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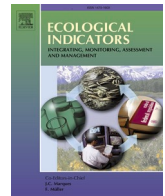
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Original Articles

Regime shift in the interaction between domestic livestock and the deer-tiger food chain

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ABSTRACT

The effects of grazing on wildlife have received considerable attention. Depending on factors such as its intensity and duration, grazing can impact higher-level species along the food chain through competition for available resources with wild herbivores. However, relatively few studies have investigated whether there are tipping points at which grazing intensity begins to seriously impact wildlife. In particular, studies that assess the impact of overgrazing on food chains that include carnivores remain scarce. We developed a time dynamic, age-structured model for the wild ungulates-Amur tiger trophic chain, including cattle grazing as a disturbance. We explored 1) the impact of cattle grazing intensity on the long-term behaviour of the wildlife population; 2) the effect of demographic parameters on wildlife population viability; and 3) the temporal dynamic impact of periods of heavy grazing on the population trajectory. Our results showed that increasing cattle density reaches a tipping point, triggering a rapid and significant shift in wildlife population size. Below the tipping point, wildlife can coexist with grazing livestock; when cattle density exceeds the tipping point, wild ungulate and tiger populations move towards extinction. In the case of heavy grazing, the dynamics of the wild ungulate population was more affected by its intensity, and the dynamics of the Amur tiger population was more affected by its duration. Our model and results suggest that theoretically wildlife conservation and cattle production can coexist but that serious regime shifts in wildlife populations may occur if grazing intensity exceeds a tipping point. These findings provide new insights useful for developing policies related to balancing livestock and wildlife conservation.

1. Introduction

Grazing from domestic cattle can strongly influence plant communities and ecosystem processes in a variety of habitats by altering vegetation composition and productivity and species diversity (Liu et al., 2015). Herbivory, especially when it involves large herbivores such as domestic cattle, tends to reduce aboveground primary productivity (Frank et al., 2018), homogenize the natural variability of grasslands upon which wildlife populations depend (Fuhlendorf & Engle, 2001) and force wild ungulates to shift their distribution to less preferred habitats (Schielz & Rubenstein, 2016). The continued increase in the demand for milk and meat, especially beef, worldwide in recent decades has led to a dramatic increase in cattle grazing (Bai et al., 2018). Beef production has become a major driver of biodiversity loss globally (Selinske et al., 2020). For example, in Indonesia, cattle grazing has had

a significant negative impact on the occupancy of carnivores and their ungulate prey in protected areas (Pudyatmoko, 2017), and in grazed areas of Iran, large carnivores and herbivores have even disappeared (Soofi et al., 2018). In particular, the disturbance caused by excessive cattle grazing limits the survival and spread of wild cervids due to depredation of available vegetation resources in understory (Wang et al., 2017), and the continuing decrease in the density of key ungulate prey species may be one of the major threats to the survival of large carnivores in many areas (Sandom et al., 2018). In turn, the loss of the top carnivores in the food chain might also initiate unexpected cascading effects throughout the entire chain (Estes et al., 2011), potentially leading to its collapse.

While overgrazing is argued to enhance vegetation destruction and regime shifts in unbalanced ecosystems (Wright, 2017), multiple studies have shown that cattle grazing might stimulate aboveground production

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(McNaughton, 1985; Odadi et al., 2011), maintain and create habitat heterogeneity (Veblen & Young, 2010). When properly managed, livestock can even be used as a tool to manage rangelands in a way that increases ecosystem health or wildlife habitat (Augustine et al., 2011; Keesing et al., 2018; Keesing et al., 2018; Welsh et al., 2018), which means under mild to moderate grazing regimes, domestic herbivores may not have negative effects on native wildlife populations and may even have a positive effect. This supports the view that grazing by domestic cattle can co-exist or not with wildlife depending on its quantity (Bestelmeyer et al., 2018; Krausman et al., 2009). Tipping points might separate grazing pressures that can co-exist with the grassland-based trophic chain with grazing pressures that lead to the collapse of the ecosystem (Ims et al., 2008; Ims & Fuglei, 2005). For example, threshold-crossing events related to cattle grazing influence on ecosystems were documented in the historical records of New Zealand (Parsons & Nalau, 2016; Whitehead et al., 2014) and western North America (Loeser et al., 2007; Morris & Rowe, 2014) due to the introduction of livestock.

On the China-Russia border, wildlife, especially the large endangered species Amur tiger (*Panthera tigris altaica*), is facing a threat as a consequence of overgrazing (Wang et al., 2017). Conservation of endangered large carnivores such as Amur tiger and other species that require large home range and intact food chains, requires the establishment of large protected areas and national parks (Goheen, 2018). However, due to the limited extension of protected areas, managers have to consider including human-occupied landscapes as supplementary conservation venues (Western, Russell, et al., 2009; Woodroffe & Ginsberg, 1998). With the establishment of the Northeast Tiger and Leopard National Park (hereinafter referred to as the NTLNP) in northeastern China, the transboundary Amur tiger subpopulation in the Changbai Mountains along the China-Russia border has gradually increased to approximately 40 individuals and has begun to extend its distribution into China (Feng et al., 2017; Hebblewhite et al., 2014; Wang et al., 2016). However, cattle grazing is a mainstay of the local industry. In particular, in the Changbai Mountains, cattle grazing has been increasing over the past 30 years (Wang et al., 2016). Throughout the yearly growing season, cattle are left unattended, freely roaming across the national park, competing with other herbivores for understory resources. This competition not only influences the growing season but also results in a shortage of food resources during the non-growing season. The pressures caused by free-ranging cattle on sympatric wild herbivores such as sika deer (*Cervus nippon*) is particularly acute (Feng et al., 2021b). Because the distributions of tigers and their territory are closely associated with those of their principal prey (Karanth et al., 2004; Miquelle et al., 2010), grazing can have a cascading effect throughout the food chain by altering the abundance of the prey on which Amur tigers subsist (Schlietz & Rubenstein, 2016). This effect is considered to limit the further expansion of the Amur tiger population in the Changbai Mountains (Feng et al., 2021a; Feng et al., 2021b), and rational management of cattle grazing in this area is therefore urgently required.

Finding the tipping points in grazing systems and the mechanisms behind, investigating the relationship between grazing, key prey (sika deer), and top predators (Amur tigers), and assessing the threats of overgrazing and undesired regime shifts are pressing needs. Exploring the possibility of coexistence between grazing cattle and wildlife conservation and the theory of food chain collapse due to overgrazing are key to softening the conflict between livestock production and nature conservation. Most existing studies on this topic have examined the structure of rangeland or the species abundance of wildlife by comparing grazed vs. ungrazed conditions (Schlietz & Rubenstein, 2016; Wells et al., 2022). Due to the absence of long-term continuous field data and experiments, modelling has become a central tool that is used in most of the work that explores the impact of grazing (Koch et al., 2008; Scheffer et al., 2001). For example, Brierley et al. (2018) used a climate-vegetation model to demonstrate that pastoralism has slowed the

deterioration in vegetation caused by climate change, and Kowal et al. (2019) used a coupled forage-grazer model to predict the viability of livestock production and herbivorous wildlife habitat. However, the effects of grazing not only impact herbivorous wildlife but are also transmitted through the food chain to higher trophic levels. There are few current studies that examine the dynamics of herbivore-large predator populations under disturbances caused by different grazing intensities in a food chain.

In this study, we explored the following research questions. (1) Is there a tipping point of cattle grazing intensity that leads to a shortage of food resources for deer and that in turn causes regime shifts in the ungulate-tiger food chain? (2) What are the demographic parameter values that allow involved populations to remain viable? (3) How would the temporal dynamics of tiger and deer populations be affected by grazing impulse perturbations of various intensities and durations? To address these questions, we developed a multispecies mathematical model of population dynamics. In this work, questions (1) and (2) are addressed via the numerical exploration of the long-term (regime) behaviour of the model, and question (3) is addressed through analysis of the time trajectories of perturbed population dynamics.

2. Materials and methods

2.1. Study area

Our study area covers the entire NTLNP in China and the Land of Leopards National Park in Russia, a total area of 18,000 km² (Fig. 1). At least 38 Amur tigers have been identified in this area in total (Feng et al., 2017). The density of sika deer, in the core range of the Amur tiger is 0.58 ± 0.11 individuals/km² (Xiao, 2014). The elevation of the rugged landscape ranges from 5 m to 1477 m, and the area has a temperate continental monsoon climate that supports a temperate coniferous broad-leaved mixed forest. Due to long-term deforestation, many low-elevation forests in these areas have been transformed into secondary deciduous forests (Wang et al., 2016). The main prey species of Amur tigers in this area are sika deer, wild boar (*Sus scrofa*) and Siberian roe deer (*Capreolus pygargus*) (Kerley et al., 2015). The area has been subjected to cattle grazing, particularly on the Chinese side (Feng et al., 2021b). The grazing pressure has steadily increased over the past three decades, reaching an average grazing density of 8 individuals/km² and even 11 individuals/km² in heavily grazed areas (Li et al., 2016). During this period, cattle were observed to be left unattended, roaming freely from spring to fall (April to October) in this area (Wang et al., 2016).

2.2. Model framework

The aim of the proposed model is to describe the ecological processes that are most relevant to the interaction between grazing cattle and the wild ungulates-Amur tiger trophic chain. The model is time-discrete and spatially implicit (populations are described in terms of density per unit area). The parameters mainly refer to populations in NTLNP. The state variables are the density of Amur tigers and sika deer by age and status (e.g., pregnant females); the density of grazing cattle is not considered a state variable because it is not part of the food chain dynamics but is considered a parameter that we varied to study the response of the food chain variables.

