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Review Paper

Ecological thresholds and large carnivores conservation: Implications for the Amur tiger and leopard in China

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ABSTRACT

The ecological threshold concept describes how changes in one or more factors at thresholds can result in a large shift in the state of an ecosystem. This concept focuses attention on limiting factors that affect the tolerance of systems or organisms and changes in them. Accumulating empirical evidence for the existence of ecological thresholds has created favorable conditions for practical application to wildlife conservation. Applying the concept has the potential to enhance conservation of two large carnivores, Amur tiger and leopard, and the knowledge gained could guide the construction of a proposed national park. In this review, ecological thresholds that result from considering a paradigm of bottom-up control were evaluated for their potential to contribute to the conservation of Amur tiger and leopard. Our review highlights that large carnivores, as top predators, are potentially affected by ecological thresholds arising from changes in climate (or weather), habitat, vegetation, prey, competitors, and anthropogenic disturbances. What's more, interactions between factors and context dependence need to be considered in threshold research and conservation practice, because they may amplify the response of ecosystems or organisms to changes in specific drivers. Application of the threshold concept leads to a more thorough evaluation of conservation needs, and could be used to guide future Amur tiger and leopard research and conservation in China. Such application may inform the conservation of other large carnivores worldwide.

1. Introduction

Large carnivores are top predators that can play important roles in structuring ecosystems and regulating ecosystem function (Ripple et al., 2014). Factors such as long life histories, low population densities, low reproductive rates, and the need for large home ranges to obtain prey make large carnivores vulnerable to persecution and recovery difficult (Ripple et al., 2014). Moreover, conflicts between large carnivores and humans or livestock may impede large carnivore survival (Madden, 2008). In 2014, 61% of the world's large carnivores (average adult body masses ≥15 kg) were listed as threatened (vulnerable, endangered, or critically endangered) by the International Union for the Conservation of Nature (IUCN), and 77%

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of species were undergoing population declines (Ripple et al., 2014). Large carnivore conservation is a growing worldwide dilemma.

Amur tiger (*Panthera tigris altaica*) and leopard (*Panthera pardus orientalis*) are sympatric large carnivores distributed in northeast China and the Russian Far East. Both species are endangered and protected by the governments of China and Russia. In December 2015, the Chinese government began to design a centrally controlled national park that stretches across Heilongjiang and Jilin provinces and aims to provide a coherent management system to protect Amur tigers and leopards. There are also livestock losses and human fatalities caused by wild animals which have created economic losses and aggravated human-wildlife conflicts in this developing and populous country (Liu et al., 2011). Hence, construction of a relatively people-free national park may provide conservation measures that could benefit with other large carnivores, help reduce human-wildlife conflicts, and halt natural resource exploitation in the national park. We argue that the future outcome for the two large cats in the national park is dependent on ecological thresholds.

Within certain limits, wildlife populations and ecosystems are expected to have the flexibility to compensate for fluctuations in environmental factors to maintain population or ecosystem conditions (Vogt et al., 2015). Changes in environmental factors exceed the range that the ecosystem or wildlife populations can compensate would cause state shifts. State shifts often occur nonlinearly with rapid speed, and recovery can be challenging. The ecological threshold or tipping point concept is used to describe the maximum or minimum values of environmental factors the system could tolerate, beyond which a small change in one or more key factors would result in a rapid state change (Bennett and Radford, 2003). Sometimes, there may be multiple stable states within a range of environment conditions, and a state change could be caused by a small fluctuation at any point within this range (Scheffer and Carpenter, 2003); that is, the entire range could be treated as one or more ecological thresholds. Of particular relevance are thresholds which when crossed, lead to loss or recovery of ecosystem functions and biodiversity (Bestelmeyer, 2006). Desertification to form the Sahara Desert is a good example that illustrates this concept (Demenocal et al., 2000). Vegetation cover had fluctuated around a smoothly decreasing rainfall trend for thousands of years before it abruptly became a desert from a verdant landscape vegetated with annual grasses and shrubs between 5000 and 6000 years ago. The rapid collapse happened within decades to centuries when summer insolation crossed a threshold value of 470 W/m^2 (Demenocal et al., 2000).

Since the ecological threshold concept was introduced by May (1977), it has been repeatedly scrutinized by ecologists (Briske et al., 2006; Li and Yuan, 2017). The practical application in biological conservation and sustainable ecosystem management also has been attractive (e.g. Huggett, 2005). In general, the utilization of knowledge about ecological thresholds in conservation has been classified as helpful in four ways: (1) to define the sensitivity of a species to threatening processes, (2) to manage the tradeoffs between biodiversity conservation efforts and human activities, (3) to set targets for habitat retention, restoration and recovery, and (4) to develop landscape designs for biodiversity conservation (Huggett, 2005).

The focus of thresholds on the maximum or minimum tolerance of systems to different environmental factors or drivers makes the concept ideal for setting rules or goals for natural resource management to keep or recover environmental conditions within tolerated ranges (Choquenot and Parkes, 2001). In this sense, the ecological threshold concept corresponds well to the "ecological protection red line" emphasized by the Chinese government (Li, 2014). The red line was defined as spatial boundaries and values of managed factors that require strict implementation and relate to natural ecological services or functions, environmental quality and safety, and the utilization of natural resources (Li, 2014). The red line represents quantitative indices that, once overstepped, can cause irreversible damage. For Amur tiger and leopard conservation and construction of the proposed national park, knowledge of possible threshold effects and the identity of environmental factors involved could help in park design, institution of regulations, and conservation practices. For example, the threshold values of habitat fragmentation for Amur tiger survival and dispersal are important reference points for national park location and ecological corridor construction. Similarly, knowledge of the frequency of human activities that would cause Amur leopard to avoid areas could be used to set rules limiting these activities. Or, if we understood the snow depth threshold that, once exceeded, would cause food searching difficulties and mass mortality of ungulate prey, managers could provide supplementary feeding stations for ungulates once the critical snow depth is reached.

