Is there a future for Amur tigers in a restored tiger conservation landscape in Northeast China?

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Abstract

The future of wild tigers is dire, and the Global Tiger Initiative's (GTI) goal of doubling tiger population size by the next year of the tiger in 2022 will be challenging. The GTI has identified 20 tiger conservation landscapes (TCL) within which recovery actions will be needed to achieve these goals. The Amur tiger conservation landscape offers the best hope for tiger recovery in China where all other subspecies have most likely become extirpated. To prioritize recovery planning within this TCL, we used tiger occurrence data from adjacent areas of the Russian Far East to develop two empirical models of potential habitat that were then averaged with an expert-based habitat suitability model to identify potential tiger habitat in the Changbaishan ecosystem in Northeast China. We assessed the connectivity of tiger habitat patches using least-cost path analysis calibrated against known tiger movements in the Russian Far East to identify priority tiger conservation areas (TCAs). Using a habitat-based population estimation approach, we predicted that a potential of 98 (83–112) adult tigers could occupy all TCAs in the Changbaishan ecosystem. By combining information about habitat quality, connectivity and potential population size, we identified the three best TCAs totaling over 25 000 km^2 of potential habitat that could hold 79 (63–82) adult tigers. Strong recovery actions are needed to restore potential tiger habitat to promote recovery of Amur tigers in China, including restoring ungulate populations, increasing tiger survival through improved anti-poaching activities, land-use planning that reduces human access and agricultural lands in and adjacent to key TCAs, and maintaining connectivity both within and across international boundaries. Our approach will be useful in other TCLs to prioritize recovery actions to restore worldwide tiger populations.

Introduction

Wild tiger *Panthera tigris* numbers have dramatically dropped to less than 3200 in the world, because of tiger poaching, poaching of their ungulate prey, and habitat destruction exacerbated by rapidly growing human populations and economies in Asia (Dinerstein *et al.*, 2007). Tigers face a dire future, and recovery will take commitment of world leaders and governments (Walston *et al.*, 2010). At the 2010 St. Petersburg Tiger Summit hosted by Russia, tiger range countries committed to doubling the population of wild tigers by the next year of the tiger in 2022 through the Global Tiger Initiative (Wikramanayake *et al.*, 2011). To achieve this ambitious goal, a number of large-scale tiger conservation landscapes (TCLs) were identified (Wikramanayake *et al.*, 2011) that will need to be actively restored to ensure a viable future for wild tigers. Identifying and prioritizing smaller-scale recovery areas and actions within these

large-scale TCLs are the next steps needed to actively recover tigers (Walston et al., 2010; Wikramanayake et al., 2011).

Successful restoration of TCLs is an enormous conservation challenge, and recovery of tigers in China is no exception (Dinerstein et al., 2007) where the South China P. t. amoyensis, Indochinese P. t. corbetti and Bengal tiger P.t. tigris (Luo, 2010) may already be effectively extinct. Recent surveys suggest that while there is no viable population of Amur tigers P. t. altaica in Northeast China, since 2002, there have been at least 16 different immigrating increasing reports of tigers in Northeastern China mainly along the Russian border (Zhou et al., 2008) from the adjacent Russian population of 430–500 tigers (Miquelle et al., 2006). Despite the ongoing threats of tiger poaching, prey depletion and habitat fragmentation to Amur tigers in China, growing national government support for tiger recovery, the presence of large forested areas through eastern Jilin and Heilongjiang provinces, and dispersal from connected populations in Russia provide a good foundation for tiger recovery.

To recover tigers in TCLs around the world, potential tiger habitat needs to be first identified and prioritized within these landscapes (Smith, Ahearn & Mcdougal, 1998; Cianfrani et al., 2010; Walston et al., 2010; Wikramanayake et al., 2011). Carnivore habitat is conceptually a combination of sufficient prey density, biophysical and landcover resources, and low mortality from human causes (Mitchell & Hebblewhite, 2012). Tiger habitat is generally considered as forested areas with high densities of large ungulate prey, with protection from human-caused mortality (Smith et al., 1998; Wikramanayake et al., 2004; Carroll & Miquelle, 2006). After identifying potential habitat, connectivity between habitat patches needs to be assessed (Schadt et al., 2002; Linkie et al., 2006) and potential population size of recovered tigers determined (Boyce & Waller, 2003) to help prioritize conservation in discrete habitat patches. Land-use planning in identified tiger habitat is a vital step in the recovery process because it integrates tiger recovery actions with political and economic development agendas (Walston et al., 2010; Wikramanayake et al., 2011).

Our objective was to develop an approach to identify priority tiger recovery areas within a greater TCL. We focused on identifying politically and scientifically defensible tiger recovery areas for Amur tigers in Northeast China by (1) defining potential tiger habitat for recovery using three different methods developed by different stakeholder teams (Loiselle et al., 2003); (2) identifying connectivity between large patches of potential tiger habitat to identify larger tiger conservation areas (TCAs); (3) estimating potential tiger population size in priority conservation areas if full restoration were to occur; and (4) prioritizing conservation areas for recovery efforts in the Northeast China using a combination of criteria including habitat quality, connectivity and potential population size of recovered tigers. While focused on the Amur tiger, our approach shows promise for implementing the global tiger initiative's conservation policies within TCLs throughout tiger range and other endangered carnivores.

Methods

Study area

Our study area was a 218 785-km^2 portion of the Changbaishan ecosystem in the Jilin and Heilongjiang Provinces in Northeast China and Southwest Primorye, Russia, and adjacent Sikhote–Alin Mountain ecosystem (Fig. 1) in southern Primorski Krai, Russia. While Changbaishan and the Sikhote–Alin ecosystems have been considered a single TCL (Wikramanayake et al., 2011), tiger populations appear to be genetically distinct between them (Henry et al., 2009). Both areas are mountainous landscapes with average elevations from 800 to 1000 m (max 2500 m). The climate is temperate continental monsoonal with average precipitation from 519 to 1336 mm and 20 to 50 cm average snow depth in winter. The average temperature in January is −19°C and the average temperature in July is 20.5°C. Vegetation is very diverse, ranging from temperate to boreal, and is characterized by major land cover types of Korean pine Pinus koraiensis mixed with deciduous forests of birch and oak, mixed coniferous forests at higher elevations, alpine areas, meadows, natural shrublands, coniferous plantation forests, and agricultural areas (see Li et al., 2010 for more details). The majority of forests have been logged, and combined with human-induced fire, many low-elevation forests have been converted to secondary deciduous forests. There are over 370 towns or larger settlements in the Chinese part of the Changbaishan ecosystem with over 11.7 million people, and 75 towns/cities with 1 million people in southern Primorye, Russia. Ungulate species in approximate order of importance in the diet of tigers (Miquelle et al., 1996), include red deer Cervus elaphus, wild boar Sus scrofa, sika deer Cervus nippon and Siberian roe deer Capreolus pygargus. The area also has a diversity of sympatric carnivores including the sole remaining population of critically endangered Far Eastern leopards Panthera pardus orientalis, wolves Canis lupus, Eurasian lynx Lynx lynx, Asiatic black bear Ursus thibetanus and brown bear Ursus arctos. Thus, successful tiger recovery in this landscape may ensure a future for many other rare and endangered species in northern Chinese forested ecosystems (Hebblewhite et al., 2011).