The core range of the Amur tiger along the China-Russia border overlaps highly with that of the sika deer (Dou et al., 2019), and the sika deer is the dominant species in the core range of the Amur tiger and has a high density (Xiao, 2014) (Table S7). In addition to the sika deer, there are other ungulates herbivores in the area, mostly wild boars and roe deer, which supplement the Amur tigers' predation on the sika deer and need to be taken into account in the model. So, to more clearly demonstrate the dynamics between ungulates and Amur tigers, we transformed wild boar and roe deer by body weight (Table S2) to sika deer, with a transformation relationship of 1:1 for wild boar to sika deer

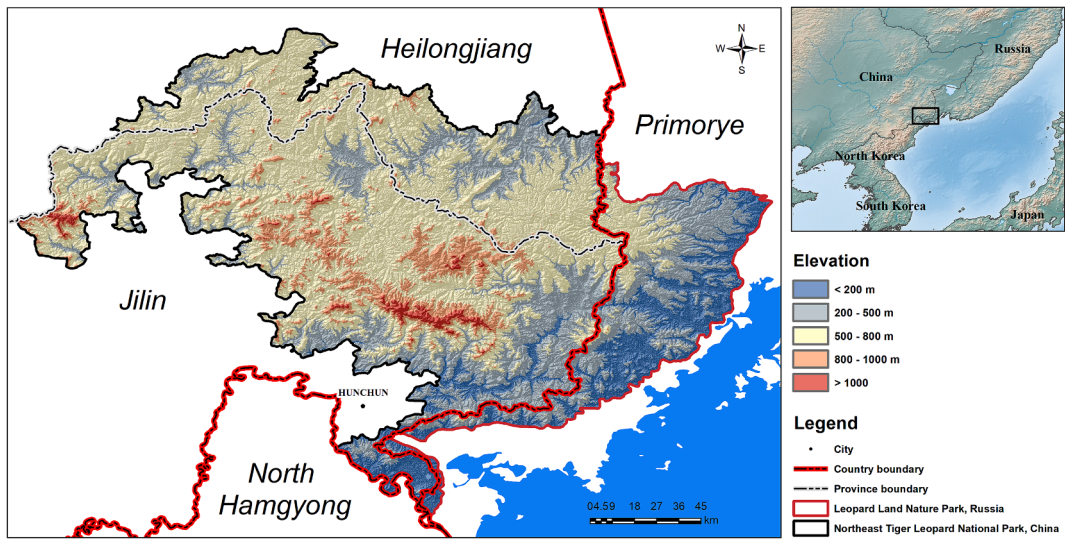


Fig. 1. Map of study area.

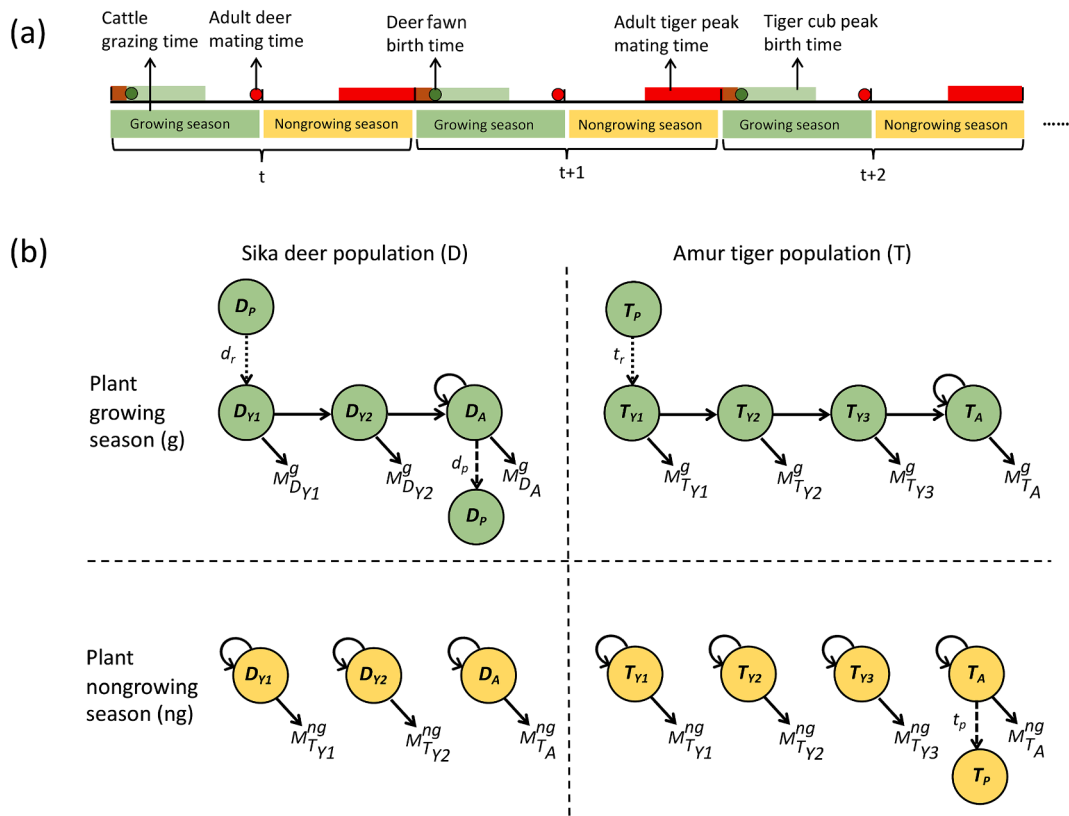


Fig. 2. Life-cycle graphs of sika deer and Amur tiger populations. Panel (a) shows the timing of pregnancy and births of female sika deer and Amur tigers. The red and green bars at the top represent the peak mating and birth times, respectively, of tigers, and the red and green dots represent the mating and birth times, respectively, of deer. Panel (b) shows the life cycles of deer (left) and tigers (right). The sika deer population is divided into three age classes: D_{Y1} includes fawns (animals ≤ 1 year old), D_{Y2} includes subadults (1 year old $<$ animals ≤ 2 years old), and D_A includes adults (animals > 2 years old). The Amur tiger population is divided into four age classes: T_{Y1} includes cubs (animals ≤ 1 year old), T_{Y2} includes juveniles (1 year old $<$ animals ≤ 2 years old), T_{Y3} includes subadults (2 years old $<$ animals ≤ 3 years old), and T_A includes adults (animals > 3 years old). The solid line in Panel (b) represents the direct transitions of individuals among age classes; the dashed line represents the temporary division of pregnant females from adults, and the dotted line represents the movement of the offspring of pregnant females into the cub/fawn class. D_P and T_P represent pregnant females in the deer and tiger populations, respectively. d_p and t_p are the pregnancy probabilities of deer and tiger, respectively. d_r and t_r are the successful reproduction rates of deer and tiger, respectively. M_X^g and M_X^{ng} represent individuals who died in different age classes during the growing and nongrowing seasons, respectively; the arrows starting and arriving at the same age class represent survival and have a probability equal to $1 - M_X^g$ and $1 - M_X^{ng}$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and 3:1 for roe deer to sika deer. Densities of each ungulate species were derived from camera monitoring data of NTLNP (Table S7).

Because vegetation biomass availability and life-cycle-related events of the species considered vary with season (Odadi et al., 2011), we considered seasonal time steps characterized by different dynamics (Fig. 2). The first season is the *plant growing season* (May to October, hereinafter referred to as the *growing season*, symbol *g*); the second season is the *plant nongrowing season* (November to April, hereinafter referred to as the *nongrowing season*, symbol *ng*). During the growing season, there is sufficient plant biomass to permit grazing, and farmers drive their cattle into the wildlife protection areas during this season (Wang et al., 2016) (Fig. 2a). As in the model of Accatino & De Michele (2013), each time step represents one year, and each step is partitioned into two sub-steps representing the two seasons.

Because sika deer and Amur tigers reach sexual maturity at 3 and 4 years of age respectively, and the biological characteristics of individuals of different ages prior to adulthood differ from those of adult individuals, we divided the populations into age classes. The sika deer population was divided into 3 age classes: D_{Y1} (fawns, *i.e.*, animals ≤ 1 year of age); D_{Y2} (subadults, *i.e.*, animals between 1 and 2 years of age); and D_A (adults, *i.e.*, those > 2 years of age). The Amur tiger population was divided into 4 age classes: T_{Y1} (cubs, *i.e.*, animals ≤ 1 year of age); T_{Y2} (juveniles, *i.e.*, individuals between 1 and 2 years of age); T_{Y3} (subadults, *i.e.*, individuals between 2 and 3 years of age; and T_A (adults, *i.e.*, individuals > 3 years of age) (Fig. 2b). Density assignment to different age classes is based on the observed age structure of the population for Amur tiger (Feng et al., 2017), while for sika deer it is based on estimates from monitoring camera data (Table 1). Only adult individuals are involved in reproduction. Adult sika deer mate during the growing season (mostly during September and October), and pregnant female deer (D_p), if the pregnancy is successful, give birth in the next growing season (from early May to late June) after a gestation period of approximately 229 days (McCullough et al., 2008). Among Amur tigers, mating occurs almost year-round, but the peak mating time is from February to May, mainly during the nongrowing season. If the pregnancy is successful, pregnant tigers (T_p) give birth after a gestation period of approximately 105 days, mainly during the next growing season from May to August (Miquelle et al., 2010) (Fig. 2). During the growing season, newborns enter the fawn/cub class (D_{Y1} , T_{Y1}), and, with the exception of individuals in the adult class (D_A , T_A), which remain in that class until death, the individuals within each age class move to the next age class (Fig. 2b). Mortality occurs due to natural death, lack of food resources, and predation. The survival of sika deer fawns (D_{Y1}), as well as that of cubs and juveniles of the Amur tiger (T_{Y1} , T_{Y2}), depends on their mothers.

2.3. Mathematical model

In the two seasons, sika deer and Amur tigers of all age classes experience natural mortality MN_X^S , with $S \in \{g, ng\}$, $X \in \{D_{Y1}, D_{Y2}, D_A, T_{Y1}, T_{Y2}, T_{Y3}, T_A\}$. Model parameterization and initialization of variables are based on relevant studies and on reasonable estimates of the small population of Amur tiger and its prey populations. Please refer to Supplementary Information for more details.

