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# Land sharing and land sparing reveal social and ecological synergy in big cat conservation

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ABSTRACT

Global biodiversity conservation has recently focused on the roles of land management strategies of land sharing vs. land sparing. However, few studies have evaluated the roles of social and ecological interactions in modifying the effectiveness of land management for top predator conservation. Using a 65-year dataset from northeastern China, we evaluated the roles of government social policies in resolving human-wildlife conflicts and improving human livelihood. From 1998 to 2015, both big cat populations and their habitats have increased. Concurrently, regional human population density decreased by 59.6%, forest volume logged was reduced by 62.6%. Consequently, increases of key prey species were observed during the same periods. Although populations remained small, the annual finite rate of increase was 1.04 for the Amur tiger population and 1.08 for Amur leopards from 1999 to 2015. Habitat areas occupied by big cats increased significantly. Overexploitation of forest resources and big cat declines under previous unsustainable land use are progressively being reversed under land sparing. Large economic investment and intense human-relocation projects coupled with efforts to reduce poaching and illegal hunting and trapping demonstrate a complex social and ecological synergy in big cat conservation in China.

## 1. Introduction

Top predators have been used as surrogate, umbrella and flagship species in biodiversity conservation due to their indispensable ecological and socioeconomic roles in ecosystems (Ripple et al., 2014). However, many carnivores have suffered substantial population declines, geographic range contractions, habitat loss and fragmentation (Ceballos and Ehrlich, 2002; Morrison et al., 2007). For wide-ranging large carnivores like tigers and leopards, conservation of viable populations is complex and challenging because of the need to maintain extensive permeable landscapes to facilitate movement and involvement of political and socioeconomic issues arising from high habitat restoration costs and human-carnivore conflicts (Wikramanayake et al., 2004; Athreya et al., 2013). Some large carnivore populations have shown recovery due to forest restoration, increased ungulate prey, and reduced anthropogenic disturbance (e.g., poaching, livestock grazing, habitat destruction). Recovering large carnivores either coexist with humans in modern, crowded landscapes in Europe (Chapron et al., 2014) or live in separation from humans in preserves or wilderness areas in Africa (Packer et al., 2013) and North America (Gompper et al., 2015). These different successes represent an ongoing debate about land-sharing and land-sparing models for conservation. Both models or strategies are key for understanding how landscape management and conservation protect and help the recovery of populations of key species. Conservation practice will benefit from understanding the mechanisms, by which each model contributes to population recovery, or whether a combination of strategies is required.

During the past six decades, the Chinese government has committed to eradicating poverty and improving the lives of more than one billion people with rapid economic growth, particularly after 1978. China has become the world's second largest economy since 2010. However, much of China's economic growth depended on the exploitation of natural resources, at the cost of the environment (Ma and Melville, 2014). Prior to the 1990s in northeastern China a high density of forest workers

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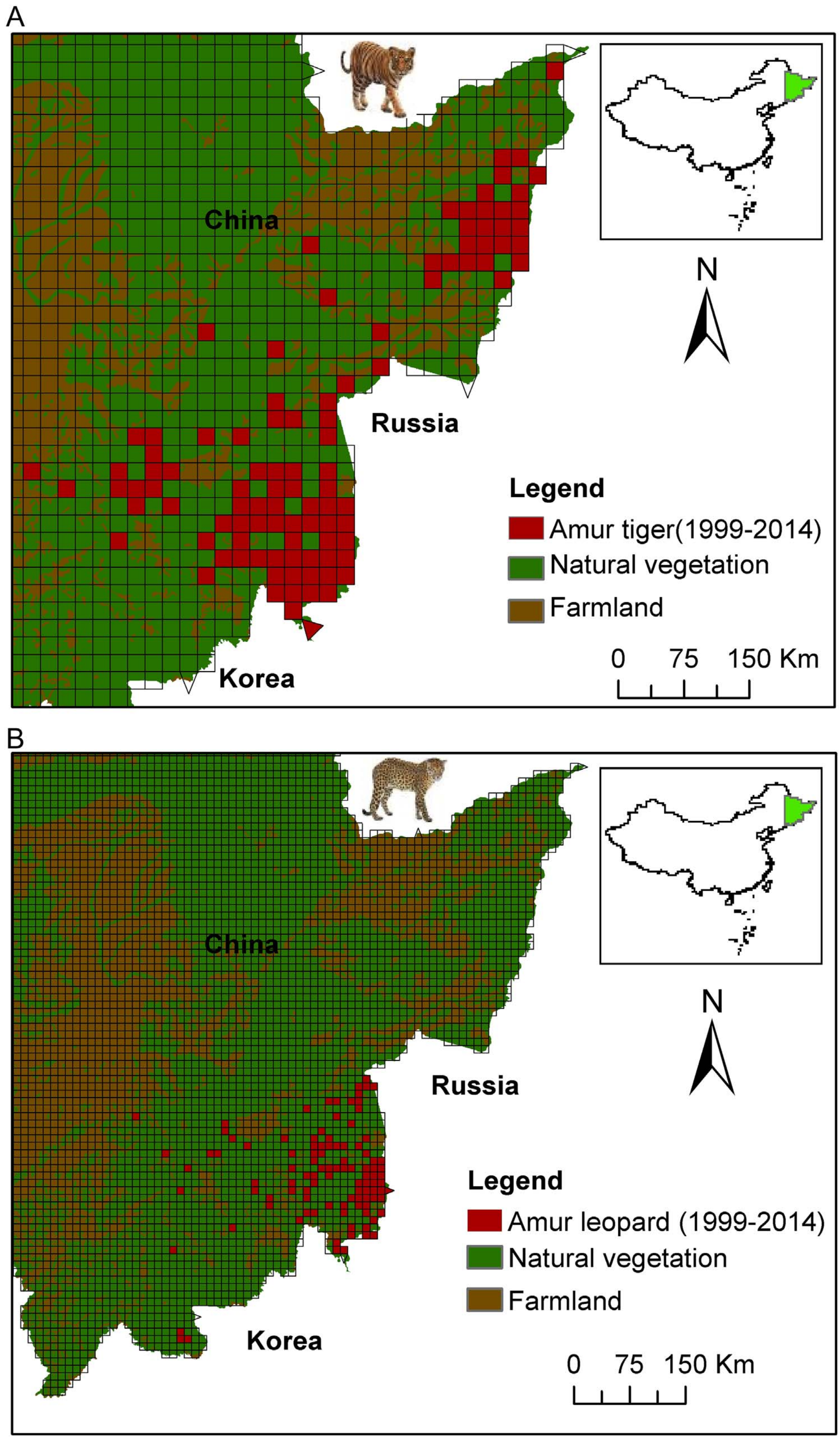