Tiger habitat modeling

To identify potential tiger habitat in China, we used a simple ensemble habitat modeling approach (Araujo & New, 2007; Thuiller et al., 2009) that averaged three habitat models (Fig. 2). We used the average of three models because of the uncertainty inherent in all habitat models (Barry & Elith, 2006) and to facilitate collaborative approaches in conservation planning among three different stakeholders [Chinese government, World Wide Fund for Nature (WWF) and Wildlife Conservation Society (WCS)] in Northeast China (Loiselle et al., 2003). Averaging all three models increased buy-in from all three stakeholders instead of competing models when their accuracy to predict tiger
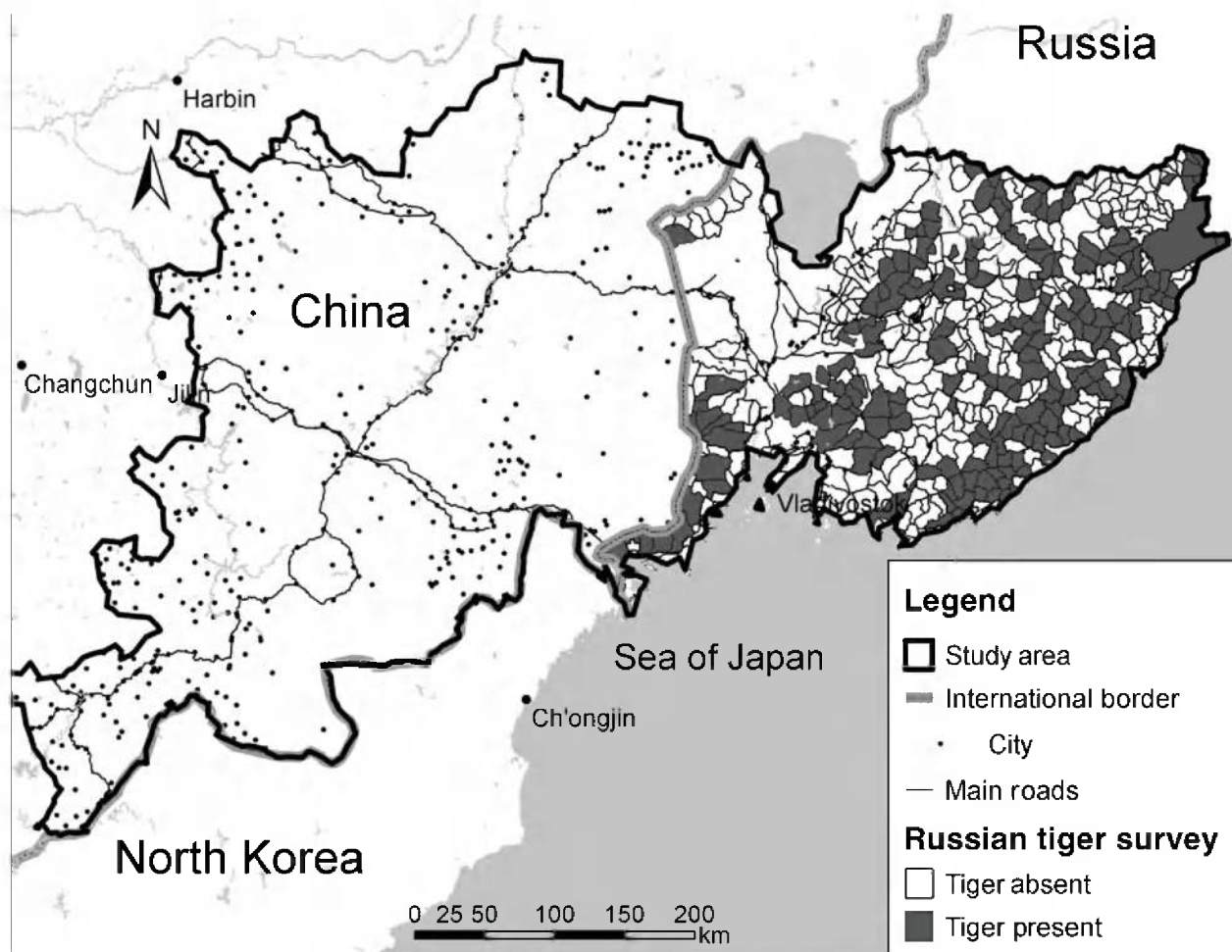
Figure 1 Location of the study area in the Changbaishan ecosystem in Northeast China and the southern Sikhote–Alin ecosystem in the Russian Far East, showing locations of the 2005 Russian winter tiger survey units where tigers were and were not present.

habitat in China was unknown because of tiger absence. We developed two complementary data-driven empirical models based on tiger data in the Russian Far East, which were then extrapolated to Northeast China; environmental niche factor analysis (ENFA, Hirzel *et al.*, 2002) and resource selection functions (RSF, Manly *et al.*, 2002). The third method used expert knowledge of Amur tiger and its habitat requirements within China to define an expert-based habitat suitability model across Russia and China following methods explained in more detail in Xiaofeng *et al.* (2011). We first describe the tiger data used to develop empirical models, landscape covariates, and then the three habitat modeling approaches.

Russian tiger surveys

We used tiger track data collected during a range-wide survey in February and March 2005 across all tiger habitat in the Russian Far East using survey methods that are reported in detail elsewhere (Carroll & Miquelle, 2006; Miquelle *et al.*, 2006), so we only briefly review them here.

The southern Primorye Krai portion of the study area was divided into 486 sampling units averaging 131 km². Within each sampling unit, an average of 89 km of transects (totaling 11 473 km) were surveyed by vehicle, snowmobile or on foot/skis. We only used sample units with > 25 km of survey effort to ensure detection probability was 1.0 (Carroll & Miquelle, 2006, Hebblewhite, unpubl. data). The number and location of 595 fresh (≤ 24 h) tiger tracks were used elsewhere to estimate tiger abundance using snow tracking – density algorithms developed in the Russian Far East (Miquelle *et al.*, 2006, Stephens *et al.*, 2006).

