areas most strongly predicted for *P. przewalskii* were restricted to the eastern part of the Qinghai-Tibet Plateau. Besides the regions around Qinghai Lake, predicted suitable habitats covered some regions next to the northeastern and southern parts of Qinghai Lake and other scattered locations on the Loess Plateau and Hetao Ordos middle high plain (Fig. 3d, e). For *P. picticaudata*, the area of highest suitability was identified as the Qinghai-Tibet Plateau, including the Chinese provinces of Gansu,

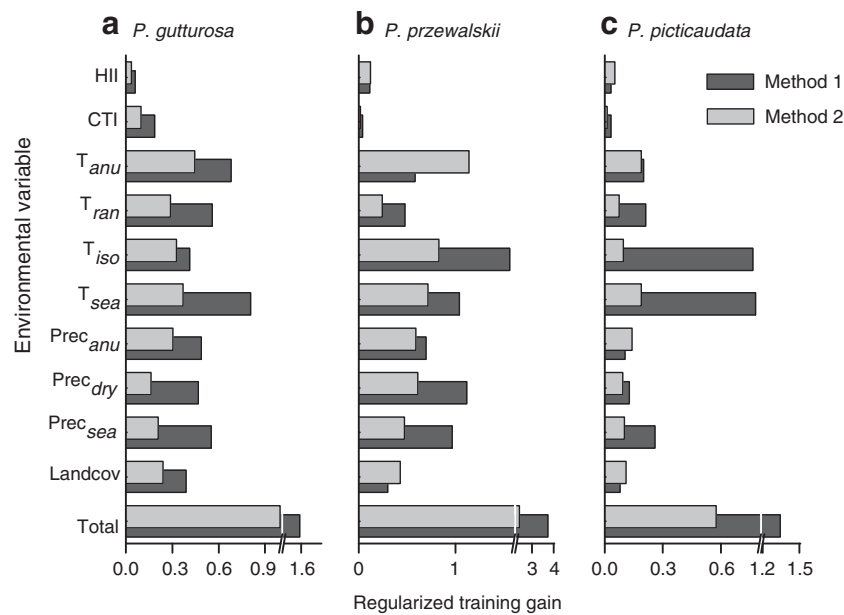


Fig. 2 Jackknife analyses of the importance of environmental variables in developing species distribution models for the three *Procapra* species using two methods of defining the extent of study region in relation to overall model quality or “total gain” (method 1, black bar, models calibrated using the large study region, and method 2, gray bar, models calibrated using the smaller study region and then projected to

the larger one). For each variable, the bars show the regularized gain achieved with training data of variable used in isolation. *HII* human influence index, *CTI* compound topographic index, T_{anu} annual mean temperature, T_{ran} mean diurnal range, T_{iso} isothermality, T_{sea} temperature seasonality, $Prec_{anu}$ annual precipitation, $Prec_{dry}$ precipitation of the driest month, $Prec_{sea}$ precipitation seasonality, *Landcov* land cover

Qinghai, Sichuan, and Tibet; moderately suitable areas were recognized in the southwestern Xinjiang and

southern Shaanxi provinces of China, and in the Ladakh region (Fig. 3g, h).

