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RESEARCH ARTICLE

Post-Soviet fire and grazing regimes govern the abundance of a key ecosystem engineer on the Eurasian steppe, the yellow ground squirrel *Spermophilus fulvus*

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Abstract

Aim: Grazing intensity and fire patterns across the Eurasian steppes have changed dramatically over the past decades due to the collapse of the Soviet Union in 1991, and Kazakhstan is now a global fire hotspot. The implications of these changes for ecosystem functioning are largely unclear. We aimed to understand the effects of changed grazing intensity and fire frequency on a key ecosystem engineer, the yellow ground squirrel *Spermophilus fulvus*, on a very large scale.

Location: Kazakhstan.

Methods: Ground squirrels were surveyed in an area of ca. 100,000 ha in the dry steppe of central Kazakhstan, using hierarchical distance sampling at more than 200 random points, stratified by fire frequency and livestock grazing intensity. We modelled abundance as a function of different variables, grouped at the landscape scale (fire and grazing), meso-scale (soil and vegetation structure) and at burrow scale (plant traits such as palatability, digestibility and nutrient content).

Results: Ground squirrels prefer areas of a high wormwood cover (*Artemisia* spp.) and high plant species richness, which are moderately grazed, preferably by cattle, with only rare fire occurrence. High squirrel densities were also related to the availability of nitrogen-rich plants of high nutritional value for herbivores.

Main Conclusions: Yellow ground squirrels seem to reach their density optima by balancing trade-offs between optimal foraging in areas of short, nutrient-rich vegetation and a good visibility of approaching predators. Post-Soviet changes in grazing pressure, resulting in higher fire recurrence rates due to grass encroachment and litter accumulation (i.e. fuel for wildfire), have likely affected the abundance of burrowing mammals and associated biodiversity across huge parts of the Eurasian steppes and semideserts.

KEYWORDS

burrowing mammal, grassland, habitat models, Kazakhstan, land-use change, livestock grazing, wildfire

1 | INTRODUCTION

Ecosystem engineers are organisms that directly or indirectly control the availability of resources for other organisms by causing physical state changes in biotic or abiotic materials (Jones et al., 1997). They increase habitat and niche availability for other taxa and have a considerable, positive influence on biodiversity globally (Romero et al., 2015). They also affect ecosystem functioning by changing vegetation cover and structure, biogeochemical cycles (e.g. nutrient and carbon cycling) and food webs (Jones et al., 1994). Due to their functional links to other biodiversity and ecosystem components, declines in ecosystem engineers can affect biodiversity disproportionally (Yeakel et al., 2020). A loss of ecosystem engineers can trigger cascades of declines in further species that depend on the habitat created and species interacting with these (e.g. predators, parasites) (Coleman & Williams, 2002). Ecosystem engineers enhance ecosystem stability (Yeakel et al., 2020).

An especially important group of terrestrial ecosystem engineers is small, social, burrowing mammals, such as pikas, marmots, prairie dogs and ground squirrels (Beca et al., 2022; Davidson et al., 2012). Among these, ground squirrels (e.g. *Spermophilus* spp., *Cynomys* ssp.) play an important role in the formation and functioning of many grassland ecosystems (Davidson et al., 2012; Lacher Jr et al., 2019). These terrestrial rodents are (semi-)fossorial and live in family groups or colonies that build extensive burrow systems (Wilson et al., 2016) (Figure S1). They are an important component of food webs and ecosystem engineers because they create habitat and niches for other plants and animals, such as nesting cavities for birds (Lacher Jr et al., 2019). Their digging activity loosens and mixes the soil, which accelerates nutrient cycling, increases soil carbon sequestration and enhances local plant species diversity (Beca et al., 2022; Davidson & Lightfoot, 2008; Pang & Guo, 2017). Despite the ground squirrels' importance as ecosystem engineers, many aspects of their ecology such as habitat selection, response to fire, grazing and other disturbances remain unstudied. This is unfortunate because many populations show declines or are fragmented (Van Horne et al., 2007). Declines of ground squirrels, and associated losses of ecosystem functions, are driven by habitat degradation caused by agricultural conversion, seasonal droughts, invasive plant species and inadequate pasture management (Van Horne et al., 2007). A major reason for declines is the conversion of their grassland habitat to cropland and the intensive use of pastures (Ceballos et al., 2010; Hoogland, 2013). Conversion to cropland and ploughing usually results in habitat loss (Hoogland, 2013; Tokarsky, 2011). Direct persecution as pest is another severe threat that has resulted in dramatic declines of some species, for example black-tailed prairie dog *Cynomys ludovicianus* or speckled ground squirrel *Spermophilus suslicus* (Hoogland, 2013; Shilova, 2011; Wilson et al., 2016).

Most ground squirrel species inhabit open grasslands, which to a large extent were shaped and maintained by the grazing of large herbivores (Wesche et al., 2016, Wilson et al., 2016). In the Central Asian arid grasslands, ground squirrels historically coexisted with numerous species of large mammals, such as Saiga Antelope *Saiga tatarica*, Wild Ass *Equus hemionus* and Przewalski's horse *E. przewalskii*, (Wesche et al., 2016). At the end of the 20th century, most of these were extinct or had declined to very small populations and had generally been replaced by domestic livestock (Robinson & Milner-Gulland, 2003).

Livestock grazing and grassland fire patterns (e.g. fire frequency and the size of burns) influence ground squirrel populations in different ways (Bylo et al., 2014; Cheng & Ritchie, 2006; Davidson et al., 2010; Yensen et al., 1992). The ecological effects of grazing of both wild herbivores and domestic livestock are cumulative and interact strongly. Among them are biomass consumption, changes in vegetation structure and productivity and trampling followed by a change of soil structure and surface water runoff. These effects are particularly complex in transitional ecosystems or ecotones, such as semi-deserts, due to the vegetation mosaics that prevail there (Abaturov, 1984).

The ecological consequences of grazing for ground squirrels are often contradictory (Figure 1): ground squirrels compete with large ungulates for food resources, but grazing also promotes short swards providing a good view of the surroundings, a situation that is preferred by many of these species. Nutrient availability is an important determinant of ground squirrel abundance and survival that influences hibernation success and the risk of predation, as squirrels have to travel larger distances to forage in areas where nutrient-rich vegetation is scarce (Van Horne et al., 2007). At the same time, relatively short vegetation promoted by grazing provides ground squirrels, as mainly diurnally active social animals, a better opportunity for visual observation and avoidance of predators using alarm calls (Wilson et al., 2016). Thus, many ground squirrels (e.g. little ground squirrel *Spermophilus pygmaeus*, spotted ground squirrel *Xerospermophilus spilosoma* and others) (Cao et al., 2016; Wilson et al., 2016) tolerate high grazing pressure.