Landscape covariates

We used geographic information system (GIS) landscape variables (see Supporting Information for more detail) thought to explain tiger habitat based on other studies (Wikramanayake *et al.*, 2004; Carroll & Miquelle, 2006; Linkie *et al.*, 2006). These included biophysical resources including topographic variables (elevation, slope, aspect) from a 100-m resolution digital elevation model, and four
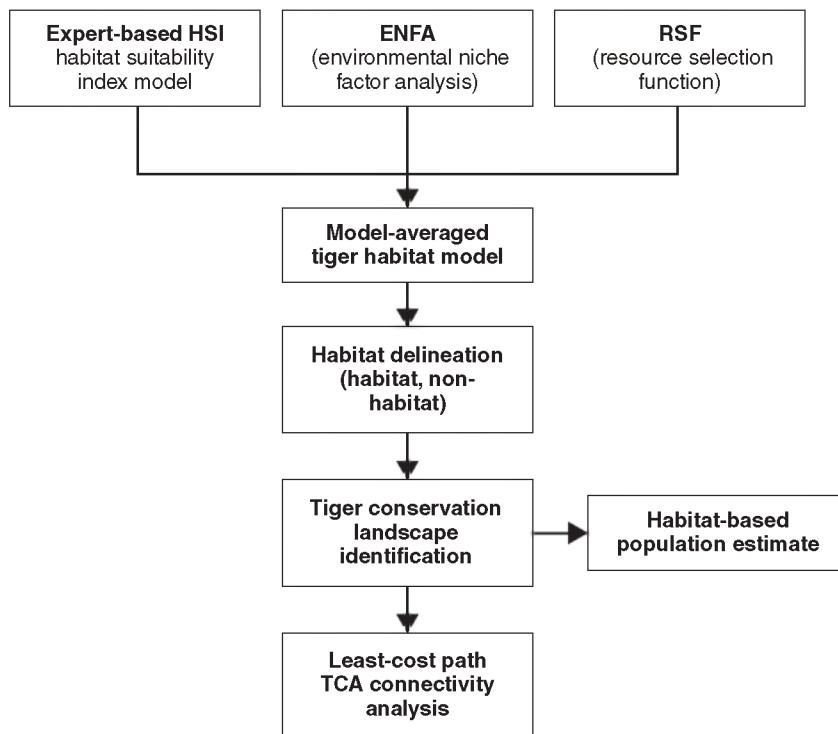
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│ Expert-based HSI│   │      ENFA       │   │       RSF       │
│habitat suitability│  │(environmental niche│ │(resource selection│
│   index model   │   │ factor analysis)│   │    function)    │
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                    │tiger habitat model│
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                    │Habitat delineation│
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            │Tiger conservation│─────▶│  Habitat-based  │
            │   landscape     │      │population estimate│
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            │ Least-cost path │
            │TCA connectivity │
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Figure 2 Schematic for identification of Amur tiger habitat in the Changbaishan study area in Northeast China.

key 30-m land cover communities, Korean pine mixed with deciduous forests, deciduous forests, coniferous forests plus other natural landscapes, and human-dominated landscapes. We also used remotely sensed measures of net primary productivity (NPP) derived from the moderate resolution imaging spectroradiometer (MODIS) satellite data (1-km resolution, MOD17A3 data product, Running *et al.*, 2004) as well as the percent of the 2005 winter (November 1 to April 30). Each MODIS pixel was covered by snow as measured by the MODIS satellite (250-m resolution, MOD10A product, Hall *et al.*, 2002), Finally, we used human use data at a 100-m resolution including human settlements classified as towns (< 20 000 people) or cities (≥ 20 000), and roads divided into low-use roads (mostly logging roads), secondary roads (unpaved or rarely used paved roads) with moderate levels of traffic and primary roads (highways and main access roads) with high traffic volumes. Despite the importance of ungulate prey as habitat for carnivores like tigers (Karanth *et al.*, 2004), the absence of standardized and reliable prey data across China prevented inclusion of prey density. However, we examined prey in habitat models for the Russian portion of the study area elsewhere (Li *et al.*, 2010; Mitchell & Hebblewhite, 2012), which we return to in the discussion.

Ecological Niche Factor Analysis (ENFA)

ENFA (Hirzel *et al.*, 2002; Basille *et al.*, 2008) relates covariates at the spatial location of a species compared with covariates available within a study area to a reduced number of uncorrelated and standardized factors in a procedure similar to a principal components analysis. The first factor that is extracted is the marginality, which measures how species' locations differ from the average conditions in the study area. The next factors explain species' specialization (a measure of the niche breadth) by comparing what is used by the species with the available range of environmental conditions within the study area (Hirzel *et al.*, 2002). We laid out a customary 2 × 2-km grid across Southern Primorye in Russia, and considered the 441 grid cells with ≥ 1 tiger track as a 'presence' data point. We computed the analyses in Biomapper 4.0 (Hirzel *et al.*, 2007) and included only uncorrelated ($r < 0.7$) covariates in the ENFA, averaged across the 2-km^2 grid using a 5-km radius moving window (to approximate the spatial scale of the sampling unit in the RSF, see later), and standardized data before analysis. The model derived from data in Russia was then interpolated/extrapolated to the Changbaishan region using the tool 'Extrapolate' in Biomapper 4.0 to interpolate/extrapolate the model using the harmonic mean algorithm (Hirzel *et al.*, 2006). We validated the ENFA using Boyce *et al.*'s (2002) k-folds cross-validation Spearman rank correlation index.

RSF modeling

RSFs (Manly *et al.*, 2002) were estimated in Russia by comparing resource covariates in used ($n = 198$) and unused ($n = 288$) survey units following a presence–absence (used–unused) design. We evaluated tiger selection at the scale of the survey unit using mean covariate values (density of

roads, % forest type 1, etc, Supporting Information Table S1) for survey units using ArcGIS 9.3 (ESRI, Redlands, CA, USA) Zonal Statistics function. Used and unused sampling units were then contrasted with fixed-effects logistic regression, which yields a true probability between 0 and 1 when detection probability is near 1.0 (Manly *et al.*, 2002). To extrapolate results from the RSF developed in Russia to the Changbaishan ecosystem, we used a moving window analysis to spatially scale variables using a circular moving window with a 6.6-km radius, equivalent to the 131-km² survey unit. First, we screened variables for collinearity using a cut-off of $r = 0.7$ and with variance inflation factors, and assessed nonlinear effects using quadratics (Hosmer & Lemeshow, 2000). We then created a set of models for which we conducted model selection using Akaike information criteria. We tested for model goodness of fit using the likelihood ratio chi-squared test (Hosmer & Lemeshow, 2000) and evaluated the predictive capacity of the top model using pseudo-r^2, the logistic regression diagnostic receiver operating curves (ROC) and classification success. We evaluated the predictive capacity of the RSF also using k-folds cross validation (Boyce *et al.*, 2002).

The expert habitat suitability model

The expert modeling approach was described by Xiaofeng *et al.* (2011) who identified potential tiger habitat in a broader area than just the Changbaishan region in Northeast China. The expert model was developed using an application of rule-based habitat suitability functions (independent of the ENFA or RSF models) to existing large forest patches ($\geq$ 500 km²) in ArcGIS 9.2 (ESRI, Redlands, CA, USA). Based on this initial constraint, four GIS landscape covariates described earlier were included in the expert model: land cover type, elevation, proximity to roads and a settlement disturbance factor (which included village density and a multiplier for large settlements). We then estimated arbitrary cost functions for the four variables as predictors of habitat suitability for tigers, with the lower the cost, the higher the value of the parameter for tiger (see Xiaofeng *et al.*, 2011 and Supporting Information Table S2 for details). For example, median elevations (400–800 m) were considered the most suitable for tigers (cost score of 1), middle and upper elevations (200–400 m and 800–1500 m) were assigned a cost score of 2, and lower (< 200 m mostly populated by humans) and high elevations (> 1500 m) were considered the poorest habitat (cost score of 4) (Supporting Information Table S2). Mixed-coniferous (Korean pine) with deciduous forests, and deciduous broadleaved forests were considered the best tiger habitat (cost = 1), pure deciduous stands 'good' (cost = 2) habitats, coniferous forests shrublands, or wetlands as poor habitats (cost = 6), and human-dominated land covers (i.e. agricultural, cities) ranked as not-suitable (cost = 15). Cells > 5 km from primary roads and > 3 km from secondary roads were ranked the highest suitability (cost = 1), 2–5 km from primary roads and 1–3 km from secondary roads as good habitat (cost = 2) and areas close to roads (0–2 km from primary roads, 0–1 km from secondary roads) as poor habitat with a cost of 6. Finally, village density was ranked as the highest quality (cost = 1) when < 2 villages/100 km², good when 3–6, poor when 7–19, and unsuitable when < 10 km from a city or 5 km of a county center or 2 km from a town (Supporting Information Table S2). These values were assigned to cells of 200 m² across a grid covering both the Changbaishan ecosystem in China and Sikhote–Alin in Russia. The resultant potential habitat suitability index was calculated as: tiger habitat value = elevation + land cover + road proximity + settlement density, with habitat suitability values ranging from 4 (most suitable) to 37 (unsuitable). We rescaled the expert model between 0 and 100 where 100 was the highest suitability, and 0 the lowest (see Li *et al.*, 2010; Xiaofeng *et al.*, 2011).

