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Review

Collapse and recovery of livestock systems shape fire regimes on the Eurasian steppe: a review of ecosystem and biodiversity implications

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Abstract

Shifts in fire regimes can trigger rapid changes in ecosystem functioning and biodiversity. We synthesize evidence for patterns, causes and consequences of recent change in fire regimes across the Eurasian steppes, a neglected global fire hotspot. Political and economic turmoil following the break-up of the Soviet Union in 1991 triggered abrupt land abandonment over millions of hectares and a collapse of livestock populations. The build-up of vegetation as fuel, rural depopulation and deteriorating fire control led to a rapid increase in fire size, area burned and fire frequency. Fire regimes were also driven by drought, but likely only after fuel had accumulated. Increased fire disturbance resulted in grass encroachment, vegetation homogenisation and decreasing plant species diversity. Feedback loops due to the high grass flammability are likely. Direct and carry-on effects on birds, keystone small mammals and insects were largely negative. Nutrient cycling and carbon balance changed, but these changes have yet to be quantified. The regime of large and frequent fires persisted until ca. 2010, but shifted back to a more grazing-controlled regime as livestock populations recovered, reinforced by increasing precipitation. Key future research topics include the effects of future climate change, changing pyrodiversity and pyric herbivory on ecosystem resilience. Ongoing steppe restoration and rewilding efforts, and integrated fire management, will benefit from a better understanding of fire regimes.

Keywords: burned area, fire frequency, pyrodiversity, restoration, rewilding, burrowing mammals

1. Introduction

Fire is an important driver of the evolution, structure and functioning of ecosystems (Keeley & Pausas 2022) and their biodiversity (He et al. 2019). In the Anthropocene, fire regimes, i.e. the timing, location, frequency, and size of fires, are changing (Kelly et al. 2023, Sayedi et al. 2024). Fire as a disturbance agent has become more intense and widespread due to human activity, including in ecosystems that were historically neither fire-prone nor fire-adapted (Kelly et al. 2020). Climate change modulates ignition and fuel flammability (Liu et al. 2010, Jones et al. 2022). Land-use change drives changes in fuel availability, with declines in fuel e.g. through increasing livestock grazing pressure, and increases where land is abandoned (Pausas & Fernández-Muñoz 2012). These processes contribute to abrupt changes in fire regimes (Pausas & Keeley 2014), including their intensification in some parts of the world (Grau-Andrés et al. 2024), and a decrease in fire disturbance in others (Kelly et al. 2023, Sayedi et al. 2024).

Wildfires can trigger feedback loops (e.g. via fire-related greenhouse gas emissions, alteration of carbon stocks and changed land surface albedo) that accelerate climate change (Sommers et al. 2014). Changing fire regimes have important implications for biodiversity, ecosystem resilience and functioning, as well as human livelihoods. It is important to understand fire regime shifts to develop policies for human adaptation, climate change mitigation and biodiversity conservation (Kelly et al. 2023).

Recent advances in mapping changing fire regimes, and their implications for humans, ecosystems and biodiversity, were largely concentrated in fire-prone systems, such as the Mediterranean or savannas in Africa and Australia. Conceptual advances were often also tested in very restricted areas despite their global importance in changing socio-ecological systems. An example is “pyric herbivory”, i.e. interactions between fire and grazing by wild and domestic ungulates (Fuhlendorf et al. 2009).

As most grasslands globally, the Eurasian steppes, grasslands stretching from Eastern Ukraine to the Altai mountains over a belt of 4000 km, have evolved and been shaped by grazing and fire (Feurdean & Vasiliev 2019). They are one of the “hottest fire hotspots” globally, as fires are frequent, intense and large compared to other global hotspots (Archibald et al. 2013, Kelly et al. 2023). Fire regimes were partly shaped by humans over at least the past 1000 year in the steppe (Leys et al. 2018, Rudaya et al. 2020), and there is evidence for fire as a tool for pasture management by nomadic tribes since the 18th century (Smelansky et al. 2015). However, fire disturbance was especially dynamic over the past 40 years, with a rapid increase in the 1990s and a more recent decrease in fire area and frequency. New regional fire hotspots created by the Russian invasion into Ukraine and associated land abandonment add to the current dynamics (Yailymov et al. 2023).