Grazing intensity also drives fire regimes across the grasslands of the world (Bond & Keeley, 2005; Fuhlendorf et al., 2009). Fire is another major biomass consumer in grasslands, especially when grazing intensity is low, vegetation and litter accumulate and provide fuel for wildfires (Freitag et al., 2021; Fuhlendorf et al., 2009). As a natural phenomenon, wildfire played an important role in shaping grassland ecosystems in the past, but current fire regimes in the majority of grasslands are the results of interaction of both natural and anthropogenic processes (Pausas & Keeley, 2014). Fire is likely to affect ground squirrels mainly indirectly, through the change of vegetation structure, because the squirrels hibernate belowground in late summer, at the peak of fire season (Loboda et al., 2012). However, unlike grazing, frequent fires cause mostly negative effects on burrowing rodents, by promoting plant communities dominated by tall grass stands, which these mammals usually avoid (Freitag et al., 2021; Hoogland, 2013; Shilova et al., 2011) (Figure 1).

The impacts of fire and grazing on small mammals are comparatively well studied for the American prairies and Australia (Griffiths & Brook, 2014). In contrast, studies from the Eurasian steppes remain scarce (Coggan et al., 2018) and are rarely quantitative. The lack of studies from the Eurasian steppes results also in significant

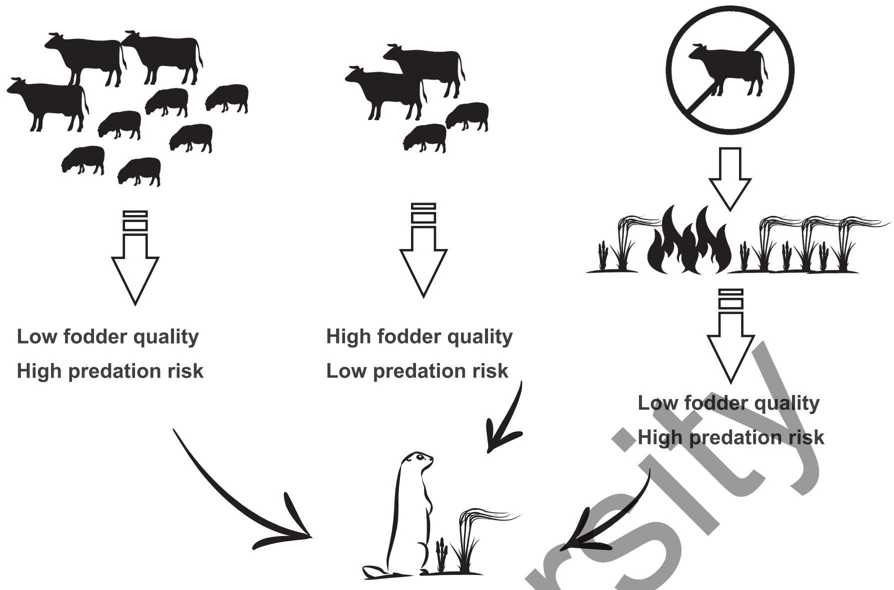

FIGURE 1 Schematic representation of potential determinants of ground squirrel abundance. Domestic livestock density drives – Via biomass consumption and vegetation height – Foraging quality, predation risk and fire patterns. We here suggest that in the system studied, there is a level of livestock grazing intensity that balances the positive and negative impacts of these factors, and is therefore preferred by the ground squirrels.

bias in international conservation assessments, as this ecozone is disproportionally species-rich in small mammals, and particularly ground squirrels (genus *Spermophilus*) (Beca et al., 2022; Wesche et al., 2016).

The steppes of north-central Kazakhstan were traditionally used by nomadic herders and remained comparatively undisturbed by the beginning of 20th century (Wesche et al., 2016). Conversion to arable lands began in 1906 with the Stolypin reforms in the Russian Empire (Dubrovskij, 1963). During Soviet times (1922–1991) the extensive conversion continued and pushed nomadic herders farther south to dry steppe and semi-desert areas (Kerven et al., 2021). This was accompanied by a transition first to a semi-nomadic lifestyle and then finally to complete sedentarization by the early 1990s. All these changes resulted in currently highly imbalanced grazing patterns. Livestock concentrates now around settlements which causes high grazing pressure there (Kamp et al., 2016; Robinson & Milner-Gulland, 2003), whereas vast steppe areas remain ungrazed (Dara et al., 2020), which leads to biomass accumulation and more frequent and intensive fires (Dara et al., 2019). Additionally, the dramatic decline of the populations of wild ungulates such as the Saiga Antelope *Saiga tatarica* (Robinson & Milner-Gulland, 2003) in post-Soviet decades has resulted in decreased grazing independent of animal husbandry (Dara et al., 2019; Dubinin et al., 2011). How these habitat changes have been influencing small mammal populations in Kazakhstan is largely unknown.

We aimed to understand how fire and grazing drive the abundance of the yellow ground squirrel *Spermophilus fulvus*, one of the most common and widely distributed ground squirrels in the dry steppes and semi-deserts of Kazakhstan. Due to their locally high abundances, yellow ground squirrels are important ecosystem engineers and an important prey for consumers on higher trophic levels, especially birds of prey such as the globally threatened Steppe Eagle (*Aquila nipalensis*). For details on the species ecology see the Text S1.

We predicted that ground squirrel population density (as an indicator of habitat preference) is driven by a connected set of variables that act on three spatial levels, namely fire and grazing regimes, vegetation and soil structure and vegetation composition (Figure 2).

We hypothesized that ground squirrel abundance:

1. Peaks in areas of intermediate grazing pressure at the landscape scale (where *colony* establishment is decided) because this resolves a trade-off between high fodder-availability (enough vegetation biomass) and high predator visibility (low vegetation).
2. Decreases with increasing fire frequency and increases with time since fire at the landscape scale because frequent fires result in vegetation homogenization and dense grass swards (Brinkert et al., 2016; Freitag et al., 2021) that are avoided by the ground squirrels.
3. Is driven on a colony scale (where decisions are made to build *burrows*) by soil substrate and vegetation that provide both cover but also access to nutritious and digestible plants.

2 | METHODS

2.1 | Study area

Our study area stretches across 101,800 ha in the transition zone of dry steppe and desert steppe ecozones in the southern Kostanai Region, Kazakhstan (centered on 56.66°N 65.05°E near the village of Stepnyak, Figure 3). The area hosts globally important populations of *Spermophilus fulvus*. The region has a semi-arid, strongly continental climate with an annual precipitation sum of approx. 300 mm and a mean temperature of 3.3°C (Wesche et al., 2016). Monthly temperature averages range between −17°C in January and 22°C in July, but temperatures can exceed 40°C in summer and −50°C in winter (Amangeldy weather station, http://www.globalbioclimatics.org/).