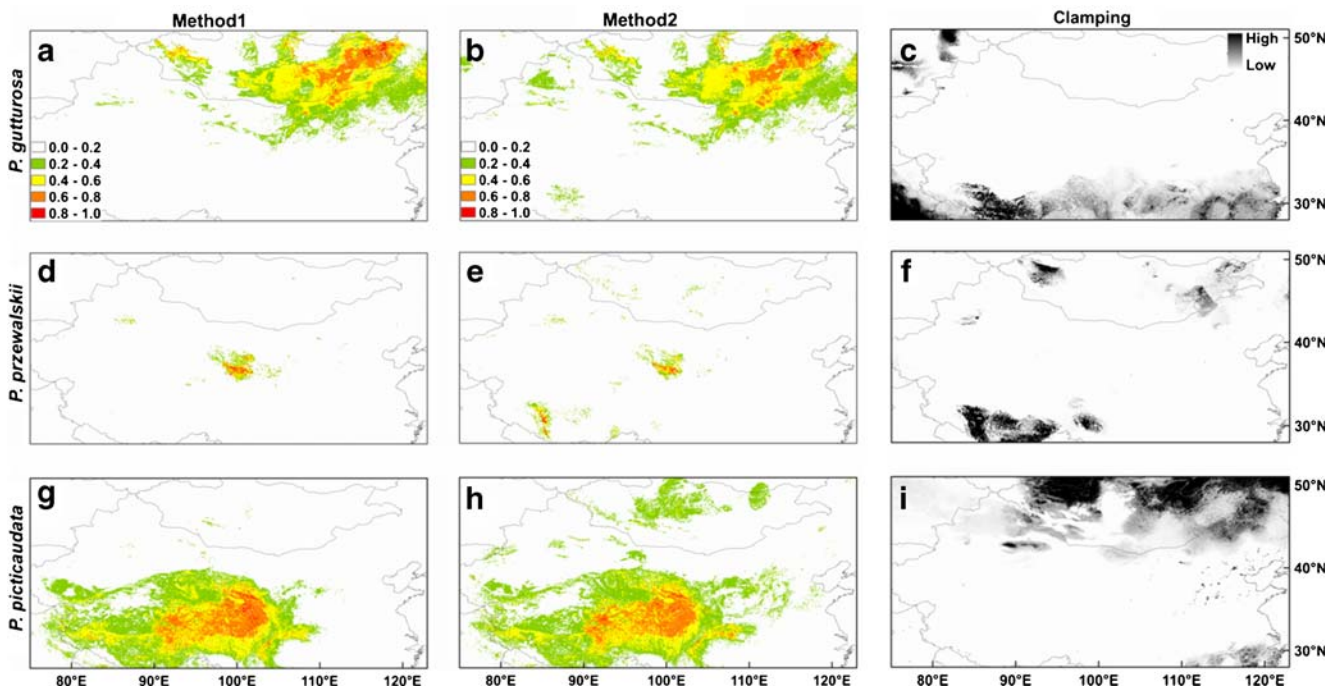


Fig. 3 Predicted probability distributions of *Procapra*: *P. gutturosa* (a, b), *P. przewalskii* (d, e), and *P. picticaudata* (g, h) with the two methods for defining the study region (method 1, models calibrated using the large study region, and method 2, models calibrated using the smaller study region and then projected to the larger one). Value ranges from 0 (lowest probability) to 1 (highest probability). In method 2, for

respective species (c, f, i), the level of clamping is revealed, if any, corresponding to each map pixel. Clamping occurs when values of environmental variables fall outside the range of environmental values in the models (see text); here, successively darker blacks show increasing levels of clamping. See Fig. 1 for the position of localities of each gazelle

The predictions for each gazelle varied depending on the method of defining the extent (Fig. 3). The predicted areas from SDMs using method 1 were more compact compared with those predicted using method 2. The predicted highly suitable area was larger in method 1 than in method 2. The projections generated in method 2 showed larger areas of low and moderate suitability than in method 1. Moreover, predictions with highly suitable habitats were restricted to areas near the known localities of the focal gazelle in method 2, while these predictions were less concentrated in such areas in method 1.

Clamping in method 2 varied greatly between gazelles (Fig. 3c, f, i). For *P. gutturosa*, areas with a high degree of clamping occurred primarily in lowland regions from eastern coastal to central mainland China and the southern margin of the Qinghai-Tibet Plateau, areas that are very unlikely to be suitable for this species. In contrast, clamping for *P. przewalskii* was minimal in most of the study region and areas of high clamping occurred in extremely cold alpine areas of the southwestern Qinghai-Tibet Plateau. Areas of high clamping for *P. picticaudata* included most of Mongolia and the northeastern Xinjiang and Inner Mongolia provinces of China.

Quantitative assessments of interpredictivity

Measures of interpredictivity varied depending on the method of defining the extent and species (Table 2). Models of *P. gutturosa* predicted localities of *P. przewalskii* slightly better than models of *P. przewalskii* predicted localities of *P. gutturosa*, while the inverse pattern occurred for *P. gutturosa* and *P. picticaudata*. Additionally, models of *P. picticaudata* predicted localities of *P. przewalskii* much better than models of *P. przewalskii* predicted localities of *P. picticaudata*. For the binary predictions, the potential distribution of *P. picticaudata* omitted 8.8 % localities of *P. przewalskii* using method 1 and performed slightly worse (14.7 %) in method 2. For the other two pairs, however, the potential distribution of gazelles would fail to predict most of the known localities of cross-species in methods 1 and 2.

Potential sympatric range

The models revealed substantial yet narrow sympatric ranges between *Procapra* species, but the estimates were different between the two methods of defining the extent (Fig. 4a, b). Compared with method 1, the binary predictions in method 2 revealed a larger predicted area for both *P. gutturosa* and *P. przewalskii* but a smaller area for *P. picticaudata*. However, method 2 led to larger potential sympatric ranges for all the three pairs of gazelles than method 1: range sizes for *P. gutturosa*–*P. przewalskii*, *P. gutturosa*–*P. picticaudata*, and *P. przewalskii*–*P. picticaudata* were $2.11 \times$

10^3 , 1.86×10^3 , 5.57×10^4 km², respectively, in method 1, and 2.47×10^4 , 4.67×10^4 , 1.52×10^5 km², respectively, in method 2. Both method 1 and method 2 predictions identified somewhat sympatric ranges across *Procapra*, of approximately 130 and 3.84×10^3 km², respectively. Additionally, proportions of potential sympatry between gazelles varied depending on not only the method of defining the extent but also the way of calculating these proportions (Table 3).