Despite its global importance, changes in fire regimes across the Eurasian steppes and their ecosystem implications remain patchily studied and poorly synthesized. This is unfortunate as the area comprises a massive proportion of the worlds intact grasslands (Scholtz & Twidwell 2022), still holds extensive, low-input, socio-ecological pastoralist systems (Kerven et al. 2021), harbours many globally threatened and often endemic species (Kamp et al. 2016), provides opportunities for ecosystem-scale restoration and rewilding (Baumann et al. 2020) and contributes extensively to global food security (Wesche et al. 2016).

We systematically reviewed the literature and data to answer three main research questions: (1) How have fire regimes changed across the Eurasian steppe since 1980? (2) What were the drivers of observed changes? (3) How do grassland fires, and changes in fire regimes, affect biodiversity and ecosystem properties?

2. Study region and methods

We constrained our review to the Eurasian steppes, grasslands stretching from Eastern Ukraine to the Altai mountains characterized by frequent, intense and large fires (Archibald et al. 2013; Yin et al. 2021; Kelly et al. 2023, Supplementary Online Material, Fig. S1–S4). Nearly all of the Ukrainian steppe was converted to cropland already in the 19th century, therefore most fires now originate from stubble burning. In contrast, across Kazakhstan and the adjacent Russian steppes, large expanses of natural grasslands still exist, often bordered by secondary grasslands on abandoned cropland (Lesiv et al. 2018, Fig. S5). Here, fires are much larger than in Ukraine. We excluded the Asian steppes in Siberia, Mongolia and China, because they differ strongly in climate and biotic composition (Wesche et al. 2016). In Mongolia and China, but not in the steppes of Russian Siberia, high livestock densities largely suppress fire (Loboda et al. 2012; Hao et al. 2021). We also included the semi-deserts (Olson et al. 2001) in European Russia and Kazakhstan, as these are part of the global fire hotspot (Shi & Touge 2022) and form a gradual transition zone from steppe to desert vegetation in Central Asia (Wesche et al. 2016, Fig. S2). We here consider the period 1980 to 2023, because of especially rapid and abrupt land-use change on the steppes and perceivable climate change.

We conducted a systematic review following Foo et al. (2021). We formulated research questions, followed by a scoping search, literature mapping and a tailored, iterative, scoping-based literature search, including forward and backward searches. We also searched Russian-languages sources and reviewed data on land use (trends in arable land and livestock numbers) and fire patterns. For details on the methods see Text S1.

3. Fire regime change 1980 to 2020

Fire regimes are characterized by fire size, fire interval (recurrence rate), seasonality, intensity, and spread pattern (horizontal vs. vertical, Krebs et al. 2010). Fire area and fire size across the steppes of Kazakhstan were rather stable during the 1980s until ca. 1995 (Bhagwat et al. 2024, Fig. 1), but increased rapidly and abruptly in the late 1990s. A high-intensity regime persisted until ca. 2005 (Kazakhstan), but burned area decreased again from 2005 to 2015 (Fig. 1). In the Russian steppes, the period of high fire intensity lasted until ca. 2010 (Smelansky et al. 2015; Pavleychik et al. 2022). Global maps suggest an increase in burned area from 3.79 to 15.5 Mha^{-1} across the steppes in the late 1990s (Mouillot & Field 2005). Regionally, increases in burned area in the mid-1990s were extreme. In the Russian dry Volga steppes, the area burned was virtually zero in the period 1985–1995, but increased dramatically to 20% of a 19,000 km^2 study area between 1996 and 2007 (Dubinin et al. 2010). Fire return rates increased to every two to three years in some areas, and ca. 30% of local hotspots burned every five years or more often (Shinkarenko 2015). Across Northern Kazakhstan, the area burned increased sevenfold, and the number of fires eightfold between 1990 and 2000. Between 2000 and 2016, the number of fires declined slightly, but the very large size of fires remained stable, especially in steppe grassland (Dara et al. 2020b). In Western Kazakhstan, fire frequency was ten times higher in 2001–2010 compared with 1986–2000 (Pavleichik & Sivokhip 2023; Shinkarenko et al. 2023). In steppes of the Russian Altai, the number of fires and fire areas continued to increase until 2014, with a decrease in fire interval (Ponomarev et al. 2016).