The dominating soil types are humus-rich Kastanozem and alkaline Solonetz soils. Vegetation communities are dominated by

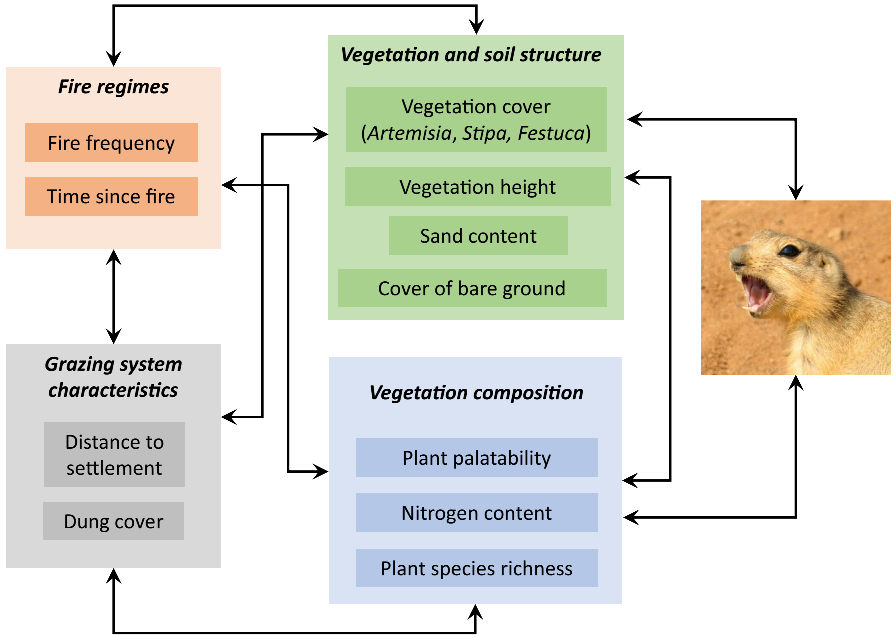

FIGURE 2 The four sets of factors that were anticipated to drive squirrel habitat selection as mirrored by population density. Fire and grazing were assumed to act on the landscape scale, whereas vegetation structure and soil factors were expected to affect abundance on an intermediate (meso-) scale and vegetation composition on the microhabitat (plot) scale. Arrows connect variables with suspected and observed interdependencies. Relationships were expected to be either positive, negative or hump-shaped.

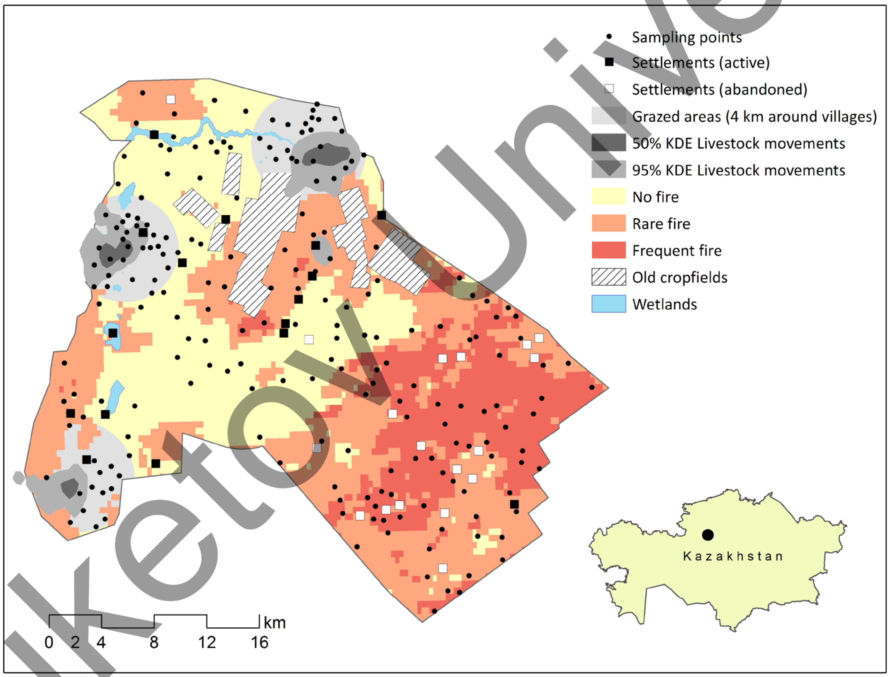

FIGURE 3 Overview map of the study area (1018 km^2) and its location in Kazakhstan (inset). The study area was stratified by fire frequency (three levels: Unburnt (no fire in the period 2000–2015), rarely burnt (1–2 fires in the period 2000–2015) and frequently burnt (3–5 fires in the period 2000–2015) and grazing pressure (high intensity grazing and low intensity grazing). Grazing intensity was estimated before fieldwork started as buffers of 4 km around inhabited settlements and livestock stations based on Kamp et al. (2012). Intensive grazing zones were verified by tracking livestock with GPS collars (spatial 50% and 95% kernel density estimates, KDE, are depicted). Fire frequency was calculated from the MODIS burnt area product (cf. text). The “old cropfields” were abandoned in the early 1990s.

bunch grasses (e.g. *Festuca* spp., *Stipa* spp.), wormwood (*Artemisia* spp.) and dwarf shrubs (*Atriplex cana*, *Spiraea hypericifolia*) (Freitag et al., 2021). The area is sparsely populated. Since the break-up of the Soviet Union in 1991, large parts of the villages were abandoned and most sheds and wells collapsed (Dara et al., 2019). Livestock is nowadays kept by private households for subsistence and driven out of the villages by local shepherds daily.

2.2 | Sampling design

We used a stratified random sampling approach to select sites for point counts. The study area was stratified by fire frequency and grazing intensity (Figure 3). Fire frequency (derived from the MODIS burnt area product from the year 2000 to 2015 at a resolution of 500 m, Giglio et al., 2018) was classified into three levels:

unburnt (no fire in the period 2000–2015), rarely burnt (1–2 fires in the period 2000–2015) and frequently burnt (3–5 fires in the period 2000–2015). During the field survey, we noted signs of recent fire during fieldwork and updated fire frequency and time since fire where not detected by MODIS. In the study area, sheep and cattle generally remain within a 4 km radius of the active settlements (Hankerson et al., 2019; Kamp et al., 2012); therefore, we defined the area in a radius of 4 km around settlements and livestock stations (Figure 3) as high intensity grazed areas. One reactivated livestock station was discovered later in the field and was therefore not included in the stratification. After removing permanent waterbodies and abandoned arable fields (mapped based on their shape and spectral phenology by visually inspecting Landsat TM/ETM+ images from May 1978, 1993 and 2015), we randomly placed 65 sampling points in the areas of high grazing intensity (500 m minimum distance between sampling points) and 50 points in each of the three fire frequency strata, with low grazing intensity. The minimum distance between sampling points was 750 m. Some of the points were not accessible during fieldwork; therefore, the final sample consisted of 204 points.

2.3 | Habitat variables

Grazing intensity was characterized by the distance of the sampling point to the nearest active settlement or livestock station and quantified by counting the number of dung piles per species in a 100 m × 2 m strip transect centered on each sampling point (Brinkert et al., 2016). Vegetation and soil structure were characterized by cover estimates from standard vegetation relevées. All vascular plant species in a 10 m × 10 m vegetation releveé were determined and for each species, projected percentage cover was estimated (nomenclature followed Czerepanov, 1995). For measuring soil parameters, we sampled electric conductivity (eC, surrogate of soil salinity), pH and sand content on every sampling point from two depths (5–30 cm and 30–60 cm) (for more details see Freitag et al., 2021). All habitat parameters are listed in the Table S1. Information on sampling plant traits and aboveground biomass quality is available fromText S2.