**Fig. 1.** Habitat areas (41,200 $km^2$) occupied by the Amur tigers (A) and habitat areas (10,200 $km^2$) occupied by Amur leopards from 1999 to 2014 (B). Red squares represent the habitat areas occupied by big cats.

congregated in several regions. Large-scale forest logging lasted for almost 50 years (until 1998) across China including the Northeast (Fig. 1b). Consequently, forest resources were over-exploited with serious impacts on regional biodiversity. Ungulates, such as sika deer (*Cervus nippon*) and red deer (*C. elaphus*) became endangered or locally extinct in northeast China (Jiang et al., 2015). During this period, the majority of Amur tiger habitat (*Panthera tigris altaica*) was lost (Yu et al., 2009), and severe drought and massive flooding shocked the national economy and compromised human safety (Xu et al., 2006; Zong and Chen, 2000). The Amur tiger population declined from 200 tigers of the 1950s to 14 tigers of 1999 (Yu et al., 2009). In China, < 10 free-ranging Amur leopards (*Panthera pardus orientalis*) were found in 1998 (Yang et al., 1998). The ensuing socioeconomic and ecological losses made the Chinese government to initiate Natural Forest Protection Program (NFPP) in 1998, with aims of protecting and restoring forests. This program represents one of the largest government investments and spatially extensive environmental rehabilitation efforts in the world (Hyde et al., 2003). It covers all state-owned natural forest regions including the historical range of the endangered big cats in northeastern China.

Recent reports have demonstrated improvement in the populations and habitats of the Amur tiger and the Amur leopard in China over the past two decades (Wang et al., 2016; Jiang et al., 2015). Both forest management and natural preserves were involved in the restoration. Recent studies have found the correlates of recent big cat population and habitat increases, but were restricted to only big cat habitat and population distributions. Specifically, Wang et al. (2016) used camera trap data to assess tiger and leopard populations and distributions, and Jiang et al. (2014, 2015) investigated habitat suitability and potential habitats of Amur leopards and Amur tigers. Yet, no studies have considered the long-term effects of human and socioeconomic factors on the conservation of these two big cats. It would be beneficial to compare the long-term effects of temporal changes in forest management practice, human population changes, the costs of management actions, and subsequent effects on the big cat and prey populations. Doing so would help elucidate mechanisms that inform the roles of land sparing vs. land sharing, and the extent to which these strategies are mutually exclusive vs. synergistic.

Quantitative analyses of the relationships between human livelihood and biodiversity conservation are necessary to test for synergies between social and ecological aims of conservation investments (Persha et al., 2011). Trade-offs or synergies between biodiversity conservation and eradication of poverty may also reveal conservation needs and opportunities (Naughton-Treves et al., 2005). However, few studies of top predators have focused on these interactive relationships across both social and ecological dimensions (Persha et al., 2011). Here we investigated the relationships among landscape conservation investments, forest logging volume, number of relocated foresters (i.e., shifts in livelihoods), and habitat areas occupied by Amur tigers and Amur leopards in the current core range of the Amur tiger and Amur leopard in northeastern China.

The government actions of relocating humans together with basic predator-prey theory led us to hypothesize several steps towards recovery of Amur tigers and Amur leopards. First, relocation of humans (land sparing) led to increases in forest standing biomass (Hypothesis 1). Second, increases in forest biomass and decrease in human disturbance (i.e. poaching, cow grazing, non-timber collection etc.) led to subsequent increases in ungulate prey abundance (supporting land sharing or sparing; Hypothesis 2). Third, reductions in human density led to decreased poaching of big cats and ungulate prey (supporting land sparing; Hypothesis 3). Last, we predicted a subsequent increase in the population size and distributional range of the big cat species following both prey increases and reduced human disturbance (Hypothesis 4). We also discussed the extent, to which the timing of events allows us to separate out the effects of removal of human effects vs. recovery of forest biomass, and hence determine whether land sharing, land sparing models, or some mix of the two are involved.

