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RESEARCH ARTICLE

Climate change and landscape fragmentation jeopardize the population viability of the Siberian tiger (*Panthera tigris altaica*)

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Abstract The Amur tiger, a flagship species of the boreal forest ecosystem in Russian Far East and northeastern China, has declined dramatically in population and geographic distribution due to human caused habitat fragmentation and poaching over the past century. The fate of this largest feline species will also be influenced by the worsening impacts of climate change. In this paper we assess the possible effects of climate change (three scenarios from the 2007 IPCC Report) on the Amur tiger by integrating species distribution modeling (SDM) and population viability analysis (PVA). We projected the potential and realized suitable habitat distributions to examine the impacts from anthropogenic factors, and evaluated the changes of suitable habitat and extinction risk for 100 years under climate change. The realized suitable habitat was projected to be more severely fragmented than the potential suitable habitat because of human-related factors. The potential suitable habitat would expand northward under all climate change scenarios considered. However, the tiger population would suffer the largest decline and highest extinction risk in the next 100 years under the worst climate change scenario (A1B) even though the size of potential habitat would be greatest. Under climate change, the tiger population could persist for the next century only if the size and quality of current habitat patches would remain intact. In addition, our study demonstrated that using SDM alone could grossly overestimate the geographic distribution of the Amur tiger, and that coupling SDM and PVA could provide important insights into conservation planning to mitigate the effects of climate change.

Keywords Amur tiger · Species distribution modeling (SDM) · Population viability analysis (PVA) · Climate change · Russian Far East · China

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Introduction

Human activities have contributed significantly to climate change since the 1750 s, resulting in increased surface temperatures and altered precipitation patterns around the globe (IPCC AR4 WG1 2007, AR4 WG2 2007). The effects of climate change on species range shifts (including contraction and expansion) have been well documented (Walther et al. 2002; Thomas et al. 2004; Parmesan 2006; Schwartz et al. 2006; Verboom et al. 2010; Koomen et al. 2012; Wasserman et al. 2012). The climate of the Russian Far East and Northeastern China is expected to become warmer and drier in the coming decades (Hansen et al. 1999; Gong and Ho 2002; Lapenis et al. 2005), and these changes will most likely affect the distribution of the habitat and populations of endangered species in the region.

Dominated by mixed boreal forests, the Russian Far East-Northeastern China region is the most biologically diverse area at that latitude, supporting a large number of rare and endemic plant and animal species (Bogatov et al. 2000; Cushman and Wallin 2000; Li et al. 2009; Tian et al. 2009). As a flagship species in this region, the Amur tiger has suffered a sharp decline in population during the past century, from more than 3,000 to fewer than 600 individuals, and its habitat has been significantly diminished and fragmented (Matyushkin et al. 1996; Miquelle et al. 2006; Tian et al. 2009, 2011b). Numerous studies have shown that poaching, prey scarcity, and habitat loss and fragmentation are major threats to the population persistence of the Amur tiger (Nowell and Jackson 1996; Carroll and Miquelle 2006; Hötte 2006; Dinerstein et al. 2007; Goodrich et al. 2008). However, few studies have examined the possible effects of climate change on the fate of this species.

In response to the climate change, species may adapt to the changing environment, shift their distribution ranges, or go extinct (Holt 1990; Wiens et al. 2009). To study how species change with climate, species distribution models (SDMs), which project species' suitable habitat using niche theory and empirically-derived statistical relationships, are increasingly used (Raxworthy et al. 2003; Thuiller et al. 2005; Elith and Leathwick 2009; Wiens et al. 2009). However, assessing the effects of environmental changes on endangered species by focusing only on habitat shifts may not be adequate, as the more detailed information on population dynamics can be crucial in determining the long-term persistence of these species (Keith et al. 2008). As a model-based method, population viability analysis (PVA) has been used to identify key factors affecting population persistence, project future population dynamics, and help design biodiversity conservation strategies by evaluating the extinction risk during a specified period of time (Boyce 1992; Burgman and Possingham 2000; Beissinger 2002; Morris et al. 2002; Doak et al. 2009; Shaffer 2009; Wu 2009; Tian et al. 2011a). Recently, Keith et al. (2008) demonstrated that integrating stochastic population models with bioclimatic habitat models could improve the prediction of species extinction risks under climate change.

The main goal of this study, therefore, was to explore the impacts of future climate change on the probability of long-term persistence of the Amur tiger by coupling the species distribution modeling with PVA. Through comparison of projected potential habitat with realized habitat, and also via a series of controlled simulation experiments based on the climate change scenarios, we addressed the following questions: (1) how would human density and land use affect the area of suitable habitat for the Amur tiger in the face of climate change? (2) How would different climate change scenarios affect the geographic distribution and population viability of the Amur tiger over the next 100 years? (3) Could species distribution modeling alone be adequate to assess the fate of the Amur tiger under climate change?

Methods

Study area

Our study area includes the Russian Far East, Northeastern China, and Northwestern North Korea (40°–60°N, 115°–145°E), which covers the historical distribution area of the Amur tiger at the end of 20th century (Fig. 1). This region includes Sikhote-Alin Mountains in Russia, Greater and Lesser Khingan (Xing'an) Mountains, Changbai Mountains, and Wanda Mountains in northeastern China (Carroll and Miquelle 2006; Tian et al. 2009). The major forests are Korean pine forests, which are the most biologically diverse forests in the region and the preferred habitat of the Amur tiger (Carroll and Miquelle 2006; Miquelle et al. 1999, 2010a). Among the most common ungulates are red deer (*Cervus elaphus*), Sika deer (*Cervus nippon*), Siberian roe deer (*Capreolus pygarus*), and wild boar (*Sus scrofa*) (Bogatov et al. 2000; Carroll and Miquelle 2006; Cushman et al. 2009), and red deer and wild boar are preferred prey

Fig. 1 Study area. The *dots* denote the locations of tigers according to field surveys

species of tigers (Hayward et al. 2012). The northern part of the region is dominated by coniferous fir, spruce, and larch forests. Siberian musk deer (*Moschus moschiferus*) and Eurasian elk (*Alces alces*) are also common at higher altitudes, but the Amur tigers are extremely rare in spruce-fir forests. A large portion of forests in this region has been subjected to selective or clear cutting and fire induced by human activities during recent decades (Zheng et al. 1997; Cushman and Wallin 2000, 2002; Li et al. 2009). These anthropogenic perturbations have fragmented the landscape and transformed many primary forests into secondary broad-leaved forests (Cushman et al. 2009; Li et al. 2009).