2.4 | Squirrel counts

From the 3rd to the 30 May 2016, we surveyed adult ground squirrels using distance sampling (Buckland et al., 2015) at the 204 sampling points. Traditional methods of estimating ground squirrel densities (burrow counts, mark-recapture) (Karaseva & Telitsyna, 1996) are time consuming and expensive. We aimed to find a labor-saving method for the rapid assessment of ground squirrel populations which could be used across the large areas of Kazakh steppes. We tested distance sampling, a widely used method of indirect estimation of species densities and abundances (Buckland et al., 2004). It is often used for estimatign densities of large- and medium-sized mammals (Jathanna et al., 2003; Ruette et al., 2003), but has been applied only rarely for visual counts of small mammals. Where it was used, e.g. for marmots in alpine environments, results were either comparable to those obtained with more labour-intensive approaches such as mark recapture (Pelliccioli & Ferrari, 2014), or were biased low (Corlatti et al., 2017). Distance sampling allows estimating animal densities while simultaneously accounting for factors that affect detection probability (Buckland et al., 2004; Kéry & Royle, 2015). By May, adult ground squirrels emerge from hibernation, but the offspring is still mainly in the burrows. Our derived densities are thus estimates of the adult breeding population.

The surveys were conducted by two teams consisting of two observers each. At each site, the observers simultaneously counted the number and estimated the distance to each squirrel within a 500 m radius using a laser range finder (Bushnell Scout 1000). To those individuals, which vocalized but remained hidden in the vegetation, we estimated approximate distances based on aural cues. Counts were conducted during the peaks of squirrels' activity between 9:00–11:00 am and 04:00–07:00 pm To minimize disturbance, we left the survey car and walked up the final 700 m to each sampling point and waited for 5–10 min until squirrels emerged from burrows and started vocalizing. Distance measurements by human observers can be imprecise and biased (summary in Yip et al., 2020), but we assume that our estimates were little biased compared to those from other habitats such as forests, because: (i) observers were trained and distance estimation was calibrated among all observers before sampling started, and at two further occasions during the fieldwork period, (ii) the flat steppe allowed the use of laser range finders up to distances of 300 m due to a lack of obstacles such as trees, (iii) there was no interference of background noise (when estimating distances based on aural cues) due to the lack of people and traffic in our study area and (iv) we classified distances into bins during analysis (see below).

We acknowledge that for estimating detection probability, measurements of objects need to be statistically independent. This is likely not the case for animals living together in one burrow, and earlier ground squirrel distance sampling surveys have used 'clusters' of animals as sampling units (Jathanna et al., 2008). We decided against the use of clusters because densities were often very high and it was difficult to partition spread-out aggregations of animals into meaningful clusters, and animals at distances >100 m were often mixing constantly, making assignments to burrows difficult. We do not assume that this influences the results strongly, as rarely more than two animals were observed emerging together from a single burrow.

Only adult individuals were counted in cases where offspring emerged from burrows towards the end of the fieldwork period. Since the colonies of *S. fulvus* are founded by females, they tend to guard their plots more actively, while males might hide in the burrow without vocalizing (Sludsky, 1969). Therefore, we assume that a certain percentage of animals (mainly males and sub-adults) were missed, and the derived numbers represent conservative density estimates.

2.5 | Data analysis

We used a hierarchical distance sampling modelling framework for closed populations to estimate population densities, while accounting for varying detection probability of the study species (Kéry & Royle, 2015). Raw distances were converted to classes of 20 m intervals. The data was truncated at 300 m distance, as the probability of detection at the distance >300 m sharply dropped, and observers tended to round the distance measure ('heaping') which resulted in spikes of the observed number in at 350 and 400 m in histograms of the distribution of distances (Figure S3). Our tests also revealed that distances were not always reliably measured beyond 300 m by the range finders, further justifying this approach.

We first fitted univariate models using the 'distsamp' function in package 'unmarked' in R (Chandler, 2020), using both half-normal or hazard-rate functions, to explore the strength and shape of the relationships of predictors and ground squirrel abundance. Models using either function were compared with Akaike's information criterion (AIC). The hazard-rate function assumes constant detection probability up to a certain distance, from which on decaying detection probability is modelled. The half-normal function assumes a decay in detection probability starting directly at the observer. Hazard-rate models performed consistently better than half-normal models, so we used hazard-rate models for inference throughout.

We expected that ground squirrel detectability would decrease with increasing vegetation height (and therefore visibility) and would vary among observers, so we first fitted all models using mean vegetation height and observer identity as covariates in the detection part. As there was little support for an influence of these variables on detection probability (see results), we re-fitted all univariate models without any covariates in the detection part and based our inference on this set of models. As we expected hump-shaped responses for a number of variables, mirroring an optimum selected along the gradient of the variable, we also included variables as squared terms.

In a second step, those variables that showed a significant relationship with animal density in univariate models were used in four sets of multi-variable models that represented the predicted spatial response levels in habitat selection (grazing, fire patters, vegetation structure and plant traits). A maximum of four variables in the same model were allowed for each set of variables for reasons of parsimony. Correlated variables (Spearman's $r > 0.7$) were included alternatingly. An automated procedure (function 'dredge' implemented in R package 'MuMIn'; Barton, 2009) was used for this. Models within 2 AIC units of that model with the smallest AIC were considered as receiving equal support from the data. Relative variable importance $w_+(j)$ was calculated as the sum of Akaike weights over all models including the respective explanatory variable (Anderson & Burnham, 2004).

3 | RESULTS

3.1 | Overall ground squirrel density and population size

There was only weak support for an effect of vegetation height (σ parameter estimate 0.001 ± 0.0007 SE, $p = .0779$) in a model containing both variables and no support for an effect of observer (Table S2). In the following, inference is therefore based on models that contained covariates only in the abundance part of the model.

Overall mean ground squirrel density across the study area was 0.965 ± 0.039 SE animals/ha (confidence interval: 0.891–1.044) based on the estimate from an intercept-only half-normal model (AIC = 6701.17) and 0.623 ± 0.020 SE (confidence interval: 0.584–0.664) based on an intercept-only hazard-rate model (AIC = 6573.70), with no covariate effects on detection probability or abundance included (sample size $n = 2539$ observed animals for both models). Extrapolating the density from the hazard-rate model (that had a considerably lower AIC) to the 1018 km^2 study area yielded a total population size 69,651 (range: 65,291 to 74,235) adult ground squirrels. An extrapolation based on the half-normal model yielded a 35% higher population size (107,887 adult ground squirrels, range 99,613 to 116,719), illustrating the sensitivity of the approach to choosing a suitable decay function for detection probability with distance to observer.

3.2 | Relationships of ground squirrel abundance and environmental parameters

At the landscape scale, univariate models of parameters mirroring grazing intensity suggested a clear optimum of ground squirrel habitat selection (expressed by high abundances) at intermediate levels of grazing (ca. 10 dung piles per 200 m grazing transect) (Table 1, Figure 4), suggesting that we can accept our first hypothesis. A positive relationship was found with cattle grazing intensity, whereas the response to increasing sheep and goat grazing pressure was negative (Table 1, Figure 4). At the landscape scale, ground squirrel densities decreased with distance to villages and livestock stations, suggesting a general preference for grazed areas. Fire had a negative effect on ground squirrel densities, as increasing fire frequencies were associated with lower densities, and densities recovered with years since the last fire event (Table 1, Figure 4), suggesting that we can accept our second hypothesis.