## 2. Methods

### 2.1. Forest management data collection and analysis

To test the relationship between conservation costs and human population removal, and between human population decline and increases in forest biomass, we selected 31 forest bureaus (69,605 $km^2$) and 10 nature reserves (4050 $km^2$) for data collection and surveys within the current range of the Amur tiger and Amur leopard in northeast China. The total survey area of 73,659 $km^2$ comprised the current range of the tiger and leopard (Table S1, Fig. S1). Most of the forest bureaus were established in the 1950s and have had commercial logging for > 60 years (Table S1). Apart from one nature reserve, most natural reserves were established after 2000 (Table S1). We compiled the annual records of relevant variables from 1950 to 2015. Those variables included conservation investments, forest logging volumes, the amount by which forest stock growth exceeded logging volume (hereafter net forest stock growth), plantation areas, number and density of forest workers, compensation costs of wildlife-human conflicts, and, human welfare benefits provided by resettlement-assistance projects for forester relocations from each forest bureau and nature reserve.

We used linear or nonlinear regression to test the relationships between annual forest management investment amounts, forest logging volumes, net forest stock growth, density of forest workers, and habitat areas occupied by Amur tigers and Amur leopards after the initiation of the natural forest protection project in 1998. We regressed logarithmically transformed poaching numbers on time to quantify the linear increase rates of the Amur tigers poaching from 1998 to 2006 and from 2007 to 2015. All statistical tests were two-sided tests at the significance level of 0.05 and carried out using by Prism (GraphPad Prism, Prism 5.0; www.graphpad.com).

### 2.2. Population size and habitat distribution of Amur tiger and Amur leopard

We obtained data on the abundance and habitat distribution of the Amur tigers and Amur leopards from the literature published in China since the 1950s (Yu et al., 2009), which we summarized below. Historical population size was assessed using snow-track line transect methods based on big cat footprint identification from 1998 to 2015.

In the core habitat of Laoyeling, Zhangguagncailing and Wandashan, we deployed > 1500 camera traps covering almost 2900 $km^2$ covering this core big cat distribution area since 2013. Camera traps were set up at a density of 1 pair per 10 $km^2$ and were checked every 3 months from 2013 to 2015.

Based on population size from both camera trap data and historical reports (Yu et al., 2009), we estimated the realized population growth rate of the Amur tiger population as $R = [\ln(N_{2015})\text{-}\ln(N_{1999})]/t$, where $N_{1999}$ is tiger population in 1999, $N_{2015}$ is population size in 2015, and $t = 16$ (years) (Berryman and Turchin, 2001). We converted annual population growth rate $R$ to finite rate of increase ($\lambda$) using the equation $\lambda = e^R$. With relatively low survival rates (e.g. 85%), at least 100 individuals of a tiger population should be required for ensuring long-term persistence (Chapron et al., 2008). We predicted how many years 100 individuals of Amur tigers will be realized according to this increase rate (Berryman and Turchin, 2001). We also conducted similar calculations for Amur leopards.

From 1998 to 2015, we recorded 779 occurrences of Amur tiger in this region, including 355 killings of prey or livestock, 51 fecal samples (determined by DNA analysis), and 345 sets of footprints and 71 photographs from camera traps. Also, 643 occurrences of Amur leopard were found, including 24 killings of prey or livestock, 36 fecal samples (determined by DNA analysis), 133 sets of footprints, and 459 photos from camera traps. We established the national tiger and leopard information database in the Feline Research Center of the Chinese State Forestry Administration. Habitat loss is normally a strong indicator of population declines (Dinerstein et al., 2007). To estimate habitat areas occupied by the big cats, we first created two gridded polygons, covering the entire study region, at the spatial resolutions of 20 km × 20 km and 10 km × 10 km, respectively, using ArcGIS software (Environmental Systems Resource Institute, ArcGIS 10.0; www.

esri.com). The two spatial resolutions were chosen according to average home range sizes of female Amur tigers or Amur leopards (Goodrich et al., 2010; Hebblewhite et al., 2011). Then we determined the occurrence frequencies of Amur tigers within a 400-$km^2$ grid cell and those of Amur leopards within a 100- $km^2$ grid cell, respectively, using Hawth's Analysis Tools for ArcGIS (http://www.spatialecology.com/htools/download.php). A grid cell with a non-zero ($> 0$) occurrence frequency was considered occupied. The annual sum of all occupied grid cells was used to estimate the annual total habitat area occupied by each big cat species. The total areas occupied over the past 15 years are shown in Fig. 1 (A) for Amur tigers and Fig. 1 (B) for Amur leopards. We tested for relationships between annual total habitat areas occupied by big cats and socioeconomic and forest variables using linear or non-linear regression models.

We collected ungulate prey density data from 2010 to 2014 over an area of 878 $km^2$ in Jilin Wangqing Nature Reserve using snow track sample plots (Qi et al., 2015). We did a total of 33 plots in 2010–2011, 14 plots in 2012–2013, and 10 plots in 2013–2014. Each plot with the area of approximately 10 $km^2$ (i.e., 5 km $\times$ 2 km) consisted of five parallel 5 km transect lines separated by 500 m. We only used animal tracks within 24 h after snowfall to calculate the number of individuals of each prey species in each plot (Qi et al., 2015) and hence, we calculated ungulates prey density. Prey abundance data were not available across the whole study area for the entire study period. Furthermore, to estimate the efforts to reduce poaching on tiger and prey and numbers of snares encountered, we collected the records of patrols for removals of steel snares as well as data on steel snare density in the Jilin Wangqing Nature Reserve in both 2009 and 2015.