In this article, we examine how different forms of ecological thresholds affect Amur tiger and leopard populations and their ecosystems directly or indirectly, primarily through a perspective of bottom-up effects. We considered threshold effects that could arise from climate and weather events, habitat and anthropogenic disturbance, vegetation, prey, and competitors. Examination of which of these factors are important to conservation of the species and ecosystems, and why, allows us to provide practical answers to two overarching questions that are relevant to conservation of large carnivores around the world: 1) How to make conservation and management measures more explicit and practical for the Amur tiger and leopard, and 2) What general recommendations can be made to applying concepts about ecological thresholds to the conservation of large carnivores? We suggest that ecological thresholds research should be conducted as an important part of Amur tiger and leopard conservation and national park construction, as well as applied to large carnivore conservation in other areas.

2. Thresholds caused by climate and weather events

Climate change has drawn wide societal interest and concern. Changes in mean climate state as well as related increases in extreme events could have profound effects both on the distribution and behavior of species (Seddon et al., 2016) and on ecosystem structure and function (Doughty et al., 2015). The effects of climate change stresses on plants and their ecosystems often are nonlinear. Examples of changes include the suggestion that a global increase of temperature of 3–4 °C is predicted to

result in a rapidly increasing rate of dieback of the Amazon rainforest (Cox et al., 2004). Similarly, decreased frequency of extreme cold events is expected to cause a poleward expansion of mangroves in response to geographical shifts in the location of their minimum temperature response threshold (Cavanaugh et al., 2014).

Effects of climate change on vegetation, such as plant communities and harvesting time, are expected to affect animal communities through changes in interspecific interactions and species distributions. For example, as climate warms, thermophytes would gain an advantage in competition with cold-tolerant plants and consequently, species that consume hardy plants would be more limited than species that consume thermophilic plants. More generally, Seddon et al. (2016) used an autoregressive model to analyze the relative response rates of ecosystems to climatic variability (air temperature, water availability and cloud cover). They identified nine sensitive ecological biomes that are close to critical thresholds of climate variability for ecosystem change, including parts of the boreal forest belt worldwide that encompass Amur tiger and leopard habitats. Many of the forests in Amur tiger and leopard ranges in China are secondary or planted forests with low plant species richness, which are expected to be especially sensitive to environmental disturbance because of their species-poor communities (Lugo, 2010). Ultimately, changes in distribution and abundance of herbivores would affect higher trophic level species through the food web, ultimately, large carnivores such as the Amur tiger and leopard could be affected. Although there is no direct evidence for effects on large carnivores, the effects on species at the bottom of the food web have been studied extensively (Visser et al., 1998; Kaiser-Bunbury et al., 2017). Thus, thresholds should be further studied to learn about how much change in climate would result in forest degradation, and in turn, impact Amur tigers and leopards through their prey.

For animals, rapid temporal shifts in temperature or other environmental conditions may result in changes in daily activity patterns to match the energetic costs of different conditions (Bellard et al., 2012). Ecologists also have begun to explore effects of climate change on life-history attributes of animals, including the timing of reproduction, reproductive success, and the timing of autumn migration (Visser et al., 1998). Other studies have looked at effects on geographical distributions, species interactions (Both and Visser, 2001), and population dynamics (Pounds et al., 1999). In a meta-analysis of 694 animal and plant species, Root et al. (2003) concluded that during the last 50 years climate change caused species to show an average of 5.1 days earlier timing per decade in key phenological events. Climate change may also increase asynchrony in predator-prey systems (Parmesan, 2006), which may lead to local extinction of a predator species. For Amur tiger and leopard, the influence of climate change could be direct, or indirect, and a variety of potential mechanisms are relevant. Although long-term evolution benefits Amur tiger and leopard adapt to the cold climate, climate warming and the accompanying amount and distribution changes in precipitation and snowfall could directly change their activity patterns, reproduction timing, reproductive success, and geographical distribution. In contrast, prey condition directly determines the survival and distribution of predators. There also are direct influences of climate change on prey distributions, activity patterns, and life-history attributes which would indirectly affect the Amur tiger and leopard. Thus, climate-driven threshold effects likely are complex for Amur tigers and leopards.

Extreme climate events also may play an important role in driving ecosystems or wildlife populations to shift states (Parker et al., 1984; Visser et al., 1998). A small amount of evidence suggests that ecosystems with large predators may be particularly vulnerable to shifts resulting from extreme events. Extreme weather may destroy germinating seeds, reducing forest regeneration (Bradford, 2005), and potentially reducing the productivity of plants or creating a mismatch between peak food availability and peak food demands of the animals (Visser et al., 1998). Extreme weather such as snowstorms also may cause direct death of ungulates. It was reported that a snow depth of 40−60% of the chest height of an ungulate greatly increased the energy cost of activity, and could threaten winter survival (Parker et al., 1984). Ungulate deaths reduced the availability of prey for large carnivores and were speculated to be able to cause shifts in predator geographical distributions (Serrouya et al., 2015). For Amur tigers and leopards the potential effects of such thresholds remain unknown.

It has been predicted that, during future winters, northern China will experience greater warming than other areas, and precipitation will increase in the northern region of northeast China but decrease in the southern part of the region (Qin et al., 2006). Research on threshold effects of climate change and weather events on vegetation, ungulate populations and Amur tiger and leopard themselves could help managers adjust control strategies for human activity in response to climate-induced changes in activity patterns of wild animals (Podolski et al., 2013). Managers could also develop and apply supplementary feeding plans that extend current feeding beyond winter to include times when there is a mismatch between peak food availability and peak food demands of the animals (Visser et al., 1998). Such responses to extreme weather events may form part of a climate change adaptation strategy that benefits tigers, leopards and the whole ecosystem.

3. Thresholds due to habitat loss and anthropogenic disturbances

A specific range of conditions is needed for the daily activities (e.g., food gathering, mating) of most mammal species. In particular, large carnivores need large and relatively stable ranges, with a sufficient prey population for their survival (Powell, 2000). For Amur tigers, GPS collar data showed that the average fixed kernel range of adult female Amur tigers was as large as 401 km^2 ($\pm$205 km^2; Hernandezblanco et al., 2015). The core area of an adult female Amur leopard was estimated to be 23.3 km^2 (Rozhnov et al., 2015). Male Amur tigers and leopards usually had larger ranges than females. Learning about the minimum habitat requirements for the persistence of these two large carnivore species based on their autecology and synecology is an important first step to design a national park with sufficient habitat areas to maintain Amur tiger and leopard populations.