The rapidly increasing trend in burned area was reversed around 2005 (Fig. 1). Between 2002 and 2016, the total area burned declined by 53% in Northern Eurasia, with grassland fires accounting for 93% in this trend; Kazakhstan contributed 47% of the total area burned and 84% of the decline (Hao et al. 2021; Yin et al. 2021). A decreasing trend in burned area was also observed on the meadow steppes of European Russian and Western Siberia in 2000–2021 (Bondur et al. 2022).

Fire seasonality follows a bimodal pattern. In April and May, relatively small and localized fires occur in agricultural areas of the more productive steppes due to stubble burning (Nemkov & Sapiga 2010; Dara et al. 2020b). From July to October, large fires of up to 500,000 ha burn especially in the steppes in the south of the study region, where the plant biomass is dry and highly flammable due to more arid climatic conditions (Dubinin et al. 2010; Dara et al. 2020b; Bondur et al. 2022). These patterns are also traceable in the atmosphere from black carbon emissions, with a clear peak in May and two later peaks in August and October (Hao et al. 2016). The decrease in fire area between 2003 and 2015 went along with decreasing black carbon emissions across the Eurasian steppe between 2003 and 2015 (Hao et al. 2016).

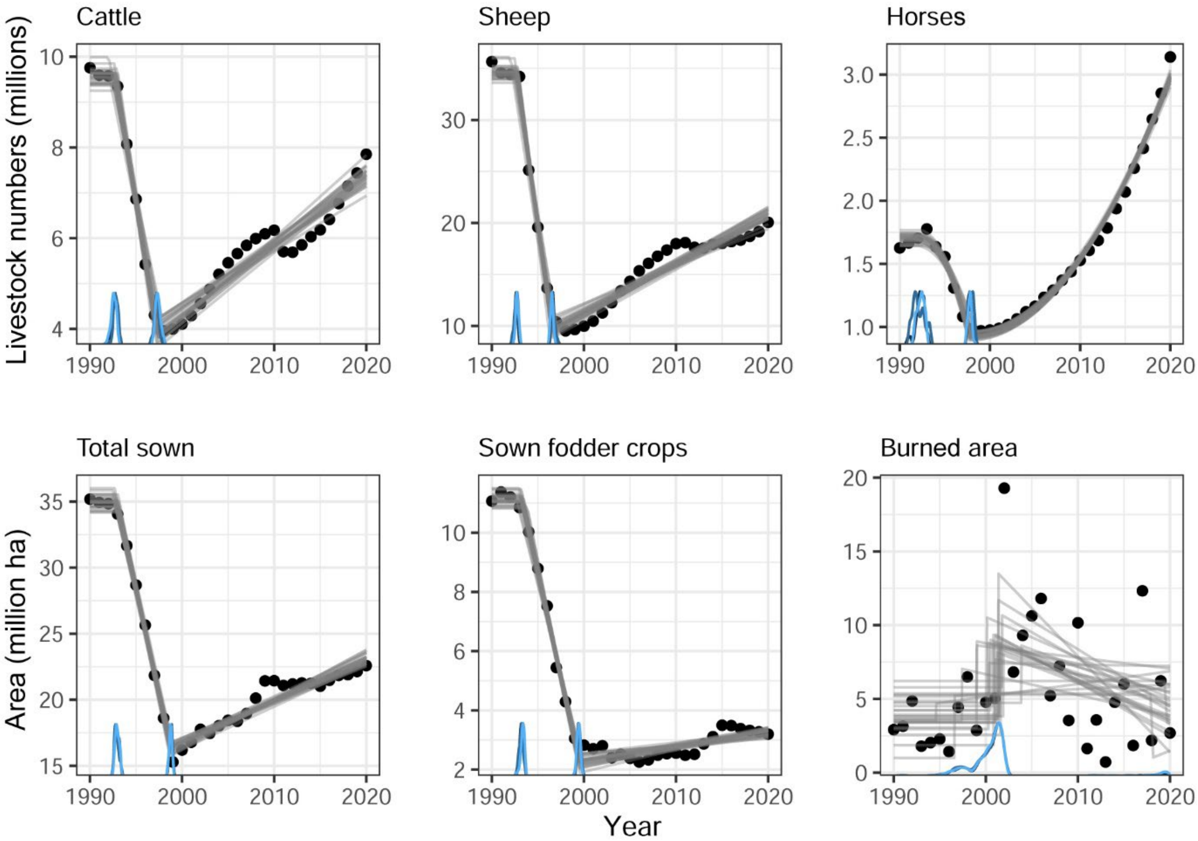

Figure 1: Livestock numbers and sown area across Kazakhstan, and mapped burned area across the forest steppe, steppe and semi-desert ecozones of Kazakhstan (based on AVHRR and MODIS products, 1990 to 2020). Black dots are raw data, grey lines are fitted partial regression lines drawn randomly from the posterior distribution (illustrating uncertainty in the predictions), blue lines are the posterior density of estimated change points (cf. Text S1 for methods).