All studies were conducted in accordance with the guidelines approved by The American Society of Mammalogists (Sikes and Gannon, 2011). Our camera trapping protocol was approved by the Expert Committee of Feline Research Center of Chinese State Forestry Administration. Data are available by contacting G.J.

## 3. Results

Most Amur tigers in China live near the Sino-Russia border, but we obtained a camera-trap image of two individuals (one male and one female) 270 km south of the border, indicating the successful dispersal of Amur tigers into the interior of northeastern China. We also recorded breeding Amur tigers and breeding Amur leopards (Shi et al., 2015; Jiang, 2014). Furthermore, we found the current range of Amur leopards to be 48,000 $km^2$ and to contain 37 suitable habitat patches for Amur leopards, which may harbor about 195 Amur leopards in northeast China (Jiang et al., 2015).

The Chinese government invested \$4.476 billion of U.S. dollars (USD) within the current range of big cats, including \$2.723 billion in NFPP (Fig. S2a), \$0.013 billion in human-wildlife conflict compensation (Fig. S2b), \$1.712 billion in human settlement improvement for relocations (Fig. S2c), and \$0.027 billion in nature reserve protection. The total amount of annual NFPP investment steadily increased from 1998 to 2015 ($R^2 = 0.78$, $n = 17$, $P < 0.001$; Fig. S2a). From 2007 to 2014, annual rates of livestock killing by big cats increased by 31%. To mitigate the conflict between the livelihoods of local people and big cats or forest recovery (Fig. S2b), the Chinese government initiated the forester resettlement project in 2008. The government constructed welfare housing to relocate foresters from forest farms or villages to large towns or cities and helped most relocated foresters to shift to other careers and livelihoods independent of forest resources (Fig. S2c).

Annual NFPP investment per square km averaged \$2927 and linearly increased from \$1098 to \$3930 ($R^2 = 0.76$, $n = 17$, $P < 0.001$; Fig. 2a). Consistent with Hypothesis 1 and land sparing, the NFPP policy initiated in 1998 caused mean total human density to fall from $17.77 \times 10^4$ $km^{-2}$ in 1999 to $7.18 \times 10^4$ $km^{-2}$ in 2015 (Fig. 2b, Fig. S3a), and almost 100,000 people changed careers during this period (Fig. S3a). From 1999 to 2015, annual mean population density of foresters decreased from 2.73 to 1.07 $km^{-2}$ ($R^2 = 0.95$, $n = 17$, $P < 0.001$; Fig. 2b). Moreover, there were no human residents in the forest areas of 2861 $km^2$ within 9 of 31 forest bureaus inside the current range of the big cats from 2008 to 2015. Concurrent with human population declines, annual total forest logging volume linearly declined from $5.51 \times 10^6$ to $2.06 \times 10^6$ $m^3$ from 1999 to 2015 ($R^2 = 0.88$, $n = 17$, $P < 0.001$; Fig. S3b). Annual mean logging volume decreased from 117 $m^3/km^2$ to 30.3 $m^3/km^2$ from 1998 to 2015 ($R^2 = 0.90$, $n = 17$, $P < 0.001$; Fig. 2c), and forest logging entirely ceased in northeastern China in April 2015. Consistent with Hypothesis 1, annual mean net forest stock growth increased from 66.62 $m^3/km^2$ in 1999 to 232.45 $m^3/km^2$ in 2014 ($R^2 = 0.61$, $n = 16$, $P = 0.004$; Fig. 2d). Forest area increased at a rate of 368 $km^2$/year from 1995 to 2015, and the total area reforested between 1995 and 2015 was 7736 $km^2$ (Fig. S2d).

Annual mean costs of NFPP per $km^2$ were inversely related to the number of foresters per $km^2$ ($R^2 = 0.68$, $n = 17$, $P = 0.002$; Fig. 3a) and mean forest logging volume per $km^2$ ($R^2 = 0.74$, $n = 17$, $P < 0.001$; Fig. 3b), but were positively related to mean net forest stock growth ($R^2 = 0.45$, $n = 16$, $P = 0.069$; Fig. 3c).

Consistent with Hypotheses 2 and 3, the total recorded number of Amur tigers poached by snares was five individuals from 1998 to 2015: four individuals from 1998 to 2006 and one individual from 2007 to 2015, suggesting that management approaches improved protection of the tiger and may facilitate population growth. In addition, patrolling records showed a snare density of 0.4 snares/km in 2009 compared to only 0.1 snares/km for prey or tiger by catch during line transect survey in 2015 in Jilin Wangqing Nature Reserve.

The rate of tiger population decline paralleled increases in human population density and mean forest logging volume and decreases in net forest stock growth (Fig. 2b–d). However, as predicted by Hypothesis 4, the Amur tiger population size recovered from 14 tigers in 1999 to 27 animals based on our camera trap data from 2013 to 2015, similar to 26 individuals or more reported by Wang et al. (2016). Furthermore, the number of Amur leopards increased from approximately 10 leopards in 1998 (Yang et al., 1998) to 42 individuals in 2015 (Wang et al., 2016). Thus, the annual finite rate of increase ($\lambda$) of the Amur tiger population from 1999 to 2015 was 1.04, so that China's wild Amur tiger population could potentially grow to 100 individuals by 2050. In addition, the rate $\lambda$ for increase of the Amur leopard population from 1999 to 2015 was 1.08, and the wild Amur leopard population could potentially grow to 100 individuals by 2025.

