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Population viability of the Siberian Tiger in a changing landscape: Going, going and gone?

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ABSTRACT

The Amur tiger (*Panthera tigris altaica*) is a flagship species of the boreal forest ecosystem in northeastern China and Russia Far East. During the past century, the tiger population has declined sharply from more than 3000 to fewer than 600 individuals, and its habitat has become much smaller and greatly fragmented. Poaching, habitat degradation, habitat loss, and habitat fragmentation have been widely recognized as the primary causes for the observed population decline. Using a population viability analysis tool (RAMAS/GIS), we simulated the effects of poaching, habitat degradation, habitat loss, and habitat fragmentation on the population dynamics and extinction risk of the Amur tiger, and then explored the relative effectiveness of three conservation strategies involving improving habitat quality and establishing movement corridors in China and Russia. A series of controlled simulation experiments were performed based on the current spatial distribution of habitat and field-observed vital rates. Our results showed that the Amur tiger population could be viable for the next 100 years if the current habitat area and quality were well-maintained, with poaching strictly prohibited of the tigers and their main prey species. Poaching and habitat degradation (mainly prey scarcity) had the largest negative impacts on the tiger population persistence. While the effect of habitat loss was also substantial, habitat fragmentation per se had less influence on the long-term fate of the tiger population. However, to sustain the subpopulations in both Russia and China would take much greater conservation efforts. The viability of the Chinese population of tigers would rely heavily on its connectivity with the largest patch on the other side of the border. Improving the habitat quality of small patches only or increasing habitat connectivity through movement corridors alone would not be enough to guarantee the long-term population persistence of the Amur tiger in both Russia and China. The only conservation strategy that allowed for long-term persistence of tigers in both countries required both the improvement of habitat quality and the establishment of a transnational reserve network. Our study provides new insights into the metapopulation dynamics and persistence of the Amur tiger, which should be useful in landscape and conservation planning for protecting the biggest cat species in the world.

1. Introduction

The Amur tiger (*Panthera tigris altaica*), also known as the Siberian Tiger, is the biggest and northernmost of the 6 extant tiger subspecies and one of the most charismatic endangered mammals. The population of the Amur tiger has declined sharply during the past century (Jackson, 2000; Carroll and Miquelle, 2006; Tian et al., 2009). In the 1890s, the Amur tiger was found in Russia Far East, northeastern China, eastern Mongolia, and the Korean peninsula, with a total number of more than 3000 individuals. Field surveys in the past few decades indicate that the current tiger population has dropped below 600 (Matyushkin et al., 1980; Pikunov, 1988; Matyushkin, 1998). The distribution areas of the tigers are now restricted to one large habitat patch and two smaller ones in Russia Far East, and a few scattered small patches in northeastern China near the Russia-China border (Li et al., 2009; Tian et al., 2009).

The primary causes for the dramatic decline of the tiger population include poaching, habitat degradation, habitat loss and fragmentation caused by logging, roads, human settlements, and agriculture (Matyushkin et al., 1996; Nowell and Jackson, 1996; Zheng et al., 1997; Matyushkin, 1998; Karanth and Stith, 1999;

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Miquelle et al., 1999; Cushman and Wallin, 2000; Kerley et al., 2002; Tian et al., 2009). It is of great importance to understand how these factors will together affect the population viability of the Amur tiger in the future (Carroll and Miquelle, 2006; Linkie et al., 2006; Miquelle et al., 2006). Although a number of studies in the past several decades have investigated the demographic characteristics of the Amur tiger and the effects of poaching on its population dynamics, a comprehensive understanding of how these multiple factors would impact the population viability in the long run is still lacking. To help achieve such understanding, simulation experiments based on population viability analysis (PVA) can be quite useful (Wu et al., 1993; Larson et al., 2004; Tian et al., 2011).

PVA is a generic term for model-based methods that evaluate the extinction risk of endangered species during a specified period of time (Shaffer, 1987; Boyce, 1992; Burgman and Possingham, 2000; Beissinger, 2002). PVA has been used to identify key factors affecting population persistence, project future population dynamics of endangered species, and help design biodiversity conservation strategies (Lindenmayer et al., 1993; Beissinger and Westphal, 1998; Morris et al., 2002; Doak et al., 2009; Shaffer, 2009). As the problems of endangered species grow greater and more urgent than ever, PVA has become one important approaches to studying and protecting biodiversity (Morris and Doak, 2002; Doak et al., 2009; Shaffer, 2009; Wu, 2009; Tian et al., 2011).

The main objectives of our study were: (1) to examine the effects of habitat degradation, habitat loss, habitat fragmentation, and poaching on the long-term survival of the Amur tiger; and (2) to explore the effectiveness of different conservation measures: improving habitat quality in China, establishing movement corridors, and establishing a Russia-China reserve network. Specifically, through a series of controlled simulation experiments based on the current habitat distribution pattern and field-observed vital rates of the Amur tiger, we addressed the following research questions: (1) How will habitat degradation, habitat loss, habitat fragmentation, and poaching affect population abundance and viability of the Amur tiger over the next 100 years? (2) Will conservation measures for improving habitat quality, establishing corridors, and establishing a transnational reserve network be sufficient to enhance the long-term population viability of the Amur tiger?

2. Materials and methods

2.1. Study area

Our study area is located in Russia Far East and northeast China (42°20′ to 51°10′N, 127°85′ to 140°21′E), including Primorski Krai and southern Khabarovski Krai in Russia and eastern Jilin Province and eastern Heilongjiang Province in China (Fig. 1). The geographical distribution range of the Amur tiger extends approximately 300,000 km^2, bounded by the Gur River to the north, east Mongolia to the west, North Korea to the south, and the Sea of Japan to the east. This vast region is mainly within the northern temperate and cold temperate zones, and characterized by a monsoon climate with cold and windy winters, except for the eastern slope of the Sikhote-Alin Mountains where a warmer and moister climate is found. The highest elevation in this region is nearly 3000 m above sea level. The extremely cold climate sets the northern limit of the Amur tiger's distribution.

The Sikhote-Alin Mountains in Russia and Changbai Mountains and Wandashan Mountains in China are currently the major distribution areas for the Amur tiger (Carroll and Miquelle, 2006; Tian et al., 2009). The northern part of the Sikhote-Alin mountains are dominated by coniferous fir, spruce, and birch forests, whereas Korean pine broad-leaved forests are the dominant vegetation type in the southern part of these mountains. The Korean pine broad-leaved forests are the most biologically diverse forests

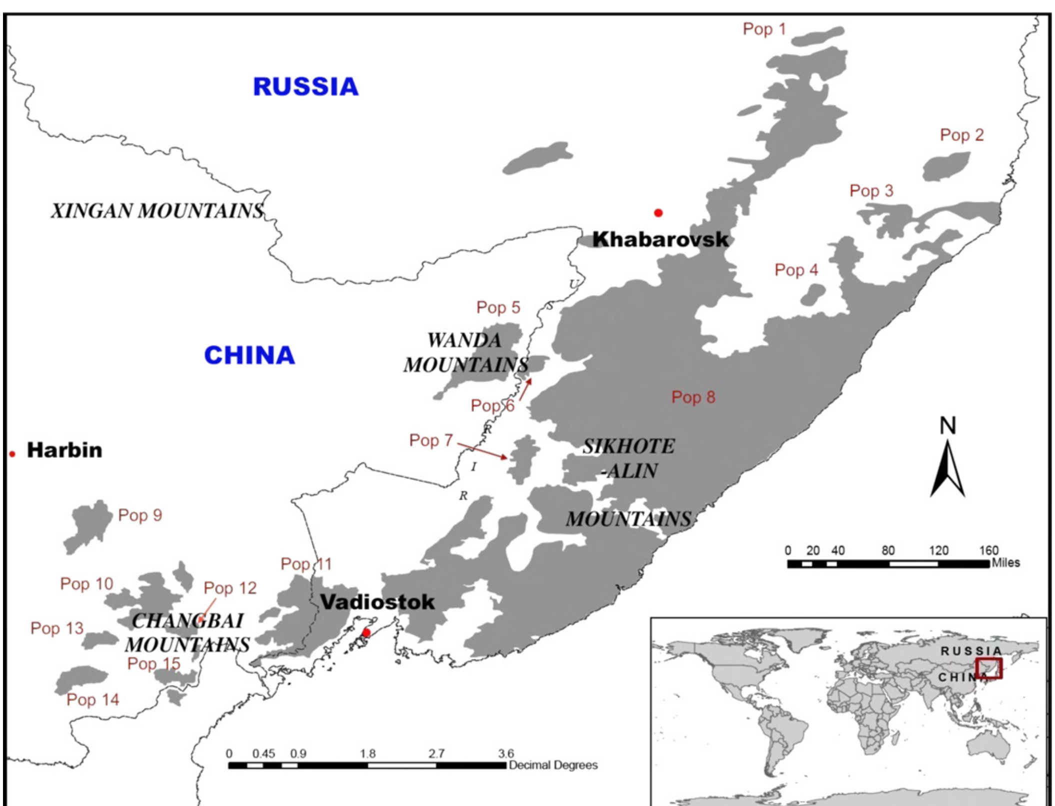

Fig. 1. The distribution area of the Amur tiger in Russia Far East and northeastern China. The darkened areas represent habitat patches, surrounded by other land cover types in white.