2.3.1. Dynamics of sika deer populations in the growing season

During the growing season, newborn deer are included in class D_{Y1}^g , whereas the surviving fawns and subadults of the previous season are transferred to the next class. Predation of adult deer occurs and affects the fawns; if a mother is predated, her fawns also die. The dynamics of sika deer populations in the growing season are described by the following equations:

$$D_{Y1,t+1}^g = D_{p,t} \cdot r \cdot d_{r,t} \cdot d_c \cdot (1 - MN_{D_{Y1}}^g - MN_{D_A}^g) - PN_{D_A,t+1}^g \cdot d_f \cdot d_{p,t} \cdot d_{r,t} \cdot d_c \quad (1)$$

Table 1

List of the parameters and initialization of variables.

Symbol	Definition	Baseline	Unit	Source
Parameters				
G	The mean vegetation biomass density of shrub-herbaceous layer	45,460	kg/km ²	Sai (2017)
$Area$	Study area	18,000	km ²	Feng et al. (2017)
U	Biomass utilization rate	0.32	–	Lü (2018)
G_c	Biomass consumption of per cattle during grazing	1817	kg	Supplementary Information 2
K	Carrying capacity density of adult Amur tiger	0.0034	individuals/km ²	Supplementary Information 2
$MN_{T_{Y1}}^g$	Natural mortality of cub tiger (age ≤ 1 year old) in growing season	0.12	–	Table S5
$MN_{T_{Y2}}^g$	Natural mortality of juvenile tiger (1 < age ≤ 2 years old) in growing season	0.05	–	Table S5
$MN_{T_{Y3}}^g$	Natural mortality of subadult tiger (2 < age ≤ 3 years old) in growing season	0.04	–	Table S5
$MN_{T_A}^g$	Natural mortality of adults tiger (age > 3 years old) in growing season	0.04	–	Table S5
$MN_{T_{Y1}}^{ng}$	Natural mortality of cub tiger (age ≤ 1 year old) in nongrowing season	0.14	–	Table S5
$MN_{T_{Y2}}^{ng}$	Natural mortality of juvenile tiger (1 < age ≤ 2 years old) in nongrowing season	0.1	–	Table S5
$MN_{T_{Y3}}^{ng}$	Natural mortality of subadult tiger (2 < age ≤ 3 years old) in nongrowing season	0.08	–	Table S5
$MN_{T_A}^{ng}$	Natural mortality of adults tiger (age > 3 years old) in nongrowing season	0.07	–	Table S5
t_f	Percentage of females among adult Amur tiger	0.75	–	Xiao (2014)
t_p	Probability of pregnancy of female Amur tiger	0.34	–	Xiao (2014)
t_c	Mean number of tiger cubs per litter	2	individuals	Wilkinson & O'Regan (2003)
t_{rmax}	The maximum successful reproduction rate of Amur tigers	0.9	–	Supplementary Information 2
a_1	Capture rates of adult Amur tigers on sika deer	0.4	–	Supplementary Information 1
h_1	Handling and ingesting times of adult Amur tigers	0.1	–	Supplementary Information 1
a_2	Capture rates of subadult Amur tigers on sika deer	0.3	–	Supplementary Information 1
h_2	Handling and ingesting times of subadult Amur tigers	0.125	–	Supplementary Information 1
CT_{Y3min}	The minimum deer predation that no longer affect subadult tiger survival	6	individuals	Supplementary Information 1

(continued on next page)

Table 1 (continued)

Symbol	Definition	Baseline	Unit	Source
CT_{Amin}	The minimum deer predation that no longer affect adult tiger survival	7.5	individuals	Supplementary Information 1
D_{min}	The minimum deer predation required to start tiger breeding in one year	10	individuals	Supplementary Information 1
D_{max}	The minimum deer predation required for max tiger reproduction in one year	20	individuals	Supplementary Information 1
S_{min}	The minimum survival of the Amur tiger due to sika deer shortage	0.6	-	Supplementary Information 1
$G_{D_{Y1}}^{g/ng}$	Biomass required for a sika deer fawn in the growing or nongrowing season	156	kg	Supplementary Information 2
$G_{D_{Y2}}^{g/ng}$	Biomass required for a subadult sika deer in the growing or nongrowing season	284	kg	Supplementary Information 2
$G_{D_A}^{g/ng}$	Biomass required for an adult sika deer in the growing or nongrowing season	348	kg	Supplementary Information 2
G_{Amin}^g	Biomass required for a female deer to be able to be pregnant	244	kg	Supplementary Information 2
G_{Amax}^g	Biomass required for a female deer to reach maximum pregnancy rate	313	kg	Supplementary Information 2
W_s	Percentage of vegetation biomass loss due to snowfall and vegetation dying	0.85	-	Yang (2018)
$R_{D_{Y1}}$	Impact index of food shortage on the additional mortality of sika deer fawns	0.5	-	Supplementary Information 2
$R_{D_{Y2}}$	Impact index of food shortage on the additional mortality of subadult sika deer	1	-	Supplementary Information 2
R_{D_A}	Impact index of food shortage on the additional mortality of adult sika deer	1	-	Supplementary Information 2
R_r	Impact index of food shortage on the sika deer reproduction	1	-	Supplementary Information 2
$MN_{D_{Y1}}^g$	Natural mortality of deer fawns (age ≤ 1 year old) in growing season	0.2	-	Supplementary Information 2
$MN_{D_{Y2}}^g$	Natural mortality of subadult deer (1 < age ≤ 2 years old) in growing season	0.1	-	Supplementary Information 2
$MN_{D_A}^g$	Natural mortality of adults deer (age > 2 years old) in growing season	0.05	-	Supplementary Information 2
$MN_{D_{Y1}}^{ng}$	Natural mortality of deer fawns (age ≤ 1 year old) in nongrowing season	0.25	-	Supplementary Information 2
$MN_{D_{Y2}}^{ng}$	Natural mortality of subadult deer (1 < age ≤ 2 years old) in nongrowing season	0.15	-	Supplementary Information 2

Table 1 (continued)

Symbol	Definition	Baseline	Unit	Source
$MN_{D_A}^{ng}$	Natural mortality of adults deer (age > 2 years old) in nongrowing season	0.06	-	Supplementary Information 2
d_f	Percentage of females among adult sika deer	0.67	-	Baskin & Danell (2003)
d_c	Mean number of deer fawns per litter	1	individuals	Ohnishi et al. (2009)
d_{pmin}	Minimum pregnancy rates of sika deer	0.1	-	Supplementary Information 2
d_{pmax}	Maximum pregnancy rates of sika deer	0.75	-	Supplementary Information 2
d_{rmax}	Maximum successful reproduction rate of sika deer	0.9	-	Supplementary Information 2
Vectors and initialization				
C	Density of cattle	9	individuals/km ²	Supplementary Information 2
F^{ng}	Food shortage index in nongrowing season	0	-	Supplementary Information 2
T_{Y1}^{ng}	Density of cubs Amur tiger in the nongrowing season	0.00033	individuals/km ²	Feng et al. (2017)
T_{Y2}^{ng}	Density of juveniles Amur tiger in the nongrowing season	0.00033	individuals/km ²	Feng et al. (2017)
T_{Y3}^{ng}	Density of subadult Amur tiger in the nongrowing season	0.00033	individuals/km ²	Feng et al. (2017)
T_A^{ng}	Density of adult Amur tiger in the nongrowing season	0.00111	individuals/km ²	Feng et al. (2017)
T_p	Density of pregnant Amur tiger	0.00044	individuals/km ²	Supplementary Information 2
D_{Y1}^{ng}	Density of sika deer fawns in the nongrowing season	0.11	individuals/km ²	Supplementary Information 2
D_{Y2}^{ng}	Density of subadult sika deer in the nongrowing season	0.11	individuals/km ²	Supplementary Information 2
D_A^{ng}	Density of adult sika deer in the nongrowing season	0.6	individuals/km ²	Supplementary Information 2
D_p	Density of pregnant sika deer	0.2	individuals/km ²	Supplementary Information 2
d_p	Pregnancy probability of sika deer	0.75	-	Supplementary Information 2
d_r	Successful reproduction probability of sika deer	0.9	-	Supplementary Information 2

Note: Some parameters cannot be cited directly and need to be calculated, see the supporting information cited for details of the inversion process.

$$D_{Y2,t+1}^g = D_{Y1,t}^{ng} \cdot (1 - MN_{D_{Y2}}^g) \quad (2)$$

$$D_{A,t+1}^g = (D_{Y2,t}^{ng} + D_{A,t}^{ng}) \cdot (1 - MN_{D_A}^g) - PN_{D_{A,t+1}}^g \quad (3)$$

Although sika deer mate at the end of the growing season and give birth at the beginning of the next growing season, only pregnant females that survive the entire nongrowing season give birth; therefore, the density of deer fawns, D_{Y1}^g , is calculated based on the number of pregnant female deer $D_{p,t}$ (details in 2.4.3) in the previous nongrowing season multiplied by the time-dependent successful reproduction rate $d_{r,t}$ (details in 2.4.8) and the average number of deer fawns per litter, d_c . Since the death of the mother leads to death of the fawns due to lack of care, the death of fawns is associated with the death of the mother in addition to their own

mortality, $MN_{D_{Y1}}^g$, which includes the natural mortality of the mother, $MN_{D_A}^g$, and the occurrence of predation. The density of fawns lost due to predation of their mothers is the density of adults predated, $PN_{D_A}^g$, (details in 2.4.6) multiplied by the percentage of females in the adult sika deer population d_f with pregnancy probability $d_{p,t}$ (details in 2.4.5), the successful reproduction rate $d_{r,t}$ (details in 2.4.8) and the mean number of deer fawns per litter d_c . Since sika deer travel in large herds and the carrying capacity of the environment for this species depends on the available vegetation biomass, we did not assign a carrying capacity for sika deer in the model but instead allowed it to be regulated by the available vegetation biomass, which is variable with grazing and seasonal changes. All parameters setting details are in [Supplementary Information 2](#) (the same below).