Tests of niche overlap

Observed niche overlap for each pair of *Procapra* species yielded niche similarity values with *D* and *I* values of 0.154 and 0.394, respectively, for *P. gutturosa*–*P. przewalskii*, 0.102 and 0.294, respectively, for *P. gutturosa*–*P. picticaudata*, and 0.260 and 0.542, respectively, for *P. przewalskii*–*P. picticaudata*. All the observed niche overlap values were significantly lower than the pseudoreplicated null distributions in niche identity tests (*t* test, $p < 0.001$). This indicates that the hypothesis that any pair of gazelles is distributed in identical environmental space should be rejected, regardless of the measure of similarity (*D* or *I*) used (Fig. 5a–c).

Discussion

Effects of the extent of the study region on predicted distribution

No question in spatial ecology can be answered without explicitly considering the scale at which data are measured or analyzed (Guisan and Thuiller 2005; Wiens 2002). The selection of an appropriate extent which is relevant for all correlative SDMs employing background, pseudo-absence, or absence data (Bahn and McGill 2007; Barve et al. 2011; Chefaoui and Lobo 2008) may help resolve debates regarding model generality/transferability across space and time (e.g., Duncan et al. 2009). Our results support the hypothesis that SDMs predict differently when different methods of defining the extent are used (Anderson and Raza 2010; Barve et al. 2011; VanDerWal et al. 2009). Of the two methods applied here, Anderson and Raza (2010) found that method 2 performed better than method 1; models using method 2 at narrower extents predicted larger suitable areas which were less concentrated in regions surrounding species' localities, as well as higher interpredictivity. In our study, the projections in method 2 revealed larger suitable areas than in method 1. Additionally, method 2 showed projections are far from the core distribution of the target species, while method 1 failed to do that (Fig. 3). This seems to agree with both Anderson and Raza (2010) and Acevedo et al. (2012). However, the qualitative assessments of the

Table 2 Measures of interpredictivity between *Procapra* species based on Maxent models made using two methods of defining the study region (method 1, left, models calibrated using the large study

region, and method 2, right, models calibrated using the smaller study region and then projected to the larger one)

	Method 1			Method 2		
	Threshold	Cross-species omission rate		Threshold	Cross-species omission rate	
Model for <i>P. gutturosa</i>	0.218	0.941 (<i>P. przewalskii</i>)	1.000 (<i>P. picticaudata</i>)	0.218	0.941 (<i>P. przewalskii</i>)	0.992 (<i>P. picticaudata</i>)
Model for <i>P. przewalskii</i>	0.478	0.994 (<i>P. gutturosa</i>)	0.962 (<i>P. picticaudata</i>)	0.198	1.000 (<i>P. gutturosa</i>)	0.939 (<i>P. picticaudata</i>)
Model for <i>P. picticaudata</i>	0.295	0.088 (<i>P. przewalskii</i>)	0.987 (<i>P. gutturosa</i>)	0.295	0.147 (<i>P. przewalskii</i>)	0.987 (<i>P. gutturosa</i>)

Cross-species omission rates provide measures of how well the model of the focal species predicts localities of other species. Omission rates constitute a threshold-dependent measure: first, we used the 10th percentile training presence threshold to yield a binary prediction from the models of focal species; then, the omission rate for localities of other species is calculated. Low omission rates indicate high interpredictivity (and high levels of niche conservatism). The threshold values are provided as additional information regarding the models, but they do not address the issue of interpredictivity

predictions indicates that using broader extents (method 1) leads to more realistic potential distributions for *Procapra* species based on the knowledge of their natural history and of the climatic and vegetational patterns in their distribution range (Jiang 2004). Specifically, *P. gutturosa* inhabits rolling arid steppes and plains; *P. przewalskii*, steppe plateaux and open valleys, including broken and undulating terrain of stabilized dunes containing steppe vegetation; and *P. picticaudata*, high-altitude plains, hills, and stony plateau (Jiang 2004). In particular, the fact that method 2 revealed

considerably suitable areas in Tibet of China for *P. przewalskii* (Fig. 3) was likely unrealistic and not substantiated by any historical data. The discrepancy between our results and those of Anderson and Raza (2010) also occurred in the measures of interpredictivity with cross-species omission rates. Applying SDMs at large scales, where climatic influences on species distribution are shown to be dominant, could minimize the impact of biotic interactions (Pearson and Dawson 2003). As Anderson and Raza (2010) used only bioclimatic variables in their study, it is reasonable to

Fig. 4 Potential sympatric ranges between *Procapra* species with the two methods for defining the study region (method 1, **a**, models calibrated using the large study region, and method 2, **b**, models calibrated using the smaller study region and then projected to the larger one). The 10th percentile training presence threshold is used