of the world at similar latitudes, and are the favorite habitat of the Amur tiger. The most common ungulates in this region include red deer (*Cervus elaphus*), Siberian roe deer (*Capreolus pygarus*), and wild boar (*Sus scrofa*). Also, Sika deer (*Cervus nippon*) are restricted to the southern part of the region, and Siberian musk deer (*Moschus moschiferus*) and Eurasian elk (*Alces alces*) are more common in spruce-fir forests at higher altitudes. A large portion of these forests has been subjected to selective or clear cutting as well as fire disturbances induced by human activities during the past several decades (Zheng et al., 1997; Cushman and Wallin, 2000; Li et al., 2009). These anthropogenic perturbations have transformed many parts of the landscape from primary forests to secondary broad-leaved forests (Cushman and Wallin, 2002; Li et al., 2009; Tian et al., 2009).

2.2. Model structure

To simulate the effects of poaching, habitat quality, habitat loss, habitat fragmentation, and conservation measures on the population viability of the Amur tiger, we used the PVA software, RAMAS/GIS (Akçakaya, 2005), which is one of the most widely used PVA tools worldwide. This software has been used to estimate and compare the population dynamics and extinction risks of a number of species as affected by different disturbance regimes, such as fires (Akcakaya et al., 2005), climate change (Lawson et al., 2010), agricultural intensification (Colling and Matthies, 2006), conservation efforts (Giordano et al., 2010), and land use change (Carroll and Miquelle, 2006; Linkie et al., 2006; Meulebrouck et al., 2009; Lawson et al., 2010). In addition, RAMAS also has been applied in population viability analysis and conservation planning for multiple species (Early and Thomas, 2007; Regan et al., 2008; Hinrichsen, 2009).

The RAMAS/GIS software package links a demographic age/stage matrix metapopulation model (RAMAS/Metapop) with a Geographic Information System (GIS) that handles the spatial information on habitat. Within RAMAS/GIS, we developed an Amur tiger-specific stage-structured model with 1-year time step to compute the population dynamics and extinction risk of the Amur tiger. Environmental and demographic stochasticities were considered in our simulations (more details below). Through a series alternative scenarios, we examined the effects of poaching, habitat degradation, habitat loss, habitat fragmentation, and three different conservation measures. In the next section, we describe the key model parameters of RAMAS/GIS that are crucial to our simulation study.

2.3. Key model parameters

2.3.1. Carrying capacity and density dependence

Each adult tiger requires a certain area of habitat for survival and reproduction, which can be considered as its home range. The average home range of the Amur tiger was reported to be from 360 km^2 (Carroll and Miquelle, 2006) to 445 km^2 (Miquelle et al., 2010a,b). Our study used the value of 440 km^2 (Goodrich et al., 2010). We derived the suitable habitat patches from the database created by the World Wide Fund for Nature (http://amur-heilong.net/GIS_site/gis_index.html). We assumed that the carrying capacity of a habitat patch depends on its size and quality and that the quality of all suitable habitat patches was similar. While habitat patches may differ in quality in reality, this assumption was necessary in order to tease out the effects of habitat loss, fragmentation, habitat quality degradation, and poaching. The carrying capacity of each habitat patch was estimated from habitat area divided by the average home range of the species. The estimation of patch carrying capacity assumed a "normal" level of prey densities as the home range size was based on field observations in undisturbed natural habitats.

Table 1
The vital rates of the Amur tiger.

Age stages	Survivorship	Fecundity
Cub (0–1)	0.6	0
Juvenile (1–2)	0.8	0
Sub-adult (2–3)	0.6	0
Adult (3+)	0.8	0.75

In our study, only adult tigers were considered in assigning initial population sizes and calculating carrying capacity for habitat patches because cubs and juveniles do not maintain their own territories. The density dependence of population growth was simulated as a "ceiling" mechanism, meaning that population growth in a habitat patch was not affected by population density before the carrying capacity of that patch was reached. When the population size of a habitat patch exceeded the carrying capacity, it was reduced to the carrying capacity of that patch. This ceiling type of density dependence seems reasonable for territorial animals and has been used in other similar studies (e.g., Larson et al., 2004).

2.3.2. Life-history attributes of the Amur tiger

Life-history attributes are an essential part of the population growth model within RAMAS/GIS. We divided the tiger population into four age stages: cubs (0–1 year), juveniles (1–2 years), sub-adults (2–3 years), and adults (≥3 years). This classification of age structure is consistent with Karanth and Stith (1999). While sub-adult tigers are more susceptible to dispersal-related mortalities, cubs are generally more sensitive to prey depletion (Karanth and Stith, 1999) and human impacts (Karanth and Sunquist, 1995; Kerley et al., 2002). Data on the age stage-specific vital rates of the Amur tiger were obtained from the existing literature (Karanth and Sunquist, 1992; Kerley et al., 2003; Carroll and Miquelle, 2006; Karanth et al., 2006; Linkie et al., 2006; Chapron et al., 2008; Miquelle et al., 2010a,b), and are listed in Table 1. The sex ratio at birth was assumed to be 1. These data on survivorship, fecundity, and sex ratio were used to construct the age stage matrix of the population growth model. Because the survival rates of male tigers are much lower than females in the wild (Smith, 1993; Goodrich et al., 2010), the actual female/male ratio for adult Amur tigers is between 5/3 and 6/5 based on field surveys (Carroll and Miquelle, 2006; Miquelle et al., 2006). However, only females were considered in our population model because there is no evidence that males are a limiting factor to the long-term persistence of the Amur tiger (Kenney et al., 1995; Chapron et al., 2008). Also, Brook et al. (2000) recommended that, to avoid an underestimate of population extinction risk, only the limiting sex should be modeled when using matrix-based PVA packages such as RAMAS/GIS.

2.3.3. Dispersal

The cubs of the Amur tiger leave their mothers to look for a vacant territory for breeding at the age of 2, and only the adults (≥3 years old) who have already settled in a territory can reproduce (Smith, 1993; Karanth and Stith, 1999; Kerley et al., 2003; Linkie et al., 2006; Goodrich et al., 2010). Sub-adults initially try to settle near their mothers' territory. If no nearby territories are available, the mortality risk for these sub-adults forced to disperse farther away will increase because of the possibilities of being attacked by adult tigers, starvation, and poaching (Matyushkin et al., 1980; Pikunov, 1988; Matyushkin, 1998; Kerley et al., 2002), leading to a decrease of dispersal rate between patches. We modeled dispersal rates between habitat patches using a built-in function of RAMAS/GIS:

$$M_{ij} = a \exp(-D_{ij}^{c/b}), \quad \text{if } D_{ij} = D_{\max}$$

$$M_{ij} = 0, \quad \text{if } D_{ij} > D_{\max}$$

where 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.

We assumed that the dispersal distances of tigers followed a normal distribution. Successful dispersal rates between patches were calculated from an edge-by-edge distance matrix using the Spatial Data Module of RAMAS/GIS.

2.3.4. Environmental and demographic stochasticities

Environmental and demographic stochasticities were considered in the population model for survival and fecundity rates of all age stages. Demographic stochasticity followed a binomial distribution, and environmental stochasticity followed a lognormal distribution (Akçakaya, 2005). We used a coefficient of variation (CV) of 0.05 for survival rates, and assumed that the stochasticity of dispersers in the sub-adult stage was twice as great (i.e., CV = 0.1). The details of how environmental and demographic stochasticities are modeled within RAMAS have been extensively documented in Akçakaya (2005) and the website of the software (http://www.ramas.com/gis-faq.htm#stoch). Genetic stochasticity was not included in our population model because no relevant data were available.

2.3.5. Habitat area and its spatial distribution

A habitat map of the Amur tiger was derived from the GIS Database of Virtual Information Center for Amur River Region (VICARR) of the World Wide Fund for Nature (WWF) (http://amur-heilong.net/GIS_site/gis_index.html). We extracted the tiger distribution area from the vector GIS database, and then converted it into a habitat map in raster format with a spatial resolution of 1 km × 1 km using ArcGIS 9.0. The raster map was then imported into the Spatial Data Module of RAMAS/GIS. Habitat patches were delineated manually based on habitat suitability for the Amur tiger in terms of vegetation type, patch size, and spatial arrangement. The area and isolation (measured by inter-patch distance) of habitat patches were computed within the GIS. We combined the patches that were closer than 10 km, which is within the radius of a circle with the size of the tiger's average home range (about 440 km^2). Also, a patch must be larger than the average home range to be qualified as potential habitat.