For Hypothesis 4, we did see the predicted effects of changes in human density, forest growth, logging volume and prey on habitat areas occupied and population sizes of big cats. A total area of 41,200 $km^2$ was occupied by Amur tigers since 1998 (Fig. 1). A total area of 10,200 $km^2$ was occupied by Amur leopards from 1999 to 2014 (Fig. 1). Furthermore, annual habitat areas occupied by Amur tigers and Amur leopards increased rapidly and linearly from 1999 to 2015 ($R^2 = 0.52$, $n = 14$, $P = 0.049$ for tigers; $R^2 = 0.86$, $n = 19$, $P < 0.001$ for leopards; Fig. 4).

Habitat area occupied by the Amur tiger was inversely related to human density ($R^2 = 0.55$, $n = 14$, $P = 0.032$; Fig. 5a), positively related to mean net forest stock growth ($R^2 = 0.63$, $n = 14$, $P = 0.011$; Fig. 5b), but not related to mean forest logging volume ($R^2 = 0.24$, $n = 14$, $P = 0.387$; Fig. 5c). Likewise, habitat area occupied by the Amur leopard also was inversely related to human density ($R^2 = 0.80$, $n = 15$, $P = 0.001$; Fig. 5d), positively related to mean net forest stock growth ($R^2 = 0.83$, $n = 15$, $P = 0.002$; Fig. 5e), and inversely related to mean forest logging volumes per $km^2$ ($R^2 = 0.79$, $n = 15$, $P < 0.001$; Fig. 5f). Ungulate prey surveys showed that population density of key prey species increased from 2010 to 2014 over an area of 878 $km^2$ in Jilin Wangqing Nature Reserve, supporting Hypothesis 3. Roe deer (*Capreolus pygargus*) density increased from 0.67 $\pm$ 0.13 individuals/$km^2$ in 2010 to 1.88 $\pm$ 0.22 individuals/$km^2$ in 2013, and then to 2.33 $\pm$ 0.52 individuals/$km^2$ in 2014. Wild boar (*Sus scrofa*)

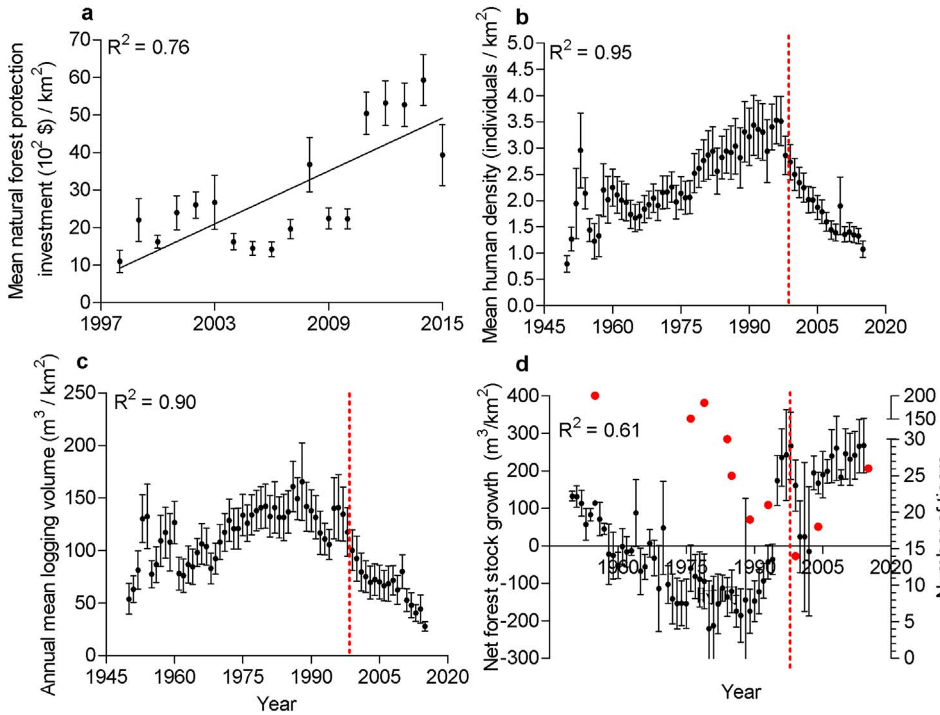


**Fig. 2.** Annual mean natural forest protection investments per square kilometer from 1998 to 2015 (**a**); annual mean human population density (**b**); annual mean logging volume (**c**); dynamics of the Amur tiger population and annual mean net forest stock growth (**d**) from 1950 to 2015. Red dashed line represents the year 1998 when natural forest protection project was implemented. Red points represent the number of Amur tigers.

density increased from 0.32 ± 0.13 individuals/$km^2$ in 2010 to 0.40 ± 0.02 individuals/$km^2$ in 2013, and to 0.93 ± 0.66 individuals/$km^2$ in 2014. Sika deer density arose from 0.03 ± 0.022 individuals/$km^2$ in 2010 to 0.06 ± 0.03 individuals/$km^2$ in 2013, and to 0.34 ± 0.34 individuals/$km^2$ in 2014. Ungulate prey population data also provided evidence for the hypothesis concerning the relationship between tiger or leopard habitat areas or population recovery and prey population density growths.