2.3.2. Dynamics of Amur tiger populations in the growing season

During the growing season, newborn tigers are included in class T_{Y1}^g , whereas cubs, juveniles and subadults from the previous season are transferred to the next age class. Only adult and sub-adult tigers are involved in predation, and the predation of adults affect the survival of cubs and juveniles. The dynamics of the Amur tiger population in the growing season are described by the following equations:

$$T_{Y1,t+1}^g = T_{P,t} \cdot t_{r,t} \cdot t_c \cdot (1 - MN_{T_{Y1}}^g - MN_{T_A}^g) \cdot S_{CT_{A,t+1}}^g \quad (4)$$

$$T_{Y2,t+1}^g = T_{Y1,t}^g \cdot (1 - MN_{T_{Y2}}^g - MN_{T_A}^g) \cdot S_{CT_{A,t+1}}^g \quad (5)$$

$$T_{Y3,t+1}^g = T_{Y2,t}^g \cdot (1 - MN_{T_{Y3}}^g) \cdot S_{CT_{Y3,t+1}}^g \quad (6)$$

$$T_{A,t+1}^g = \min(K, (T_{Y3,t}^g + T_{A,t}^g) \cdot (1 - MN_{T_A}^g) \cdot S_{CT_{A,t+1}}^g) \quad (7)$$

The density of cubs, T_{Y1}^g , is calculated based on the number of pregnant tigers, $T_{P,t}$, (details in 2.4.4) from the previous nongrowing season multiplied by the time-dependent successful reproduction rate $t_{r,t}$ (details in 2.4.7) and the mean number of tiger cubs per litter t_c . Since cubs, T_{Y1}^g , and juveniles, T_{Y2}^g , depend on their mothers, their death rate is affected not only by their own natural mortality $MN_{T_{Y1,Y2}}^g$ but also by the natural mortality of their mothers, $MN_{T_A}^g$, and by the survival rate related to prey resources, $S_{CT_A}^g$ (details in 2.4.7). The survival of subadults, T_{Y3}^g , and that of adults, T_A^g , depend on their own natural mortality $MN_{T_{Y3,A}}^g$ and on the survival rate associated with prey resources, $S_{CT_{Y3,A}}^g$ (details in 2.4.7). Cubs and juveniles of the Amur tiger do not have their own territories (Tian et al., 2011), while the territories of adult males overlap with those of 1-3adult females, and the overlap between females' territories is relatively low (Hernandez-Blanco et al., 2015; Xiao et al., 2016). Thus, in this study, habitat carrying capacity was measured in terms of female tiger home ranges, and the carrying capacity for adult tigers, K , was calculated based on the number of females that can be accommodated and the sex ratio. This carrying capacity represents the maximum density of adult Amur tigers that can be accommodated when prey resources are adequate. The adult tiger density is maintained at a level that is no greater than the carrying capacity density K .

2.3.3. Dynamics of sika deer populations in the nongrowing season

In the nongrowing season, sika deer in each age class remain in the same age class, except for mortality. The dynamics of sika deer populations in the nongrowing season are described as follows:

$$D_{Y1,t+1}^{ng} = D_{Y1,t}^{ng} \cdot (1 - MN_{D_{Y1}}^{ng} - MN_{D_A}^{ng}) \cdot (1 - MG_{D_{Y1}}) - PN_{D_{A,t+1}}^{ng} \cdot d_f \cdot d_{p,t} \cdot d_{r,t} \cdot d_c \quad (8)$$

$$D_{Y2,t+1}^{ng} = D_{Y2,t}^{ng} \cdot (1 - MN_{D_{Y2}}^{ng}) \cdot (1 - MG_{D_{Y2,t+1}}) \quad (9)$$

$$D_{A,t+1}^{ng} = D_{A,t}^{ng} \cdot (1 - MN_{D_A}^{ng}) \cdot (1 - MG_{D_{A,t+1}}) - PN_{D_{A,t+1}}^{ng} \quad (10)$$

$$D_{P,t+1} = D_{A,t+1}^{ng} \cdot d_f \cdot d_{p,t+1} \quad (11)$$

Similar to the growing season, in addition to natural mortality $MN_{D_{Y1}}^{ng}$, the survival of individuals in the fawn class, D_{Y1}^{ng} , in the nongrowing season is also linked to the natural mortality of adults, $MN_{D_A}^{ng}$, and to predation of adult deer by tigers during the nongrowing season, $PN_{D_A}^{ng}$ (details in 2.4.6). In addition, due to the scarcity of food resources in the nongrowing season, all age classes of deer have a mortality $MG_{D_{Y1,Y2,A}}$ (details in 2.4.8). The density of pregnant female deer D_P is obtained by multiplying the density of adult deer in nongrowing season, D_A^{ng} , by the percentage of females among adult sika deer, d_f , and by the probability of pregnancy d_p (details in 2.4.5).

2.3.4. Dynamics of Amur tiger populations in the nongrowing season

In the nongrowing season of each year, Amur tiger individuals of each age class remain in the same age class, except for mortality. The transitions of the Amur tiger population in the nongrowing season are as follows:

$$T_{Y1,t+1}^{ng} = T_{Y1,t}^{ng} \cdot (1 - MN_{T_{Y1}}^{ng} - MN_{T_A}^{ng}) \cdot S_{CT_{A,t+1}}^{ng} \quad (12)$$

$$T_{Y2,t+1}^{ng} = T_{Y2,t}^{ng} \cdot (1 - MN_{T_{Y2}}^{ng} - MN_{T_A}^{ng}) \cdot S_{CT_{A,t+1}}^{ng} \quad (13)$$

$$T_{Y3,t+1}^{ng} = T_{Y3,t}^{ng} \cdot (1 - MN_{T_{Y3}}^{ng}) \cdot S_{CT_{Y3,t+1}}^{ng} \quad (14)$$

$$T_{A,t+1}^{ng} = T_{A,t}^{ng} \cdot (1 - MN_{T_A}^{ng}) \cdot S_{CT_{A,t+1}}^{ng} \quad (15)$$

$$T_{P,t+1} = T_{A,t+1}^{ng} \cdot t_f \cdot t_p \quad (16)$$

The survival of cubs, T_{Y1}^{ng} , and that of juveniles, T_{Y2}^{ng} , are related to the survival of their mothers as well as to their own natural mortality $MN_{T_{Y1,Y2}}^{ng}$, which includes the natural mortality of mothers, $MN_{T_A}^{ng}$, and the survival rate related to prey resources, $S_{CT_A}^{ng}$ (details in 2.4.7). For subadults T_{Y3}^{ng} and adults T_A^{ng} , survival depends on their own natural mortality $MN_{T_{Y3,A}}^{ng}$ and on the survival rate associated with prey resources $S_{CT_{Y3,A}}^{ng}$ (details in 2.4.7). The density of pregnant female tigers, T_P , is obtained by multiplying the density of adult tigers in winter, T_A^{ng} , by the percentage of females among adult Amur tigers, t_f , and the probability of pregnancy t_p .

2.3.5. The role of grass resources and cattle grazing during the growing season

Cattle grazing influences the vegetation biomass available during the growing season of sika deer G^g in a way that can be described as follows:

$$G^g = G \cdot U - G_c \cdot C \quad (17)$$

where G is the density of available biomass for ungulates (45460 kg/km², obtained through averaging a survey of 105 sample squares in NTLNP), U is the utilization rate of available vegetation biomass (we estimated U to be 0.32 based on controlled enclosure experiments), and C is the density of cattle, whose biomass consumption is G_c (2 % of body weight multiplied by grazing days), see [Supplementary Information 2](#) for details. The availability of grass in the growing season affects the probability of sika deer pregnancy $d_{p,t}$ (Parker et al., 2009), see [Supplementary Eqs. \(1\)–\(3\)](#) for the detailed relationship. Parameters setting details are in [Supplementary Information 2](#).

2.3.6. The predatory relationship between the Amur tiger and sika deer

The density of adult sika deer preyed on by Amur tigers, $PN_{D_A}^g$, is determined by the density T_A^g , T_{Y3}^g and the per capita sika deer consumption $CT_{A,t}^g$ and $CT_{Y3,t}^g$ of adult and subadult Amur tigers, respectively, in the growing and nongrowing seasons ($S \in \{g, ng\}$), as follows:

$$PN_{D_{A,t}}^S = CT_{A,t}^S \cdot T_{A,t}^S + CT_{Y_{3,t}}^S \cdot T_{Y_{3,t}}^S \quad (18)$$

We used type II of the functional response (Holling, 1959), one of the mathematical frameworks that is most commonly used to describe feeding interactions between consumers and resources (Dunn & Hovel, 2020; Rosenbaum & Rall, 2018), to describe per capita sika deer consumption by subadult and adult Amur tigers ($CT_A^{g/ng}$ and $CT_{Y_3}^{g/ng}$). See Supplementary Eqs. (4) and (5) for details.

2.3.7. Survival of prey resources and successful reproduction of the Amur tiger

We describe the minimum survival rate of the Amur tiger under conditions of sika deer shortage as S_{min} and designate the minimum sika deer predation necessary for adult and subadult Amur tigers to meet their own survival unimpaired as CT_{Amin} and $CT_{Y_{3min}}$, respectively. These parameters depend on the presence of alternative prey such as wild boars (*Sus scrofa*) and roe deer (*Capreolus pygargus*) (Gu et al., 2018; Sugimoto et al., 2016). When the per capita consumption of sika deer in adult and subadult Amur tigers, $CT_A^{g/ng}$ and $CT_{Y_3}^{g/ng}$, is lower than the minimum predation of these two groups Amur tigers, CT_{Amin} and $CT_{Y_{3min}}$, the survival of adult and subadult Amur tigers ($S_{CT_A}^{g/ng}$ and $S_{CT_{Y_3}}^{g/ng}$, respectively) in terms of the food factor is proportionally regulated based on the minimum survival rate. When predation of sika deer is equal to or higher than the minimum level, predation of sika deer will not affect the survival of adult and subadult Amur tigers. See Supplementary Eqs. (6) and (7) for details.