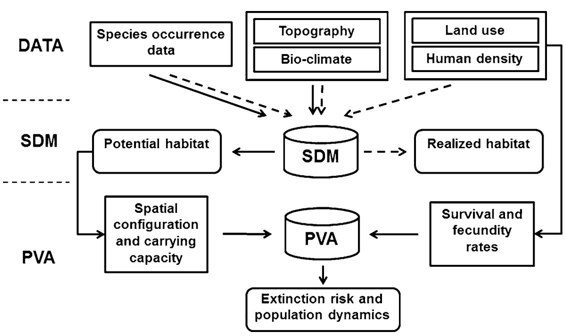

Fig. 2 Schematic representation of the modeling framework to couple species distribution modeling with population viability analysis

Modeling approach

To explore the effects of climate change on the Amur tiger's habitat shifts and population viability, we developed a modeling strategy that linked species distribution modeling (MAXENT), population viability analysis (RAMAS/GIS), and a spatial database (Fig. 2).

MAXENT is a computer program developed for modeling species geographic distributions (Phillips et al. 2006), based on the principle of maximum entropy in statistical mechanics and information theory. "Presence-only" data for the species' occurrence and a series of environmental data are required to project whether a region satisfies the requirements of the target species' ecological niche (Phillips et al. 2004, 2006; Phillips and Dudik 2008; Harte et al. 2009). In this study, we used MAXENT to project the tigers' potential habitat, and their possible response to climate change. The realized habitat was projected by combining the human related factors with environmental variables.

To simulate the population dynamics and extinction probability of the Amur tiger in 100 years, we used RAMAS/GIS (Akçakaya 2005), which has been widely applied in population viability analysis and conservation planning (Colling and Matthies 2006; Early and Thomas 2007; Hinrichsen 2009; Giordano et al. 2010; Lawson et al. 2010). The demographic parameters in RAMAS/GIS were adjusted by human-related factors (more detail below), including human density and land-use data. In an earlier study, we used RAMAS/GIS to explore how poaching, habitat degradation, habitat loss, and habitat fragmentation would affect the population dynamics and extinction risk of the Amur tiger and the relative effectiveness of different conservation corridors in China and Russia (Tian et al. 2011b).

In the current study, we linked the PVA tool with SDM to address climate change-related questions. Specifically, we used MAXENT to estimate the tigers' occurrence probabilities and produce habitat suitability distribution maps. These maps were then used as input to the Spatial Analysis Module of RAMAS/GIS to conduct population viability analysis under different climate change scenarios.

Database and model parameterization

Parameterization of MAXENT

Data on tiger presence locations were extracted from the field survey reports for the winters of 1995–1996 in the Russian Far East (Matyushkin et al. 1996) and for the winters of 1998–1999 in Northeastern China (Li et al. 2001; Jiang 2005; Sun et al. 2005; Yu 2005). There were 372 location records identified, with 355 in Russia and 17 points in China. Environmental variables affecting the tigers' distribution were divided into two types: natural environmental variables and human-related variables. The natural environmental variables included 19 bioclimate variables from the WorldClim database (http://www.worldclim.org/), which include annual mean temperature, mean diurnal range, isothermality, temperature seasonality, max temperature of warmest month, min temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter. The climate data used in our baseline scenarios were for the 2000s, which were produced by extrapolation of observed data during 1950–2000. Topographic data, including slope, altitude, and aspect, were extracted from the Shuttle Radar Topography Mission (SRTM) Digital Elevation Model (DEM) with a spatial resolution of 90 m. Human-related variables comprised human density and land-use and land-cover classes. The land-use and land cover data were derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation indices product (MOD13Q1 collection 4) of 2006. By integrating supervised and non-supervised methods, 13 classes were identified based on the field survey.

There are six features in the MAXENT model: L (linear), Q (quadratic), P (product), T (threshold), H (hinge), and C (category). We selected QPTHC combining features (since it would be redundant to use L and H features simultaneously) (Phillips and Dudik 2008) (Table 1). The MAXENT settings used in all the simulations of our study were as follows: logistic output format, 25 % as random test percentage, 1,000 max iterations, and default settings for all the other parameters (Phillips et al. 2006; Phillips and Dudik 2008) (Table 1). Ten simulations were run in batch, and the average values were then used to represent the final results.

The suitable habitat of the Amur tiger was extracted from the continuous occurrence probability map, which is one of the major outputs of MAXENT. The larger the occurrence probability was, the more suitable the habitat would be. We classified the suitable habitat into five categories—very poor, poor, fair, good and very good—according to the values with average intervals.

As a threshold-independent method for characterizing the performance of models, receiver operating characteristic (ROC) analysis was used to evaluate the

Table 1 Parameters used in MAXENT and RAMAS/GIS

Methods	Parameters	Definition	Explanation and references
SDM (MAXENT)	Features	QPTHC	Q (quadratic), P (product), T (threshold), H (hinge) and C (category)
	Training data/test data	75/25 %	75 % of sample data were used for training model
	Maximum iteration	1,000	
	Applied threshold rule	Minimum training presence	(Phillips and Dudik 2008)
PVA (RAMAS)	Density dependence	Ceiling	(Tian et al. 2011b)
	Carrying capacity	$CC = \frac{Ap}{An} \times \frac{N \times P\max}{\sum_0^N Pn}$	CC is the carrying capacity, A_p is the patch size, A_n is the tiger's home range size in Sikhote Nature Reserve (considered the best habitat because the tigers' occurrence probability was the highest there), P_n is the occurrence probability of each pixel in the habitat patch, P_{max} is the maximum occurrence probability in the study area, which is in the region of Sikhote Natural Reserves.
	Initial population numbers	See Table 2	Field survey in the winter of 1995–1996
	Life history	Cubs (0–1 year); juveniles (1–2 years); sub-adults (2–3 years); adults (≥3 years)	(Karanth and Stith 1999; Tian et al. 2011b)
	Sex ratio	Female only	
	Vital rates	$S = S0 \times \frac{\sum_0^N P_{\mathrm{LULC}}}{N \times P_{\max}}$ $F = F0 \times \frac{\sum_0^N P_{\mathrm{human}}}{N \times P_{\max}}$	S and F are the survival rate and fecundity rate of the Amur tiger in a habitat patch, P_{human} and P_{LULC} are the occurrence probabilities simulated when considering either human density or land use only in each pixel, P_{max} is the maximum occurrence probability in the study area, which is in the region of Sikhote Natural Reserves (Table 3).
	Dispersal rates	$M_{ij} = a \exp\left(-D_{ij}^{c/b}\right),\ \text{if } \mathrm{D_{ij}} = \mathrm{D_{max}};$ $M_{ij} = 0,\ \text{if } \mathrm{D_{ij}} > \mathrm{D_{max}}$	M_{ij} is the dispersal rate between patch i and patch j, D_{ij} is the distance between the two patches, D_{max} is the maximum travel distance of tigers (58 km), and a, b, and c are parameters estimated from field data. The dispersal distances was assumed to follow a normal distribution, and were computed from an edge-by-edge distance matrix using the Spatial Data Module of RAMAS/GIS(Tian et al. 2011b).
	Stochasticities considered	Environmental stochasticity and demographic stochasticity	(Tian et al. 2011b)

simulation in our study. The performance of the model could be evaluated using the value of area under the curve (AUC) (Phillips et al. 2006).