In general, expansion of human activities has increased habitat loss and imposed pressure on remaining habitat (Fahrig, 2001), hindering the identification of relationships between patch (or habitat) size and population persistence in wildlife conservation. Human activities have resulted in habitat fragmentation or loss directly, which is the principal contemporary threat to species persistence, and there are also simultaneous changes in the ability of populations to disperse and spread across landscapes (Fahrig, 2001, 2017). Additionally, wild animals often leave areas with human disturbance and engage in normal activities elsewhere. For instance, it was reported that red deer shied away from human facilities within a certain distance, and they preferred areas that were more than 8.2 km from villages and 1.6 km from forest roads (Jiang et al., 2007). Jiang et al. (2014) also found that the presence of the Amur tiger was seriously limited by railways built within 15 km, and the relative probability of tiger presence decreases obviously once a pixel of area 196 km^2 contained over 25% farmland in Wandashan region in Heilongjiang province. The avoidance of human disturbance accentuates habitat loss and consequently could be more impactful for survival than direct killing of wild animals (Jaeger et al., 2005). Thus, studies of habitat requirement of Amur tiger and leopard should take human disturbance into consideration. Estimating a habitat loss or fragmentation threshold is also crucial in designing a national park to maintain the Amur tiger and leopard populations.

In addition to habitat loss, human activities affect other aspects of the ecosystems at unprecedented rates (Leemans and Groot, 2003). For Amur tiger and leopard conservation, human activities not only destroy the habitat, but also could be lethal factors directly or indirectly. Hunting was the main reason leading Amur tiger and leopard to become endangered in China (Zhou, 2008), and is now banned (Forestry Ministry of China, 1992; The People's Government of Jilin Province, 2001). The survival of adult female Amur tigers is greatly influenced by the size and type of roads (Kerley et al., 2002). Livestock damaged vegetation and competed with ungulates, which decreased ungulate populations and threatened the local survival of Amur tigers and leopards (Li et al., 2016).

To better manage human activities, many researchers and managers have tried to identify the thresholds that indicate the tolerance of focal wildlife or ecosystems to human disturbance (Spooner and Allcock, 2006; Rodrigues et al., 2016). Instructive examples are provided by the use of thresholds to guide sustainable management and harvest of the frequency and intensity of human disturbances in rangeland and woodland (Spooner and Allcock, 2006). Species var in their sensitivity to human activities. Some generalist species (e.g. Black-throated Blue Warbler *Dendroica caerulescens*) which could adapt to multiple habitat types were able to tolerate 90% habitat loss, whereas species that are more sensitive (e.g. Bicknell's Thrush *Catharus ustulatus*) to anthropogenic changes could only survive in landscapes with 60% loss (Rompré et al., 2010). Although most of relative studies have focused on birds, it is clear that the sensitivity of large mammals to human interference also varies significantly (e.g. the differences in the avoidance distance of the Amur tiger and red deer to different human facilities mentioned before. Jiang et al., 2014; Jiang et al., 2007). Our recent research, which analyzed 3428 historical records of tigers from A.D. 218 to 2015, revealed the existence of a threshold effect of human population density on tiger extinction probability. Specifically, when human population density exceeded 400 persons/km^2, tigers had a local extinction probability of over 60% within a period of 50 years (unpublished data). Such basic information is critical to Amur tiger conservation in China.

4. Thresholds caused by vegetation

The importance of vegetation (both structure and composition) to animals is not only reflected in the food supply, but also affects the availability of thermal (heat) energy and cover (hiding) (Reimoser and Gossow, 1996). Hence, vegetation could drive threshold effects through various mechanisms. Effects of vegetation on herbivores and omnivores often happened when the quality and quantity of vegetation as food were too poor to support their survival. Beyond reduced survival, if vegetation quality or quantity falls below a minimum dietary requirement, consumers may cease to forage in an area, as described by the idea of a giving-up density (Brown, 1988). Additionally, herbivore diversity is often related to plant diversity, and often in nonlinear ways (Siemann et al., 1998). A more diverse consumer group is more conducive to the coexistence of Amur tigers and leopards (Richman and Lovvorn, 2009).

Providing shelter for animals is another key function of vegetation, and the number and quality of shelters the vegetation provides is often nonlinearly related with animal occurrence frequency. Smith and Long (1987) uncovered that the vegetation at a summed diameter at breast height above about 3.14 cm/m^2 or crown diameters greater than 4.75 cm/m^2 was required as hiding cover by elk (*Cervus elaphus nelsonii*) and the thermal cover requirement was more restrictive than hiding cover. For many other ungulate species, such a shelter effect was also measurable and the thresholds for hiding cover availability were smaller than those for thermal cover (Mysterud and Østbye, 1999). These studies have drawn attention to the importance of thermal and hiding cover availability for animals to resist harsh weather and avoid predation. Zemanova et al. (2017) assessed impacts of deforestation on habitat connectivity for large carnivores in tropical forests, showed that both amount of natural vegetation and habitat structure were important for jaguars (*Panthera onca*), and identified a threshold in habitat connectivity. Furthermore, consumers have to balance predation risk and foraging requirements, both of which could change prey activity patterns and food availability (Esparza-Carlos et al., 2016). This relationship would, in turn, influence the outcomes of vegetation management on large carnivores.

Vegetation is vital for the survival of herbivore prey, which strongly influence the survival of the tiger and leopard. Consequently, vegetation restoration in the ranges of Amur tiger and leopard should prioritize quantifying any threshold effects that arise through the influence of vegetation to the diversity and abundance of ungulates, and overwintering of individuals of both the ungulate prey and Amur tiger and leopard in this frigid region.