Habitat model averaging

We used a simple ensemble modeling approach (Araujo & New, 2007) that averaged all three habitat models to describe tiger habitat in China. To accommodate different spatial resolution (grain size) from different models, we recalculated model projections at the largest resolution of inputs, and then resampled to 500 m². We averaged models instead of weighting based on area under the curve or ROC scores because of scant tiger validation data within China for optimum model evaluation. Moreover, prior to a habitat modeling workshop in 2008, different stakeholders (Russia, China) were using different modeling approaches, with the potential for competitive and contradictory results hampering conservation. Therefore, model averaging was used as part of a collaborative stakeholder process including Russian, Chinese and western modeling approaches that would ultimately be more successful politically than competing habitat models (Loiselle *et al.*, 2003). To compare the predictions of the three modeling approaches against each other, we evaluated the correlation and linear regression between all three models from 10 000 randomly generated locations across the study area.

Potential numbers of tigers in the Changbaishan ecosystem

We used the habitat-based population method developed by Boyce & McDonald (1999) to estimate potential tiger population size within each TCA (see later) to the averaged habitat suitability model. Given the estimate for the number of tigers (N, range) in Russian (Miquelle *et al.*, 2006), and the total habitat suitability [i.e. sum of all habitat suitability scores $w(x)_i$ from 0 to 100 across all GIS pixels] quality in Russia, we estimated the total habitat suitability required per tiger and predicted the tiger population size in each TCA following:

$$\frac{\sum_{\text{Russia}} \hat{w}(x)_i}{N_{\text{Russia}}} = \frac{\sum_{\text{TCA}_j} \hat{w}(x)_i}{N_{\text{TCA}_j}} \tag{1}$$

where $\sum_j \hat{w}(x)_i$ is the summed habitat suitability for each TCA$_j$, and N is the tiger population estimate for Russia (known) and for TCA$_j$ [solved by rearranging equation (1)]. Key assumptions of this approach include: (1) the right covariates are measured; (2) similar landscape configuration of available habitats and selection patterns occur in both Russia and China; and (4) there exist similar relationships between population parameters and available habitat (Boyce & McDonald, 1999; Boyce & Waller, 2003).

Identifying and prioritizing TCAs

We used a cut-point value from the averaged Amur tiger habitat model to turn the continuous prediction of tiger habitat suitability into discrete tiger habitat patches (i.e. habitat vs. non-habitat, Liu *et al.*, 2005) that correctly classified 85% of tiger tracks collected in Russia. Potential tiger habitat patches were defined using the tool Region-Group in ArcGIS 9.2 (ESRI). Next, connectivity of these patches was assessed using a least-cost approach with the CostDistance Tool in ArcGis 9.2 (Chetkiewicz, Clair & Boyce, 2006; Zimmermann & Breitenmoser, 2007; Janin *et al.*, 2009). We used tiger habitat patches as sources for least-cost modeling, and estimated the movement cost surface between patches using an expert-based 'friction' model.

The expert-based cost surface was defined as the relative 'cost' to tiger movement on a scale of 1 (high-quality habitat and connectivity) to 1000 (insurmountable barrier) for each land cover and human covariate using expert opinion similar to the expert-based model (see Supporting Information Table S3). Villages (< 10 000 people) were buffered by 500 and 1000 m and the three larger cities (10 000–20 000; 20 000–50 000; 50 000–100 000) were buffered by 2, 3 and 5 km, respectively. All 200 × 200-m cells falling into the buffer around settlement types I–III were considered insurmountable barriers for tigers and their value was set to 1000 (high cost to movement). A value of 400 and 100 was given to cells falling into the 0–500 m and 500–1000 m distances from villages, respectively. Low-use roads were not included because they do not appear to limit movement of tigers. Secondary roads in Russia were given a value of 130 and primary roads a value of 200. Because main roads in China are generally fenced and all road categories have higher traffic volumes compared with Russia, secondary and primary roads were assigned values of 200 and 800, respectively. Land cover types commonly used by tigers (Miquelle *et al.*, 1999) were given a friction value of 1 (Korean pine mixed with deciduous forests, deciduous forests), whereas coniferous forests and other natural vegetative types (less preferred) were given a value of 10. Human-dominated lands were given a cost value of 100.

To determine which habitat patches were connected in a single TCA, we defined a threshold of the maximum accumulated costs for tigers moving between adjacent quality habitat patches (Zimmermann & Breitenmoser, 2007; Janin *et al.*, 2009). We used knowledge of tiger movement in the southern Sikhote–Alin Mountain ecosystem to calibrate the cost surface. In the Sikhote–Alin, tigers move regularly between adjacent quality habitat patches and thus, all patches can be considered to be connected to each other forming one single unit except for Southwest Primorye (Henry *et al.*, 2009). We set the threshold of the accumulated cost grid so that all habitat patches in Russia were connected except for Southwest Primorski Krai (e.g. Janin *et al.*, 2009). By applying the same threshold values to the Changbaishan ecosystem, we defined connected habitat patches greater than 400 km^2 (approximately 1 female home range, Goodrich *et al.*, 2010) as TCAs.

We prioritized TCAs for recovery using the following criteria recommended based on previous studies of carnivore landscape conservation (Wikramanayake *et al.*, 2004; Carroll & Miquelle, 2006): (1) distance from the closest source population in Russia along the least-cost path between the closest source and the respective TCA; (2) area; (3) the potential tiger population size; (4) a fragmentation index calculated as the ratio of the perimeter to the area multiplied by 1000; (5) whether tigers were currently present based on number of reports; and (6) level of isolation, ranked according to the number of linkages between the top nine TCAs (see Li *et al.*, 2010).