Parameterization of RAMAS/GIS

To simulate the population viability of the Amur tiger using RAMAS/GIS, the model was run for 100 years, with a 1-year time step and 1,000 replications of each combination of parameters. To determine suitable habitat, forest fragments less than 12 km apart were considered as functionally connected, and thus combined into one habitat patch. The inter-patch distance of 12 km was chosen the radius of a circle whose area was approximately the tiger's average home range of about 440 km^2 (360 km^2 in (Carroll and Miquelle 2006); 440 km^2 in (Goodrich et al. 2010); 445 km^2 in (Miquelle et al. 2010a, b). Fragments smaller than the average home range and far away from each other were not considered. Based on the criteria above, four suitable habitat patches were identified.

The carrying capacity of each patch was estimated using a function of patch area and patch quality (Table 1), represented by occupancy probability. The initial population number of each patch was determined from the census of tiger population in the Russian Far East and Northeastern China in the winters of 1995–1996 and 1998–1999 (Matyushkin et al. 1996; Li et al. 2001; Yu 2005 Li et al. 2008; Zhou et al. 2008). For North Korea, experts have estimated that no more than ten individuals have existed there since the 1990s (Table 2). We set the number to ten individuals in our simulations.

Tiger fecundity rates are highly related to human disturbance, here represented by human density, while land-use and land-cover are closely related to survival rates (He et al. 1997; Karanth and Stith 1999; Carroll and Miquelle 2006; Linkie et al. 2006). Two functions for the tiger vital rates were built upon this assumption (Table 1). The stage-specific vital rates of the Amur tiger in undisturbed habitat were obtained from the existing literature, which were then adjusted by multipliers reflecting effects of land-use and human density (Table 1).

The remaining parameters of RAMAS/GIS were the same as in Tian et al. (2011a, b), including the classification of age structure, sex ratio, dispersal rate function, and stochasticities considered. Most of the key parameters are listed in Table 1.

Simulation scenarios

In order to focus on the effects of climate change on the population viability of the Amur tiger, we used the same parameter settings in MAXENT and RAMAS/GIS for all simulation scenarios, including the baseline and climate change scenarios.

Baseline

In the baseline simulations, we assumed that the regional climate, as well as the quality, quantity, and spatial configuration of habitat, would not change, and that poaching of tigers and their prey in the region would be prohibited during the simulation duration. Under these conditions, we examined the differences between the potential habitat and realized habitat. Only natural environmental variables were used to estimate the potential habitat, whereas both natural and human-related variables were used for projecting the realized habitat. In addition, dispersal and no-dispersal scenarios were simulated to examine their impacts on the population viability of the Amur tiger in 100 years. The results from these simulations were then used as a baseline to assess the effects of climate change scenarios.

Climate change scenarios

The bioclimate data used in the climate change scenarios were derived from the WorldClim database (http://www.worldclim.org/). We selected the data from the Canadian Centre for Climate Modeling and Analysis (CCCma)'s Global Circulation Model (GCM). Based on the IPCC Fourth Assessment Report (IPCC AR4 WG1 2007, AR4 WG2 2007), three climate change scenarios—Special Report on Emissions Scenarios (SRES) in IPCC reports—were selected for three time periods (2020 s, 2050 s, and 2080 s): A1B, A2A, and B2A. According to the IPCC reports, the A1 and A2 scenario families are characterized by high economic development and thus high emissions, but A1 scenario family emphasizes globalization (market-driven) whereas A2 scenario family emphasizes regionalization (geographically differentiated economies). In contrast, the B1 and B2 scenario families assume a lower level of economic development and emr tiger population dynamicsissions, with B2 putting emphasis on globalization and B2 on regionalization.

Table 2 Initial population numbers of the Amur tiger in each sub-patch

Patches	Location	Cub	Juvenile	Sub-Adult	Adult	Total
Pop1	Wanda Mountains in China	1	0	0	2	3
Pop2	China-Russia Border	2	0	1	9	12
Pop3	Russia Far East	53	0	16	193	262
Pop4	North Korea	0	0	0	10	10
Total		56	0	17	214	287

Results

Baseline simulations

Potential and realized suitable habitat

We quantified the suitability of the tigers' distribution area based on occurrence probability, with the assumption that if an area is more suitable for tigers they will be more likely to occur in that area. The occurrence probability was simulated with the MAXENT software. The potential suitable habitat for the Amur tiger included a large habitat patch in southeastern Russian Far East, and some small patches near the border between North Korea and Northeastern China (Fig. 3a). The potential habitat with the highest quality was distributed in the Sikhote-Alin Mountains and the southeastern coastal area of the Russian Far East. The suitable habitat in China and North Korea were small, fragmented, and of relatively low quality.

Compared with the potential suitable habitat, realized suitable habitat of the Amur tiger considering human-related factors was much smaller and highly fragmented (Fig. 3b). The suitable habitat in China and northern Russian Far East disappeared, and the areas in North Korea and southwestern Russian Far East shrank significantly. In addition, the occurrence probability of the Amur tiger was lower in the whole simulated area.

Population viability of the Amur tiger metapopulation

Using RAMAS/GIS, four suitable habitat patches were identified based on the criteria of distance between patches, patches size, and the habitat suitability. The largest patch (pop3) with highest habitat quality was located in Sikhote-Alin Mountains of the Russian Far East; a suitable habitat patch was identified in Korea (pop4); a suitable patch was located in Wanda Mountains of Northeastern China (pop1); and another patch (pop2) was astride the border of China and Russia.