5. Thresholds of prey or herbivores

Beyond the indirect effects of vegetation on predators discussed above, predator-prey relationships have always been an important part of wildlife conservation, especially for large predators (Johnson et al., 2007). Tigers (*Panthera tigris tigris*) are known to adjust their range sizes according to prey abundance, and their density has been related to prey density (Karanth et al., 2004). Similarly, lynx (*Lynx canadensis*) in southwestern Yukon, Canada, expanded their range size from 13.2 to 39.2 km^2 when snowshoe hare (*Lepus americanus*) density declined from 14.7 to 0.2 hares/0.01 km^2 (Ward and Krebs, 1985). Some lynxes abandoned their home ranges, becoming nomadic after the density of snowshoe hares fell below 0.5 hares/0.01 km^2 (Ward and Krebs, 1985). This accords with ideas of treating giving up density as an ecological threshold (e.g. Nolet et al., 2006).

Increasing prey population density has been seen as a crucial component of large predator conservation. A study focused on the threshold effect of prey density on the interaction of two prey species, Cape buffaloes (*Syncerus caffer*) and warthogs (*Phacochoerus africanus*), and their predators, lions (*Panthera leo*) suggested that in order to attain co-existence, the buffalo population density should be maintained above half of the habitat's carrying capacity (Ddumba et al., 2012). Miller et al. (2014) advised that prey management requires insight into the minimum density required to ensure that energy requirements of predators for survival and reproduction can be met. The average successful hunt frequency of Amur tigers was one time each 6.5 days, and each individual needed to consume about 8.9 kg of prey biomass per day (Miller et al., 2013). A female individual would stop reproduction if the prey population density was less than 0.5/km^2 and prey abundance of 250−500 individual ungulates within a typical home range, although such prey numbers may sustain Amur tigers without reproduction (Li et al., 2010). Such information indicates that prey density thresholds are important for the conservation of Amur tigers and leopards, and further studies are both challenging and important.

Prey diversity also plays an important role in affecting the coexistence of different predator species (Tucker and Rogers, 2014). Prey of different sizes are available to predators of different body sizes (Dickman, 1988). Amur tigers are known to prefer wild pigs as their main prey, whereas roe deer are more likely predated by Amur leopards (Yang et al., 2018a). This difference in prey preference between Amur tiger and leopard is thought to reduce competition between these two large carnivores for food resources (Yang et al., 2018a). Moreover, spatial heterogeneity in the distribution of prey with different body sizes also facilitates prey coexistence with predators (Richman and Lovvorn, 2009), which contributes to maintaining species diversity and ecosystem stability.

In addition to their role in affecting predators based on bottom-up effects, herbivore prey also affect vegetation through top-down effects. An excessive number of herbivores, higher than the carrying capacity, can destroy the forest understory shrub layer and cause a decline in the abundance and distribution of preferred food plants (Rooney et al., 2004). To maintain biodiversity in a harvested deciduous forest, De Leo and Levin (1997) concluded a population management objective for white-tailed deer was 4 deer/km^2. For maintenance of balsam fir boreal forests in the early successional stage, Tremblay et al. (2006) estimated a compatible deer density was 7.5−15 deer/km^2. More generally, it is expected that there would be a threshold effect of herbivore density for vegetation change, and that changes in vegetation state would influence the herbivore population density, which would in turn affect predator density (Sasaki et al., 2008). Such indirect effects might explain why Qi et al. (2015) found that leopard density would decline when the total biomass of wild pig and roe deer exceeded 100−150 kg/0.25 km^2. Therefore, prey or herbivore populations should be managed to avoid too much pressure on vegetation, which could hinder the conservation of predators. A comprehensive consideration of prey diversity and abundance, bottom-up and top-down effects, makes the study of prey thresholds complex.

6. Thresholds in coexistence of the Amur tiger and leopard

As sympatric large carnivores, Amur tiger and leopard compete intensely with each other, for instance, Pianka's niche overlap index for prey resources in Russia was estimated to be as high as 0.77 (Sugimoto et al., 2016). In China, Amur tiger and leopard both prey on ungulates like wild pig, roe deer and sika deer as their main food, which consist 74% and 75% of their total food recourse respectively (Yang et al., 2018a). Because human disturbance is more serious in China than Russia, and reduces the area of habitat used by the two cat species, suitable habitat is more limited in China (Jiang et al., 2014). Competing species will avoid meeting each other, and more similar resources they share, the more exploitative competition will occur (Caro and Stoner, 2003). Amur leopards tend to use more cliffy spatial habitat components which likely helps them avoid tigers (Jiang et al., 2015), and prey preferences and temporal activity patterns are also distinct (Yang et al., 2018a, 2018b). However, this avoidance will reduce available habitat area and food resources, which could limit population recovery.

Studies in South Africa illustrate the possible consequences of competitive interactions. The minimum area required for 10 cheetah (*Acinonyx jubatus*) varied greatly given different competition pressures. It was 48−466 km^2 without other predators, whereas when with equal numbers of lions (*Panthera leo*) it was 166−2806 km^2, and when with equal numbers of leopards (*Panthera pardus*), spotted hyenas (*Crocuta crocuta*), wild dogs (*Lycaon pictus*) and lions it was 727−3739 km^2 (Lindsey et al., 2011). For sympatric large carnivores, rapid increase of one species also would be expected to intensify competition and reduce the population size of another species. Body size differences result in differences in competitive ability, and consequently the Amur leopard is expected to be a weaker competitor than the Amur tiger. Tigers occasionally also will kill leopards. Accordingly, it was found that as Indian tiger density increased from 3.31/100 km^2 to 5.81/100 km^2, the diet of leopards showed an obvious shift and population densities declined sharply in some areas (Harihar et al., 2011). However, competitive interactions could change, if resources benefit the leopard. In fact, we have found that in some of the areas where

Amur tigers and leopards coexist, leopard abundance is higher than tiger abundance, which may occur because the local terrain is more adaptive for leopard (Qi et al., 2015).

Based on this and what we know about competitive dominance, we would expect that population increases of Amur tiger would cause Amur leopards to leave the area. Consequently, managers could take steps to create more leopard preferred micro-habitats or promote the spread of leopard individuals to other areas once tiger population densities increase. Furthermore, if we knew what value the niche overlap index of food would reach, meaning that it might be possible for one of these two predators to go extinct above this overlap (threshold) value, then we could adjust or manipulate the composition and density of preferred prey in advance to facilitate coexistence.