Results

Habitat modeling

ENFA

Using the marginality (M), the preferred habitat of tigers was identified as areas including a higher mean slope, a higher frequency of deciduous forests, a greater distance from villages and large cities, a lower frequency of human-dominated landscapes, and a lower density of primary and secondary roads than available in the Russian study area (marginality scores; Table 1). An overall tolerance value T ($T = 1/specialization$) of 0.68 indicated that tigers were predominately not habitat specialists. We identified three factors (M, $S1$–2; Table 1) that accounted for 54.2% of the total specialization. Tiger distribution was restricted to a narrow range regarding the mean NPP, the mean density of primary roads, and, to a lesser extent, the frequency of deciduous forests (specialization scores S1 and S2; Table 1). The mean k-folds rank correlation was relatively high (0.82), confirming good model cross-validation, but with a relatively large standard deviation (SD) of 0.24, indicating variation in model performance. Overall marginality, M, of the ENFA model applied to the calibration data sets was 0.73, confirming that potential tiger habitat in the Changbaishan region differed from the Russian Far East. However, when interpolating and extrapolating the model to the Chinese portion of the study area (Supporting Information Fig. S2a), all habitat suitability values were within the range of the factor values in the calibration area ±10% (allowable percentage of extrapolation) and could therefore be computed. All 1802 extrapolated cells (3.2% of the area) in the Chinese portion of the study area were located in highly human-dominated areas and, consequently, their tiger habitat suit-

Table 1 Summary of ENFA and RSF empirical habitat models for Amur tigers in Southern Primorye Krai, Russian Far East, that were used to predict potential tiger habitat in the Changbaishan ecosystem in Northeast China

Landscape covariate	ENFA results[a]			RSF results[a]	
	M[b] 23.4%	S1[c] 21.3%	S2[d] 9.5%	Selectivity, β[d]	SE
Mean slope	++++	0	★★★	—[d]	—
Elevation	N/A[c]			−0.0014	0.00079*
Deciduous forests	+++	*	★★★★	2.12	0.612**
Distance to villages	+++	0	0	—	—
Distance to cities	+++	★★	*	—	—
Snowcover SD	++	0	0	−2.17	0.888**
Mixed Korean pine -deciduous forests	++	*	★★	1.78	0.722
NPP	++	★★★★★★★★	★★★★★	0.00267	0.00145*
NPP – quadratic				−1.66E-07	1.01E-07*
Coniferous forests	+	0	*	1.15	0.532**
Low-use road density	0	0	*	—	—
Mean aspect	0	0	0	—	—
Mean snow cover	−	★★	0	−2.17	0.888**
Aspect SD	−	0	0	—	—
NPP SD	−	0	0	—	—
Hillshade	−	0	0	—	—
Density of villages	N/A[d]			−64.3	27.43**
Density of cities	N/A[d]			−264.6	100.30**
Secondary roads	−	*	0	—	—
Primary roads	−	★★★★★	★★★★★★★	—	—
Human-dominated landscape.	−	*	0	−9.00	2.223*

[a]17 ENFA covariates in rank order from positive to negative effects on tigers with marginality (M) and specialization scores (S1 and S2). For the RSF model, beta coefficients indicate selection if > 0 and avoidance if < 0, and are shown with SEs and *P* values (**$P < 0.05$, *$0.05 < P < 0.10$).
[b]Positive values (+) indicate that tigers were found in locations with higher than average cell values. Negative values (–) indicate that tigers were found in locations with lower than average cell values. The greater the number of symbols, the higher the correlation; 0 indicates a very weak correlation.
[c]Any number > 0 means the species was found occupying a narrower range of values than available. The greater the number of symbols, the narrower the range; 0 indicates a very low specialization.
[d]Was not retained because of collinearity.
ENFA, environmental niche factor analysis; NPP, net primary productivity; RSF, resource selection function; SD, standard deviation; SE, standard error.

ability values were zero. These results confirmed that extrapolation from Russia to China was appropriate.

RSF

Tigers selected areas with low densities of cities and villages, intermediate NPP, and intermediate elevations, while avoiding areas with high snowfall (Table 1, Supporting Information Fig. S2b). In terms of land cover, tigers preferred deciduous forests, Korean pine, then coniferous/other natural land cover types, and strongly avoided human-dominated areas (Table 1). The overall model was significant (likelihood ratio $\chi^2 = 51.5$, $P = 0.0001$), demonstrated good model fit (Hosmer & Lemeshow goodness of fit test, $\chi^2 = 4.45$, $P = 0.77$), and had reasonable measures of model fit and validation with a ROC score of 0.77, a pseudo-R^2 of 0.15 and k-folds cross-validation spearman rank correlation of 0.712, suggestive of lower cross-validation success, but with narrower predictions (SD = 0.10) compared with the ENFA. The optimal cut-point probability for discriminat-

ing habitat from non-habitat was 0.42, which resulted in 75% correct classification of units.

Expert habitat suitability index model

We developed cost functions for each of the four variables (Xiaofeng *et al.*, 2011) and then summed values of all layers to develop an assessment of potential tiger habitat, with scores of each grid ranging from 4 to 37, which were then rescaled to 0 to 100.

Habitat model averaging

Overall, the three models were reasonably correlated with each other, but not high enough to suggest using only one model. The pair-wise correlation coefficients between the ENFA and RSF model was $r = 0.49$; the ENFA and Expert model, $r = 0.52$; and the RSF and the Expert model, $r = 0.38$. All three models showed similar positive correlations as predicted habitat quality improves, but the RSF and

ENFA models (which were calibrated against known tiger occurrence in Russia) tended to predict more low-quality habitat than the expert model. We used the rescaled (between 1 and 100) average of all three habitat models to represent tiger habitat suitability (Fig. 2).

Identifying TCAs

Nine TCAs were identified from the cost-distance analyses after patches < 400 km² were removed (Fig. 3, Table 2). Two TCAs, Hunchun–Wangqing (TCA 1) and Mulin (TCA 4; Fig. 3) are shared with Russia: 78.7 and 40% of their area is located in China, respectively. Changbaishan (TCA 2; Fig. 3) is likely shared with Korea, but lack of cooperation limited our ability to include Korea in analyses. The size of the TCAs ranged from 440 to 14 230 km², and totaled 22% of the Changaishan ecosystem, mostly concentrated in mountainous regions (Table 2). Hunchun-Wangqing, Changbaishan, South Zhangguangcailing and Mulin encompass important protected areas, with the proportion of effectively protected area ranging from 4.7% (TCA 3) to 13.4% (TCA 2) (Table 2). All TCAs have low village densities (range: 0–0.35 villages per 100 km²) compared with the overall area in China (4.3 villages per 100 km²). Secondary road density was also much lower in TCAs (range: 2.3–6.8 km/100 km²) compared with overall area in China (15.5 km/100 km²) except for TCA 6 and TCA 9. Based on all factors, including predicted population size of tigers, we ranked the top four TCAs as the Hunchun-Wangqing complex (TCA 1), southern Changbaishan (TCA 2), southern Zhangguangailing (TCA 3) and Mulin (TCA4).