Table 3 The maximum vital rates of the Amur tiger

Age stages	Survivorship	Fecundity
Cub (0–1)	0.90	0
Juvenile (1–2)	0.80	0
Sub-adult (2–3)	0.75	0
Adult (3+)	0.85	0.85

Baseline scenarios, as mentioned before, assumed no human effects and changes in environmental conditions. The results of the baseline simulations showed that the viability of the entire metapopulation did not differ significantly between the dispersal and no-dispersal scenarios (but the viability of subpopulations did, as discussed below). In both scenarios, the mean abundance of the Amur tiger continued to increase from about 200 individuals in the beginning to about 100 % of the carrying capacity (about 450) in 100 years (Fig. 4a). The probability of extinction at the end of the simulation for the entire metapopulation (i.e., terminal quasi-extinction probability) was negligible (Fig. 4b). The risk of metapopulation percent decline (the percentage of the metapopulation decline) during 100 years was quite low in general (Fig. 4c). For example, there was a 60 % probability that the metapopulation would not decline at all, and the probability of the metapopulation falling below 450 individuals was 10 %.

The four subpopulations differed in their dynamics of mean population abundance in the two dispersal strategies (Fig. 5). Metapopulation trajectory was predominantly determined by the largest patch (pop3) in the central Sikhote-Alin Mountains, the only sub-population that had no local extinctions in 100 years in both dispersal strategies (Fig. 5). The two small subpopulations (pop1 and pop2) were closely connected to the largest sub-population, persisting for the next 100-year span in the dispersal scenario. But these were all sink subpopulations whose local extinctions were rescued by immigrants from the largest subpopulation (pop3). The subpopulation (pop4), most distant from pop3, went extinct rather quickly (Fig. 5). In the non-dispersal scenario, all three small subpopulations went extinct quickly (Fig. 5).

Impacts of climate change

Suitable habitat shifts

Changes in the number and area of suitable habitat patches under different climate change scenarios were quantified using MAXENT and RAMAS/GIS (Table 4). Our results showed that tigers' suitable habitat moved northward in different extents in response to different climate change scenarios. According to the IPCC Assessment Report 4, A1B is a scenario with rapid economic development, high-energy requirements, and greater climate change. In this scenario, the suitable habitat of the Amur tiger also expanded widest and the most far northward. Compared to the baseline scenario, from the 2000 s to the 2020 s, the suitable habitat changed slightly, bounded by the historical distribution area to the north. During the period from 2020 s to 2050 s, the suitable habitat spread westward to the Siberian region in Amur Krai. Until the 2080 s, the climate condition in most of the Siberian region would satisfy the potential persistence of the Amur tiger. The Greater and Lesser Khingan Mountains in Northeastern China would become suitable habitat; while the population distributed in southern Primorski Krai would move northward. However, the occurrence probability of the Amur tiger in the whole region would decline (Fig. 6).

In the A2A climate change scenario, the size of suitable habitat was smaller than that in the A1B scenario, with lower assumed energy use and emissions. From the 2020 s to the 2050 s, the suitable habitat would move northward. In the 2050 s, the southern boundary of suitable habitat would move northward, but the entire area would expand to the north border of historical distribution area at the end of the 19th Century, and the occurrence probability would be much lower across the whole range. The suitable habitat in China would disappear beginning in 2050. In the 2080 s, suitable habitat would keep moving northward, but the shifts would be less than that in the A1B scenario, and the occurrence probability would be lower. The suitable habitat distributed in the Lesser Khingan Mountains would disappear consequently (Fig. 7).

The climate in the B2A scenario changes the most conservatively due to projecting the lowest-level economic development and a strategy of sustainable energy use. The results showed that potential suitable habitat in this scenario changed very little, the suitable habitat in North Korea moved northward to the China-Russia-North Korea border region, and the occurrence probability in the northern part of the suitable habitat increased from the 2000 s to the 2020 s (Fig. 8). The suitable habitat from the 2050 s to the 2080 s were smaller than that in scenarios A1B and A2A, the largest suitable habitat patch was divided into two patches, and the occurrence probability declined significantly. The suitable habitat in China would disappear after 2050 s (Fig. 8).

Based on our projection of potential suitable habitat, there is a positive relationship between the distance of potential habitat shifts and climate change. Tigers' suitable habitat in A1B scenario moved the most northward, and expanded to the largest extent; while in the most conservative scenario, B2A, the suitable habitat shifted the least.

Population viability analysis

The metapopulation's size increased quickly in response to climate change in the A1B and A2A scenarios over the first few decades of the simulation, and then began to decline until extinction at the 2060 s (Fig. 9a). Climate change led to considerably higher risks for quasi-extinction (Fig. 9b). In the A1B and A2A scenarios, the probability of decline for 100 % of their population was 1, which means that the probability of extinction was 1 (Fig. 9b, c). The probability of the population reaching 140 individuals (about 50 % of their initial population) was 75 % in scenario B2A (Fig. 9b, c). Although the population in B2A increased less than that of the other two climate change scenarios, the population did not go extinct and it was more stable. The suitable habitat in A1B scenario was the largest in size, but the suitability of