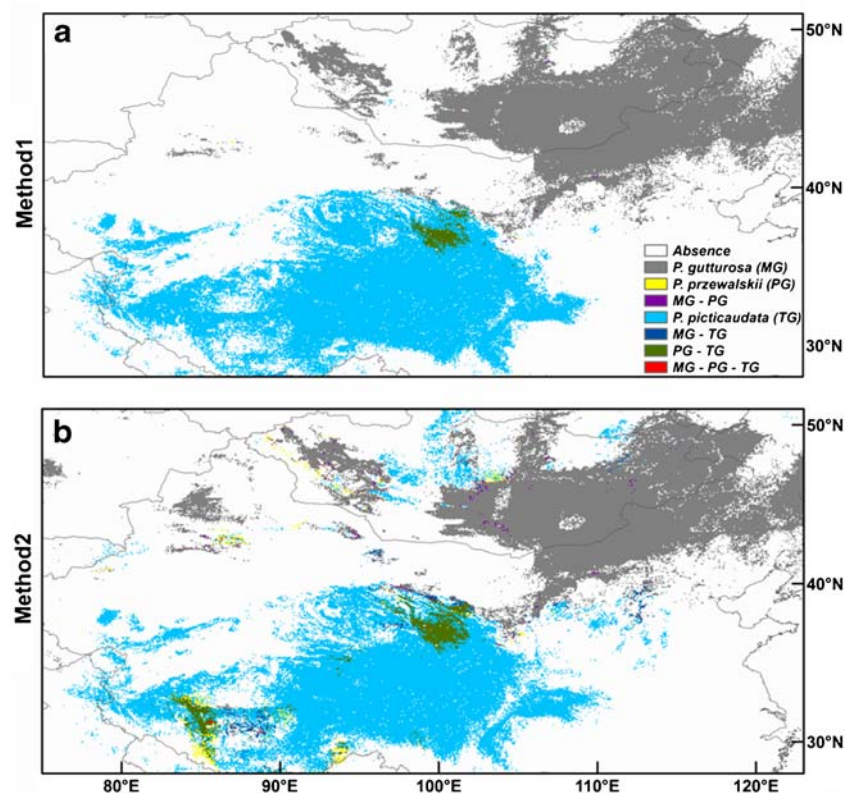


Table 3 Measures of proportional geographic overlap for the potential distributions of *Procapra* species, for each method of defining the study region (method 1, models calibrated using the large study region,

and method 2, right, models calibrated using the smaller study region and then projected to the larger one)

Proportional geographic overlap based on number of pixels in	Species pair	Method 1	Method 2
Overlap relative to larger study region	<i>gutturosa</i> – <i>przewalskii</i>	1.377×10^{-4}	1.610×10^{-3}
	<i>gutturosa</i> – <i>picticaudata</i>	1.210×10^{-4}	3.041×10^{-3}
	<i>przewalskii</i> – <i>picticaudata</i>	3.630×10^{-3}	9.896×10^{-3}
	Three gazelles	8.344×10^{-6}	2.503×10^{-4}
Overlap relative to prediction of <i>P. gutturosa</i>	<i>gutturosa</i> – <i>przewalskii</i>	8.370×10^{-4}	9.683×10^{-3}
	<i>gutturosa</i> – <i>picticaudata</i>	7.356×10^{-4}	1.829×10^{-2}
	Three gazelles	5.073×10^{-5}	1.505×10^{-3}
Overlap relative to prediction of <i>P. przewalskii</i>	<i>gutturosa</i> – <i>przewalskii</i>	3.560×10^{-2}	0.107
	<i>przewalskii</i> – <i>picticaudata</i>	0.939	0.655
	Three gazelles	2.157×10^{-3}	1.657×10^{-2}
Overlap relative to prediction of <i>P. picticaudata</i>	<i>gutturosa</i> – <i>picticaudata</i>	7.254×10^{-4}	0.185
	<i>przewalskii</i> – <i>picticaudata</i>	0.022	0.060
	Three gazelles	5.003×10^{-5}	1.523×10^{-3}
Overlap relative to prediction of either species	<i>gutturosa</i> – <i>przewalskii</i>	4.156×10^{-4}	4.858×10^{-3}
	<i>gutturosa</i> – <i>picticaudata</i>	3.652×10^{-4}	9.175×10^{-3}
	<i>przewalskii</i> – <i>picticaudata</i>	0.011	0.030
	Three gazelles	2.519×10^{-5}	7.551×10^{-4}

All results are for predictions of the species' potential distributions in the larger study region (even though the models for method 2 were calibrated in the smaller study region), and after converting the continuous prediction to a binary one based on the threshold indicating equal test sensitivity and specificity. The proportional geographic overlap was calculated in three ways based on overlap between potential distributions of *Procapra* species as a proportion of: (1) the number of pixels with data in the larger study region; (2) the number of pixels in the prediction for each respective species alone; and (3) the number of pixels predicted for either species. The last measure provides the best single indicator of the amount of geographic overlap between the predictions of gazelles (Anderson and Raza 2010)