Based on the above criteria, we reduced the 22 patches in the original WWF map to 15, as shown in Fig. 1. According to their size and spatial configuration, the 15 patches fell into 4 general types. Type I included only one patch (pop8 in Fig. 1), the largest patch in central Sikhote-Alin Mountains of Russia Far East, accounting for about 80% of the tiger habitat in the distribution region. Type II consisted of 6 patches (pop1, pop3, pop4, pop5, pop6, and pop7) which are small in area but close to the largest patch (within 58 km, the maximum travel distance of female tigers). Type III was composed of 3 isolated patches (pop2, pop9, and pop11) that vary in size and are farther away from the largest patch. Type IV included 5 small patches (pop10, pop12, pop13, pop14, and pop15), forming a loose cluster near the China-Russia border. This habitat map with 15 patches was then used in RAMAS/GIS as part of the input to run the demographic stage-based population viability analysis model.

2.4. Simulation schemes

We simulated the population dynamics and extinction risk of the Amur tiger following a series of scenarios, as described below in detail. For each scenario, the simulation duration was set to 100 years (i.e., 100 one-year time steps), and the model was run 1000 times (i.e., 1000 replications). We assumed that habitat patches each were not fully occupied at the beginning of a simulation, and set the initial population size of each habitat patch to one third of its carrying capacity. The initial subpopulation sizes of a connected set of habitat patches influence the persistence of the metapopulation (e.g., Wu et al., 1993). Our preliminary simulation with different initial population sizes has confirmed that this is also the case here. However, in order to focus on the effects of habitat attributes and human activities on the Amur tiger population viability, we used the same set of initial subpopulation sizes for all simulation scenarios.

2.4.1. Baseline scenario

In this scenario, we simulated the population dynamics and extinction risk of the Amur tiger in the next 100 years, assuming that during the simulation duration: (1) there will be no changes in the quality, quantity, and spatial configuration of habitat, and (2) there will be no poaching of tigers or killing of their prey. The results from this scenario were then used as a baseline to assess the effects of other scenarios.

2.4.2. Habitat degradation

Habitat degradation due to logging, fires, and other human activities leads to prey scarcity which in turn results in a decrease in the fecundity of tigers. Tigers may adjust their behavior to cope with the problem of declining habitat quality by expanding their home range within the distribution area of suitable habitat (Smith et al., 1987; Sandell, 1989; Karanth et al., 2004; Miquelle et al., 2010b). In general, female tigers tend to maintain home range large enough to ensure adequate resources for rearing young and, in the same time, small enough to minimize travel and defense costs (Smith et al., 1987; Sandell, 1989; Miquelle et al., 2010b). Thus, the home range size of female tigers is inversely related to habitat quality (in terms of prey density) as well as patch carrying capacity (Sandell, 1989; Karanth et al., 2004; Miquelle et al., 2010b). To simulate this situation, we designed five scenarios of habitat degradation. The first scenario reduced fecundity by 10% for 10 years from the beginning of simulation, and then increased it linearly by 1% per year until the original fecundity was reached. In the same time, the carrying capacity of habitat patches was decreased by 1% per year until reaching 90% of its original value in the baseline scenario. The other scenarios of habitat degradation followed the same procedures, but had a 20%, 30%, 40% and 50% initial decrease in fecundity and a 80%, 70%, 60% and 50% ultimate decrease in the patch carrying capacity.

2.4.3. Habitat loss

To simulate habitat loss, we developed five scenarios: reducing the size of each patch by 10%, 20%, 30%, 40%, and 50%, respectively. In reality, habitat loss inevitably leads to changes in the degree of habitat fragmentation or connectivity. However, to avoid the compound effects of habitat fragmentation, we assumed the distances between patches remained the same so that the effects of habitat loss could be isolated.

2.4.4. Habitat fragmentation

Habitat fragmentation, if defined broadly, includes both habitat loss and habitat fragmentation per se. In this study, we used the term to refer only to the increase in the degree of patch isolation or the decrease in the degree of patch connectivity (Fahrig, 1997, 2003). We had five scenarios for habitat fragmentation: decreasing successful dispersal rates between patches by 20%, 40%, 60%, 80%, and 100% (i.e., zero dispersal), respectively. In this case, the size of each patch remained the same.

2.4.5. Poaching

Poaching has been one of the most important factors affecting the population decline of the Amur tiger (Nowell, 2000; Carroll and

Miquelle, 2006; Tian et al., 2009). To simulate the effects of poaching on tiger population viability, we ran three scenarios: removing 2%, 4%, 6%, 8% and 10% of tigers each year from each subpopulation for 50 years starting in the 10th year during the simulation. The duration of poaching was set to 50 years because it roughly corresponds to the time over which poaching has been going on in this region and also because it allows us to see if the tiger population is able to recover from the devastation of poaching.

2.4.6. Conservation strategies

We designed three different conservation strategies to explore possible measures to improve population viability of the Amur tiger. In the first strategy, Improving Habitat Quality in China (IHQC), the quality of the current habitat patches (including pop9, pop10, pop12, pop13, pop14, and pop15) in China was improved through conservation efforts (e.g., turning suitable habitat areas into nature reserves). To examine the effects of this conservation strategy on the tiger population viability, we simulated 5 levels of the strategy separately. That is, the improvement of habitat quality was assumed to increase fecundity by 10%, 20% and 30%, 40%, and 50%, respectively, for a period of 10 years. The patch carrying capacity was increased accordingly by the same percentages. These changes in IHQC mirrored the two habitat degradation scenarios discussed earlier.

The second conservation strategy, Establishing Movement Corridors (EMC), assumed that movement corridors increased the successful dispersal rates by 100% (i.e., doubled). Two scenarios were constructed: placing corridors between habitat patches within China only and constructing corridors between all the patches near the China-Russia border to form a transnational movement corridor.

The third conservation strategy, Russia-China Reserve Network (RCRN), combined elements in both IHQC and EMC. Here we assumed a 50% increase in fecundity due to habitat quality improvement and doubled successful dispersal rates due to movement corridors. Three scenarios were considered under the RCRN strategy: (1) increasing the quality and connectivity of habitat patches within China only, (2) increasing the quality and connectivity of habitat patches in both China and Russia, and (3) increasing the quality and connectivity of habitat patches in both countries, and establishing a transnational protection zone that enclosed pop10, pop11, pop12, pop13, pop14, and pop15, with areas among them also fenced in Fig. 1.

These conservation strategies are feasible in principle, but practically challenging, if not impossible, because of logistical and political reasons. Nevertheless, exploring the effectiveness of these strategies based on a set of explicitly stated assumptions provides needed insight into these issues.

3. Results

3.1. Baseline scenario

Under the baseline scenario, which assumed that there were no poaching, habitat loss and fragmentation, and habitat degradation, the mean metapopulation abundance of the Amur tiger continued to increase from about 30% of the carrying capacity in the beginning of the simulation to about 100% of the carrying capacity in 100 years (Fig. 2A). The probability of extinction at the end of the simulation for the entire metapopulation (i.e., terminal quasi-extinction probability) was negligible (Fig. 2B). The risk of metapopulation percent decline (the percentage of the metapopulation decline) during 100 years was quite low in general (Fig. 2C). For example, there was a 75% probability that the metapopulation would not decline at all, and the probability of the metapopulation falling below 200 individuals was 10%.

The 15 subpopulations differed in their dynamics of mean population abundance (Fig. 2D). The metapopulation trajectory was predominantly determined by the largest patch in the central Sikhote-Alin Mountain, the only subpopulation that had no local extinctions in 100 years (pop8 in Fig. 2D). Six small subpopulations that were closely connected to the largest subpopulation, i.e., Type II patches as discussed earlier (pop1, pop3, pop4, pop5, pop6, and pop7), persisted for the 100 years span. But they were all sink subpopulations whose local extinctions were rescued by immigrants from the largest subpopulation (pop8). For more distant subpopulations (Type III patches), pop2 and pop9 went to extinction, and pop11 did not go extinct because of its relatively large patch size, but showed a continuous decline in abundance. The subpopulations in China (Type IV, including pop10, pop12, pop13, pop14, and pop15), small in size and remote from the largest patch, went extinct rather quickly (Fig. 2D).