7. Future challenges in threshold research and applications to conservation

With the development of the ecological threshold concept, many methods also have been developed to detect threshold values. Traditional methods like the disjointed broken stick model (dBS), the hockey stick model (HS), the step function model (SF) are still widely used, but as they can often produce a change point even when a threshold does not exist, evaluating multiple alternative models is important to detect a reliable threshold (Qian, 2014). GAMs (Generalized Additive Models) are a popular method to model nonlinear relationships among variables, and Ciannelli et al. (2004) applied them to threshold detection in a method they called TGAM (T stands for "threshold Interaction"). The quickest detection method, a Bayesian approach is also very useful method and has been widely used (Carpenter et al., 2014; Cappa and Varona, 2013). With the development of statistical methods, many software packages have also been developed, which are listed partially by Andersen et al. (2009). Although most of the aforementioned methods consider only the detection of threshold effects between a single response variable and single independent variable, Baker and King (2010) introduced a method Threshold Indicator Taxa ANalysis (TITAN) to detect community thresholds by assessing the synchrony of taxa change points to the same driver. In fact, few variables are expected to work in isolation in nature, and the outcomes of single independent variable models are often unreliable and even misleading, which could result in a failure of protection practices (Huggett, 2005). This is also the main reason some ecologists are skeptical about ecological thresholds and points to the need to consider multiple responses and drivers (Huggett, 2005).

As illustrated by the foregoing discussion and published literature, threshold responses are often caused by several interacting factors rather than one particular driver (van der Ree et al., 2004; Huggett, 2005). For example, climate change may influence the food availability and then influence the density and distribution of animals (Both et al., 2006). Species interactions are also directly affected by climate change (Tylianakis et al., 2008). Determining threshold range sizes for predator persistence may be misconstrued because of habitat fragmentation, competitors, climate change, and the availability of prey. None of these factors are independent from human activities. The potentially confounding effect of multiple interacting variables produces complex threshold responses, making threshold identification much more difficult (Bennett and Radford, 2003). Today, the popular approach to take the interaction between variables in threshold detection is to analyze the threshold effect of variation in one variable under different gradients of another variable (Suding and Hobbs, 2009). Developing new and improved methods for detecting threshold values in the case of interaction of multiple environmental variables will greatly aid the development of threshold theory and its application to conservation and management.

Interactions between variables also make the application of thresholds context-dependent. For instance, it would be misleading to extrapolate the threshold values of minimum habitat area for Amur tiger survival in pristine habitats to landscapes where human activity, habitat fragmentation, low prey abundance or other factors affect the habitat utilization of Amur tigers. Because of temporal and spatial variation in these processes and characteristics, there is not a threshold value that is universally applicable (Huggett, 2005). We therefore argue that ecological threshold studies should focus on a specific limited area and that limiting factors should be studied integrally to find those relevant to each step of conservation and management.

The construction of a national park for tiger and leopard conservation aims to restore populations of these two species and the whole ecosystem. It requires a huge investment of money, and natural and human resources, the ongoing enhancement and expansion of human activities and huge costs raise more challenges. We believe that thresholds could be an appropriate tool to realize efficient conservation with limited resources under some conditions. For instance, knowing the minimum forest habitat area required to ensure the survival and coexistence of Amur tigers and leopards could avoid allocating so much land for conservation that it creates a conflict with resource extraction needs and necessitates more human migration out of areas to be conserved. Maintaining human disturbances under threshold values in key habitat patches and corridors areas could be used to maintain an extensively permeable habitat landscape for the dispersal of large predators (Chapron et al., 2014). Furthermore, threshold knowledge provides quantitative indicators for developing reasonable objectives and measures to manage the habitat, vegetation and prey population. Amur tiger and leopard national park construction represents a good opportunity to practice such information and methods, knowledge of the mechanisms of biome resilience from threshold study would finally benefit to the construction.

A sequence of next steps is sensible for research and applications of threshold ideas to Amur tiger and leopard conservation, as well as other large carnivore species. First, we should have a map of bottom-up effects in their habitat landscape and consider all of the relevant drivers for a particular area and situation. These drivers include climate and weather events, habitat loss and other anthropogenic disturbances, vegetation, prey, and intraguild competition between the two predators. Consideration of both direct and indirect effects is important, such that vegetation will not only provide shelter for predators
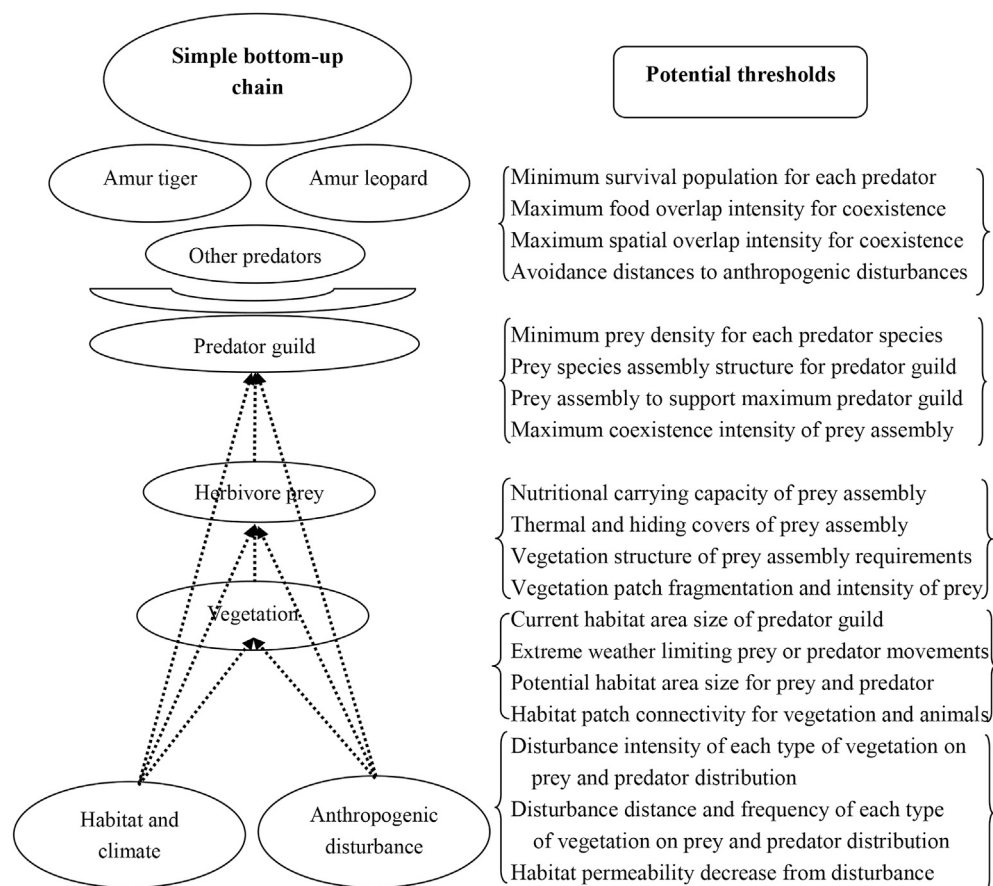
Fig. 1. Some potential thresholds, summarized in a simple bottom-up chain for large carnivores conservation.