At a meso-scale, vegetation structure was a strong driver of ground squirrel density, which increased with high cover of wormwood (*Artemisia* spp.), but decreased with increasing fescue (*Festuca* spp.) and total grass cover (Table 1, Figure 4). Densities decreased with increasing cover of bare ground and peaked at a vegetation height of ca. 32 cm. Areas of high grass cover, which are the areas with the least grazing pressure, were avoided. Areas with higher

TABLE 1 Parameter estimates with associated standard errors, *p*-values and AIC values for univariate distance sampling models (abundance part of the model, estimated λ).

Variable group	Variable	Estimate	SE	*p*	AIC
Fire & grazing	Cattle dung cover	0.054	0.006	<.001	6510.1
	Distance to settlement	−0.020	0.003	<.001	6526.8
	Time since fire	0.025	0.004	<.001	6533.7
	Horse dung cover	−0.026	0.005	<.001	6534.7
	Total dung cover	−0.003	0.001	<.001	6540.6
	Sheep dung cover	−0.007	0.002	.002	6549.3
	Fire frequency	−0.090	0.019	<.001	6552.5
Vegetation composition	Lignin content	−0.087	0.013	<.001	6534.5
	Species richness	0.025	0.004	<.001	6538.0
	Nitrogen content	−0.235	0.103	.023	6571.8
Vegetation & soil structure	Modal vegetation height	−0.001	0.000	<.001	6509.4
	Artemisia cover	0.010	0.001	<.001	6520.3
	Cover of bare ground	−0.010	0.002	<.001	6528.8
	Sand content	0.006	0.002	.001	6565.2
	Stipa cover	0.004	0.002	.009	6569.1
	Festuca cover	−0.006	0.003	.017	6569.7
	Total grass cover	−0.000	0.000	<.001	7008.2

sand content had higher ground squirrel densities (Table 1, Figure 4), probably mirroring the greater ease of burrow construction in these substrates compared to more clayey and loamy substrates.

On the plot scale, ground squirrel abundance was related to fodder/biomass quality and peaked at a nitrogen content of about 2% in plant biomass and a high palatability (measured as reduced lignin [ADL] content) (Table 1, Figure 4). Ground squirrel abundance also increased with increasing plant species richness (Table 1, Figure 4). This suggests we can accept our third hypothesis.

Fifteen variables had significant univariate relationships with ground squirrel abundance and were therefore examined further in multivariate models. Fire frequency and time since fire were highly negatively correlated (Spearman's $\rho = -0.88$, Figure S2), we therefore did not set up a multivariate fire model, but used inference from the univariate models. Multivariate models were thus setup for the variable groups 'grazing', 'vegetation and soil structure' and 'vegetation composition'. In the multivariate grazing model, we refrained from entering total dung cover as it was a linear combination of cattle, sheep/goat and horse dung cover. None of the variables representing vegetation structure and soil characteristics were strongly correlated, only grass cover and the cover of wormwood (*Artemisia* spp.) were moderately negatively correlated (Spearman's $\rho = -0.57$). None of the variables representing vegetation composition were correlated (Spearman's $\rho < 0.3$ and > -0.2) (Figure S2). We therefore entered all variables in the full model before simplification.

The best multivariate grazing model suggested that ground squirrel abundance declined with increasing distance to settlement, increased with increasing cattle dung cover and slightly decreased with increasing sheep dung cover (Table 2), suggesting again that hypothesis 1 can be accepted.

There was a single best multivariate model that suggested a positive effect of wormwood cover and higher sand content, coupled with a certain mean vegetation height, and a negative effect of much bare ground on ground squirrel abundance (Table 3). The variables wormwood cover, cover of bare ground and mean vegetation height were the most important ones across all models. Removing the variable sand content (variable importance 0.88) from the best model increased the AIC by 5.32. All models considered here were much better than an intercept only model (ΔAIC = 178.60, Table 3).

There was no single best model suggesting all three variables (vegetation palatability measured as lignin content; plant nitrogen content and plant species richness) had an effect on ground squirrel abundance (Table 4). The variable importance of nitrogen content (hump-shaped relationship) was much lower than that of palatability (hump-shaped relationship) and plant species richness (increasing squirrel densities with increasing plant species richness). All models considered here were much better than an intercept only model (ΔAIC = 58.44, Table 4). The equivocal model results on lignin content (mirroring digestibility) and nutrient availability, and their hump-shaped responses in univariate models suggest that ground squirrels cannot exploit areas of the highest availability of palatable and nutrient-rich plants due to trade-offs with vegetation height and density, thereby providing support for our third hypothesis.