## 4. Discussion

We found a transition from unsustainable forest management to land sharing and to land sparing for forest conservation in northeast China. During the same period, substantial decreases in regional human population density, forest volume logged, and known number of Amur tigers poached coincided with increases in three key prey species. Both increasing trends in big cat population sizes and increases in habitat areas occupied were also observed during the transition to land sharing and land sparing for forest conservation of northeast China.

We provided evidence of the lack of land sharing before 1999. We found that Amur tiger population size linearly decreased from 1950 to 1998 and has then increased since 1999 (Fig. 2d), while annual forest logging volume increased till 1998 and then decreased with an increasing trend of net forest stocks from 1999 to 2015 (Fig. 2 b,c). The timings and temporal sequence of the changes in forest management, population dynamics of big cats during the past 65 years provided evidence for ineffective land sharing before 1999. Specifically, the more overexploitation of forest resources led to lower forest biomass and ungulate prey and higher poaching of prey and cats. Subsequently, since the beginning of NFPP in 1998, land sparing has promoted forest biomass recovery followed by prey recovery and increases in both habitat area and abundance of big cats.

Forest management should focus on both forest resource sustainability and humane social development (Carpenter et al., 2009). Our study provides partial support for successful big cat conservation in China, although populations were still small. We cannot simply attribute the success in the recovery of the two big cats to either the land sparing or land sharing model, because it might be caused by the role of ecological synergy. The lack of land sharing between the big cats and humans led to the dramatic declines in the abundance of the two large carnivores before 1998. By contrast, implementation of land sparing, through setting the majority of forestlands aside from logging, and land sharing, through maintaining the minimal forest logging and other forest use, has increased the abundance and habitat distribution of the two big cats. This represents a step towards the goals suggested by Chapron et al. (2014), that the conservation of large carnivores should focus on preserving the ecological processes driven by large carnivores in human-dominated landscapes and the functionality of forest ecosystems with different levels of completeness (Chapron et al., 2014). Hence, we should simultaneously emphasize the social processes of conservation investment with measurable social indicators (Mace, 2014); otherwise, we may not be able to ensure ecological and conservation outcomes of conservation investments.

On the other hand, styles of land ownership also influence the effectiveness of conservation investments due to the will of land owners (Wilcove et al., 1998). One big challenge western countries face in biodiversity conservation is persuading landowners to agree to protect wildlife on the privately owned lands (McShane et al., 2011). However, land in China is state-owned. State-owned land management provides benefits for "top-down" initiatives and was shown to be beneficial despite its complexity. Considering the potential risks of nationally uniform policies and their large-scale impacts, the Chinese government first conducted a pilot project and then elevated the annual amount of investments gradually, according to the program's progress (Fig. 2a, Fig. S4). In addition, welfare housing, increasing forest stock volume, and wildlife compensation policies played an important role in resolving human-tiger conflicts and protecting human wellbeing (Jiang et al., 2014). As far as the level of conservation investment is concerned, it is remarkably similar to the funding levels (> \$3000/$km^2$) for successful lion conservation in unfenced African reserves (Packer et al., 2013).

Large carnivores have exhibited species-specific sensitivities to

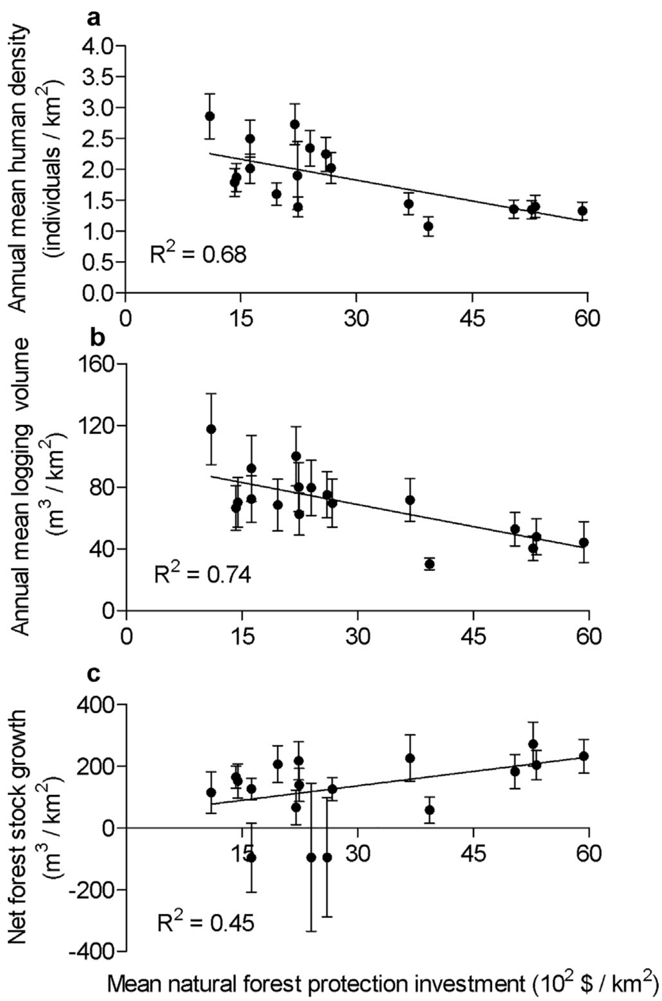


**Fig. 3.** Relationships between mean natural forest protection investment (the abscissa), annual mean human density (**a**), annual mean forest logging volume (**b**), and net forest stock growth (**c**) in 31 forest bureaus of Northeastern China from 1998 to 2015.