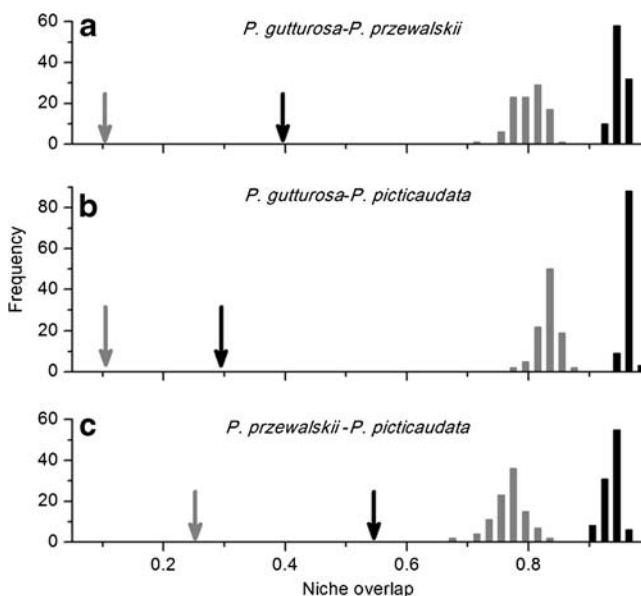


Fig. 5 Results of the identity test. The niche overlap values (arrows) for Schoener's *D* (gray) and Warren et al.'s (2008) *I* (black) are compared to the null distributions in each panel for the corresponding pair of species. The histograms represent the distribution of niche similarities obtained from pairs of pseudo-niches based on the randomization of the occurrence points of the two species

assume that different outcomes may arise when more factors (e.g., land cover or topographic complexity) are included (Pearson and Dawson 2003). The difference in either taxa or the location of the study region may also contribute to the discrepancy in the results.

Geometric shapes such as rotated rectangles and buffered minimum convex polygons, rather than the smaller rectangular extent used in method 2, have been suggested (Anderson and Raza 2010). However, if only part of an important environmental gradient is sampled, an overly constrained extent may underestimate the importance of coarse resolution factors such as climate in delimiting species' distributions and can lead to an incorrect interpretation (Barve et al. 2011; Van Horn 2002). Typically, a useful framework for assessing the environment–biota relationship is as a hierarchy (defined as being a system of interconnections wherein the higher levels constrain the lower levels to various degrees) of factors operating at different scales (Pearson and Dawson 2003; Turner et al. 2001). A refined extent for background or pseudo-absence sampling can be selected using the results of a first round of modeling based on simple, but reasonable, study regions (Anderson and Raza 2010). Therefore, the results of our study, in combination with previous studies (e.g., Anderson and Raza 2010;

Barve et al. 2011), are relevant to SMDs in many study areas. Our results can inform studies exploring sympatric ranges and niche evolution versus conservatism for related species, where analyses theoretically should be focused at the extent scale at which the phenomena of interest are dominant (Turner et al. 2001). In light of our findings and those of Anderson and Raza (2010) and Barve et al. (2011), we should be cautious of selecting the extent and recognize that the extent has been accessible to the species of interest over relevant time periods representing the ideal extent for implementing SMDs.

Potential sympatric ranges for *Procapra*

Many fossils of gazelles have been found in northern China. Before the formation of Loess Plateau in the Quaternary, gazelles were thought to be the superior herbivores when prairie and forest alternated over geological time (Jiang 2004). These gazelles are considered to be widespread historically and are likely the ancestor of *Procapra* (Jiang 2004; Lei et al. 2004). The ancestor of *Procapra* diverged along with the uplifting of the Qinghai-Tibet Plateau during the Tertiary and the Quaternary period. Subsequently, two lineages were established and evolved independently, developing *P. picticaudata* in one lineage and the ancestor of both *P. przewalskii* and *P. gutturosa* in the other (Lei et al. 2004). When the Loess Plateau formed gradually and the Hexi [Gansu] Corridor came into being, the ancestor of both *P. przewalskii* and *P. gutturosa* was split into two lineages, one of which lived on the Qinghai-Tibet and the other on the Mongolian Plateau. Because the adaptation of species to local environments is a primary force that drives morphological evolution and speciation, the ancestor of the gazelles diverged and finally generated *P. przewalskii* and *P. gutturosa* under environmental change (Jiang 2004). Potential sympatry between *Procapra* species was identified using SDMs with larger sympatric ranges revealed when using method 2 in this study. This suggests that there are habitats that can satisfy partial environmental requirements for more than one gazelle simultaneously.