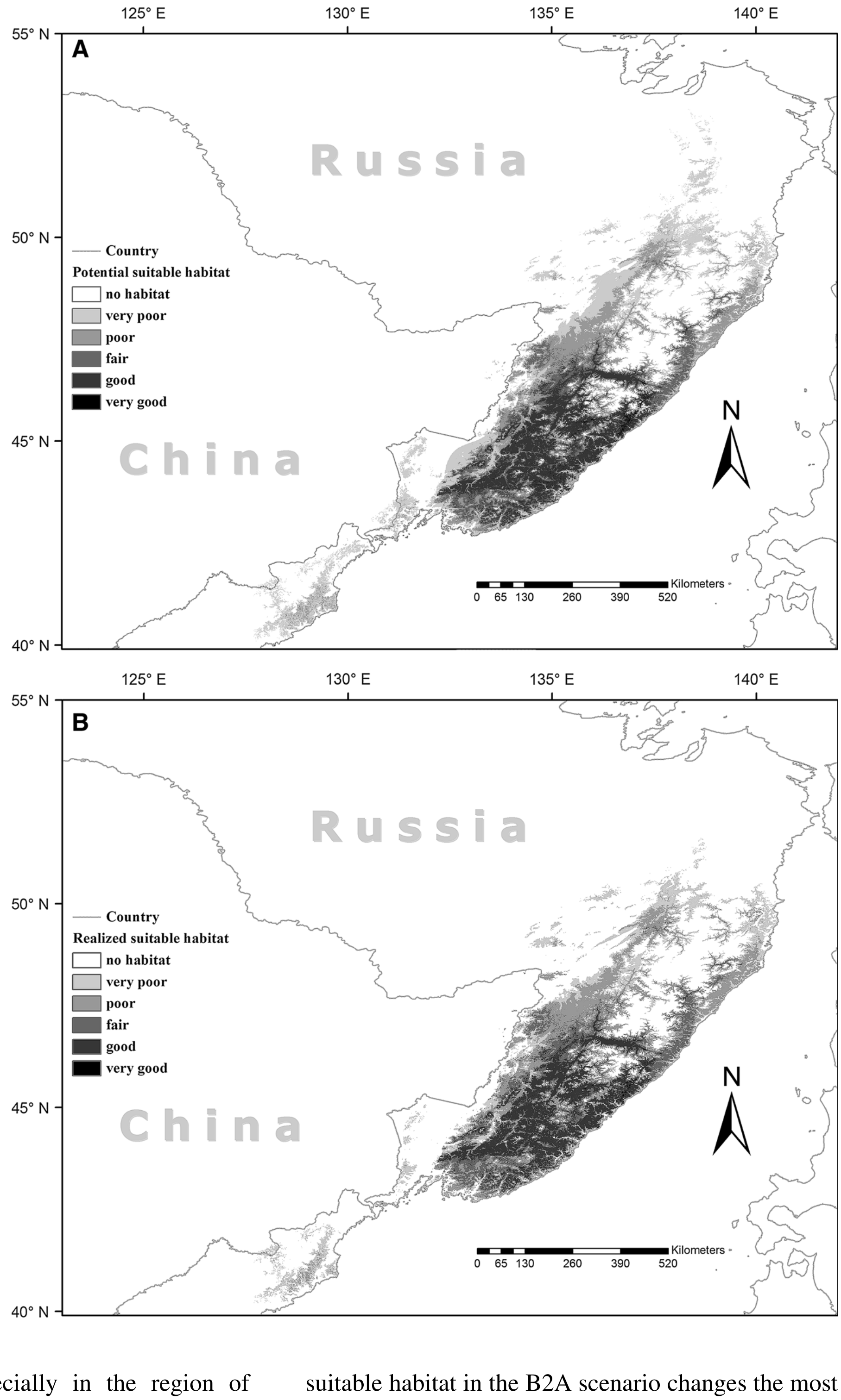

Fig. 3 The potential suitable habitat (**a**) and realized suitable habitat (**b**) for the Amur tiger projected from species distribution modeling (MAXENT). The *darkened areas* represent occurrence probability, the darker the area, the higher the occurrence probability. Here we used sensitivity-/specificity-balanced thresholds to delimit suitable and unsuitable habitats for tigers. The suitable habitat was classified into five categories: very poor, poor, fair, good, and very good with equal intervals

these areas was low, especially in the region of northern Siberia, and population viability was thus the lowest among the three scenarios. Comparatively, the suitable habitat in the B2A scenario changes the most conservatively, but the population would not go to extinction over the 100 years.

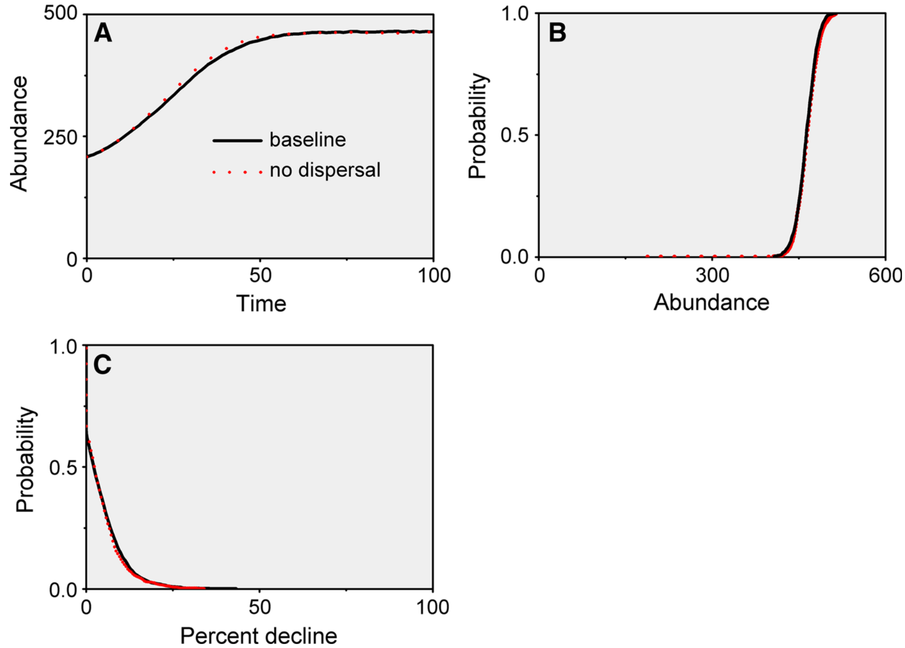

Fig. 4 Population dynamics and the viability of the entire Amur tiger metapopulation in baseline scenarios. **a** Metapopulation abundance, **b** quasi-extinction risk of the metapopulation as the probability of falling below a certain threshold size, **c** the risk of population decline as a function of the amount of population decline. In each graph, the *solid line* represents the baseline scenario with dispersal between patches, and the *dotted line* denotes the baseline scenario without dispersal

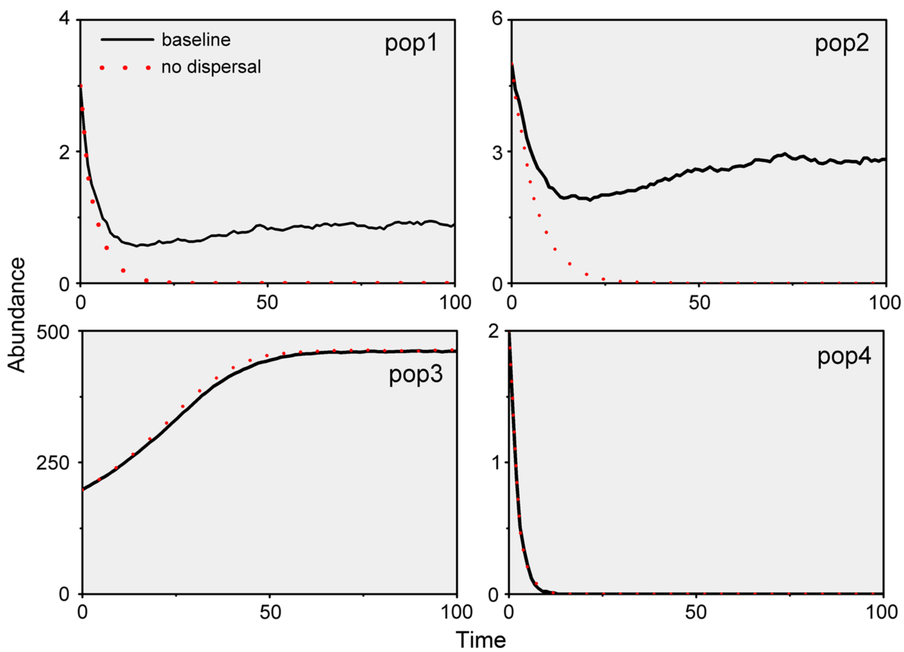

Fig. 5 Population viability of four sub-populations of the Amur tiger in baseline scenarios. In each graph, the *solid line* represents the baseline scenario with dispersal and the *dotted line* represents the baseline scenario without dispersal