3.2. Effects of habitat degradation

The metapopulation size declined quickly in response to habitat degradation in the first few decades of the simulation, and then began to sustain at a lower level than in the baseline scenario (Fig. 3A). Habitat degradation led to considerably higher risks for quasi-extinction (Fig. 3B) and population decline (Fig. 3C). When the levels of habitat degradation increased from 10% to 20% and 30%, the probability of metapopulation decline by 50% or more during the simulation time increased from 5% to 25% and 80%, respectively (Fig. 3B). This population decline probability quickly reached 100% as the level of habitat degradation increased to 40% and beyond (Fig. 3B). Habitat degradation substantially decreased population abundance in all patches (most significantly the largest patch–patch8), and sped up the local extinctions of most small subpopulations (Fig. 3D). For relatively larger patches (e.g., pop8, pop5, and pop11), there appeared to be a threshold value for the level of habitat degradation (between 20 and 30%) beyond which these subpopulations would suffer a long-term decline.

3.3. Effects of habitat loss

Habitat loss by 10%, 20%, 30%, 40%, and 50% led to the same amounts of decrease in the maximum population size for each habitat patch. In all cases the metapopulation abundance declined to a lower level (Fig. 4A). As compared to the baseline scenario, habitat loss increased the risks of quasi-extinction and population decline substantially at the metapopulation level (Fig. 4B and C). The effects of habitat loss became increasingly pronounced after 50 years. These metapopulation-level patterns emerged from the significant decreases in population abundance of all habitat patches (Fig. 4D).

3.4. Effects of habitat fragmentation

Decreasing inter-patch dispersal rates by 20%, 40%, 60%, 80%, and 100% due to increased fragmentation did not have significant effects on metapopulation dynamics (Fig. 5A) or on the risks of quasi-extinction and population decline (Fig. 5B and C). At the subpopulation level, increasing habitat fragmentation had no appreciable effects on distant patches (Type III) and small patches in China (Type IV) (Fig. 5D). However, the reduced dispersal rates had stronger effects on Type II patches (pop1, pop3, pop4, pop5, pop6, and pop7) which were more closely connected to the largest patch in Russia (Fig. 5D). But these subpopulation-level alterations did not translate into significant changes at the metapopulation level.

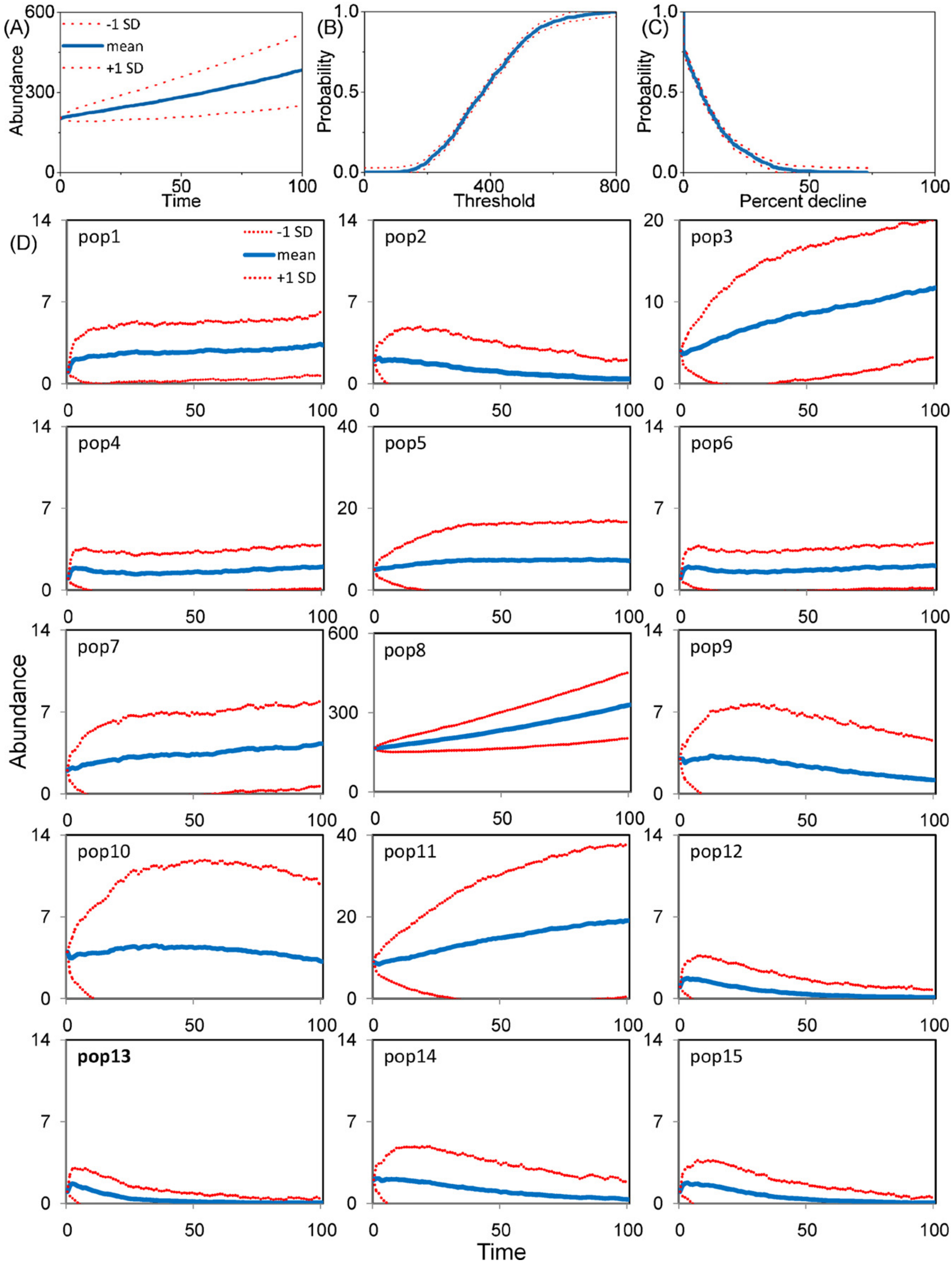

Fig. 2. Simulation results of the baseline scenario. (A) metapopulation dynamics, (B) the quasi-extinction risk of the metapopulation as the probability of falling below a certain threshold size in the next 100 years (e.g. there was a 50% probability that the metapopulation fell below the threshold of 400 individuals), (C) the risk of population decline during the next 100 years as a function of the percentage of population decline (e.g., the probability that the metapopulation declined by 25% or more during the simulation was about 10%), and (D) changes in mean subpopulation abundance of the 15 habitat patches (based on 1000 simulation runs). In (A) and (D) the solid line is the mean population abundance, and the dotted lines denote ±1 standard deviation); and in (B) and (C) the dotted lines represent the 95% confidence intervals.