directly but also provide food for prey survival, which indirectly benefits the predators. A next logical step would be to attempt to identify key factors that could influence or alter the condition of species of concern. The final step is to detect if these factors, and their interactions, exhibit threshold responses and what are the threshold values (Fig. 1). Regardless of the extent to which the ambitious agenda for research and conservation can be conducted, applying theory and thinking about thresholds can make conservation policy and practices more complete. Threshold research should be a regular content of the national park construction and be executed throughout the Amur tiger and leopard conservation.

Declaration of competing interest

This manuscript is not published and is not being considered for publication elsewhere. All authors agree with the contents of our manuscript and its submission to Global Ecology and Conservation, and declare no conflict of interest.

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Appendix A. Supplementary data

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References

Andersen, T., Carstensen, J., Hernández-García, Emilio, Duarte, C.M., 2009. Ecological thresholds and regime shifts: approaches to identification. Trends Ecol. Evol. 24 (1), 0–57.

Baker, M.E., King, R.S., 2010. A new method for detecting and interpreting biodiversity and ecological community thresholds. Methods Ecol. Evol. 1 (1), 25–37.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15 (4), 365–377.

Bennett, A.F., Radford, J.Q., 2003. Know your ecological thresholds. Think. Bush (2), 1–3.

Bestelmeyer, B.T., 2006. Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious. Restor. Ecol. 14 (3), 325–329.

Both, C., Visser, M.E., 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411, 296–298.

Both, C., Bouwhuis, S., Lessells, C.M., Visser, M.E., 2006. Climate change and population declines in a long-distance migratory bird. Nature 441 (7089), 81–83.

Bradford, K.J., 2005. Threshold models applied to seed germination ecology. New Phytol. 165 (2), 338–341.

Briske, D.D., Fuhlendorf, S.D., Smeins, F.E., 2006. A unified framework for assessment and application of ecological thresholds. Rangel. Ecol. Manag. 59 (3), 225–236.

Brown, J.S., 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behav. Ecol. Sociobiol. 22 (1), 37–47.

Cappa, E.P., Varona, L., 2013. An assessor-specific bayesian multi-threshold mixed model for analyzing ordered categorical traits in tree breeding. Tree Genet. Genomes 9 (6), 1423–1434.

Caro, T.M., Stoner, C.J., 2003. The potential for interspecific competition among african carnivores. Biol. Conserv. 110 (1), 0–75.

Carpenter, S.R., Brock, W.A., Cole, J.J., Pace, M.L., 2014. A new approach for rapid detection of nearby thresholds in ecosystem time series. Oikos 123 (3), 290–297.

Cavanaugh, K.C., Kellner, J.R., Forde, A.J., Gruner, D.S., Parker, J.D., et al., 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. Proc. Natl. Acad. Sci. U.S.A. 111 (2), 723–727.

Chapron, G., Kaczensky, P., Linnell, J.D., von Arx, M., Huber, D., et al., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346, 1517–1519.

Choquenot, D., Parkes, J., 2001. Setting thresholds for pest control: how does pest density affect resource viability? Biol. Conserv. 99 (1), 29–46.

Ciannelli, L., Chan, K.S., Bailey, K.M., Stenseth, N.C., 2004. Nonadditive effects of the environment on the survival of a large marine fish population. Ecology 85 (12), 3418–3427.

Cox, P.M., Betts, R.A., Collins, M., Harris, P.P., Huntingford, C., et al., 2004. Amazonian forest dieback under climate-carbon cycle projections for the 21st century. Theor. Appl. Climatol. 78 (1–3), 137–156.

Ddumba, H., Mugisha, J.Y.T., Gonsalves, J., Kerley, G.I.H., 2012. The role of predator fertility and prey threshold bounds on the global and local dynamics of a predator–prey model with a prey out-flux dilution effect. Appl. Math. Comput. 218 (18), 9169–9186.

De Leo, G.A., Levin, S., 1997. The multifaceted aspects of ecosystem integrity. Conserv. Ecol. 1 (1), 3.

Demenocal, P., Ortiz, J., Guilderson, T., Adkins, J., Sarnthein, M., et al., 2000. Abrupt onset and termination of the african humid period: rapid climate responses to gradual insolation forcing. Quat. Sci. Rev. 19 (1–5), 0–361.

Dickman, C.R., 1988. Body size, prey size, and community structure in insectivorous mammals. Ecology 69 (3), 569–580.

Doughty, C.E., Metcalfe, D.B., Girardin, C.A.J., Amézquita, F.F., Cabrera, D.G., et al., 2015. Drought impact on forest carbon dynamics and fluxes in Amazonia. Nature 519 (7541), 78–82.

Esparza-Carlos, J.P., Laundré, J.W., Hernández, L., Dávalos, L.I.I., 2016. Apprehension affecting foraging patterns and landscape use of mule deer in arid environments. Z. Saugetierkd 81 (6), 543–550.

Fahrig, L., 2001. How much habitat is enough? Biol. Conserv. 100 (1), 65–74.

Fahrig, L., 2017. Ecological responses to habitat fragmentation per se. Annu. Rev. Ecol. Evol. Syst. 48 (1) annurev-ecolsys-110316-022612.