Discussion

Changes in potential and realized suitable habitat

Though climate models have been successfully used to project the distribution of plants and animals at large scales (Guisan and Zimmermann 2000; Rahbek and Graves 2001; Whittaker et al. 2001), they have been questioned for lacking important details on species interactions and dispersal processes (Davis et al. 1998; Iverson et al. 1999; McCarty 2001; Thuiller et al. 2003, 2004). Thuiller et al. (2004) estimated the

Table 4 The number and area of suitable habitat patches of the Amur tiger in different climate change scenarios

Scenarios	2000 s (baseline)		2020 s		2050 s		2080 s	
	No. of patches	Area (km^2)	No. of patches	Area (km^2)	No. of patches	Area (km^2)	No. of patches	Area (km^2)
A1B	4	238,237	5	329,037	5	470,339	6	487,874
A2A	4	238,237	3	272,668	1	384,304	3	399,480
B2A	4	238,237	4	311,785	2	331,231	3	399,968

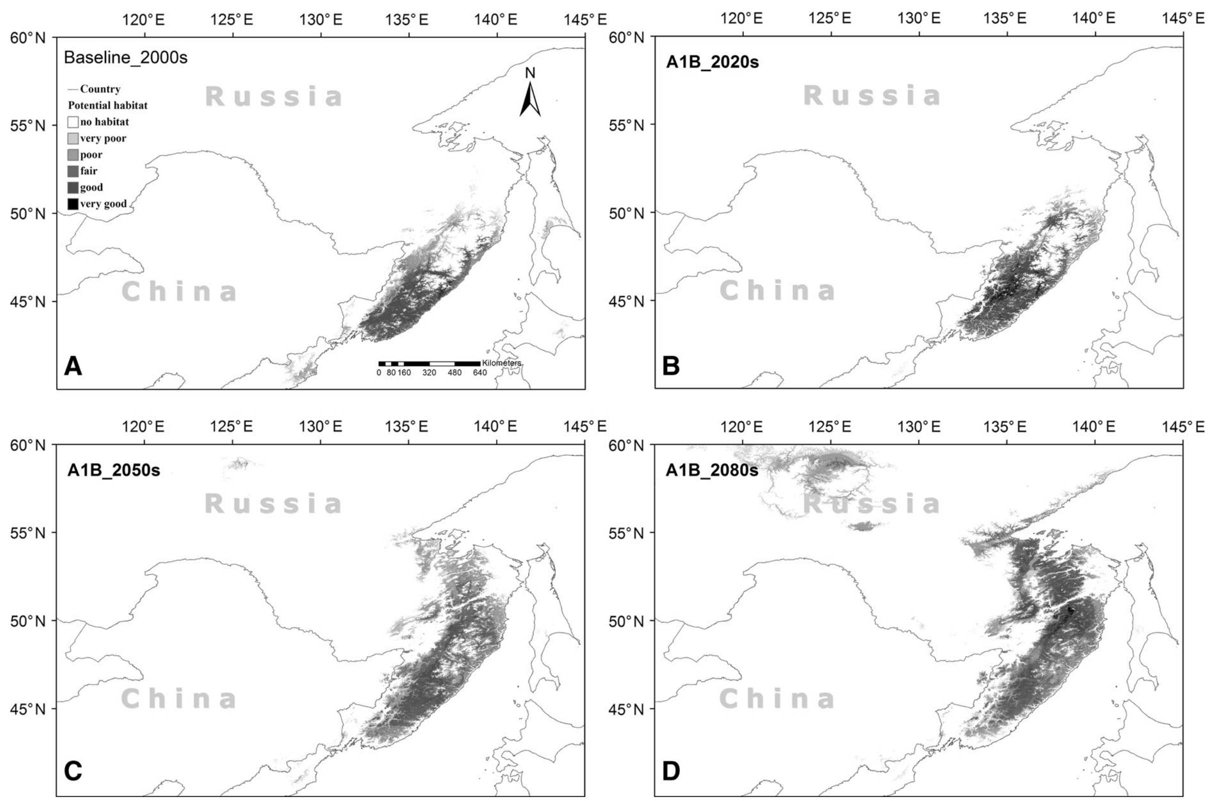

Fig. 6 The potential suitable habitat for the Amur tiger in the A1B scenario in the 2000 s (**a**; the same as the baseline scenario), 2020 s (**b**), 2050 s (**c**), and 2080 s (**d**). *Darkened areas* represent occurrence probabilities; the darker the color, the higher the occurrence probabilities

effects of human-related factors on species distribution using the Artificial Neural Network (ANN) to compare the differences between simulation based only on climate data and simulations considering both climate and human effects. Their results showed that human-related factors did not affect the distribution projections significantly. However, the study by Pearson et al. (2004) showed that considering human-related factors would increase the accuracy of simulation results. Research by Lorenzen et al. (2011) suggested that "although climate change alone can explain the extinction of some species, a combination of climatic and anthropogenic effects appears to be responsible for the extinction of others".