The coupling of temporal and spatial changes in fire regimes (”pyrodiversity”) can also change overall landscape diversity and heterogeneity, which drives e.g. biodiversity (Jones and Tingley 2022). Changes have seldom been mapped over larger areas, but an analysis for the Western Palearctic suggested that the steppe biome had a much higher pyrodiversity than any other biome (Pausas 2022). Pyrodiversity effects on ecosystem functioning and biodiversity have rarely been studied, especially outside North America and Australia, and in grasslands. Across our study area, pyrodiversity, measured as the Shannon diversity H′ in time since last fire across 15 x 15 km grid cells (cf. Text S1), was 0.60 ± 0.003 SE across the study region in 2001 to 2010, a period with high fire disturbance. It declined to 0.38 ± 0.002 SE in 2011 to 2023, when fire disturbance was much lower (Fig. 2).

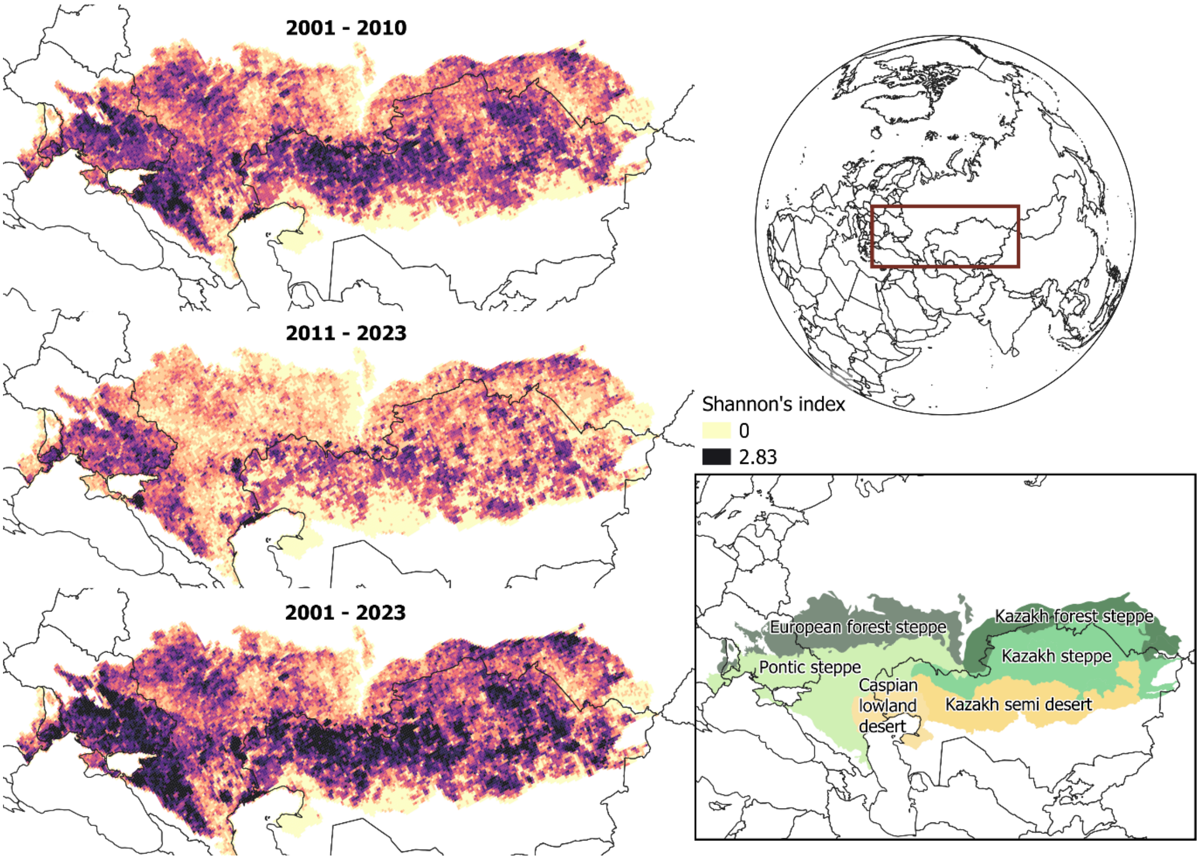

Figure 2: Pyrodiversity in 15 x 15 km grid cells across the study region (inset, main ecozones after Olson et al. 2001). Pyrodiversity is displayed as the Shannon diversity in fire frequency across all 500 x 500 m MODIS burned area product pixels per 15 km grid cell for the periods 2001–2010, 2011–2023. Darker colours indicate a higher diversity. Cf. Text S1 for methods.

4. Drivers of changing fire regimes

4.1 Land-use change

The increase in fire disturbance during the 1990s was largely caused by land-use change following the break-up of the Soviet Union in 1991 (Dara et al. 2020a; Pavleichik & Sivokhip 2023; Shinkarenko et al. 2023). The transition from a state-controlled, socialist, to a free market-economy meant the collapse of state farms over the entire area of the Russian and Kazakh steppes in the early 1990s (Fig. 1). This loss of rural infrastructure and employment triggered massive rural outmigration (Baumann et al. 2020). Both processes resulted in the abandonment of 40–60 million ha cropland across the former Soviet Union (Lesiv et al. 2018). At least 12 million ha (ca. 50% of the Soviet-period cropland) were abandoned across the Kazakh steppes around the year 2000 (Fig. 1, Fig. S5) and similar amounts across the Russian steppes, making the former Soviet Union a global hotspot of cropland abandonment (Daskalova & Kamp 2023).