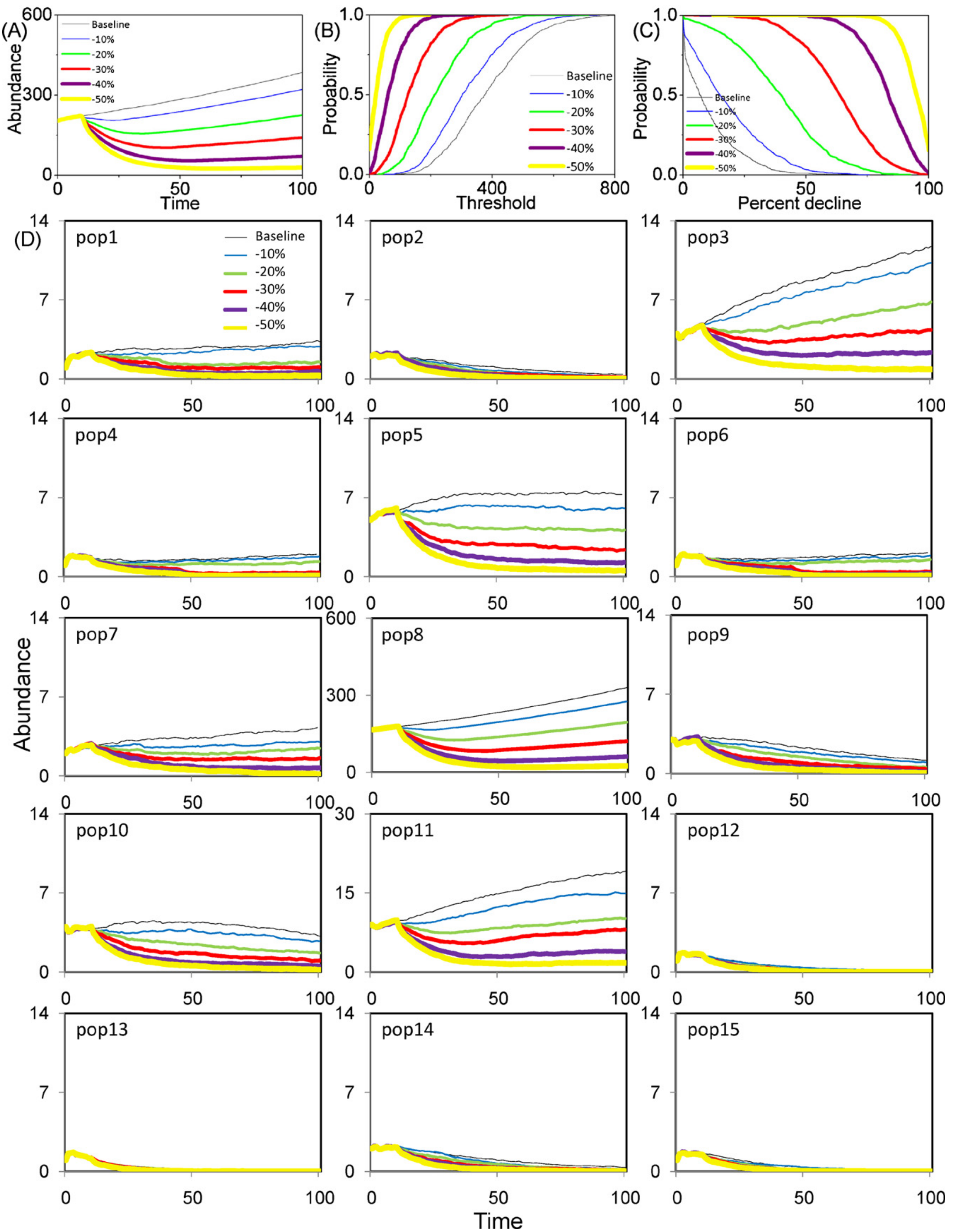

Fig. 3. Effects of habitat degradation on the population dynamics and viability of the Amur tiger. (A) metapopulation abundance, (B) quasi-extinction risk of the metapopulation as the probability of falling below a certain threshold size, (C) the risk of population decline as a function of the amount of population decline, and (D) subpopulation dynamics. In each graph, the thinnest line represents the baseline scenario, and the other lines with increasing thickness represent 5 levels of habitat degradation: 10%, 20%, 30%, 40%, and 50% reduction in fecundity for 10 years, respectively.

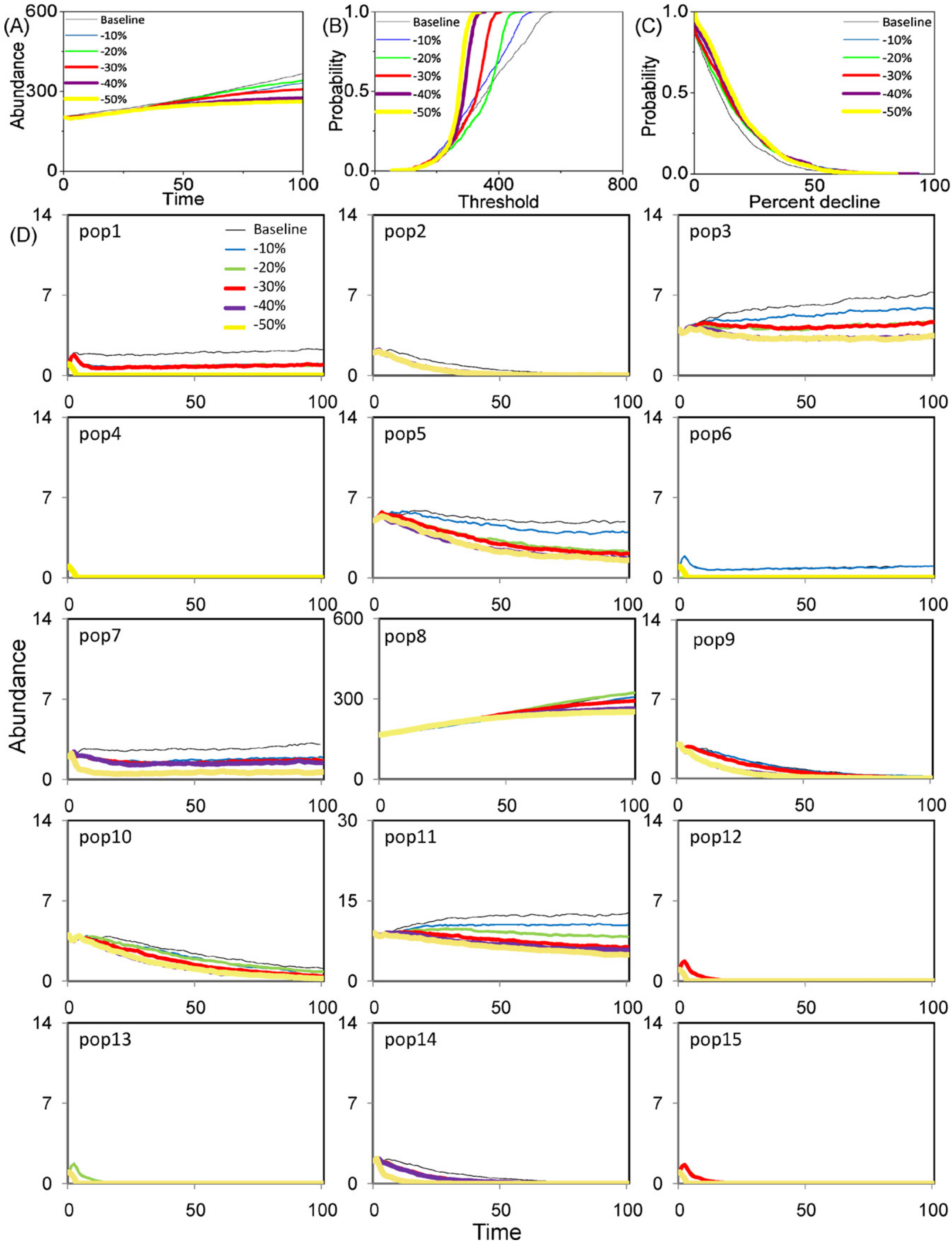

Fig. 4. Effects of habitat loss on the population dynamics and viability of the Amur tiger. (A) metapopulation dynamics, (B) quasi-extinction risk of the metapopulation as the probability of falling below a certain threshold size, (C) the risk of population decline as a function of the amount of population decline, and (D) subpopulation dynamics. In each graph, the thinnest line represents the baseline scenario, and the other lines with increasing thickness represent 5 habitat loss scenarios: decreasing patch size by 10%, 20%, 30%, 40%, and 50%, respectively.