Potential numbers of tigers in the Changbaishan ecosystem

In contrast to the geographic split between the Chinese (63%) and Russian (37%) portions of the Changbaishan ecosystem, Russia contained 56% of tiger habitat, confirming higher-quality habitat on the Russian side of the border (Fig. 1). There was an estimated 181 (range of 160–203)
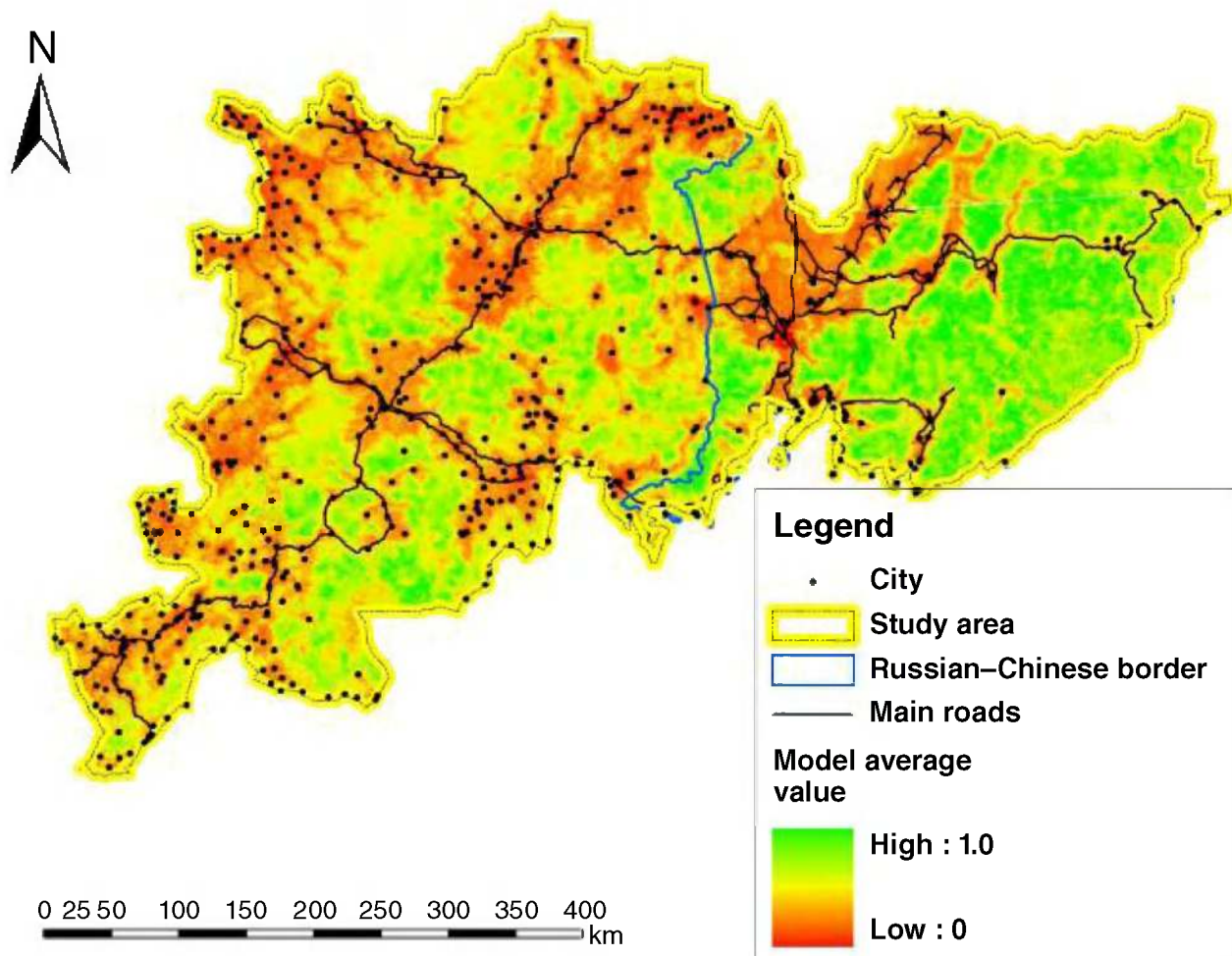

Figure 3 Potential Amur tiger habitat for the Changbaishan and Russian Far East study areas based on the ensemble averaged resource selection function, environmental niche factor analysis and expert habitat model.

Table 2 Prioritization and ranking of the nine identified Amur TCA in the Changbaishan ecosystem, Northeast China

TCA #	TCA	Area (km²)	% TCA protected	Villages (#/100 km²)	Secondary roads (km/100 km²)	Median habitat rank (0–100)	Potential tiger population N, SD[b]	Distance from source (km)[c]	Isolation[d]	Fragmentation index[e]	Tiger observation	Priority rank
1	Hunchun[a]	14 239	12.8	0.24	6.2	58.2	33 (29.4–38.9)	0	3	0.74	218	1
2	Changbaishan	8 420	13.4	0.32	6.8	55.1	24 (20.9–26.5)	184	5	0.71	0	2
3	Southern Zhangguangcailing	5 373	4.7	0.35	6.3	53.9	15 (13.1–16.6)	260	3	0.81	7	3
4	Mulin[a]	3 231	7.8	0.09	6.1	54.9	7 (6–9.1)	0	1	0.97	8	4
5	Huadian	2 686	0	0.22	2.3	51.6	7 (6.2–7.9)	375	4	1.04	0	6
6	Northern Zhangguangcailing	2 626	0	0.34	10.5	48.3	7 (5.9–7.5)	140	1	1.34	0	8
7	Baishan Tanghua – J'ian	864	0	4.05	4.8	49.9	2 (1.9–2.5)	551	2	1.41	0	9
8	Lushui-Dongjiang	632	0	0.31	3.5	47.1	2 (1.5–1.9)	318	2	0.72	0	5
9	Jingyu-Jiangyuan	440	0	0	17.0	51.1	1 (0.9–1.4)	459	3	0.70	0	6

[a]Part of the management zone is located in Russia.

[b]Habitat-based population estimate for adult tigers calculated according to Boyce & McDonald (1999).

[c]Distance from source = distance along the least-cost path to the closest tiger source population (Southwest Primorye Krai and Pogranichnyi Russia).

[d]Isolation = # potential main connections with other TCAs with accumulative costs ≤309 261 (=costs of the connection between Changbaishan and Baishan Tonghua-Ji'an).

[e]Fragmentation index = ratio of the perimeter to the area multiplied by 1000.

SD, standard deviation; TCA, tiger conservation areas.

adult/subadult tigers in the southern Russian Far East study area in 2005 (Miquelle *et al.*, 2006). This translates into roughly 445 km² per tiger, reassuringly close to home range estimates for female tigers (Goodrich *et al.*, 2010). We predicted a total of 98 (83–112) tigers across the nine main tiger conservation units (Table 2), but the top four TCAs contained 79 (80%) of those tigers, and only three TCAs contained habitat for > 10 tigers: Hunchun, Changbaishan and South Zhangguangcailing (Table 2). The estimates for the transboundary TCAs (1 and 4) do not include the number of tigers present on the Russian side of the zone.