The successful reproduction rate $t_{r,t}$ is linked to the number of sika deer eaten. Below a threshold D_{min} , tigers are unable to reproduce. Above a threshold D_{max} , the successful reproduction rate reaches its full potential $t_{r,max}$. Between D_{min} and D_{max} , the successful reproduction rate increases linearly between 0 and $t_{r,max}$ (see Supplementary Eqs. (8) and (9) for details). In the next part of the analysis, we refer to D_{max} as *tiger dependency on sika deer*.

2.3.8. Effects of nongrowing season food resources on reproduction and survival of sika deer

During the nongrowing season, snowfall and dying vegetation reduce the available vegetation, causing food shortages for the sika deer population and affecting sika deer survival in the nongrowing season and reproduction in the following growing season.

The vegetation biomass available in the nongrowing season G_t^{ng} is as follows:

$$G_t^{ng} = \max(0, (G - GC_t^g) \cdot (1 - W_s)) \cdot U \quad (19)$$

$$GC_t^g = G_{D,t}^g + G_C \cdot C \quad (20)$$

where GC_t^g represents biomass consumption by all herbivores in the growing season, W_s is the percentage of vegetation biomass loss due to snowfall and death of vegetation, and $G_{D,t}^g$ is the biomass required for the sika deer during the growing season, see Supplementary Eq. (3) for details.

We used the food shortage index F_t^{ng} to measure the food shortage experienced by sika deer during the nongrowing season (see Supplementary Eqs. (10) and (11) for details). The probability of successful reproduction of sika deer in the next growing season, $d_{r,t}$, and the additional mortality of sika deer caused by the shortage of available biomass, MG_x , depend on the food shortage index F_t^{ng} , and this relationship is described in Supplementary Eqs. (12) and (13).

All parameters and initial values involved in the model are listed in Table 1.

2.4. Scenario setting

As a preliminary step, we wanted to understand the regime

behaviour of the system; for this reason, we explored the time trajectory along a very long horizon (1000 years) with the purpose of capturing the long-term regime behaviour, including its steady states and cycles, after a transient time period dependent on initial conditions. We used the model in three ways to answer different research questions. Because the model has a large number of state variables and parameters, an analytical treatment of the model was challenging and outside the purpose of our analysis. In this study we wanted to explore some key scenarios through numerical model exploration.

First, we explored the influence of grazing pressure on the population densities of sika deer and Amur tiger in terms of regime dynamics. To achieve this, we identified long-term behaviour in the simulations and explored how the densities in regime conditions changed across a range of cattle density C (from 0 to 15 individuals/km² using an interval of 0.01 individuals/km²), encompassing both observed densities and potential realistic more severe grazing scenarios. We also explored D_{max} (from 0 to 30 individuals using a value interval of 0.1 individuals) to determine the influence of the dependence of Amur tiger breeding on sika deer on population development. In addition, higher vegetation biomass utilization rate and lower nongrowing season biomass loss rates (caused by winter snowfall and plant dieback) could, to some extent, mitigate the effects of grazing on wild ungulates and are important factors influencing the survival of ungulates. We therefore also tested biomass utilization rate U (from 0.3 to 0.6 using an interval of 0.05) and nongrowing season biomass loss rate W_s (from 0.5 to 0.9 using an interval of 0.05) on steady-state wildlife population density at different grazing densities.

Second, we investigated the effects of the natural mortality of adults and cubs/ fawns on population dynamics. We systematically varied the natural mortality of adult and fawn sika deer, as well as adult and cub Amur tigers, throughout the entire spectrum from 0 to 1, with intervals of 0.01. This comprehensive range was chosen to theoretically assess the sensitivity of population dynamics to varying mortalities, encompassing extreme scenarios for theoretical exploration.

Third, we explored the influence of a sudden increase in grazing intensity during the growing season for a certain number of years, starting from equilibrium conditions, on the time trajectories of the populations. In particular, we explored disturbance intensities ranging from 7 to 20 individuals/km² using a value interval of 1 individual/km² and durations ranging from 0 to 30 years using a value interval of 1 year; for each combination of intensity and duration, we calculated the time required for the populations to recover under that particular scenario, i. e., the time required for the population densities to return to their equilibrium values. All simulations were performed in Python (version 3.9.7).

3. Results

3.1. Density trajectories of sika deer and Amur tiger populations at different cattle densities

The simulations showed, after an initial transient due to the initial conditions, a regime consisting of a steady state or a cycle. Fig. 3 shows simulations of sika deer and Amur tiger densities in the nongrowing seasons for selected values of cattle density. When the cattle density was below 9.813 individuals/km² (e.g., $C = 9$ individuals/km²), the sika deer population reached an equilibrium (Fig. 3a), and the Amur tiger population reached carrying capacity after transient fluctuations (Fig. 3b). For cattle densities in the range of 9.813–9.822 individuals/km² (e.g., $C = 9.813$ individuals/km²), the size of the sika deer population fluctuated cyclically after the transient, with smaller fluctuations around the maximum value reached in the cycle (Fig. 3c). Additionally, the tiger population underwent a cycle (Fig. 3d). For cattle densities greater than 9.822 individuals/km² (e.g., $C = 10$ individuals/km²), the tiger and sika deer populations rapidly became extinct (within 60 years for sika deer and 20 years for Amur tigers) (Fig. 3e, f).

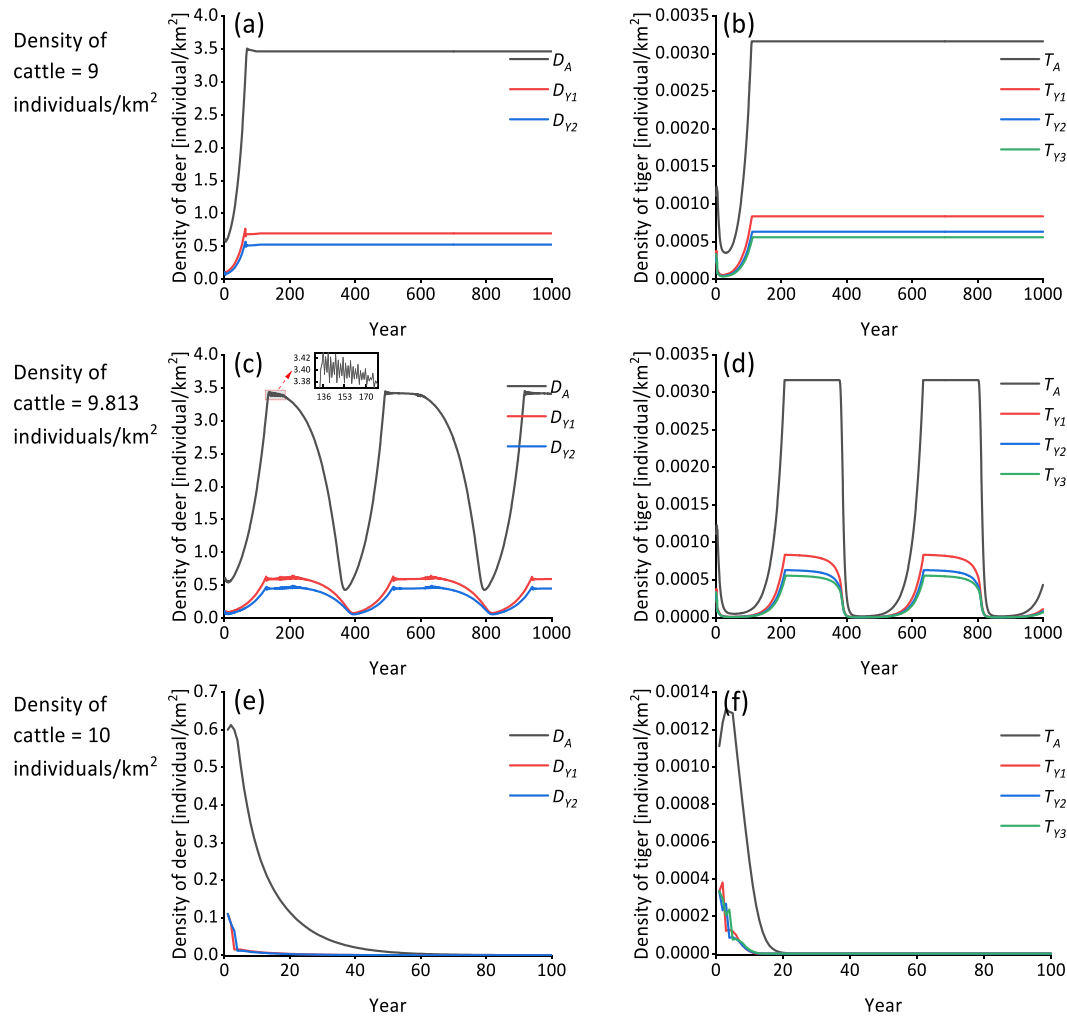


Fig. 3. Trajectories of sika deer (a, c, e) and Amur tiger (b, d, f) population densities in the nongrowing season under different cattle densities. Sika deer age classes: D_{Y1} includes fawns (animals ≤ 1 year old), D_{Y2} includes subadults (1 year old $<$ animals ≤ 2 years old), and D_A includes adults (animals > 2 years old). Amur tiger age classes: T_{Y1} includes cubs (animals ≤ 1 year old), T_{Y2} includes juveniles (1 year old $<$ animals ≤ 2 years old), T_{Y3} includes subadults (2 years old $<$ animals ≤ 3 years old), and T_A includes adults (animals > 3 years old). Please note that the time horizon showed in panels e and f is shorter (100 years) than in the other panels (1000 years) in order to make the trajectories visible.