Forestry Ministry of China, 1992. Regulations of the People's Republic of China on the implementation of terrestrial wildlife protection. Chin. J. Zool. (4), 16–20 (in Chinese).

Harihar, A., Pandav, B., Goyal, S.P., 2011. Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. J. Appl. Ecol. 48 (3), 806–814.

Hernandezblanco, J.A., Naidenko, S.V., Chistopolova, M.D., Lukarevskiy, V.S., Kostyrya, A., et al., 2015. Social structure and space use of amur tigers (*panthera tigris altaica*) in southern Russian far east based on gps telemetry data. Integr. Zool. 10 (4), 365–375.

Huggett, A.J., 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. Biol. Conserv. 124 (3), 301–310.

Jaeger, J.A.G., Bowman, J., Brennan, J., Fahrig, L., Bert, D.G., et al., 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecol. Model. 185 (2), 329–348.

Jiang, G., Qi, J., Wang, G., Shi, Q., Darman, Y., et al., 2015. New hope for the survival of the amur leopard in China. Sci. Rep. 5, 15475.

Jiang, G., Sun, H., Lang, J., Yang, L., Li, C., et al., 2014. Effects of environmental and anthropogenic drivers on Amur tiger distribution in northeastern China. Ecol. Res. 29 (5), 801–813.

Jiang, G., Zhang, M., Ma, J., 2007. Effects of human disturbance on movement, foraging and bed selection in red deer *Cervus elaphus xanthopygus* from the Wandashan Mountains, northeastern China. Acta Theriol. 52 (4), 435–446.

Johnson, C.N., Isaac, J.L., Fisher, D.O., 2007. Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. Proc. Roy. Soc. Lond. B Biol. 274 (1608), 341–346.

Kaiser-Bunbury, C.N., Mougal, J., Whittington, A.E., Valentin, T., Gabriel, R., et al., 2017. Ecosystem restoration strengthens pollination network resilience and function. Nature 542 (7640), 223.

Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A., Hines, J.E., 2004. Tigers and their prey: predicting carnivore densities from prey abundance. Proc. Natl. Acad. Sci. U.S.A. 101 (14), 4854–4858.

Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B., Hornocker, M.G., 2002. Effects of roads and human disturbance on amur tigers. Conserv. Biol. 16 (1), 97–108.

Leemans, H.B.J., Groot, R.S.D., 2003. Millennium ecosystem assessment: ecosystems and human well-being: a framework for assessment. Phys. Teach. 34 (9), 534-534.

Li, C.G., Yuan, Z., 2017. Research development and application in ecological threshold. J. Hebei For. Sci. Technol. 3, 54–57 (in Chinese).

Li, G., 2014. "ecological protection red line"- the lifeline to ensure the national ecological security. Qiushi (2), 44–46 (in Chinese).

Li, Z., Kang, A., Gu, J., Xue, Y., Ren, Y., et al., 2016. Effects of human disturbance on vegetation, prey and Amur tigers in hunchun nature reserve, China. Ecol. Model. 353, 28–36, 2017.

Li, Z., Zimmermann, F., Hebblewhite, M., Purekhovsky, A., Mörschel, F., et al., 2010. Study on the Potential Tiger Habitat in the Changbaishan Area. China Forestry Publishing House, China. Beijing.

Lindsey, P., Tambling, C.J., Brummer, R., Davies-Mostert, H.T., Hayward, M.W., et al., 2011. Minimum prey and area requirements of the vulnerable cheetah *Acinonyx jubatus*: implications for reintroduction and management of the species in South Africa. Oryx 45 (04), 587–599.

Liu, F., Mcshea, W.J., Garshelis, D.L., Zhu, X., Wang, D., Shao, L., 2011. Human-wildlife conflicts influence attitudes but not necessarily behaviors: factors driving the poaching of bears in China. Biol. Conserv. 144 (1), 538–547.

Lugo, A.E., 2010. Visible and invisible effects of hurricanes on forest ecosystems: an international review. Austral Ecol. 33 (4), 368–398.

Madden, F.M., 2008. The growing conflict between humans and wildlife: law and policy as contributing and mitigating factors. J. Int. Wildl. Law Policy 11, 189–206.

May, R.M., 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269 (5628), 471–477.

Miller, C.S., Hebblewhite, M., Petrunenko, Y.K., Seryodkin, I.V., DeCesare, N.J., et al., 2013. Estimating amur tiger (*panthera tigris altaica*) kill rates and potential consumption rates using global positioning system collars. J. Mammal. 94 (4), 845–855.

Miller, C.S., Hebblewhite, M., Petrunenko, Y.K., Seryodkin, I.V., Goodrich, J., et al., 2014. Amur tiger (*Panthera tigris altaica*) energetic requirements: implications for conserving wild tigers. Biol. Conserv. 170, 120–129.

Mysterud, A., Østbye, E., 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. Wildl. Soc. Bull. 27 (2), 385–394, 1973-2006.

Nolet, B.A., Fuld, V.N., Van Rijswijk, M.E.C., 2006. Foraging costs and accessibility as determinants of giving-up densities in a swan-pondweed system. Oikos 112 (2), 353–362.

Parker, K.L., Robbins, C.T., Hanley, T.A., 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manag. 474–488.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37 (1), 637–669.

Podolski, I., Belotti, E., Bufka, L., Reulen, H., Heurich, M., 2013. Seasonal and daily activity patterns of free-living Eurasian lynx Lynx lynx in relation to availability of kills. Wildl. Biol. 19 (1), 69–77.

Pounds, J.A., Fogden, M.P.L., Campbell, J.H., 1999. Biological response to climate change on a tropical mountain. Nature 398 (6728), 611–615.

Powell, R.A., 2000. Animal home ranges and territories and home range estimators. In: Pearl, M.C., Boitani, L., Fuller, T.K. (Eds.), Research Techniques in Animal Ecology: Controversies and Consequences. Colombia University Press, Cambridge, pp. 64–110.

Qian, S.S., 2014. Ecological threshold and environmental management: a note on statistical methods for detecting thresholds. Ecol. Indicat. 38, 192–197.

Qi, J., Shi, Q., Wang, G., Li, Z., Sun, Q., et al., 2015. Spatial distribution drivers of Amur leopard density in northeast China. Biol. Conserv. 191, 258–265.