In our study, we compared the "potential suitable habitat" (simulated using natural environmental viabilities only) and "realized suitable habitat" (simulated by also incorporating human-related viabilities) to find out if human activities significantly affect the projection of suitable habitat and viability of the Amur tiger. Our results showed that, although the area of realized suitable habitat was nearly the same as the

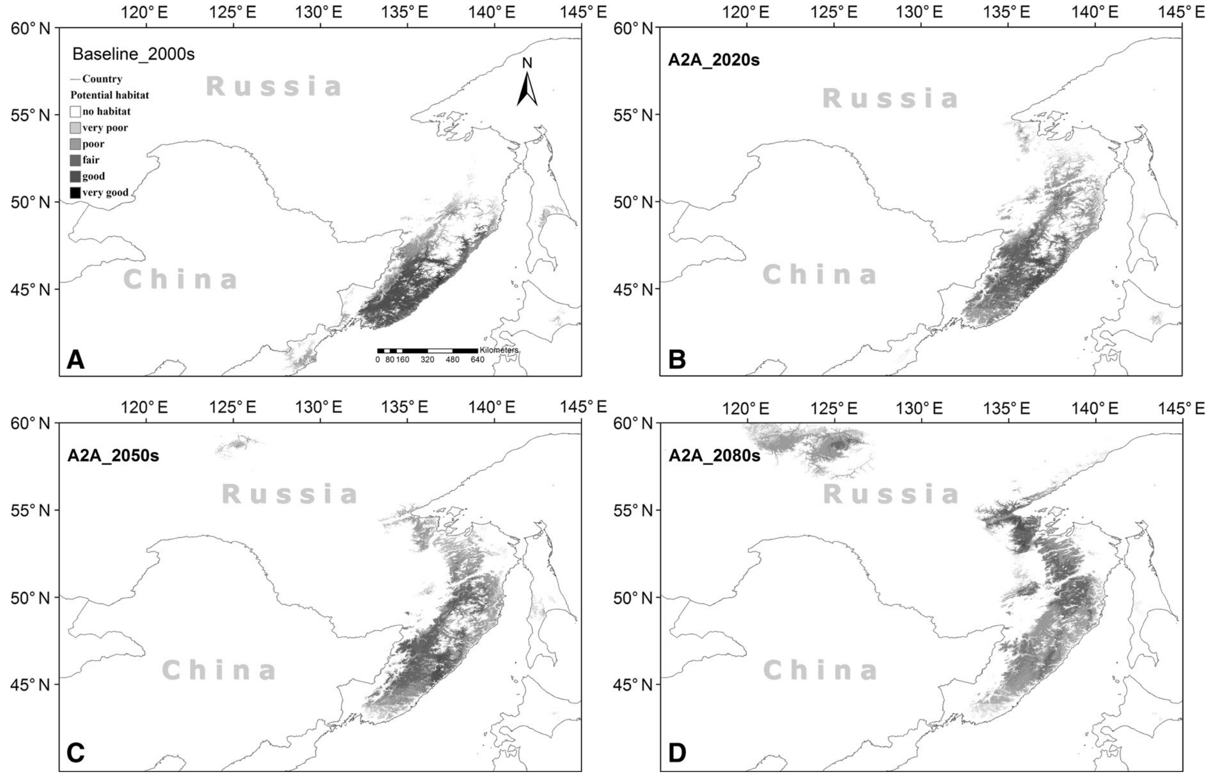

Fig. 7 The potential suitable habitat for the Amur tiger in the A2A scenario in the 2000 s (**a**), 2020 s (**b**), 2050 s (**c**), and 2080 s (**d**). *Darkened areas* represent occurrence probabilities; the darker the color, the higher the occurrence probabilities

size of the projected potential habitat, the region with high human density and disturbance had a very low suitability of habitat (occurrence probability of tigers). This means that, besides climate and topographic requirements, the most suitable habitat was located in areas with low human density and high Korean pine forest cover. This conclusion is consistent with the results of Carroll and Miquelle (2006). Thus, it is not adequate to assess the status of the Amur tiger by projecting suitable habitat only; extinction probability should also be considered.

Effects of climate change on tigers' distribution and population viability

According to our analysis, bioclimatic conditions satisfying the survival requirements of tigers would shift differentially in response to the three climate change scenarios. Our population viability analysis further indicates that the Amur tiger would go extinct fastest in the most severe scenario of climate change (A1B), although the total area of suitable habitat in this scenario was the largest. In contrast, in the least severe scenario of climate change (B2A), the total area of suitable habitat would not increase much due to temperature shifts, and the relatively stable survival and fecundity rates would allow the Amur tiger to persist for the next 100 years. Apparently, these results would be the opposite of what would have been obtained from the SDM method alone (in that case, the tiger population would be positively correlated with the total area of suitable habitat).

A key reason underlying these differences is that the expanded suitable habitat due to climate change would be dominated by spruce and fir forests. These forests are not high-quality habit for the tigers because prey densities are usually low (Tian et al. 2009, 2001b). The most favorite habitat of the Amur tiger, the Korean pine forest (Miquelle et al. 1999), has suffered intense logging and has shrunk southward during last century because of Korean pine's high price as construction material in the international market (Li et al. 2009; Shingauz and Diao 2003). Our previous study showed that poaching, habitat degradation, and habitat loss in