3.2. Effects of cattle density and dependence of tiger reproduction on deer on wildlife population density

Exploring systematically how steady-state population densities vary with changes in parameters makes it possible to generalize the insights gained through the analysed trajectories shown in Fig. 3. The trajectories show that after 400 years, the effects of the initial conditions were largely complete; therefore, we considered that the population densities at regime were the average population densities calculated over the time period extending from year 400 to the end of the simulation.

To emphasize details in the crucial region, Fig. 4 zooms into the variation in steady-state population densities of sika deer and Amur tigers, reflecting changes in cattle density from 9.6 to 10 individuals/ km^2 and in D_{\max} from 18 to 28 individuals. Our results showed a regime shift as cattle density increased, with a tipping point at ~ 9.813 individuals/ km^2 (Fig. 4a). When the cattle density exceeded the tipping point, the average deer population density decreased rapidly from 3.3 to 0 individuals/ km^2 (Fig. 4a, moving from A to C), and the average tiger population density changed from 0.0032 to 0 individuals/ km^2 (Fig. 4b, A to C). For the deer population, the tipping point of cattle density is independent of D_{\max} . In contrast, for the tiger population, a D_{\max} of ~ 24 was also a tipping point: before D_{\max} reached this point, the tiger population density was maintained at the carrying capacity, and beyond the

tipping point, the tiger population density decreased rapidly to 0 individuals/ km^2 (Fig. 4b, A to B). The decrease in the population density of Amur tigers resulted in a small increase in the average sika deer population density at steady state due to reduced predation, varying from 3.35 to 3.40 individuals/ km^2 (going from A to B in Fig. 4a).

At point A, the development of the tiger population mainly depended on its own life-history traits. In this case, because tiger dependency on sika deer is not high and the sika deer population density is not limited by cattle density, the tiger population density can be maintained at its carrying capacity. At point B, the development of the Amur tiger population was limited by insufficiency of prey.

3.3. Effect of biomass utilization rate and biomass loss during the nongrowing seasons on wildlife population density

In Fig. 5, we showed the variation in steady-state population densities of sika deer and Amur tigers due to a combination of cattle densities ranging from 0 to 15 individuals/ km^2 with vegetation biomass utilisation varying from 0.3 to 0.6 and nongrowing season vegetation loss rates varying from 0.5 to 0.9, respectively.

Overall, our results showed that decreasing grazing densities, increasing biomass utilization rate, and reducing rates of biomass loss during the nongrowing season would lead to an increase in steady-state

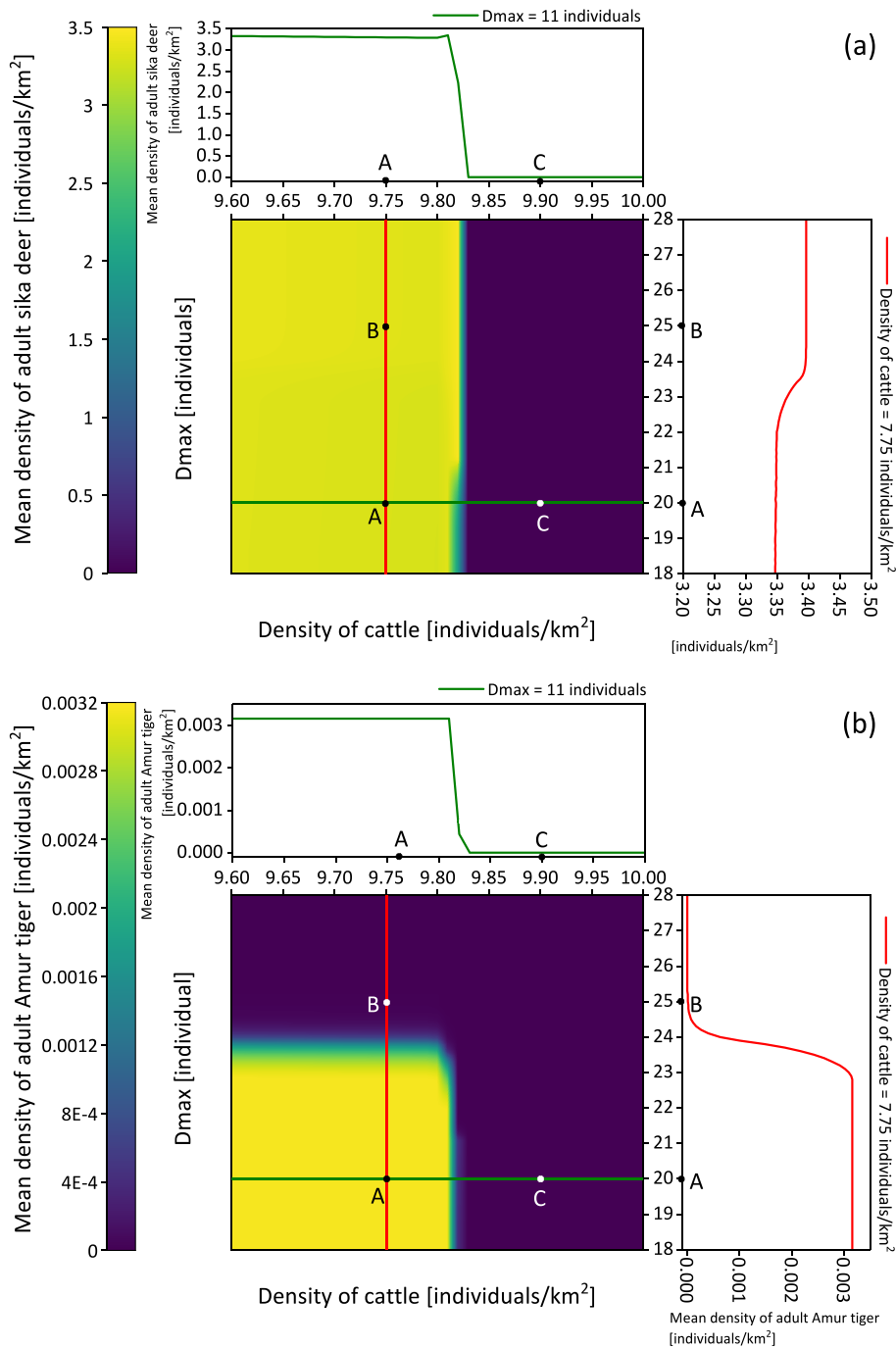


Fig. 4. Heatmap of the average density of adult sika deer (a) and Amur tigers (b) at the regime dynamics as a function of cattle density (C) and the tiger dependency on the sika deer (D_{max}).

densities of sika deer, allowing the densities of Amur tigers to be maintained at the environmental carry capacity. In addition, as biomass utilization rate increases, it would lead to an increase in the grazing density tipping point for the regime shift in wildlife populations. This means that greater grazing densities can be tolerated. However, vegetation loss rate did not result in a change in grazing density tipping point.

3.4. Effect of adult and cub mortality on population density

For cattle densities below the tipping point (e.g., 9 individuals/km²), we tested the effect of changes in the mortalities of cubs and adults on the population densities of sika deer and Amur tigers during the growing

and nongrowing seasons. The results identified certain combinations of mortalities of cubs and adults in which the populations survived (lighter areas in Fig. 6, showing positive density equilibrium values) and other combinations in which the populations went extinct (darker areas in Fig. 6). The combinations that resulted in population survival spanned parameter ranges of varying widths. The maximum natural mortality of adult deer and tiger that could maintain deer and tiger populations (lower than 0.11) was much lower than the maximum natural mortality of deer fawns and tiger cubs (lower than 0.8) in the two seasons (Fig. 6). However, very low natural tiger mortality was not always beneficial (Fig. 6d, h). With low tiger mortality, the average density of sika deer in the steady state was lower due to predation; it was 1.6–2.0 individuals/km² in the growing season (Fig. 6c) and 1.1–1.5 individuals/km² during

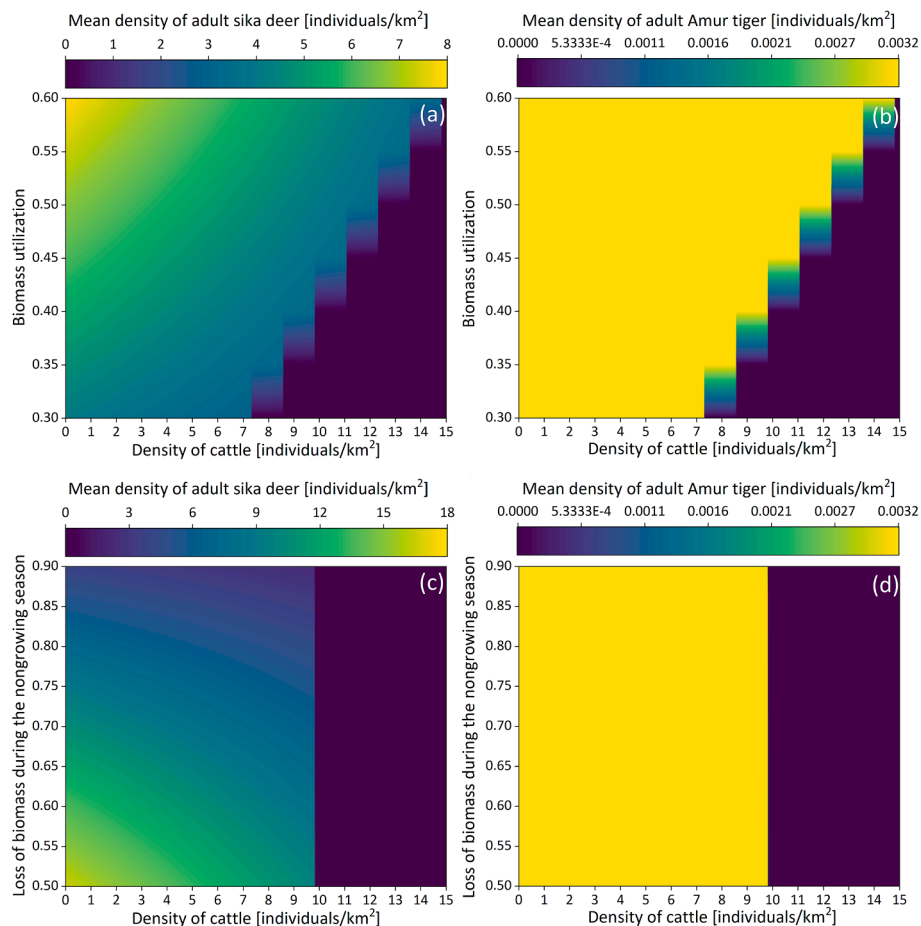


Fig. 5. Heatmap of the average density of adult sika deer (a, c) and Amur tigers (b, d) at the regime dynamics as a function of biomass utilization rate (U) and winter biomass loss rate (W_s) at different cattle density (C).