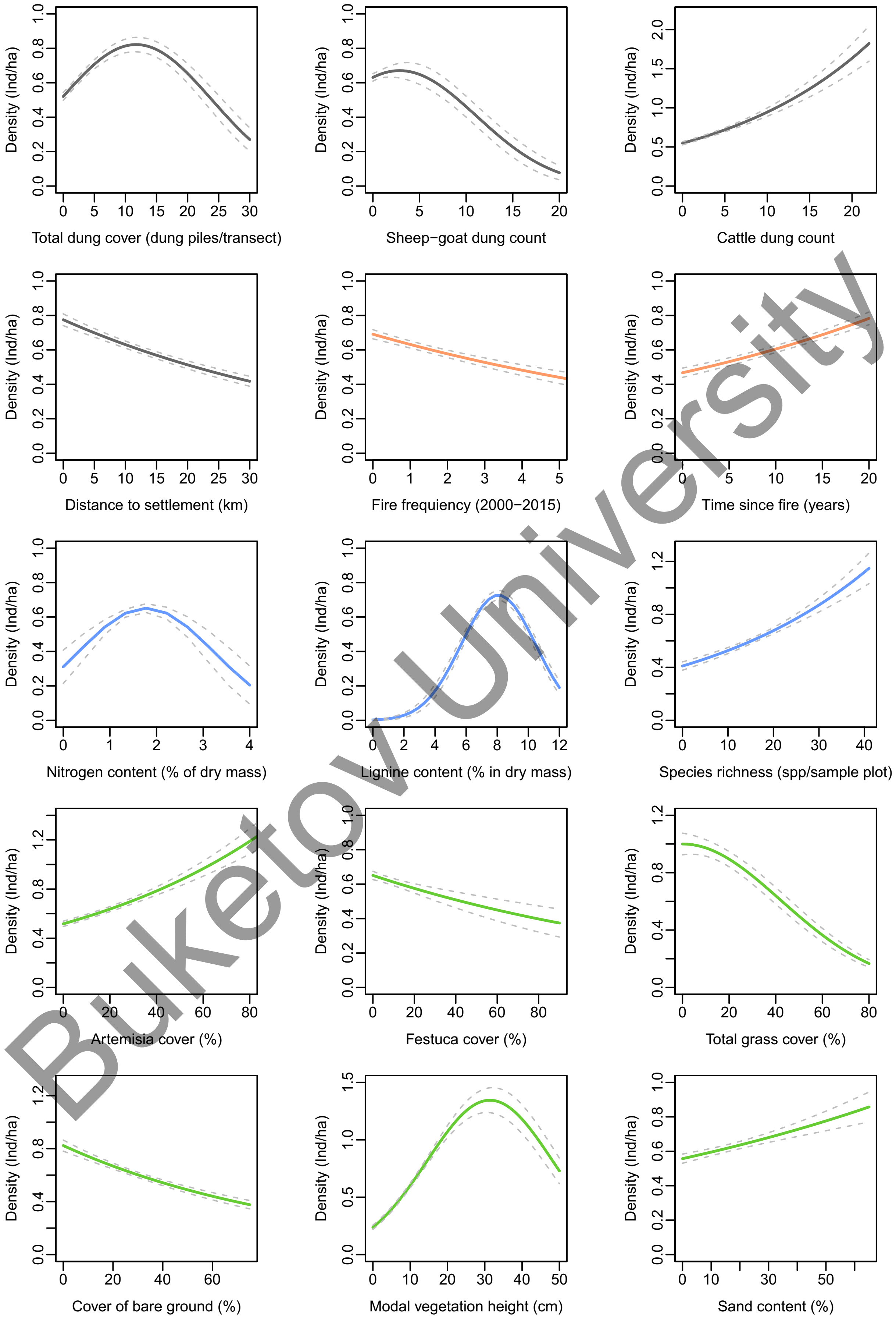
Density (Ind/ha)
0.0 0.2 0.4 0.6 0.8 1.0
0 5 10 15 20 25 30
Total dung cover (dung piles/transect)
Density (Ind/ha)
0.0 0.2 0.4 0.6 0.8 1.0
0 5 10 15 20
Sheep−goat dung count
Density (Ind/ha)
0.0 0.5 1.0 1.5 2.0
0 5 10 15 20
Cattle dung count
Density (Ind/ha)
0.0 0.2 0.4 0.6 0.8 1.0
0 5 10 15 20 25 30
Distance to settlement (km)
Density (Ind/ha)
0.0 0.2 0.4 0.6 0.8 1.0
0 1 2 3 4 5
Fire frequency (2000−2015)
Density (Ind/ha)
0.0 0.2 0.4 0.6 0.8 1.0
0 5 10 15 20
Time since fire (years)
Density (Ind/ha)
0.0 0.2 0.4 0.6 0.8 1.0
0 1 2 3 4
Nitrogen content (% of dry mass)
Density (Ind/ha)
0.0 0.2 0.4 0.6 0.8 1.0
0 2 4 6 8 10 12
Lignine content (% in dry mass)
Density (Ind/ha)
0.0 0.4 0.8 1.2
0 10 20 30 40
Species richness (spp/sample plot)
Density (Ind/ha)
0.0 0.4 0.8 1.2
0 20 40 60 80
Artemisia cover (%)
Density (Ind/ha)
0.0 0.2 0.4 0.6 0.8 1.0
0 20 40 60 80
Festuca cover (%)
Density (Ind/ha)
0.0 0.4 0.8 1.2
0 20 40 60 80
Total grass cover (%)
Density (Ind/ha)
0.0 0.4 0.8 1.2
0 20 40 60
Cover of bare ground (%)
Density (Ind/ha)
0.0 0.5 1.0 1.5
0 10 20 30 40 50
Modal vegetation height (cm)
Density (Ind/ha)
0.0 0.2 0.4 0.6 0.8 1.0
0 10 30 50
Sand content (%)

FIGURE 4 Predicted ground squirrel density (individuals per hectare) from univariate point distance sampling models (hazard-rate function throughout, no covariates entered in the detection part of the model). Colours correspond to sets of factors that were anticipated to drive squirrel habitat selection (cf. Figure 2): Dark grey: Grazing variables, orange: Fire variables, blue: Vegetation composition and plant trait variables, green: Vegetation structure variables.

TABLE 2 Comparison of an intercept model and those models with ΔAIC <2 containing grazing-related explanatory variables in the abundance part (λ) of a hierarchical distance sampling model.

	Intercept (σ)	Intercept (λ)	Dist_sett (λ)	Dung_cattle (λ)	Dung_sheep (λ)	Dung_sheep^2	df	AIC	ΔAIC	w_i
1	5.159	−0.329	−0.018	0.046	−0.086		6	6449.8	0.00	0.640
2	5.159	−0.340	−0.017	0.046	−0.066	−0.002	7	6451.5	1.54	0.297
3	5.159	−0.376	−0.015	0.044		−0.006	6	6454.4	4.64	0.063
4	5.159	−0.474					3	6573.8	124.37	<0.001
$w_+(j)$			1.00	1.00	0.94	0.35				

Note: The detection part of the model did not contain any variables, hence only the intercept (σ) is reported.

Abbreviations: AIC, Akaike's information criterion; ΔAIC, Difference of the model AIC to the AIC of the best model; w_i, Akaike weight; $w_+(j)$, Variable importance; Dist sett, Distance to nearest settlement or livestock station; dung_cattle, Cover of cattle dung; Dung_sheep, cover of sheep and goat dung (also entered as squared term).

4 | DISCUSSION

In the semi-arid steppe of Kazakhstan, the abundance of yellow ground squirrels peaked in areas where large-scale grazing pressure was high enough to prevent frequent fires. Ground squirrels were most abundant in areas of intermediate grazing pressure. These areas likely provided cover from predators, but were suitable for foraging at the same time. The vegetation in areas of high squirrel densities was characterized by cattle and horse rather than sheep grazing, intermediate grass cover, a high plant diversity and levels of intermediate plant nutrient content and plant palatability. The abundance maxima of the squirrel in these intermediate areas of plant fodder quality suggest that trade-offs between optimal foraging conditions and the visibility of predators are present.

A reliance of a minimum or intermediate level of grazing has also been documented for Black-tailed Prairie Dog *Cynomys ludovicianus* in North America (Bylo et al., 2014; Davidson et al., 2010; Knowles, 1986), Daurian Ground Squirrel *Spermophilus dauricus* in Inner Mongolia, China (Cao et al., 2016), Little Ground Squirrel *S. pygmaeus* in Kalmykia, Russia (Shilova et al., 2011) and Bobak marmot *Marmota bobak* in Northeastern Ukraine (Savchenko & Ronkin, 2018; Tokarsky, 2011). For the latter, the decrease in intensity or complete cessation of livestock grazing leads to a dramatic population decline (Shilova et al., 2011; Tokarsky, 2011).

On a meso-scale, squirrel density increased with high cover of wormwood *Artemisia* spp., but declined with increasing grass cover and bare ground. This supports the preference of a certain level of grazing: high wormwood cover is found in grazed areas, but these obviously should not be grazed so intensively that bare ground crosses a certain threshold. Areas of high grass cover (mostly genus *Stipa*) are usually avoided by ground squirrels for their low fodder quality, as they prefer more nutrient-rich and palatable plants (e.g. *Artemisia* spp., *Ceratocephala* spp., *Tulipa* spp.) (Sludsky, 1969). Apart from this, tall grass stands also decrease vertical visibility and impair communication inside the squirrel colonies, and the ground squirrels can easily be approached by mammalian and avian predators such as Red Fox *Vulpes vulpes*, Corsac Fox *Vulpes corsac*, Steppe Polecat *Mustela eversmanii*, Steppe Eagle *Aquila nipalensis* or Long-legged Buzzard *Buteo rufinus* (Sludsky, 1969). This also adds to poorer forage conditions as ground squirrels spend more time in vigilance and less time feeding (Sharpe & Van Horne, 1998).