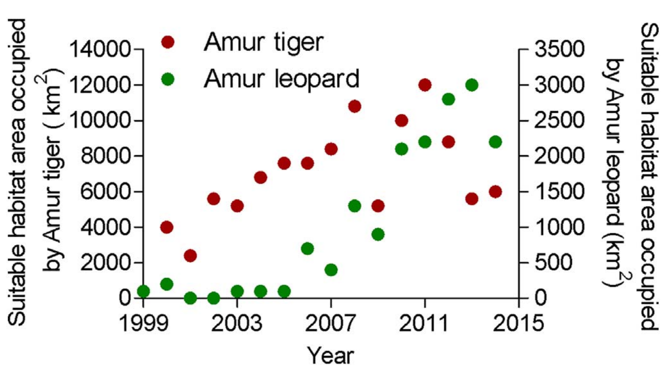


**Fig. 4.** Estimates of habitat areas occupied by Amur tigers (red points) and Amur leopards (green squares) in northeastern China after the implementation of natural forest protection project in 1998. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

changes in human population density, allowing for successful adaptation to human-dominated landscapes (Chapron et al., 2014). Our results indicate that the decline of human density enhanced the distributional expansion of both Amur tigers and leopards (Figs. 2b, 3a, 5a, d). The control of human density in the core range of big cats not only directly reduced forest harvesting volume, but also mitigated human disturbances such as forest harvesting, farmland reclamation, infrastructure construction, poaching, and human activity (Qi et al., 2015; Giller et al., 2008). Disentangling the relationship between big cat poaching and changes in human densities is more complex because poaching effects may have a time lag. For example, once steel snares have been set up, they may impose risks to wild animals for many years. With increases in the frequency of big cat occurrence, local governments have conducted patrols in the key tiger and leopard habitats to locate and remove old snares to ensure big cat safety. Consequently, our results show that snare density decreased from 2009 to 2015 in the Jilin Wangqing Nature Reserve. Coincident with this, from 2007 to 2015, the recorded number of Amur tigers poached was significantly lower than that from 1998 to 2006. Although fewer and fewer people will live in the forests, local governments will need to continue to remove old snares through patrolling.

Evidence suggests that long-term forest restoration and simultaneous controls of illegal ungulate hunting and other human disturbances have increased ungulate abundance and distribution range (Jiang et al., 2015). For example, our ungulate surveys suggested that ungulate prey density (i.e., roe deer, wild boar and sika deer) increased from 2010 to 2014 over the 878 $km^2$ Jilin Wangqing Nature Reserve. Based on the evidence of the prey driven distribution of big cats in previous studies (Jiang et al., 2015; Qi et al., 2015) and this study, we conclude that forest restoration contributed to the recovery of ungulate populations and subsequently increased the distribution range of big cats in northeastern China. Our findings provide a good example, in which big cat populations expanded in both size and habitat area used when humans retreated from forests through a combination of land sparing and sharing. Like other conservation studies, there is need to consider social problems caused by relocating people, such as the needs for infrastructure and new job opportunities. Conservationists have often ignored the social context and implications of conservation actions (Jiang et al., 2014). Our study reveals that the controlling of human density from a conservation investment standpoint may bring out synergy for social or ecological developments (Persha et al., 2011).

Several European studies have shown that the land sharing model for large carnivores to coexist with humans at high densities can be successful on a continental scale, and demonstrated that four large carnivore species live largely outside of protected areas (Chapron et al., 2014). However, on smaller regional scales in southwest Ghana and northern India, land sparing was a more promising strategy for minimizing negative effects of food production on tree and bird species biodiversity (Phalan et al., 2011). Similar to the European findings, we also found that the conservation of large carnivores may not merely rely on local nature reserve systems in China, which is the case for giant panda conservation (Liu et al., 2001; Loucks et al., 2001). The Changbaishan Nature Reserve was established for the conservation of Amur tigers in the 1960s. However, the reserve was insufficient to sustain the tiger population because the tiger has not been found in this reserve over the last 30 years. In this study, our results have demonstrated the effectiveness of landscape conservation on Amur tigers and leopards in China on a large scale (Chapron et al., 2014). After the NFPP was initiated in 1998, forestland management in northeastern China incorporated not only the large-scale land sharing model to reduce human densities, but also regional-scale land sparing model to set aside 2861 $km^2$ of unpopulated forests within the 9 forest bureaus. More generally, there is a need to integrate the land sparing and land sharing models for the conservation of large carnivores at multiple spatiotemporal scales (Chapron et al., 2014; Hurlbert, 1978; Carter et al., 2012).