the nongrowing season (Fig. 6g). In turn, the lower prey density resulted in failure of the tiger population density to reach carrying capacity because of the scarcity of prey (Fig. 6d, h). In addition, at cattle densities below the tipping point, cubs and adults of both sika deer and Amur tiger had higher maximum mortalities in the nongrowing season than in the growing season that could maintain viable populations of the two species.

3.5. Effects of enhanced grazing on population recovery

During simulations with $C = 9$ individuals/km², we introduced heavy grazing disturbances during the regime dynamics after the population reached stability by abruptly increasing C to different intensities and durations. The results are shown for a range of intensities and durations on population recovery time (Fig. 7a, d) as well as for selected values of intensities and durations for in-depth theoretical exploration to understand trends in data changes (Fig. 7b, c, e, f) and are cross-referenced among the figures using letters. Overall, as grazing intensity and duration increased, recovery times increased for the two populations (Fig. 7a, d). The observed deer population dynamics were counterintuitive at point B and within the yellowish area represented by scenario B in Fig. 7a. At this point, the deer population density initially declined to ~ 1.5 individuals/km² after the introduction of the disturbance, and the decline in population density then slowed (Fig. 7b). Initially, the decline in deer density did not affect the tiger population, which remained at the carrying capacity (Fig. 7e). However, after some years, due to a combination of tiger predation and reduced population growth due to cattle grazing, the decrease in deer population density again accelerated, leading to a decrease in the tiger population density

to a point below the carrying capacity. This nonlinear behaviour made the recovery time longer, even more than that observed at points C and D. However, for the tiger population, the recovery time was shorter in B than in C and D, and because of the nonlinear behaviour of the deer population, the effect of grazing on Amur tigers in this scenario was delayed (Fig. 7e). Increased grazing intensity resulted in longer recovery times for both the deer and the tiger populations (Fig. 7c, f). Grazing intensities lower than 17 animals/km² and heavy grazing periods shorter than 9 years, as indicated by the darker areas in Fig. 7a and d, had little effect on tiger populations but resulted in a deer density lower than the equilibrium value within less than 100 years.

4. Discussion

It is debatable whether wildlife protection and cattle rearing can coexist (Keesing et al., 2018). We explored the effects of different grazing intensities on the sika deer and Amur tiger populations in the NTLNP by constructing a deer-tiger food chain model in which cattle grazing was included as a disturbance. Our results showed a tipping point in wildlife persistence occurring along a gradient of cattle density. We also found that the long-term effects of sudden increases in grazing intensity and varying durations on the populations of the sika deer and the Amur tiger differ and that Amur tiger populations often take longer than deer populations to recover after heavy grazing disturbances have ceased.

4.1. Regime shifts due to grazing

Our results showed that cattle density causes abrupt regime shifts in

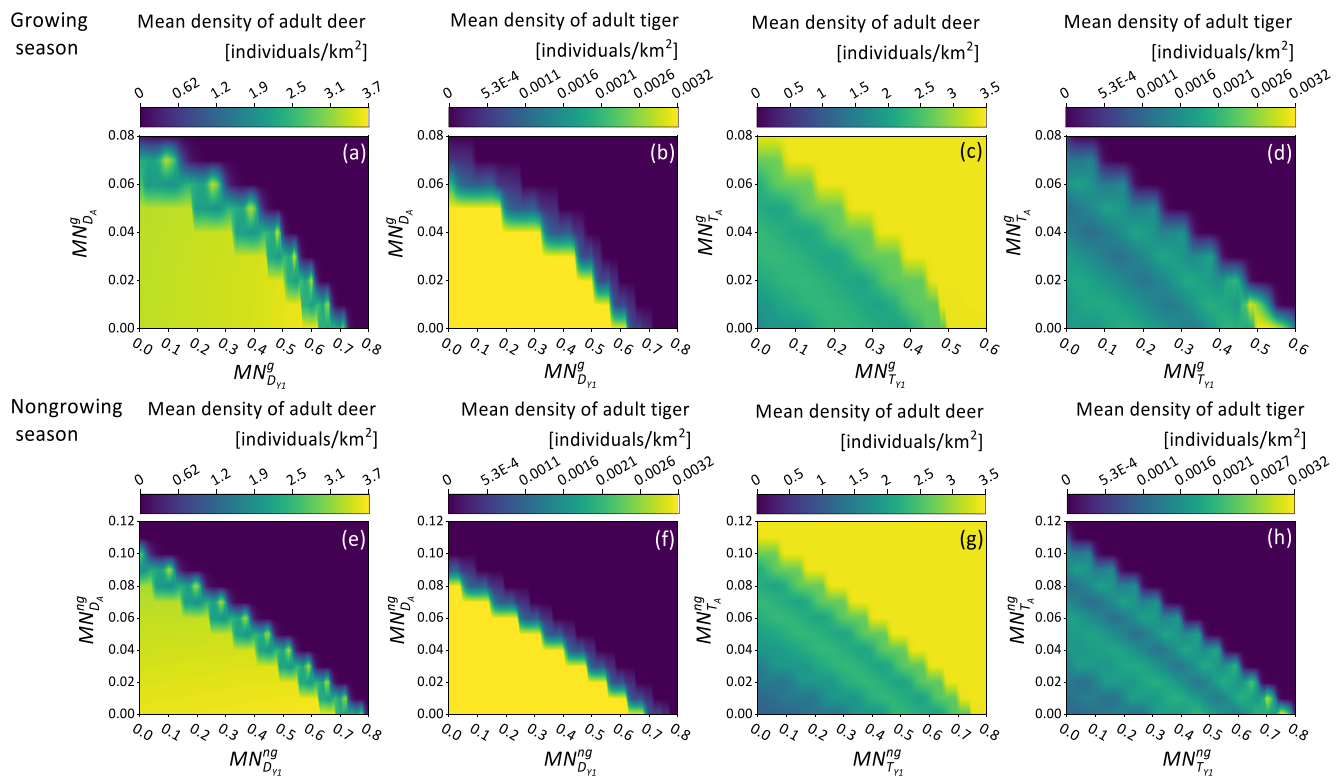


Fig. 6. Heatmap of the average density of adult sika deer (Panels a, c, e, g) and Amur tigers (Panels b, d, f, h) at the regime dynamics (calculated as averages along trajectories in the period 400–1000 years) as a function of natural mortalities of cubs/fawns (<1 year old) and adult of sika deer (>2 years old) and Amur tiger (>3 years old) during the growing season (Panels a, b, c, d) and the nongrowing season (Panels e, f, g, h). $MN_{D_{vi}}^g$, $MN_{D_A}^g$, $MN_{T_{vi}}^g$, and $MN_{T_A}^g$ are the natural mortalities of deer fawns, adult deer, tiger cubs and adult tigers, respectively, in the growing season; $MN_{D_{vi}}^{ng}$, $MN_{D_A}^{ng}$, $MN_{T_{vi}}^{ng}$, and $MN_{T_A}^{ng}$ are the natural mortalities of deer fawns, adult deer, tiger cubs and adult tigers, respectively, in the nongrowing season. All simulations are run using a cattle density of 7 individuals/km²; for the other parameters, refer to Table 1.

wildlife populations, *i.e.*, that there is a tipping point at a certain level of cattle density that leads the deer and tiger populations to rapid extinction. This tipping point in cattle density is related to vegetation biomass utilisation: the higher the biomass utilisation, the more cattle density can be tolerated. Below the tipping point, wildlife can coexist with grazing livestock. For cattle densities slightly lower than the tipping point, even a relatively small increase in grazing intensity can lead to the occurrence of cycles. In contrast, at cattle densities greater than the tipping point, sika deer and Amur tiger rapidly become extinct because sika deer are hampered by competition with cattle for food resources. The results of this simulation confirmed the hypothesis that high grazing rates can negatively influence wildlife, while appropriate grazing rates permit the coexistence of cattle with wildlife (Keesing et al., 2018; Kiffner et al., 2020; Schieltz & Rubenstein, 2016; Wells et al., 2022). This means that strategic planning of livestock grazing can conserve biodiversity if the grazing is managed in a way that minimizes competition with wildlife and facilitates high-quality grazing (Fynn et al., 2016).

The continuous increase in the number of livestock in and around the NTLNP for more than the past 30 years, as well as reduced pastoralist mobility, have led to continuous overgrazing in that area (Wang et al., 2016), resulting in land degradation, loss of vegetation diversity, and serious disturbances to wildlife (Feng et al., 2021a; Feng et al., 2021b). The average cattle density in some rangelands located within the NTLNP is 11 individuals/km² (Li et al., 2016), a density that is much higher than the tipping point predicted by the models; therefore, wildlife in these areas may be facing negative impacts from grazing, and this is an urgent need that must be addressed.