Qin, D., Ding, Y., Su, J., 2006. Assessment of climate and environment changes in China (i): climate and environment changes in China and their projection. Adv. Clim. Change Res. 2, 1–05 (in Chinese).

Reimoser, F., Gossow, H., 1996. Impact of ungulates on forest vegetation and its dependence on the silvicultural system. For. Ecol. Manag. 88 (1), 107–119.

Richman, S.E., Lovvorn, J.R., 2009. Predator size, prey size and threshold food densities of diving ducks: does a common prey base support fewer large animals? J. Anim. Ecol. 78 (5), 1033–1042.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., et al., 2014. Status and ecological effects of the world's largest carnivores. Science 343 (6167), 1241484.

Rodrigues, M.E., Roqueb, F.O., Quintero, J.M.O., Pena, J.C.C., Sousa, D.C., et al., 2016. Nonlinear responses in damselfly community along a gradient of habitat loss in a savanna landscape. Biol. Conserv. 194, 113–120.

Rompré, G., Boucher, Y., Bélanger, L., Côté, S., Robinson, W.D., 2010. Conserving biodiversity in managed forest landscapes: the use of critical thresholds for habitat. For. Chron. 86 (5), 589–596.

Rooney, T.P., Wiegmann, S.M., Rogers, D.A., Waller, D.M., 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. Conserv. Biol. 18 (3), 787–798.

Root, B.A., Price, J.T., Hall, K., 2003. Fingerprints of global warming on wild animals and plants. Nature 421, 47–60.

Rozhnov, V.V., Chistopolova, M.D., Lukarevskii, V.S., Hernandez-Blanco, J.A., Naidenko, S.V., et al., 2015. Home range structure and space use of a female amur leopard, *panthera pardus orientalis*, (carnivora, felidae). Biol. Bull. (Woods Hole) 42 (9), 821–830.

Sasaki, T., Okayasu, T., Undarmaa, J., Taheuchi, K., 2008. Threshold changes in vegetation along a grazing gradient in Mongolian rangelands. J. Ecol. 96 (1), 145–154.

Scheffer, M., Carpenter, S.R., 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol. Evol. 18 (12), 648–656.

Seddon, A.W.R., Macias-Fauria, M., Long, P.R., Benz, D., Willis, K.J., 2016. Sensitivity of global terrestrial ecosystems to climate variability. Nature 531 (7593), 229–232.

Serrouya, R., Wittmann, M.J., McLellan, B.N., Wittmer, H.U., Boutin, S., 2015. Using predator-prey theory to predict outcomes of broadscale experiments to reduce apparent competition. Am. Nat. 185 (5), 665–679.

Siemann, E., Tilman, D., Haarstad, J., Ritchie, M., 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. Am. Nat. 152, 738–750.

Smith, F.W., Long, J.N., 1987. Elk hiding and thermal cover guidelines in the context of lodgepole pine stand density. West. J. Appl. For. 2 (1), 6–10.

Spooner, P.G., Allcock, K.G., 2006. Using a state-and-transition approach to manage endangered *Eucalyptus albens* (White Box) woodlands. Environ. Manag. 38 (5), 771–783.

Suding, K.N., Hobbs, R.J., 2009. Threshold models in restoration and conservation: a developing framework. Trends Ecol. Evol. 24 (5), 0–279.

Sugimoto, T., Aramilev, V.V., Nagata, J., McCullough, D.R., 2016. Winter food habits of sympatric carnivores, Amur tigers and Far Eastern leopards, in the Russian Far East. Z. Saugetierkd 81 (2), 214–218.

The People's Government of Jilin Province, 2001. Implementation Measures for Prohibiting Hunting for Terrestrial Wild Animals in Jilin Province, vol. 20. Gazette of the people's government of Jilin Province (in Chinese).

Tremblay, J.P., Huot, J., Potvin, F., 2006. Divergent nonlinear responses of the boreal forest field layer along an experimental gradient of deer densities. Oecologia 150 (1), 78–88.

Tucker, M.A., Rogers, T.L., 2014. Examining the prey mass of terrestrial and aquatic carnivorous mammals: minimum, maximum and range. PLoS One 9 (8), e106402.

Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. Ecol. Lett. 11 (12), 1351–1363.

van der Ree, R., Bennett, A.F., Gilmore, D.C., 2004. Gap-crossing by gliding marsupials: thresholds for use of isolated woodland patches in an agricultural landscape. Biol. Conserv. 115 (2), 241–249.

Visser, M.E., Van Noordwijk, A.J., Tinbergen, J.M., Lessells, C.M., 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proc. Roy. Soc. Lond. B Biol. 265 (1408), 1867–1870.

Vogt, N.D., Pinedo-Vasquez, M., Brondã-Zio, E.S., Almeida, O., Rivero, S., 2015. Forest transitions in mosaic landscapes: smallholder''s flexibility in land-resource use decisions and livelihood strategies from world war ii to the present in the amazon estuary. Soc. Nat. Resour. 28 (10), 1043–1058.

Ward, R.M.P., Krebs, C.J., 1985. Behavioural responses of lynx to declining snowshoe hare abundance. Can. J. Zool. 63 (12), 2817–2824.

Yang, H., Dou, H., Baniya, R.K., Han, S., Guan, Y., et al., 2018a. Seasonal food habits and prey selection of Amur tigers and Amur leopards in northeast China. Sci. Rep. 8 (1), 6930.

Yang, H., Zhao, X., Han, B., Wang, T., Mou, P., et al., 2018b. Spatiotemporal patterns of Amur leopards in northeast China: influence of tigers, prey, and humans. Mamm. Biol. S1616504717302859.

Zemanova, M.A., Perotto-Baldivieso, H.L., Dickens, E.L., Gill, A.B., Leonard, J.P., Wester, D.B., 2017. Impact of deforestation on habitat connectivity thresholds for large carnivores in tropical forests. Ecol. Process. 6 (1), 21.

Zhou, X., 2008. Protection status of wild Amur tiger (*panthera tigris altaica*) and their conservation strategy. Chin. J. Wildl. 29 (1), 40–43 (in Chinese).