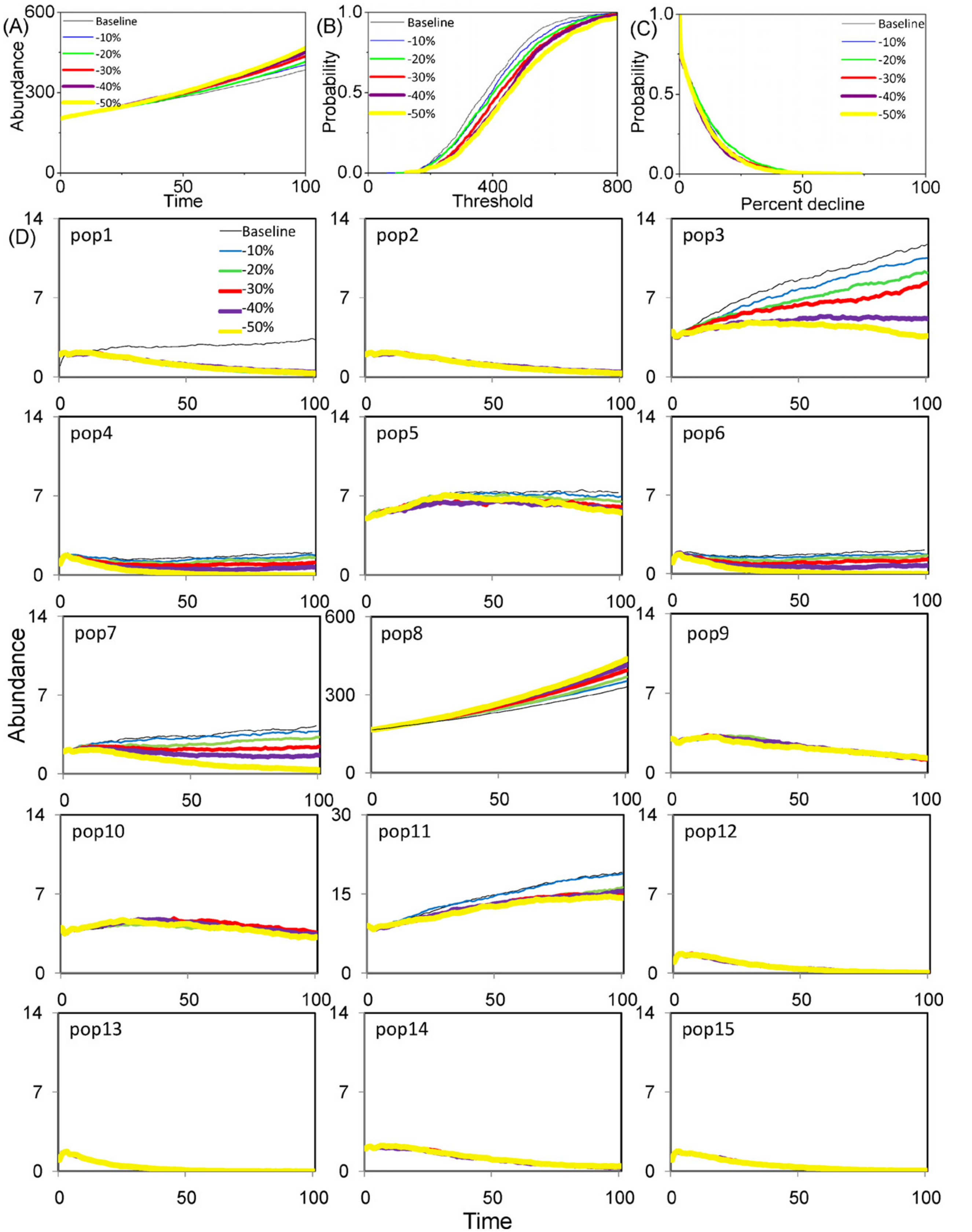

Fig. 5. Effects of habitat connectivity on the population dynamics and viability of the Amur tiger. (A) metapopulation dynamics, (B) quasi-extinction risk of the metapopulation as the probability of falling below a certain threshold size, (C) the risk of population decline as a function of the amount of population decline, and (D) subpopulation dynamics. In each graph, the thinnest line represents the baseline scenario with dispersal rates derived from the distance-based matrix of the present habitat distribution map, and the other lines with increasing thickness represent 5 habitat fragmentation scenarios with dispersal rates decreased by 20%, 40%, 60%, 80%, and 100% (i.e., no dispersal), respectively.

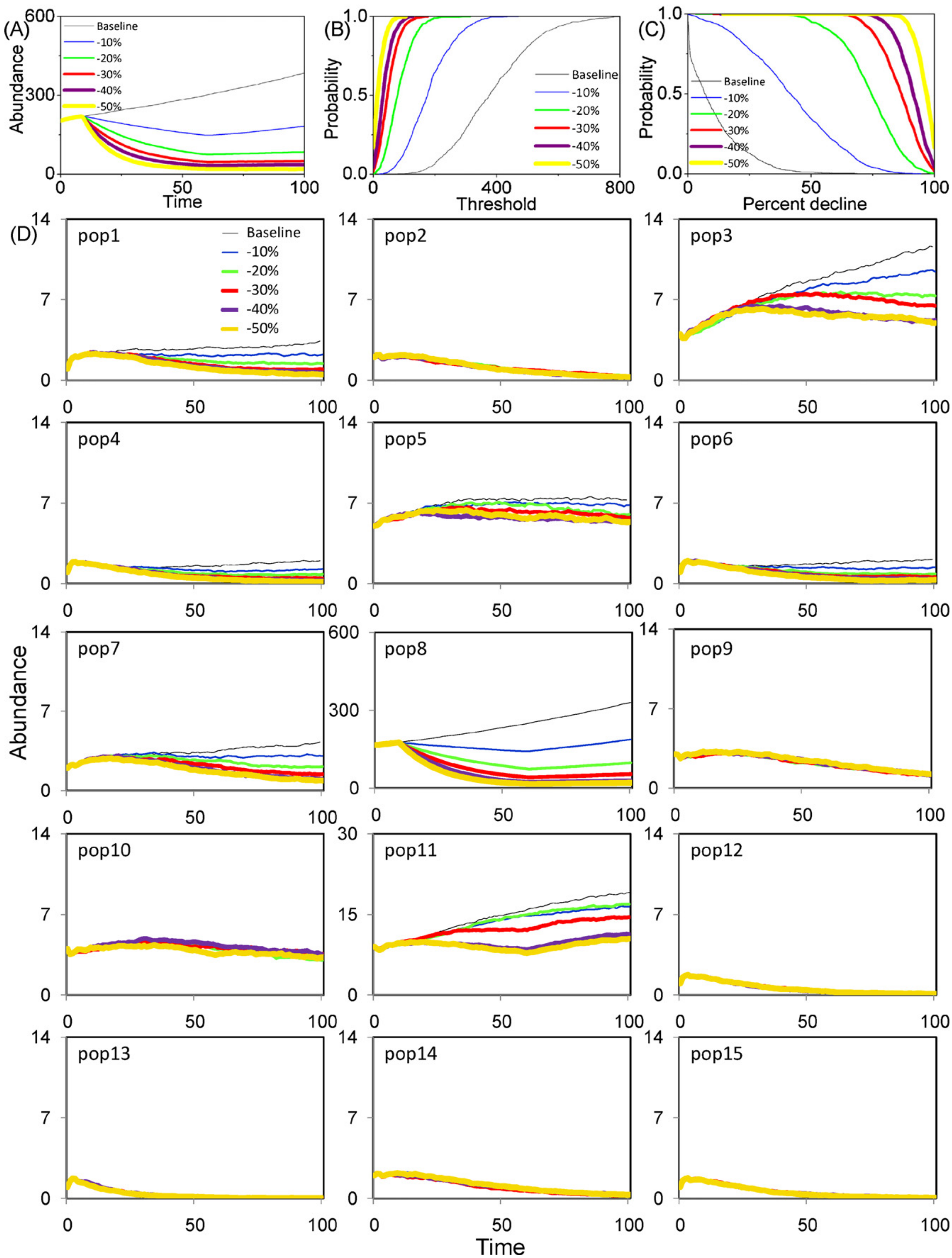

Fig. 6. Effects of poaching on the population dynamics and viability of the Amur tiger. (A) metapopulation dynamics, (B) quasi-extinction risk of the metapopulation as the probability of falling below a certain threshold size, (C) the risk of population decline as a function of the amount of population decline, and (D) subpopulation dynamics. In each graph, the thinnest line represents the baseline scenario (no poaching), and the other lines with increasing thickness represent 5 different levels of poaching intensity: 2%, 4%, 6%, 8%, and 10%, respectively.