Evaluating connectivity between tiger habitat

We identified the 12 highest-ranked potential linkages (black lines labeled from A to L in Fig. 4, Table 3) between the nine TCAs. Their lengths ranged between 1 and 68 km and accumulative costs varied sixfold between the lowest- and highest-cost corridors. Hunchun-Wangqing (TCA 1), the largest TCA, is connected to three adjacent TCAs: South Zhangguangcailing (TCA 3, 2-km connection), Mulin (TCA 4, 11 km) and Changbaishan south (TCA 2, 64 km). We identified other linkage zones ranging in length from 1 to 68 km between other TCAs (Fig. 4), but rank the three most important linkages as between TCA 1 and 4 (Fig. 4b, 11 km), between TCA 1 and 3 (Fig. 4a, 2 km), and TCA 3 and 6 (Fig. 4d, 11 km) based on relative costs and adjacency to source populations (Table 3).

Discussion

Our TCA prioritization benefited scientifically and politically from using three different habitat modeling approaches. During a 2008 habitat modeling workshop, different stakeholders (WWF, WCS, Chinese government) were approaching habitat modeling from different statistical backgrounds (e.g. RSF, ENFA, Expert model). This created the potential for competing or contradictory modeling approaches that could potentially derail conservation planning (Loiselle *et al.*, 2003). Instead, we assumed that all habitat models have differential weaknesses and strengths, and that averaging across models would increase scientific rigor (Wilson *et al.*, 2005; Araujo & New, 2007). This was especially important when no independent tiger validation data existed within Northeast China (Barry & Elith, 2006). Ultimately, only future tiger recovery will test of the accuracy of our models (Mladenoff, Sickley & Wydeven, 1999). Our approach increased political support for the identified TCAs, which were formally adopted by the Chinese government for tiger conservation planning (Li *et al.*, 2010). Moreover, all three models captured similar well-known aspects of tiger habitat: tigers avoided steep slopes or high elevations, strongly selected for Korean pine and deciduous forests, avoided high snow depth, avoided coniferous forests, and strongly avoided human villages and roads (Table 1, Smith *et al.*, 1998; Wikramanayake *et al.*, 2004; Carroll & Miquelle, 2006;
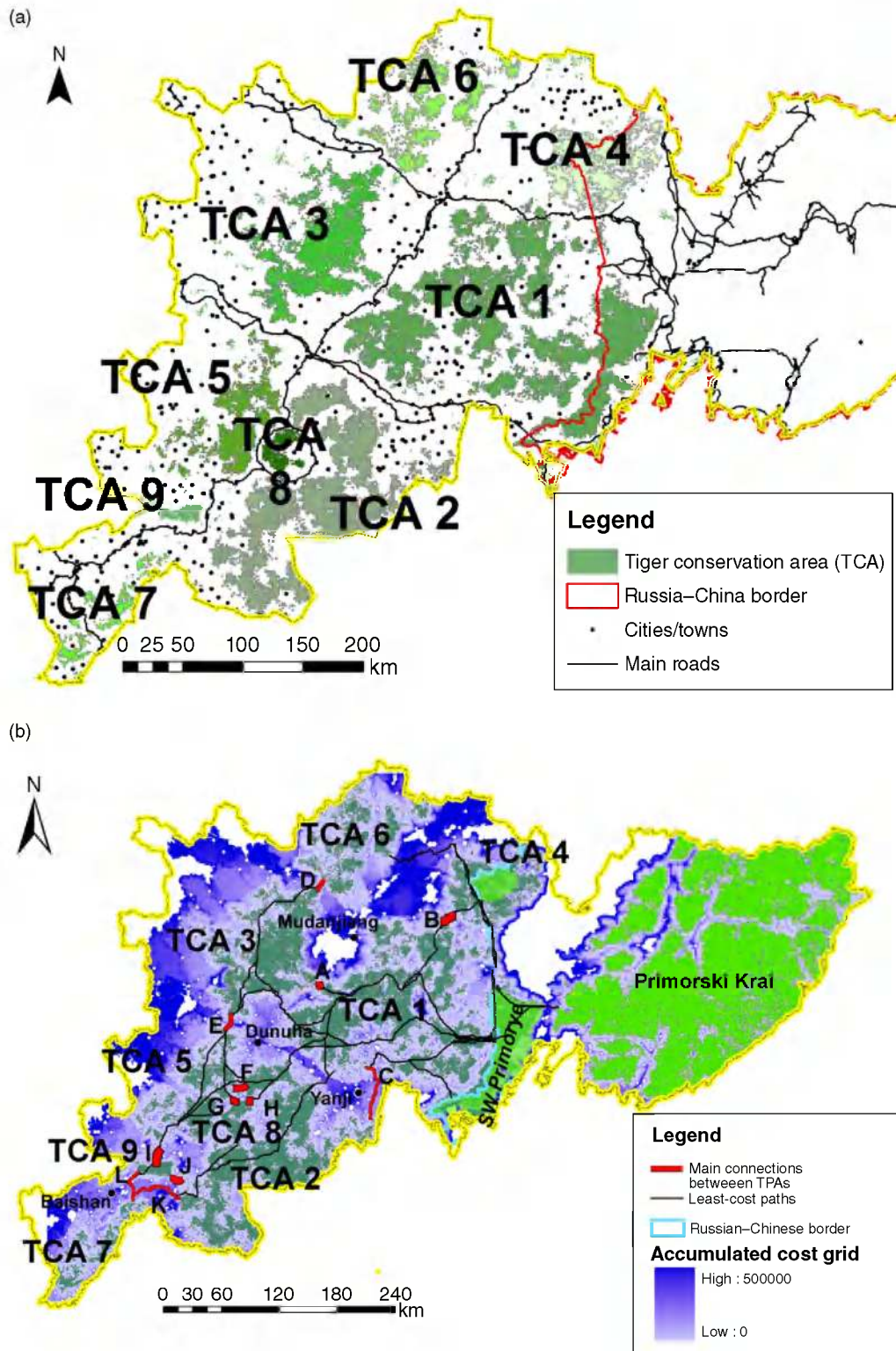
Figure 4 Tiger habitat in Northeast China showing (a) the nine tiger conservation areas (TCAs) identified from potential tiger habitat patches: Hunchun–Wangqing (TCA 1), Changbaishan (TCA 2), Southern Zhangguangcailing (TCA 3), Mulin (TCA 4), Huadian (TCA 5), Northern Zhang-guangcailing (TCA 6), Baishan Tanghua – Jian (TCA 7), Lushui-Dongjiang (TCA 8) and Jingyu-Jiangyuan (TCA 9); and (b) least-cost paths between TCAs, highlighting the twelve primary linkage zones between TCAs (labeled A–L) in red, with line thickness inversely correlated to cost.

Table 3 Characteristics of 12 potential primary linkages connecting TCA in the Changbaishan landscape, listed the shortest to the longest connecting distance

Name	Linkage	Length (km)	Accumulative costs
H	TCA 2–8	1	161 000
A	TCA 1–3	2	161 883
G	TCA 5–8	3	162 897
F	TCA 2–5	9	168 580
B	TCA 1–4	11	62 307
D	TCA 3–6	11	228 474
I	TCA 5–9	13	52 740
J	TCA 2–9	15	185 865
E	TCA 3–5	18	240 411
L	TCA 7–9	39	292 631
C	TCA 1–2	64	309 132
K	TCA 2–7	68	309 261

Name (letter) identifies each linkage in Fig. 4. Accumulative costs units are a relative value, see text for details.
TCA, tiger conservation areas.