At the burrow scale (plot level), high ground squirrel abundance was related to high plant palatability and increased with increasing plant species richness, which perhaps mirrors the higher availability of nutrient-rich herbs and annual plants compared to grass-dominated plots. Higher species richness is also correlated with increasing sand content and decreasing salinity of soils in the area (Freitag et al., 2021), and these are exactly the soils preferred by *S. fulvus* (Sludsky, 1969). Finally, higher plant-species richness is created by cattle grazing compared to sheep grazing (Tóth et al., 2018), further explaining the squirrel preference of cattle-grazed areas.

Effects of livestock density (measured by dung density) on squirrel abundance were equivocal. This might be due to a differential impact of cattle and sheep/goats on vegetation, such as clipping height and plant species selection (Abaturov, 1984). Positive effects of cattle grazing on ground squirrels and prairie dogs were documented in North America and China (Bylo et al., 2014; Cao et al., 2016; Davidson et al., 2010), but we found no evidence of negative impact of sheep grazing on ground squirrels in the literature. Another explanation could be related to the livestock management at our study site. Here, like in many areas of central Kazakhstan, sheep are herded in close vicinity of the villages or livestock stations (within 4 km). The high stocking densities lead to areas with sparse vegetation cover (10–40%) and poor in plant species (1–10 species) (Freitag et al., 2021). Although the predation risk for squirrels in such overgrazed areas is probably very low due to better visibility and

TABLE 3 Models related to vegetation structure and soil.

	Intercept (σ)	Intercept (λ)	Cov_ art (λ)	Cov_ fest (λ)	Cov_ grass (λ)	Cov_ bare (λ)	Mean_ vegH (λ)	Sand (λ)	df	AIC	ΔAIC	w_i
1	5.159	−0.922	0.011			−0.007	0.031	0.006	7	6395.2	0.00	0.879
2	5.159	−0.838	0.010			−0.007	0.033		6	6400.4	5.32	0.061
3	5.159	−0.763	0.009		−0.002	−0.008	0.033		7	6401.8	6.58	0.033
4	5.159	−0.811	0.010	−0.001		−0.008	0.033		7	6402.3	7.03	0.026
5	5.159	−0.474							3	6573.8	178.60	<0.001
$w_+(j)$			1.00	0.03	0.03	1.00	1.00	0.88				

Note: Comparison of an intercept model and those models with ΔAIC <7 containing explanatory variables related to vegetation structure and soil in the abundance part (λ) of a hierarchical distance sampling model. The detection part of the model did not contain any variables, hence only the intercept (σ) is reported.

Abbreviations: AIC, Akaike criterion; ΔAIC, Difference of the model AIC to the AIC of the best model; w_i, Akaike weight; $w_+(j)$, Variable importance; Cov_art, Wormwood cover (*Artemisia* spp.) cover; Cov_fest, Fescue cover (*Festuca valesiaca*) cover; Cov_grass, total grass cover; Cov_bare, cover of bare ground; mean_vegH, mean vegetation height; sand, Sand content in the soil.

TABLE 4 Comparison of an intercept model and those models with ΔAIC <7 containing explanatory variables related to vegetation composition as a proxy for fodder quality in the abundance part (λ) of a hierarchical distance sampling model.

	Intercept (σ)	Intercept (λ)	Lignin (λ)	Lignin^2 (λ)	N (λ)	N^2 (λ)	Richness (λ)	df	AIC	ΔAIC	w_i
1	5.158	−5.820	1.267	−0.078			0.019	6	6515.6	0.00	0.436
2	5.158	−5.759	1.213	−0.074	0.083		0.021	7	6516.2	0.50	0.340
3	5.160	−5.607	1.201	−0.073	0.081	0.009	0.020	7	6517.1	1.34	0.223
4	5.159	−0.474						3	6573.8	58.44	<0.001
$w_+(j)$			1.00	1.00	0.33	0.22	1.00				

Note: The detection part of the model did not contain any variables, hence only the intercept (σ) is reported.

Abbreviations: AIC, Akaike's information criterion; ΔAIC, Difference of the AIC to the AIC of the best model; w_i, Akaike weight; $w_+(j)$, Variable importance; Lignin, Palatability measured as lignin content; N, Plant nitrogen content; richness, Plant species richness on plot level.

proximity to anthropogenic infrastructure (wild predators tend to avoid them, Kerven et al., 2021), their density is limited by the extreme scarcity of food resources. Contrastingly, cattle are herded or freely roam within much larger distance (ca. 5–10 km) from the settlements (Kamp et al., 2012). This promotes a moderate grazing pressure at about 6 km from the settlements where sheep/goat grazing intensity decreases, but the proportion of cattle is high. We did not have enough data to estimate the effects of horse grazing, but we expect them to have similar positive effects, as at our study site as in many areas of Kazakhstan horses are freely roaming in small groups at large distances from the villages providing low and medium grazing pressure.

The negative impact of fire frequency on squirrel abundance might again be explained by a change of vegetation structure. More frequently burnt areas at our study site were associated with low grazing pressure and grass-dominated communities (Freitag et al., 2021), which are avoided by squirrels. The fodder quality in such habitats likely is also limited, as squirrels usually prefer more palatable plants with high specific leaf areas and leaf nitrogen content such as *Poa bulbosa and Artemisia spp.* over bunch grasses such as *Festuca valesiaca* and *Stipa* spp. with low nutritional value due to high leaf dry matter content and low leaf nitrogen content (Freitag et al., 2021). As other burrowing small mammal, yellow ground squirrels themselves enhance the occurrence of ruderal plants with higher nutritional value by regular topsoil disturbance and inputs of nitrogen in available forms (e.g., ammonium and nitrate ions) from their excretion products. A similar enrichment of ruderal species could also be found by Valkó et al. (2021) for the vegetation of steppe marmot burrows in Kazakhstan.

Studies that investigate habitat preferences of social, burrowing mammals on different spatial levels are generally rare, with the macro-habitat level dominating (Kostelnick et al., 2007; Olimb et al., 2022). Similar to our results, an effect of grazing intensity on ground squirrel abundance through a change of vegetation structure was also shown for upland habitats in Saskatchewan, Canada (Bylo et al., 2014). Vegetation structure (plant height and cover of bare ground) and composition (palatability, cover of forbs) had a high importance in black-tailed prairie dog (*Cynomys ludovicianus*) habitat selection in Mexico (Avila-Flores et al., 2010) and golden-mantled ground squirrels (*Callospermophilus lateralis*) in Colorado, USA (Aliperti et al., 2022).