Habitat loss and fragmentation throughout the grasslands as well as hunting represent substantial threats to gazelle populations (Clark et al. 2006; Mallon 2008). Although large herds of Mongolian gazelles still exist, their range in the Inner Mongolia grasslands of China has retreated to the North because of increasing human activities (Mallon 2008). Because *P. przewalskii* is only found around Qinghai Lake (Hu et al. 2010b; IUCN SSC Antelope Specialist Group 2008), *P. przewalskii* and *P. gutturosa* are therefore described as more than 500 km away from each other (Jiang 2004). Although most populations of *P. przewalskii* and *P. picticaudata* are isolated, some actual sympatry does occur between them (Li et al. 2008, 2010). However, sympatry

may be uncommon now because of the rarity of *P. przewalskii* and disparate habitat preferences between gazelles (Schaller 1998). *P. przewalskii* occurs in more arid habitats and uses a narrower elevational band than *P. picticaudata*, and *P. gutturosa* currently survives exclusively on the plains (Clark et al. 2006; Hu and Jiang 2011; Jiang 2004). We identified the most important environmental variables affecting the potential distribution of these gazelles, as understanding why species distributions terminate at their existing boundaries is a critical issue for SDMs. Our results suggested that annual mean temperature is important for all three gazelle species when using method 2, although it was only highly important for *P. gutturosa* when using method 1 (Fig. 2). Because climate change is projected to induce changes in the distribution range (Hu and Jiang 2011; Lawler et al. 2009; Pearson and Dawson 2003), the future climate may lead to a distribution shift of *Procapra* species and alter their potential sympatry. Additionally, based on the shrinking of distributions mainly induced by human activities (Clark et al. 2006; Jiang 2004; Mallon and Jiang 2009), *Procapra* species have not achieved their distribution limits, especially for *P. przewalskii* (Hu and Jiang 2010). If we reduce human activities and construct migration passages within their potential ranges, gazelles may again expand to their historical ranges, and more actual sympatric ranges will emerge.

Regions where the distributions of related species contact one another may provide opportunities for hybridization and introgression of genetic material from one taxon to the other and induce a number of possible consequences, such as the establishment of stable hybrid zones or a total breakdown of reproductive isolation (Barton 2001). SDMs could be used to clarify evolutionary relationships through the identification of potential hybrid zones between sibling and/or sympatric species (e.g., Martínez-Freiría et al. 2008). *Procapra* is a monophyletic clade with three species evolving from the common ancestor (Jiang 2004). *P. przewalskii* and *P. picticaudata* can occur in the same area with some dietary overlap and mixed-species groups (Li et al. 2008, 2010), and even individuals of intermediate morphological traits. Specifically, a female *P. przewalskii* mated with a male *P. picticaudata* and gave birth to a hybrid which survived from 2003 to 2005. This anecdote suggests that hybridization may occur between *Procapra* species (Jiang, unpublished data).

As expected, besides the actual sympatry for the pair of *P. przewalskii* and *P. picticaudata* in the Upper Buha River, our results revealed more potential sympatric ranges between gazelles. We expect that these ranges may satisfy the environment requirements for coexistence of two or three gazelle species. Although *P. przewalskii* and *P. picticaudata* often occur in mixed-species groups and are suggested to eat similar diets in the actual sympatry, they may

avoid food competition by occupying different foraging areas (Li et al. 2008, 2010). Therefore, beyond local scales, it is reasonable to sustain sympatric ranges between these gazelles. Moreover, gazelles found in Shandan County in the north side of the Qilian Mountains could be *P. gutturosa* (Hu and Jiang, unpublished data). It would be significant to identify *P. gutturosa* in the Hexi Corridor, as the southern margin of this gazelle is currently on the frontier between China and Mongolia. Thus, three gazelles could occur within an approximately 250 km diameter circle surrounding Qinghai Lake. Because *P. przewalskii* is more closely related to *P. gutturosa* than to *P. picticaudata* (Jiang 2004), and *P. gutturosa* have long distance nomadic movements (Olson et al. 2010), there could be sympatry and mixed-species groups for *P. przewalskii* and *P. gutturosa*, and even the opportunity for hybridization. Additionally, the potential sympatry for *P. gutturosa* and *P. picticaudata* suggests that they may have formed mixed groups and even hybridized in the past. These opportunities are also probable across the three gazelles.

Niche divergence

Quantifying niche relationships between related and/or partly sympatric species is of fundamental interest in ecology, since they provide a solid basis for further experimental or observational work and raise questions about mechanistic underpinnings of broad-scale biogeographic patterns (Buckley et al. 2010; Peterson et al. 1999). The application of newly developed techniques (e.g., Warren et al. 2008) for inferring the divergence between *Procapra* species found strong inter-specific variation in the observed environmental niches. Additionally, our results showed that the niche overlap was associated with geographic distance (GD) but not with phylogenetic distance (PD; also see Warren et al. 2008) among *Procapra* species: the *P. gutturosa*–*P. picticaudata* pair had the lowest niche overlap with the longest GD and moderate PD, while *P. przewalskii*–*P. picticaudata* possessed the highest niche overlap with the shortest GD but the longest PD (Jiang 2004). Based on our results, the over-riding importance of divergence between *P. gutturosa* and *P. picticaudata* and the more distantly related set of *P. przewalskii*–*P. picticaudata* indicates that ecological differentiation may play an important role in both the origin and ongoing development of species in this related group of gazelles.