Linkie *et al.*, 2006). Based on the statistical convergence between models, and the conservation planning benefits, we recommend model averaging as a useful approach to prioritize tiger recovery areas within other TCLs across Asia, and other recovering carnivore populations.

Our results suggest that the top four TCAs represent a viable opportunity for the Chinese government to meet its commitments of recovering Amur tigers by the next year of the tiger, 2022, under the Global Tiger initiative. Within these top four TCAs, there was habitat for a total of 72 adult Amur tigers. While not a large potential population by itself, if connectivity is maintained with the adjacent Sikhote–Alin population in Russia (400–500 individuals, Miquelle *et al.*, 2006), the Changbaishan–Sikhote–Alin meta-population would be one of the largest wild tiger populations in the world (Dinerstein *et al.*, 2007; Walston *et al.*, 2010). The connectivity between Russia and China is also encouraging, as tigers are already dispersing successfully from Russia to China, emphasizing reintroduction of captive animals is not needed (Hayward & Sommers, 2009). Recovery of tigers in the Changbaishan ecosystem will be contingent on maintaining and improving connectivity with Russia and within China, increasing tiger survival by reducing tiger and ungulate poaching (Karanth *et al.*, 2004; Chapron *et al.*, 2008), and reducing fragmentation from incompatible human land uses in and around TCAs (Kerley *et al.*, 2002; Carroll & Miquelle, 2006).

The highest priority TCA is the Hunchun–Wangqing area, which has the largest connected network of habitat patches, is contiguous with source populations in Russia, and has the largest potential number of tigers. Tigers are already present in Hunchun and Wangqing, much of which is in protected areas already, and recovery efforts such as removal of snares are already underway (Yu *et al.*, 2006). The Changbaishan is the second largest TCA, and while it has potential to hold up to 24 adult animals, tigers have not been reported in the Changbaishan for ≥ 15 years, and the

least-cost distance from a source population (184 km) is very far. Southern Zhangguangcailing and Mulin, the remaining two top-ranked TCAs, both have potential linkages (2 and 11 km) to Hunchun–Wangqing, and Mulin is also connected to suitable habitat in Russia. Efforts should be made to ensure further habitat loss does not occur, and to maintain or restore linkages (Chetkiewicz *et al.,* 2006) with the Hunchun–Wangqing area through tiger-friendly 'green' infrastructure (Quintero *et al.*, 2011) such as wildlife crossing structures (Clevenger & Waltho, 2005) in identified movement corridors (Colchero *et al.*, 2010) across transportation networks.

Despite these encouraging results, our Amur tiger habitat model may overestimate tiger habitat quality because of the lack of information about ungulate prey densities, one of the key components of tiger habitat (Karanth *et al.*, 2004). Using tiger-based RSF models developed on the Russian side of the border, Li *et al.* (2010) showed that predictive capacity and performance was greatly improved in RSF models that included spatial prey covariates for red deer, wild boar and roe deer (Li *et al.*, 2010). In supporting analyses within the Russian portion of the study area, the ungulate-RSF model predicted lower habitat quality than an RSF based on just GIS covariates (Supporting Information, Fig. S3; see also Mitchell & Hebblewhite, 2012). Similar analyses done for the critically endangered Far eastern leopard in Southwestern Primorye Krai also confirm that including spatial prey density tends to predict lower habitat quality than expected just based on land cover-type covariates alone (Hebblewhite *et al.*, 2011). This emphasizes the potential for overestimating tiger habitat quality in China if ungulate prey densities are lower than Russia, and the key role of reducing poaching on ungulates and increasing ungulate densities will play in Amur tiger recovery in China (Chapron *et al.*, 2008).

Our model averaging approach to understand the habitat needs of recovering carnivores or active restoration of carnivores (Hayward & Sommers, 2009) will help overcome reliance on a single modeling method. With recent advances in sophisticated species distribution modeling approaches (e.g. BIOMOD, Thuiller *et al.*, 2009), carnivore ecologists will be able to construct robust ensemble models of up to a dozen different modeling approaches. Moreover, although our approach identified habitat for Amur tiger under current conditions, a looming question for tiger and carnivore recovery in general will be the interacting effects of changing human land use and climate change (Carroll, 2007).

Conservation recommendations

Recent debate has centered on whether tiger conservation should focus on critical 'source sites' (Walston *et al.*, 2010) or across wider landscapes (Wikramanayake *et al.*, 2011). For the Amur tiger, dependent on the one hand on prey densities for high reproductive rates (Chapron *et al.*, 2008), and on the other, on large habitat patches (Goodrich *et al.*, 2010), both are critically needed. Our results emphasize the importance

of restoring connected habitat first to promote natural dispersal, survival and recolonization of Amur tigers in Northeast China. The priority should be to increase tiger habitat quality in the Hunchun and adjacent TCAs, where dispersing tigers from Russia are regularly appearing (Li *et al.*, 2006). Tiger habitat quality must be increased by reducing livestock density and thus, tiger–human conflicts (Yu *et al.*, 2006), increasing survival rates of tigers and their ungulate prey through removal of snares (Yu *et al.*, 2006), and reducing human activity through regional land-use planning surrounding TCAs (Miquelle *et al.*, 2005). Although the challenges are great, we are encouraged that local and national governments have recognized TCAs as a basis of Amur tiger conservation in China (Li *et al.*, 2010). Maintaining connectivity of TCAs within China and across the China–Russian border will also be critical to recovery, and our linkage zone analysis focuses immediate conservation attention on several key linkages under threat, but ensuring 'source sites' where breeding female tigers are secure in Northeast China is a necessary first step toward recovery.

Acknowledgements

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Southern portion of Primorski Krai area surveyed for Amur tigers in the Russian Far East showing sampling unit design used in resource selection function with sampling units (polygons) where tigers were present (in red) or absent (grey) were treated as a used-unused design to develop RSF models for extrapolation to the Chinese portion of the Changbaishan study area.

Figure S2. (a) Potential tiger habitat predicted by the ENFA model in the Changbaishan landscape in Northeast China and the southern Russian Far East. All cells are shown (direct, interpolated and extrapolated). (b) Predicted habitat for the Amur Tiger from a resource selection function (RSF) model in the Changbaishan landscape in Northeast China and the southern Russian Far East. Major cities (> 50 000) and major roads are shown. (c) Potential tiger habitat, as predicted by the expert model excluding data on prey densities. The higher the value (towards color green) the better the habitat potential.

Figure S3. Comparison of predictions of the environmental spatial covariates-only RSF model (GIS Habitat) and the same RSF model with covariates of relative density of the top three prey species for Amur tigers in the southern portion of their range in the Russian Far East.

Table S1. Predictor variables included in the three complementary Amur tiger habitat modelling approaches, Environmental Niche Factor Analysis (ENFA), Resource Selection Function (RSF) modelling, and the expert-opinion based model.

Table S2. Cost allocations of five predictor variables used in the Expert Model: the lower the cost, the higher the value in terms of habitat suitability for tigers

Table S3. Friction values of the environmental variables for Amur tiger habitat connectivity modeling based on expert opinion. Values ranging from 1 (easy to cross) to 1000 (impossible to cross). RFE = Russian Far East.

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