Across the Eurasian steppes, livestock numbers increased steadily in Soviet times since the 1930s, and numbers peaked during the late 1980s (Kamp et al., 2016). The collapse of the Soviet Union resulted in a sharp decline of livestock populations in the 1990s, as the transition from a state-controlled to a market economy meant a collapse of the state farming systems, and as animals were used as a trade currency by the rural population in times of economic hardship: in Kazakhstan, sheep declined from 36 million animals in 1990 to 9.5 million in 1998 (−73%) and cattle from 9.8 million to 4.0 million (−60%, Kamp et al., 2016). Populations of the most important wild grazer, the Saiga Antelope *Saiga tatarica*, also collapsed in the 1990s (decline of 96%, Milner-Gulland et al., 2001). This massive loss of grazing animals in less than a decade resulted in a very large decrease of grazing pressure across the Eurasian steppe (Dara et al., 2020) and was mirrored in adjacent regions of Russia (Dubinin et al., 2010). The lack of grazing over vast areas resulted in biomass accumulation that provided fuel for an increased fire frequency with wildfires burning over huge areas (Brinkert et al., 2016; Dubinin et al., 2011; Freitag et al., 2021). Frequent fires created feedback loops and lock-in stages (Freitag et al., 2021), i.e. where fires burnt frequently, woody plants and annuals disappeared and were replaced by tall-growing grasses, that in turn accumulated more fuel for new fires (Freitag et al., 2021). We here provide first quantitative evidence that this increasing grass dominance in the steppes might have affected burrowing animals, as these seem to avoid ‘undergrazed’ areas of high fire frequency. The mentioned processes have happened over millions of square kilometres from the Caucasus to the Altai mountains (Kamp et al., 2020) and would have resulted in massive population declines of ground squirrels and likely other important burrowing mammals.

We suggest that the described changes in small mammal populations might have affected ecosystem functioning considerably. Small, burrowing, colonial mammals are keystone species regarding trophic interactions (Davidson et al., 2012). The yellow ground squirrel is the main prey of several apex predators, and some of these such as the Steppe Eagle *Aquila nipalensis* (now Endangered on the IUCN red list) have been strongly declining after the collapse of the Soviet Union (BirdLife International, 2022). Equally important, small mammals are important ecosystem engineers on the steppe, and their burrowing activities are important for the carbon cycle and promote plant and insect biodiversity (Valkó et al., 2021). A decline of the yellow ground squirrel could have affected the availability of flowering plants for pollinating insects, as shown for steppe marmots (Valkó et al., 2021). As the described changes in grazing and fire have happened over millions of square kilometres, these changes might have affected ecosystem functioning on a continental scale.

The described changes have several implications for conservation. Restoring natural grazing to reduce fuel load on the steppe and inhibit high fire recurrence rate are crucial. Indeed, conservation efforts to restore Saiga antelope populations in Kazakhstan are successful (Knight, 2022). Similar efforts are currently being made to bring back extinct grazers such as Kulan (*Equus hemionus*) (Kaczensky et al., 2021). A second lever to steer fire frequency is the grazing of domestic animals (Dubinin et al., 2011). With an increasing demand for meat, and a stabilization of the agricultural sector in Kazakhstan, domestic livestock numbers are now recovering (Kerven et al., 2021; Robinson et al., 2017). We here show that free-ranging livestock at intermediate densities (likely mirroring traditional grazing systems) is important for the health of the steppe ecosystem. This suggests that incentives to keep the traditional, socio-ecological grazing systems of rural Kazakhstan alive will provide large benefits for biodiversity and ecosystem functioning. Conservation policies should therefore provide incentives for this type of grazing and avoid subsidizing feedlot-based livestock systems that are currently on the rise in some regions (Dara et al., 2020). Interestingly, a mitigating effect of increasing numbers of free-ranging livestock on fire frequency seems already visible (Hao et al., 2021). Livestock managers should be encouraged to graze steppe at intermediate densities, to avoid overgrazing and ‘undergrazing’. Finally, Kazakhstan currently sees a strong increase in sheep numbers, but a less clear increase in cattle numbers. Cattle grazing has sometimes been shown to provide larger biodiversity benefits (Tóth et al., 2018), so agricultural, and perhaps conservation policies, should also promote free-ranging cattle and horse rather than sheep grazing. Active suppression of fire ended across vast areas of Kazakhstan as these became depopulated (Baumann et al., 2020) and fire services collapsed due to the economic collapse of the Soviet Union in 1991. A revival of fire monitoring and combat in Kazakhstan seems necessary for some areas, but much more difficult to implement in comparison to fire-suppressing livestock management. However, a close monitoring of grazing pressure, fire patterns and biodiversity responses is much needed across the Eurasian steppes, ideally combining remote sensing (Dara et al., 2020), socio-economic (Kerven et al., 2021) and ecological fieldwork.

4.1 | Methodological implications of the distance sampling approach

Visual counts were shown to be a good rapid means for monitoring populations of ground squirrel and prairie dogs (Menkens et al., 1990), although often the results of such assessments are biased low and represent rather indices of abundance (Corlatti et al., 2017). Distance sampling may increase the accuracy of such estimates as it accounts for detection probability, but has so far only rarely been used for social, burrowing mammals. A few distance sampling assumptions were likely difficult to meet in our case (Buckland et al., 2004). The degree of violation varies in our study (Table S3). Measures of exact distances as required in distance sampling methodology can be difficult to obtain in flat, uniform grassland areas without structures that can be used to point laser range finders at, and some animals would remain hidden behind vegetation or belowground. To overcome this, observers may decide for counting only visible individuals, or using interval measures instead of raw distances to account for vocalizing animals also, which would also mitigate of ‘heaping’ we encountered (Table S3, Figure S3). Extended waiting time before starting counts and the use of playback of social calls to stimulate emergence from burrows may significantly increase detection probability (Downey et al., 2006). Finally, squirrel social behaviour might vary depending on habitat type, land use and colony size (Sharpe &

Van Horne, 1998). Extending the work to other habitats and land-cover types might increase the precision in abundance estimation. Our distance-sampling-based densities were close to the density estimates produced with more traditional methods such as winter burrows entrance counts in early spring in similar habitats in Kazakhstan (Sludsky, 1969). We are therefore confident that the patterns we describe here are robust.

5 | CONCLUSIONS

We here provide the first quantitative evidence that post-Soviet changes in grazing and fire regimes have strongly affected the abundance of small mammals, over very large areas and with important implications for ecosystem functioning. Given that the steppes of Kazakhstan are a global hotspot of bioturbating mammals (Beca et al., 2022), our results seem globally relevant. We could further show that habitat selection by small, burrowing, social mammals is driven by factors acting on several spatial levels. Our research therefore closes an important research gap in the old-world grasslands. However, we only scratch the surface: The implications of changing land use, ecosystem properties and disturbance regimes are still not understood for the majority of the taxa inhabiting the vast steppes of Eurasia. It is largely unclear, how interactions between abiotic drivers such as grazing and fire, and biotic processes such as competition and predation affect biodiversity. An improved monitoring of biodiversity and ecosystem processes is much needed to inform conservation and guide practical management and agricultural policies across the vast Eurasian steppes.

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CONFLICT OF INTEREST

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The dataset collected for this research is available from the Dryad repository: https://doi.org/10.5061/dryad.q83bk3jn5

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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