The taxonomy and evolutionary relationships in *Procapra* were once an issue of great contention, and the evolution of *Procapra* and the uplift of the Qinghai-Tibet Plateau may be closely related (Jiang 2004). Our niche identity tests showed evidence for niche divergence across *Procapra* species. Although these differences cannot explain patterns of true evolutionary divergence among all lineages in *Procapra*, they could simply and practically

reflect the fact that *Procapra* species are largely allopatric and thus are exposed to different environmental backgrounds. Moreover, where such ecological niche divergence is implicated, it has often been interpreted as evidence for, or at least consistent with, ecological speciation theory, which is suggested to play a significant role in lineage generation (Rundle and Nosil 2005; Schluter 2009).

Conclusions

What properties of organisms and their environments inevitably lead to the evolution of discrete species (Turelli et al. 2001)? Although this is an abstract and difficult question, some aspects of it can be demonstrated since rapid niche evolution could be linked with speciation (Orr and Smith 1998). SDMs can provide spatially explicit maps to display the spatial configuration of suitable habitats, which can be helpful to dissect the biogeographical relationships between related species. The evidence for niche divergence across the whole geographical range of *Procapra* species supports the idea that ecological speciation plays a substantial role in lineage generation. Moreover, a changing climate can alter species distributions as well as niche evolution (Hu and Jiang 2011; Wake et al. 2009). To conduct valid tests of hypotheses for niche evolution versus conservatism, our results indicate that the ideal extent for SMDs of interest is the extent that has been accessible to the target species over relevant time periods (Barve et al. 2011).

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References

- Acevedo P, Jiménez-Valverde A, Lobo JM, Real R (2012) Delimiting the geographical background in species distribution modelling. *Journal of Biogeography*. doi:10.1111/j.1365-2699.2012.02713.x
- Acevedo P, Ward AI, Real R, Smith GC (2010) Assessing biogeographical relationships of ecologically related species using favourability functions: a case study on British deer. *Divers Distrib* 16:515–528
- Anderson RP, Peterson AT, Gomez-Laverde M (2002) Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. *Oikos* 98:3–16