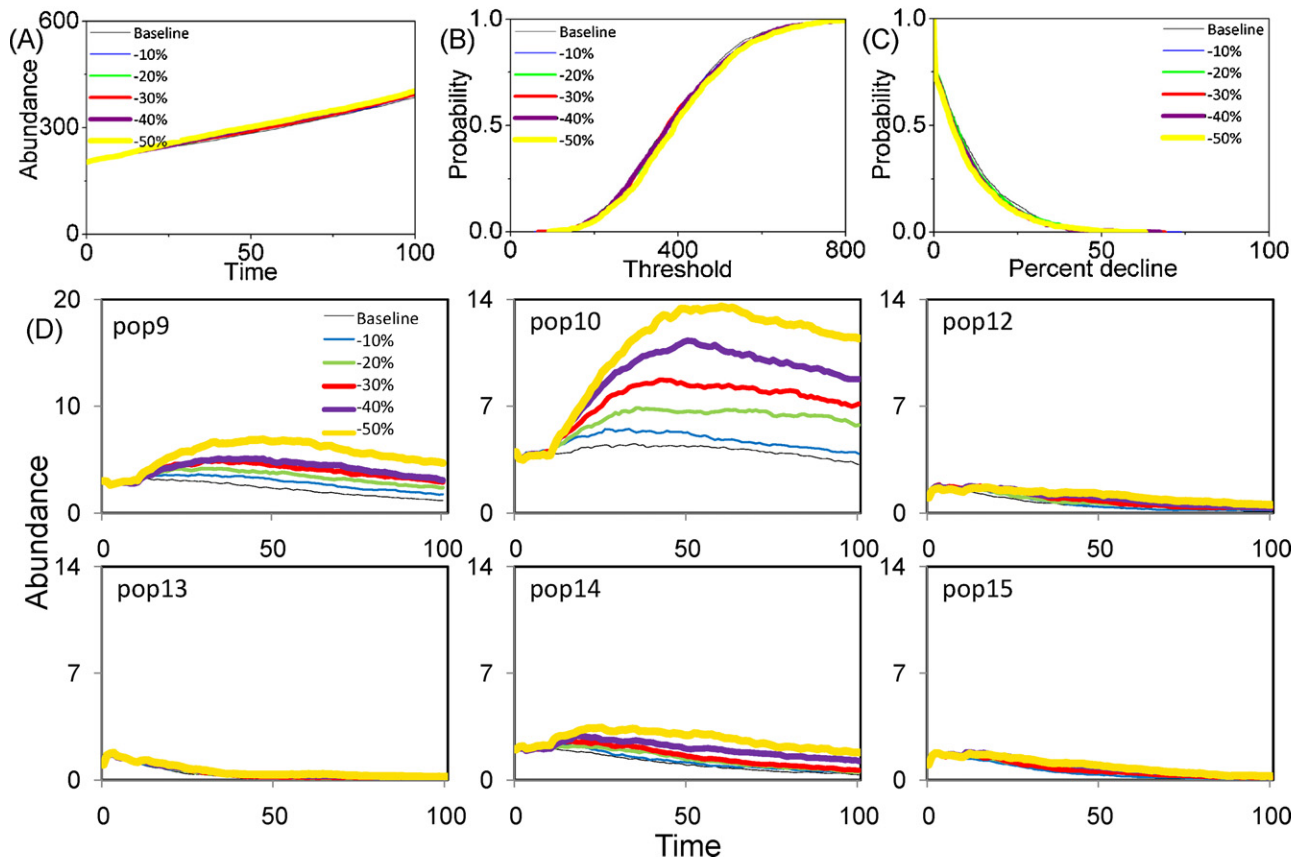

Fig. 7. Effects of the first conservation strategy, i.e., Improving Habitat Quality in China (including all patches within China). (A) metapopulation dynamics, (B) quasi-extinction risk of the metapopulation as the probability of falling below a certain threshold size, (C) the risk of population decline as a function of the amount of population decline, and (D) subpopulation dynamics. In each graph, the thinnest line represents the baseline scenario, and the other lines with increasing thickness represent 5habitat quality improvement scenarios – i.e. increasing habitat quality by 10%, 20, 30%, 40%, and 50%, respectively.

3.5. Effects of poaching

Metapopulation abundance declined significantly with all three poaching scenarios (Fig. 6A). When poaching rates increased from 2%, 4%, 6%, 8% to 10% (percentage of each subpopulation removed each year for 50 years), the quasi-extinction probability and risks of population decline increased rapidly (Fig. 6B and C). After poaching stopped, the metapopulation was not able to recover in the following 50 years. While the probability of the metapopulation declining to 200 individuals was less than 10% in the baseline scenario, it rose to 70% in the 2% poaching scenario and to 100% in all other poaching scenarios. The risks of population decline by 50% or more increased from 0 in the baseline model to 35% when poaching rate was 2%, to 95% when poaching rate was 4%, and to 100% when poaching rates were higher (Fig. 6C). Poaching resulted in a substantial reduction in the subpopulation abundance of all patches (most importantly, the largest patch–patch8), and drove small patches to extinction quickly (Fig. 6D).

3.6. Effectiveness of different conservation strategies

The first conservation strategy – Improving Habitat Quality in China – had essentially no impact on metapopulation dynamics or the probabilities of quasi-extinction and population decline (Fig. 7A–C). It did not have appreciable effects on population abundance of any habitat patch, except for pop10 with the greatest habitat quality improvement (Fig. 7D). Even in the case of pop10, the higher level of population abundance was not able to overcome the declining trend, leading the subpopulation eventually to local extinction.

Under the second conservation strategy – Establishing Movement Corridors, neither within-China nor transnational corridors had any noticeable effects on metapopulation dynamics, or the risks of quasi-extinction population decline (Fig. 8A–C). At the subpopulation level, the EMC strategy prevented two Chinese habitat patches from local extinction, but had little effects on the fate of other patches (Fig. 8D).

The three scenarios of the third conservation strategy – Russia-China Reserve Network – all had positive effects on the dynamics of both the metapopulation and Chinese subpopulations, as well as the risks of quasi-extinction and population decline of the metapopulation (Fig. 9A–D). Increasing the quality and connectivity of habitat patches within China only or in both countries through movement corridors increased the total population size of Chinese habitat patches, but could not prevent them from going extinct in the long run. Establishing a transnational protection zone enclosing pop10, pop11, pop12, pop13, pop14, and pop15, in combination with increasing the quality and connectivity of habitat patches in both countries, substantially increased the overall metapopulation abundance (Fig. 9A) and the total tiger population in China (Fig. 9B). Accordingly, the risks of population decline and extinction probabilities decreased significantly for the entire metapopulation (Fig. 9C and D). Importantly, this was the only scenario that allowed for the long-term persistence of the Chinese tiger population (Fig. 9B).

4. Discussion

All wild tigers are in an increasingly endangered state today (Dinerstein et al., 2007), and this is particularly true for the

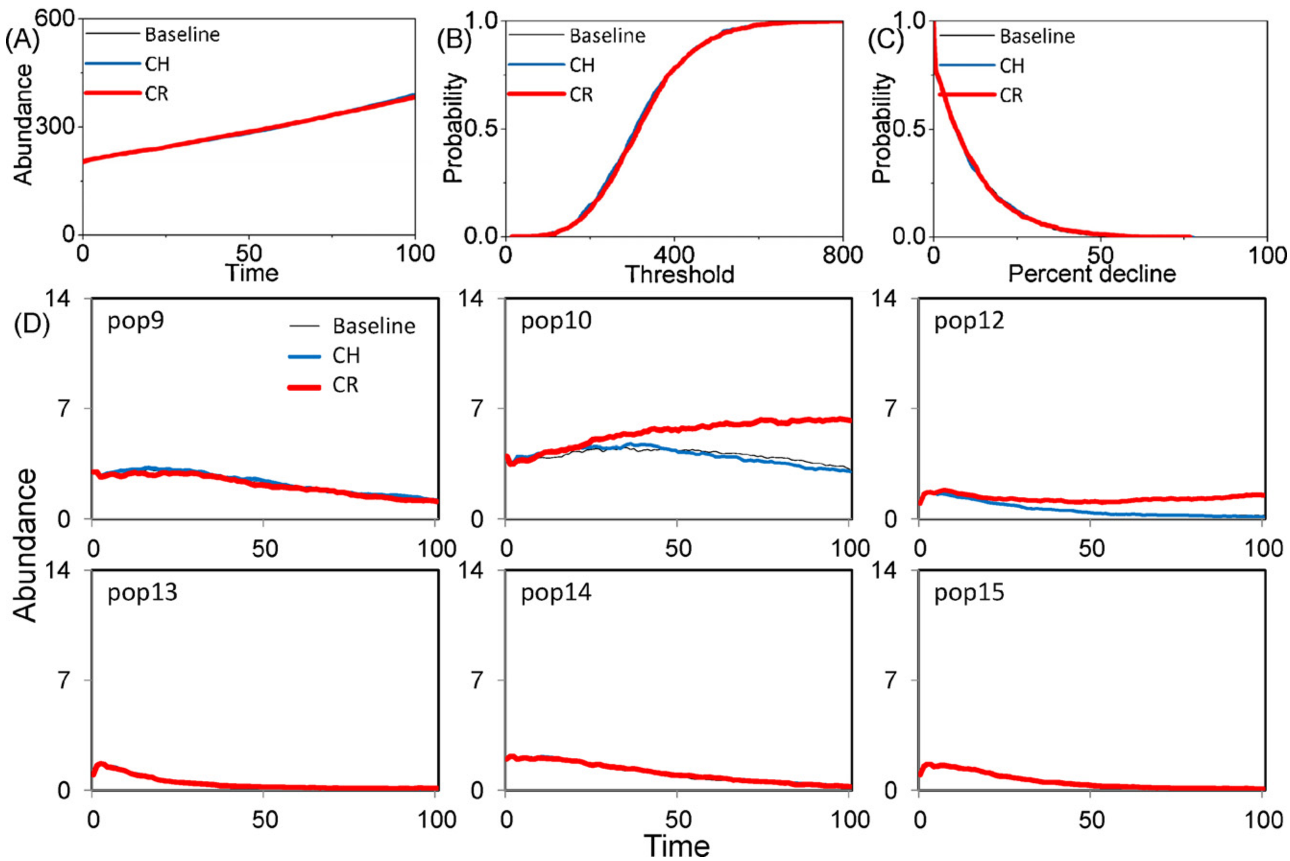

Fig. 8. Effects of the second conservation strategy, i.e., Establishing Movement Corridors. (A) metapopulation dynamics, (B) the quasi-extinction risk of the metapopulation as the probability of falling below a certain threshold, (C) the risk of population decline as a function of the amount of population decline, and (D) subpopulation dynamics. CH denotes establishing corridors between patches within China only (excluding pop11), and CR stands for establishing corridors between patches in both China and Russia to form a cross-border movement corridor (including pop11).