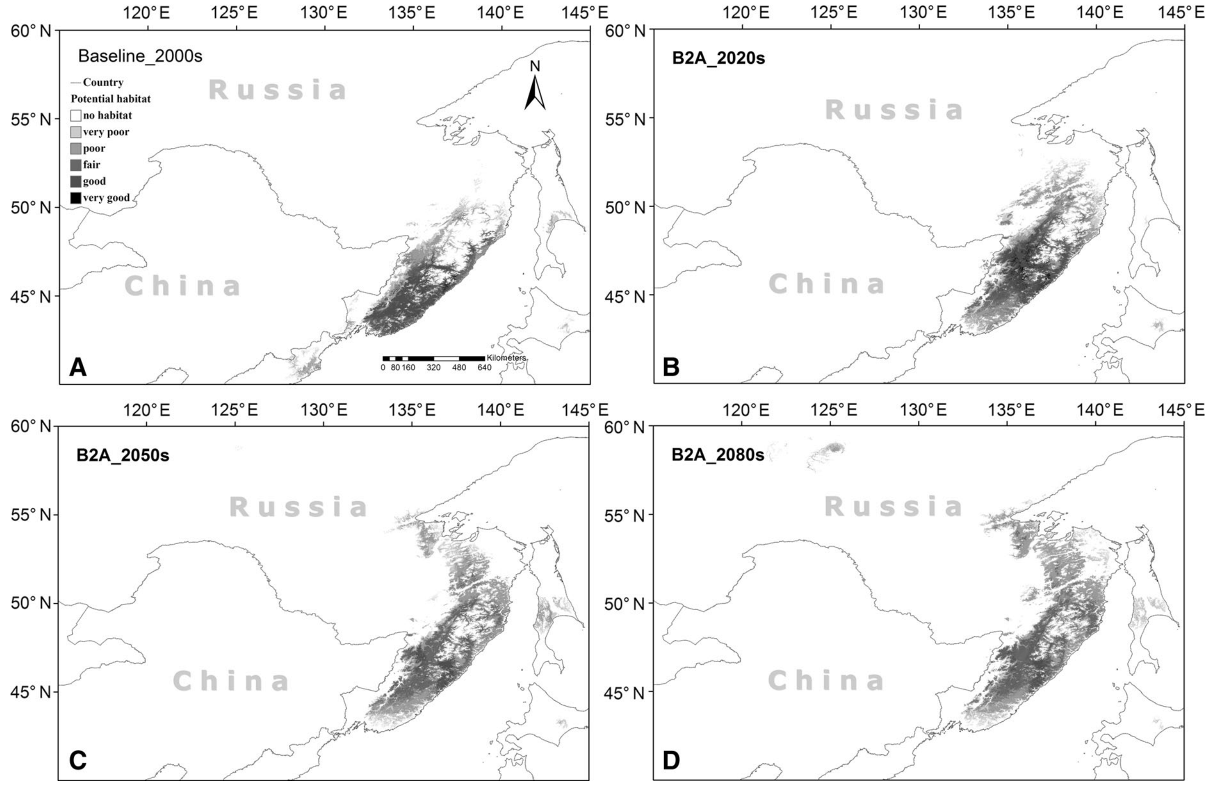

Fig. 8 The potential suitable habitat for the Amur tiger in the B2A scenario in the 2000 s (**a**), 2020 s (**b**), 2050 s (**c**), and 2080 s (**d**). *Darkened areas* represent occurrence probabilities; the darker the color, the higher the occurrence probabilities

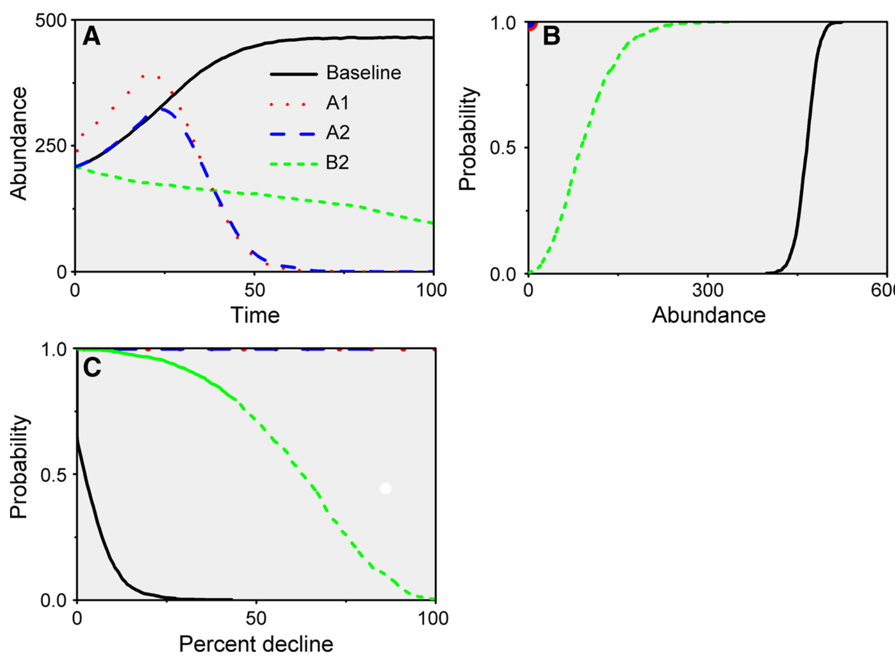

Fig. 9 Population dynamics and viability of the Amur tiger under climate change scenarios: **a** metapopulation abundance, **b** quasi-extinction risk of the metapopulation, **c** the risk of population decline. In each graph, the *solid line* represents the baseline scenario, and the different *dotted lines* represent three climate change scenarios (A1B, A2A, and B2A)

this region could drive the Amur tiger to extinction within the next century. The results of this current study indicate an even gloomier future for the Amur tiger: climate change will likely exacerbate the habitat-related problems and thus increase the possibility of extinction for these largest cats in the world over the next 100 years.

Methodologically, our study demonstrates that neither SDMs nor PVA alone is adequate enough to assess how climate change will affect the fate of the Amur tiger. Similar conclusions have been made concerning other endangered species elsewhere (e.g. Keith et al. 2008). Combining these two modeling approaches, however, seems an effective way of exploring the possible impacts of climate change in a spatially explicit, landscape-specific fashion, providing valuable information for conservation planning and ecosystem management.

Implications for conservation

To mitigate the impacts of climate change on the population viability of the Amur tiger, landscape and regional conservation planning is needed. Based on our study, here we make three suggestions. First, it is necessary to build nature reserves and corridors between isolated suitable habitat patches to increase permeability of the matrix. Although the Amur tiger has great dispersal ability, habitat fragmentation still negatively affects its population persistence, especially for small and geographically isolated populations. As shown in our study here, increasing inter-patch connectivity increases the abundance of subpopulations. To ensure the long-term persistence of the Amur tiger under climate change, therefore, it is necessary to have a nature reserve network well-connected through animal movement corridors, which retains the primary quality habitat that exists now.

Second, as the scarcity of prey was one of the primary contributors to the decrease in the population size of the Amur tiger during the last century (Karanth and Stith 1999; Schwartz et al. 2006; Tian et al. 2009), the introduction of prey species into the potential suitable habitat should be an effective and feasible way to enhance the tigers' viability. Prey density is indeed the primary criterion for evaluating the quality of suitable habitat.

The last, but not the least, suggestion is not only to protect the extant Korean pine forests, but also to expand them into some neighboring potential habitat that is currently dominated by fir and spruce forests. In places where temperature and precipitation are appropriate now and in future due to climate change, such reforestation and human-directed forest succession efforts would help the tigers adapt to the possible impacts of climate change in the next 100 years. Because the rate of evolutionary response (Etterson and Shaw 2001) and distribution shifts (McLachlan et al. 2005) for plants are much slower than that of climate change, these human efforts seem necessary.

It is important to note that the Amur tiger is already in great danger, and may go extinct before the deleterious consequences of climate change fully manifest. So, in addition to establishing nature reserves, prey introduction, and habitat expansion, any effective conservation strategy for long-term persistence of the Amur tiger must also ensure that there will be no poaching, habitat destruction, prey depletion, and substantial changes in the forest stand structure of tigers' habitat (Carroll and Miquelle 2006; Hötte 2006; Dinerstein et al. 2007; Tian et al. 2009; Han et al. 2012).

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