The recovery of big cats, like other large carnivores, is limited by their low annual population growth rates and by diseases. The annual finite rate of increase of China's Amur tiger population is similar to that (1.046) of the Russian Amur tiger population during its increasing phase over 41 years (Miquelle et al., 2015). Long-term monitoring is needed for the assessments of the success or failure of the recovery (Miquelle et al., 2015). Short-term monitoring may not be adequate owing to the lack of data for sensitive ecological indicators and slowly

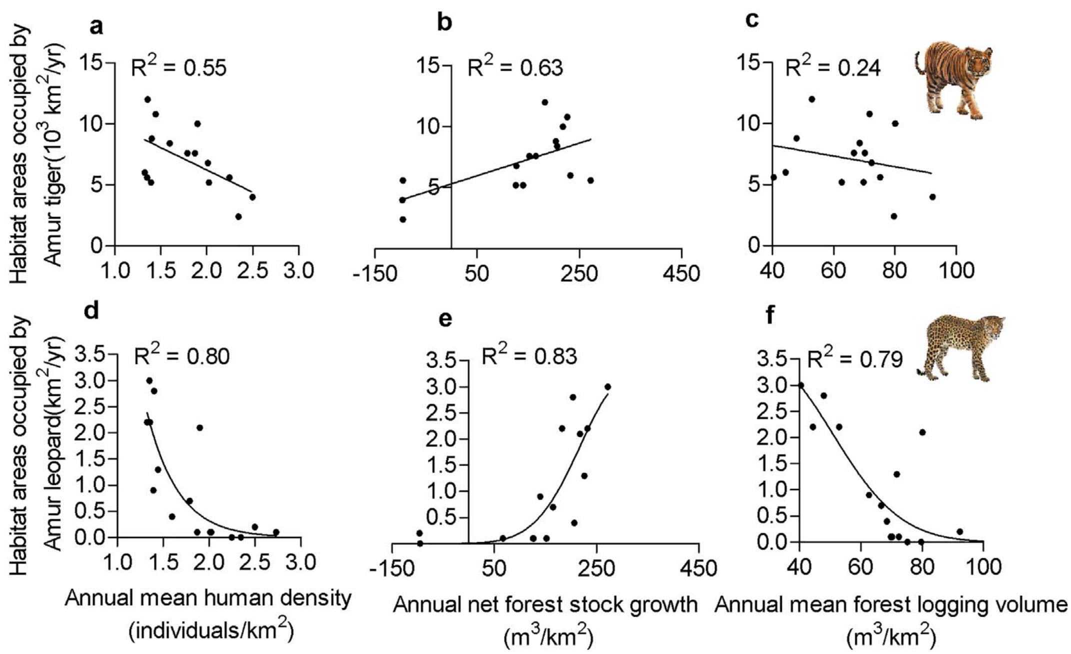


**Fig. 5.** Linear relationships between habitat areas occupied by big cats (the ordinate), annual mean human density (**a**), mean net forest stock growth (**b**), and mean forest logging volume (**c**), and nonlinear relationships between habitat areas occupied by big cats (the ordinate), annual mean human density (**d**), mean net forest stock growth (**e**), and mean forest logging volume (**f**) since the beginning of natural forest protection in 1998.

changing populations of long-lived species. At the early stages of big cat conservation, we can use indirect social, economic, primary production (i.e., habitat vegetation improvement, etc.) or prey indicators to measure the success of conservation activities. Only after a relatively long period of conservation may we link the habitat area or population abundance of big cats to conservation investment indicators. Up to now, there is not a published time limit on the life-span of the NFPP from the Chinese government. China's central government still continues to fund the forest protection under the on-going forest harvest ban in northeastern China. Moreover, a series of centrally controlled large national parks (14,600 $km^2$) for tigers and leopards has been scheduled to be established step by step across the big cat habitat landscape (Li et al., 2016). The new National Park Initiative will ensure the long-term protection and conservation of big cats in northeastern China (Kathleen, 2016). Except the Amur tiger and Amur leopard national park pilot, the Chinese government is planning to establish other 8 national parks, including Sanjiangyuan national park pilot (123,100 $km^2$), giant panda (*Ailuropoda melanoleuca*) national park pilot (27,000 $km^2$), Hubei province Shennongjia national park pilot (1170 $km^2$), Zhejiang province Qianjiangyuan national park pilot (252 $km^2$), Hunan province Nanshan national park pilot (635.94 $km^2$), Fujian province Wuyishan national park pilot (982.59 $km^2$), Beijing Great Wall national park pilot (59.91 $km^2$), and Yunnan Shangri-La Pudacuo (602.1 $km^2$). It is urgent to assess how much areas of both national parks and international or national ecological corridors are needed to maintain extensive permeable landscapes for Amur tiger and leopard survival (Chapron et al., 2014; Ekroos et al., 2016). Based on this study, historical declines of the big cat population were accompanied with human encroachment, forest harvest intensification, and then the occurrence of natural disasters and conservation decision-making (Fig. S4). With the progress of conservation, some new social or ecological problems may occur. Increasing tiger-human conflicts (mainly killing livestock) also occurred simultaneously with the tiger recovery (Fig. S2b). Consequently, attention should be paid to large-scale synergistic effects between big cats or other large carnivores and human livelihoods to improve conservation and future recovery potential with sustainable forestland management. At the same time, we also should pay attention to differences in habitat and prey requirements between the two big cats. Critically endangered Amur leopards are more vulnerable while competing with sympatric Amur tigers (Jiang et al., 2015). Hence, the balanced conservation of sympatric big predator guild may be a future challenge for conservationists. The findings of this study provide great lessons of land management strategies not only for big cats, but also for other large carnivore guilds and habitat conservation under complex social and ecological synergy worldwide.

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