Amur tiger in Russian and China (Jackson, 2000; Carroll and Miquelle, 2006; Miquelle et al., 2009; Tian et al., 2009). A better understanding of how different factors affect the population dynamics and extinction risk of the Amur tiger is both urgent and important. This need was the primary motivation of our study. Through a series of simulation experiments, we have gained new insights into the effects of habitat degradation, habitat loss, habitat fragmentation, and poaching on the population dynamics and

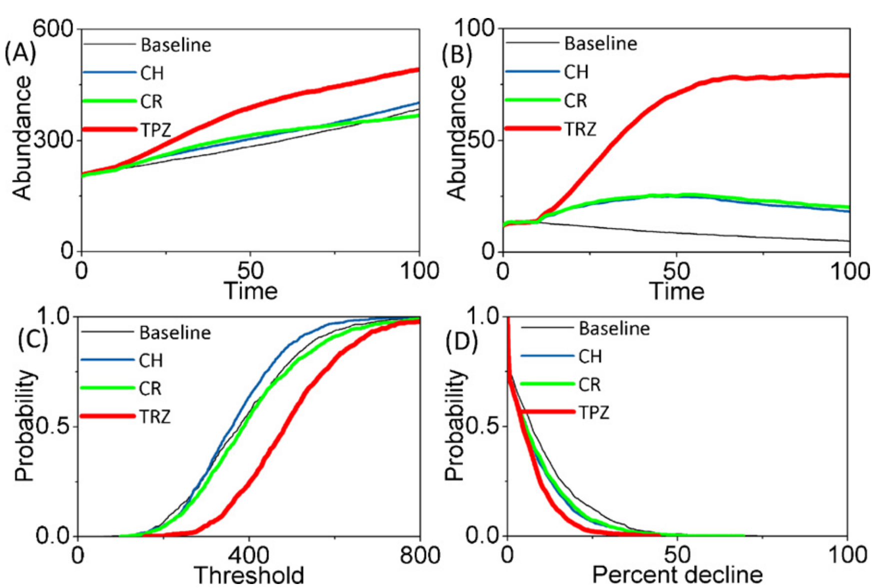

Fig. 9. Effects of the third conservation strategy (Russia-China Reserve Network) on the persistence of the Amur tiger population. (A) metapopulation dynamics, (B) the abundance dynamics of the Chinese tiger population, (C) the quasi-extinction probability of the entire metapopulation, (D) the risks of population decline of the entire metapopulation. CH, CR, and TRZ denote the three scenarios of the third conservation strategy, respectively: (1) increasing the quality and establishing corridors within China only (CH), (2) increasing the quality and establishing corridors in both China and Russia (CR), and (3) increasing the quality and establishing corridors in both countries and establishing a transnational reserve network (TRZ).

extinction risk of the Amur tiger. We discuss discuss them in detail below.

4.1. Effects of habitat degradation

The baseline scenario leads to an increase in the metapopulation size towards the carrying capacity, but this does not mean that the Amur tiger will persist if the current situation with the species continues. This is because of two assumptions in the baseline scenario: (1) there will be no changes in the quality, quantity, and spatial configuration of habitat, and (2) there will be no poaching of tigers or killing of their prey. In reality, neither of these two assumptions is met adequately at present. Our results demonstrated that habitat degradation could drastically reduce the population abundance and increase population extinction risk of the Amur tiger at both the metapopulation and subpopulation levels. Habitat degradation had greater impacts on the tiger population viability than habitat loss. A key assumption here was that habitat degradation led to reductions in both patch carrying capacity and population fecundity, whereas habitat loss only affected patch carrying capacity.

While habitat loss has been widely considered as a major threat to the persistence of the tigers, the importance of habitat quality is yet to be fully recognized in research and practice. The availability of prey (especially large ungulates such as boars and deer) may be the most important limiting factor to the population persistence of the Amur tiger in the immediate future (Karanth and Stith, 1999). This is supported by our results that habitat degradation (related to prey scarcity) had much greater impacts on tiger population dynamics than other factors examined. Thus, maintaining high-quality habitat should focus on prey densities as well as vegetation on which prey species depend on.

4.2. Effects of habitat loss versus habitat fragmentation

Habitat loss and habitat fragmentation have been widely recognized as the major cause for biodiversity decline, and significant research has examined their effects on endangered species (Fahrig, 1997, 2003; Wu, 2008, 2009). Because habitat loss and habitat fragmentation take place concurrently in the real world, distinguishing between the effects of habitat loss and habitat fragmentation per se is difficult in empirically based studies (Fahrig, 2003, 1997; Smith et al., 2009). However, separating these two kinds of effects can be quite important for biodiversity conservation as they may suggest rather different practical measures. Simulation modeling, as demonstrated by our study, provides a powerful approach to dealing with this problem.

Our results showed that the Amur tiger metapopulation was more sensitive to habitat loss than to habitat fragmentation per se. The carrying capacity of a patch decreased with habitat loss, and when it dropped below the minimum viable population, the subpopulation of that patch will go extinct locally in a short term. This result suggests that increasing habitat connectivity may alleviate, to some extent, the problem of habitat loss. The largest patch (about 80% of the total habitat area) played the most essential role in determining the long-term viability of the tiger metapopulation. Consequently, the effects of habitat loss on subpopulations differed with the degrees of connectivity between the subpopulation of consideration and the largest patch. Most subpopulations would go extinct in the long run without a continuous influx of immigrants from the largest patch (which is more than 100 times as many as population in small patches) – an important feature of the metapopulation dynamics of the Amur tiger given the current distribution pattern of its habitat. However, for the largest and relatively stable patch, catastrophes caused by disease or climate change may have important effects on the probability of population extinction than these scenarios we simulated. In these cases, the small patches connected to the largest patch may help avoid its extinction.

4.3. Effects of poaching

Poaching tigers for their valuable parts has been widely recognized as the most direct and significant threat to the persistence of tigers (Check, 2006; Li et al., 2009; Nowell, 2000; Tian et al., 2009). Based on an individual-based model, Kenney et al. (1995) found that poaching substantially increased the probability of population extinction, and that the tiger population could not bounce back once a threshold poaching intensity was passed. Using a resource selection model and a spatially explicit population model, Carroll and Miquelle (2006) also found that the regional popualtion of the Amur tiger was sensitive to poaching. However, Karanth and Stith (1999) used a stage-based model to compare the effects of poaching and prey depletion on tiger population viability, and found that tigers were highly resilient to poaching because of their high reproductive potential. Karanth and Stith (1999) concluded that prey depletion was the primary cause for the decline of the tiger population.

Our simulation results indicate that both poaching and habitat quality deterioration (including prey scarcity) may have major negative effects on the population viability of the Amur tiger. Chapron et al. (2008) pointed out that Karanth and Stith (1999) and other similar studies may have overestimated the effects of prey depletion by decreasing fecundity rates too much throughout the simulation. The extremely high sensitivity of population viability to both poaching and habitat quality at all intensity levels in our study suggests that downplaying the impacts of poaching may be dangerously misleading in the case of the Amur tiger.

4.4. Conservation implications

To increase the population viability of the Amur tiger in a rapidly changing world, practical and effective conservation measures are urgently needed. These measures will mostly likely involve improving the quality of existing habitat patches and establishing movement corridors to increase habitat connectivity. However, given the life history attributes of the Amur tiger and the current spatial pattern of its habitat, our study suggests that such conservation measures have to be done on a grand scale in order to be effective.

Our results indicate that, although there are at least 15 habitat patches for the Amur tiger, the persistence of this species hinges critically on the largest one in Russia. Increasing habitat quality and connectivity of small patches alone would not have a major impact on the population viability. In particular, the habitat patches within China seem too small to support viable local populations. Small habitat patches are population “sinks” and can “drain” the largest subpopulation in the metapopulation system (Wu et al., 1993). Our study here showed that in a number of cases increasing patch connectivity resulted in a decrease in population abundance of the largest patch (pop8). In contrast, in a population viability analysis of the Sumatran tiger in Indonesia based on camera trap and field survey data, Linkie et al. (2006) concluded that small subpopulations could enhance their persistence by increasing their habitat connectivity to large subpopulations as immigrant tigers would offset poaching losses.

Our results also showed that the Russian population of tigers could persist without the subpopulations in China, but the viability of the Chinese population of tigers depended closely on the fate of the tigers on the other side of the border. Conservation efforts to improve the habitat quality of small patches only or increasing habitat connectivity through movement corridors alone would not be enough to guarantee the long-term population persistence of the Amur tiger in both Russia and China. To ensure the long-term persistence of the Amur tiger in both countries would require the improvement of habitat quality of the existing patches as well as the establishment of a transnational reserve network. To implement this strategy would undoubtedly take considerable financial resources and political will, and its feasibility deserves to be examined further.

In conclusion, our study provides new insights into the metapopulation dynamics and persistence of the Amur tiger, and useful information for landscape and conservation planning to protect the biggest cat species in the world. For any conservation plan to be effective, poaching of tigers and their prey must be eliminated by strictly reinforcing existing laws and regulations and creating new ones, when necessary, at all levels of government. Also, it is critically important to take measures now to make sure that the largest habitat patch in Russia will be fully protected. Finally, large-scale collaborations between China and Russia, involving scientists, governmental agencies, and financial sectors, seem indispensable if wild tigers are to be seen on both sides of the border in the long run.

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