- Anderson RP, Raza A (2010) The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nepheleomys*) in Venezuela. *J Biogeogr* 37:1378–1393
- Araújo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under climate change. *Glob Ecol Biogeogr* 16:743–753
- Araújo MB, New M (2007) Ensemble forecasting of species distributions. *Trends Ecol Evol* 22:42–47
- Bahn V, McGill BJ (2007) Can niche-based distribution models outperform spatial interpolation? *Glob Ecol Biogeogr* 16:733–742
- Barton N (2001) The role of hybridization in evolution. *Mol Ecol* 10:551–558
- Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher SP, Peterson AT, Soberón J, Villalobos F (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol Modell* 222:1810–1819
- Braunisch V, Suchant R (2010) Predicting species distributions based on incomplete survey data: the trade-off between precision and scale. *Ecography* 33:826–840
- Buckley LB, Davies TJ, Ackerly DD et al (2010) Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proc R Soc B-Biol Sci* 277:2131–2138
- Chefaoui RM, Lobo JM (2008) Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecol Modell* 210:478–486
- Clark EL, Munkhbat J, Dulamtsereen S, Baillie JEM, Batsaikhan N, King SRB, Samiya R, Stubbe M (2006) Summary conservation action plans for Mongolian mammals. Zoological Society of London, London
- Costa GC, Schlupp I (2010) Biogeography of the Amazon molly: ecological niche and range limits of an asexual hybrid species. *Glob Ecol Biogeogr* 19:442–451
- Doebeli M, Dieckmann U (2003) Speciation along environmental gradients. *Nature* 421:259–264
- Duncan RP, Cassey P, Blackburn TM (2009) Do climate envelope models transfer? A manipulative test using dung beetle introductions. *Proc R Soc B-Biol Sci* 276:1449–1457
- Eliith J, Graham CH, Anderson RP et al (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151
- GLC (2003) Global Land Cover 2000 database. European Commission, Joint Research Centre. <<http://gem.jrc.ec.europa.eu/products/glc2000/glc2000.php>>. Cited 10 Oct 2009
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8:993–1009
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978
- Hu J, Hu H, Jiang Z (2010a) The impacts of climate change on the wintering distribution of an endangered migratory bird. *Oecologia* 164:555–565
- Hu J, Jiang Z (2010) Predicting the potential distribution of the endangered Przewalski's gazelle. *J Zool* 282:54–63
- Hu J, Jiang Z (2011) Climate change hastens the conservation urgency of an endangered ungulate. *PLoS One* 6:e22873
- Hu J, Ping X, Cai J, Li Z, Li C, Jiang Z (2010b) Do local communities support the conservation of endangered Przewalski's gazelle? *Eur J Wildl Res* 56:551–560
- IUCN SSC Antelope Specialist Group (2008) *Procapra przewalskii*. In: IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4. Available at: <http://www.iucnredlist.org/>. Accessed 20 Dec 2010
- Jiang Z (2004) Przewalski's Gazelle. China Forestry Publishing House, Beijing
- Lawler JJ, Shafer SL, White D, Kareiva P, Maurer EP, Blaustein AR, Bartlein PJ (2009) Projected climate-induced faunal change in the Western Hemisphere. *Ecology* 90:588–597
- Lei R, Jiang Z, Hu Z, Yang W (2004) Taxonomic status of *Procapra* and the classification of Chinese antelopes and gazelles. *Acta Zootaxon Sin* 29:622–627
- Li Z, Jiang Z, Beauchamp G (2010) Nonrandom mixing between groups of Przewalski's gazelle and Tibetan gazelle. *J Mammal* 91:674–680
- Li Z, Jiang Z, Li C (2008) Dietary overlap of Przewalski's gazelle, Tibetan gazelle, and Tibetan sheep on the Qinghai-Tibet Plateau. *J Wildl Manage* 72:944–948
- Lobo JM, Jiménez-Valverde A, Real R (2008) AUC: a misleading measure of the performance of predictive distribution models. *Glob Ecol Biogeogr* 17:145–151
- Lomolino M, Riddle B, Brown J (2006) Biogeography. Sinauer Associates, Sunderland
- Mallon DP (2008) *Procapra gutturosa*. In: IUCN Red List of Threatened Species, IUCN 2010 Version 2010.4. Available at: <http://www.iucnredlist.org/>. Accessed 21 Dec 2010
- Mallon DP, Bhatnagar YV (2008) *Procapra picticaudata*. In: IUCN Red List of Threatened Species, IUCN 2010. Version 2010.4. Available at: <http://www.iucnredlist.org/>. Accessed 21 Dec 2010
- Mallon DP, Jiang Z (2009) Grazers on the plains: challenges and prospects for large herbivores in Central Asia. *J Appl Ecol* 46:516–519
- Martínez-Freiria F, Sillero N, Lizana M, Brito JC (2008) GIS-based niche models identify environmental correlates sustaining a contact zone between three species of European vipers. *Divers Distrib* 14:452–461
- Olson KA, Fuller TK, Mueller T, Murray MG, Nicolson C, Odonkhuu D, Bolortsetseg S, Schaller GB (2010) Annual movements of Mongolian gazelles: nomads in the Eastern Steppe. *J Arid Environ* 74:1435–1442
- Orr MR, Smith TB (1998) Ecology and speciation. *Trends Ecol Evol* 13:502–506
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob Ecol Biogeogr* 12:361–371
- Peterson AT, Soberón J, Sánchez-Cordero V (1999) Conservatism of ecological niches in evolutionary time. *Science* 285:1265–1267
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Modell* 190:231–259
- Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31:161–175
- Putman R (1996) Competition and resource partitioning in temperate ungulate assemblages. Chapman & Hall, London
- Real R, Barbosa AM, Rodríguez A, García FJ, Vargas JM, Palomo LJ, Delibes M (2009) Conservation biogeography of ecologically interacting species: the case of the Iberian lynx and the European rabbit. *Divers Distrib* 15:390–400
- Rundle HD, Noss P (2005) Ecological speciation. *Ecol Lett* 8:336–352
- Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The human footprint and the last of the wild. *BioScience* 52:891–904
- Schaller G (1998) Wildlife of the Tibetan steppe. University of Chicago Press, Chicago
- Schluter D (2009) Evidence for ecological speciation and its alternative. *Science* 323:737–741
- Svenning JC, Normand S, Kageyama M (2008) Glacial refugia of temperate trees in Europe: insights from species distribution modelling. *J Ecol* 96:1117–1127
- Turelli M, Barton NH, Coyne JA (2001) Theory and speciation. *Trends Ecol Evol* 16:330–343

- Turner M, Gardner R, O'Neill R (2001) Landscape ecology in theory and practice: pattern and process. Springer-Verlag, New York
- USGS (2009) HYDRO1k elevation derivative database. <http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/gtopo30/hydro>. Cited December 2008
- Van Horn B (2002) Approaches to habitat modeling: the tensions between pattern and process and between specificity and generality. In: Scott JM, Heglund PJ, Haufler JB et al (eds) Predicting species occurrences: issues of scale and accuracy. Island Press, Washington, pp 63–72
- VanDerWal J, Shoo LP, Graham C, William SE (2009) Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecol Modell* 220:589–594
- Wake DB, Hadly EA, Ackerly DD (2009) Biogeography, changing climates, and niche evolution. *Proc Natl Acad Sci USA* 106:19631–19636
- Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* 62:2868–2883
- Wiens J (2002) Predicting species occurrences: progress, problems, and prospects. In: Scott JM, Heglund PJ, Haufler JB et al (eds) Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, pp 739–749