In addition, tigers prefer medium-sized and large prey such as sika deer and wild boar (Hayward et al., 2012), and their successful

reproduction likely depends on adequate densities of these preferred species (Miquelle et al., 2018). Our results show that when the Amur tiger's preference for sika deer exceeds in overdependence, it increases the risk of tiger extinction. This is due to the density of sika deer that fails to meet the predation requirements for tigers to attain the necessary reproductive rate for population sustainability. This suggests that conservation of prey for the Amur tiger cannot be limited to a single species: increasing the participation of multiple medium- and large-prey species in the tigers' diet can prevent the tiger population from being limited by overdependence on a single species. Thus, restoration of scarce medium-sized and large prey species such as red deer (*Cervus elaphus*), together with appropriate grazing management, is crucial for conservation of the Amur tiger.

4.2. Insights from the investigation of the role of mortality

For both deer and tigers, adult mortality has a greater impact on population survival than does cub mortality (<1 year) in both seasons, implying that elevated natural mortality of adult individuals is more likely to lead to population extinction than elevated mortality of cubs. Indeed, adult individuals are closely related to reproduction, and to some extent, females determine the future development of the population (Franklin et al., 2021; Kenney et al., 2014). Moreover, cubs depend on their mothers, and increased mortality of mothers increases the death of cubs. Therefore, the survival of adult deer and tigers, especially of females, is crucial, and it is important to have good breeding habitat and low human-caused mortality (Miquelle et al., 2015). The results also show that extremely low mortalities can harm the viability of the predator population itself (Fig. 6d, h). Low predator mortality results in lower prey densities, resulting in more difficult recovery for prey

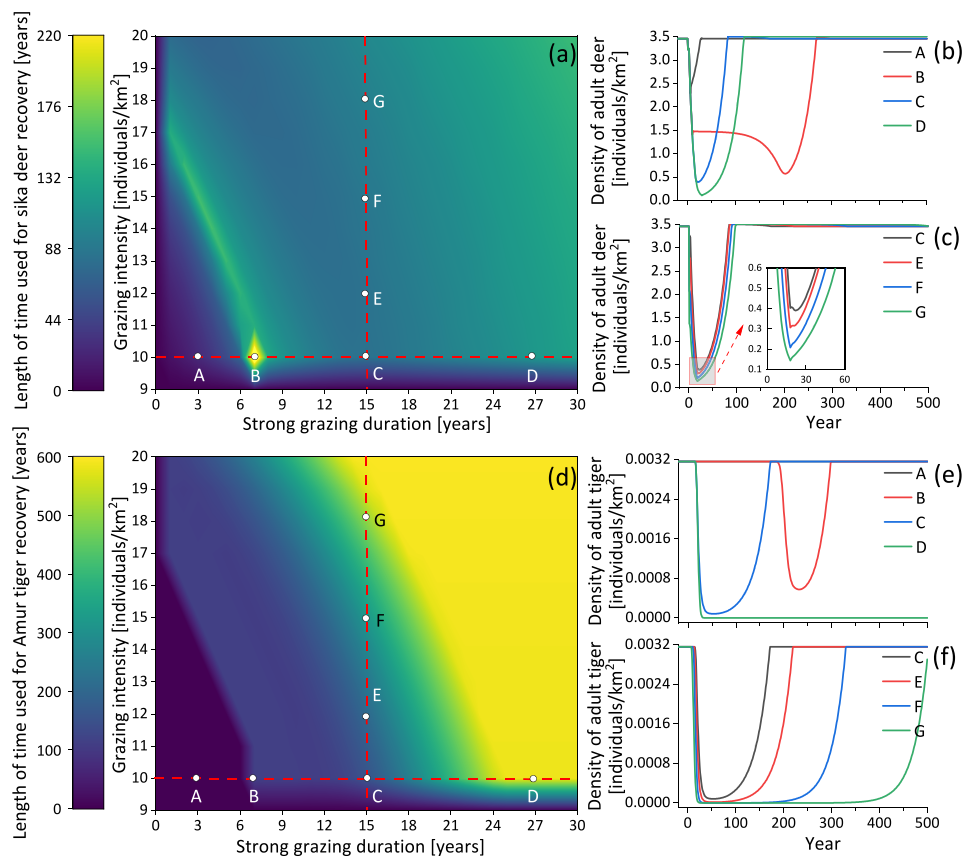


Fig. 7. Heatmap of the length of recovery time for sika deer (a) and Amur tigers (d) as a function of the length and intensity of heavy grazing. (b) Trajectories of sika deer population density under different lengths of heavy grazing at the same intensity. (c) Trajectories of sika deer population density under different intensities of heavy grazing during periods of the same length. (e) Trajectories of Amur tiger population density under different lengths of heavy grazing at the same intensity. (f) Trajectories of Amur tiger population density under different intensities of heavy grazing during periods of the same length.

populations, leading in turn to lower predator densities due to scarcity of food resources (Abrams & Quince, 2005). Thus, the recovery of top predators needs to be based on sufficient prey resources (Steinmetz et al., 2021; Wang et al., 2018). Ensuring that the sika deer population is not overly disturbed and restoring its population size is critical to recovery of the Amur tiger population.

4.3. The influence of sudden increases in grazing intensity

The analyses depicted in Figs. 3 and 4 are static, meaning that the effects of cattle density and mortality on long-term behaviour are shown. However, when the temporal dynamics are considered, it is possible to study the transient behaviours of the systems that are induced by the temporary introduction of heavy grazing disturbances. Although these transient disturbances may not affect the equilibrium in the long term, they might cause a decrease in population densities for periods longer than the time scales of transient disturbances, which are highly relevant for management time scales.

Our results indicate that for deer population, the length of the recovery time increases more with the length rather than the intensity of the heavy grazing period. For tiger populations, the trend is reversed: recovery time is more affected by the intensity of grazing than by the length of the heavy grazing period. Increases in grazing intensity and duration result in longer recovery times for the deer population, but increases within a certain range may have no effect on the tiger population. However, after grazing at certain levels of duration and intensity, the indirect effect of heavy grazing on tiger populations is larger than its direct effect on deer populations, the tiger population takes longer to recover, and the recovery time is much longer than the duration of

grazing disturbance. Nonetheless, the actual population abundance may even be lower than the simulated results, as the initial population size of the Amur tiger is very small, demographic stochasticity often occurs, and there are threats of inbreeding depression (Ning et al., 2021) and canine distemper virus (Wang et al., 2022, 2023) within the population (not included in the model) that could increase the risk of population extinction as the population size decreases. This makes it difficult for the tiger population to recover once they reach a certain low population size after a period of overgrazing, even if grazing has been adjusted to a lower level or prohibited, which is known as a quasi-extinction scenario.

4.4. Methodological considerations

Our model consisted of 7 state variable and a relatively high number of parameters. For this reason, the analytical treatment of the model was extremely challenging as well as out of scope of our study. Our analysis was based on the numerical exploration of the model, which allowed to perform local sensitivity analyses (corresponding to regions of the solution and parameter spaces related to our research questions 1) and 2)) and to explore the time trajectory, which was of high interest for research question 3).

To build a model that possesses an acceptable degree of realism, simulation requires the estimation of a number of parameters; hence, there is some degree of uncertainty associated with the model results (Shoemaker et al., 2014; Lawson et al., 2021). Therefore, this analysis identifies relative differences in future trends of wildlife populations under different grazing scenarios rather than providing an absolute and accurate prediction. In addition, certain fixed parameter settings may prove insufficient for dynamically evolving ecosystems. However, given

the theoretical nature of our study and the inherent constraints imposed by the available data, we are presently limited in adjusting the parameters over time. Consequently, our primary objective is to employ the existing model as a theoretical framework to investigate the theoretical impacts of grazing within the defined range of parameter settings, similar to approaches taken in other theoretical models (Accatino et al., 2010; Accatino & De Michele, 2013). These insights are confirmed in the literature. Researchers have found that appropriate grazing can facilitate grass growth during the growing season (McNaughton, 1985; Odadi et al., 2011); however, overgrazing can also reduce aboveground primary productivity (Brierley et al., 2018; Western, Groom, et al., 2009). Due to the impossibility of obtaining accurate parameters, we assumed that the vegetation biomass each year was not affected by the cattle density of the year before and we did not include compensatory plant growth in response to grazing. It is also worth noting that deer actively avoid livestock in shared rangelands or shift their use of sites as soon as cattle are introduced (Schielz & Rubenstein, 2016). This “social intolerance”, which is not explicitly included in our model, is also an important limitation on the expansion of the sika deer population. In addition, there are other factors, such as spatial heterogeneity and vegetation type, that may influence the effects of grazing on native wildlife. All of these points deserve further evaluation and inclusion in more refined and complex models.

5. Conclusions

This study shows, through a modelling approach, the possibility that there is a tipping point in wildlife persistence along a gradient of cattle grazing intensity. The results theoretically demonstrate that wildlife conservation and cattle production can coexist but that serious regime shifts can occur, and if overgrazing occurs for some time, the damage caused to wildlife may be irreversible or may persist for a very long time relative to time scales of disturbances. Our model shows the direct consequences of overgrazing on the small tiger population along the China-Russia border and suggests that it is critical to be proactive in reducing this threat. Therefore, establishing grazing rules and gaining local community support for adherence to these rules requires continuous and determined effort. These findings are important for guiding ecosystem management and restoration efforts across the NTLNP and provide novel insights into the tradeoffs and potential win-wins between cattle production and wildlife conservation.

CRedit authorship contribution statement

Dawei Wang: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Tianming Wang:** Supervision, Project administration. **Francesco Accatino:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Python code (Wang, et al., 2022) is available in Science Data Bank at <https://doi.org/10.57760/sciencedb.08208>.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.111870>.

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