Along with the crumbling state farms and rural outmigration, populations of domestic grazing livestock also collapsed (Robinson & Milner-Gulland 2003; Kerven et al. 2021, Fig. 1) and left vast expanses of steppe pasture abandoned (Dara et al. 2020a). Widespread poverty during the 1990s increased poaching pressure on Saiga Antelope *Saiga tatarica,* leading to a population decline from > 1 million in 1990 to a mere 30,000 animals (Milner-Gulland et al. 2001) and a further reduction of grazing pressure on the steppe.

The increase in area burned and fire frequency in the early 2000s was attributed to a build-up of flammable biomass on abandoned pastures and cropland through vegetation succession: Four to six years after destocking, accumulated fuel increased fire frequency across the Russian steppes (Nemkov & Sapiga 2010; Dubinin et al. 2011) and Western Kazakhstan (Pavleichik & Sivokhip 2023). Low grazing probability was strongly associated with high fire disturbance and in the Kazakh steppes: field data suggested that where grazing intensity fell below a threshold of ca. 250 dung piles/ha, fire frequency would increase fivefold (Freitag et al. 2021). Firefighting systems deteriorated in the 1990s due to a lack of funding and lack of infrastructure after the collapse of the state farms (Smelansky et al. 2015). Overall, a transition from a grazing-dominated to a fire-driven disturbance regime has been suggested for the 1990s (Dara et al. 2020a, Freitag et al. 2015).

The increase in fire area and fire return interval was reversed in the mid-2000s (Fig. 1), albeit not to Soviet-period levels. Total burned area decreased on the Eurasian steppes in the period

2002 to 2016 (Hao et al. 2021). This was related to decreasing net primary productivity, likely due to increasing biomass consumption by recovering livestock numbers (Fig. 1, Hao et al. 2021; Kolluru et al. 2022). Across Kazakhstan, rapid declines in cattle, sheep and horse numbers as well as area sown set in in 1992/1993, but were reversed already in 1997 to 1999, albeit slowly (Fig. 1). Horse numbers increased strongly since 1998 (Fig. 1), mirrored by a reactivation of horse pasture over large areas (Kolluru et al. 2023), but cattle and sheep numbers are still much lower than in Soviet times before 1990, which explains the delayed response of fire regimes (Dara et al. 2020b). In Russia, fire disturbance declined less, and later, as livestock numbers have not recovered yet (Pavleychik et al. 2022).

4.2 Climatic changes

Climate is an important determinant of fire regimes globally: Increasing aridity and decreasing precipitation can lead to vegetation changes with more flammable biomass (Jones et al. 2022). Increasing temperatures, often coupled with decreasing precipitation, increase "fire weather", i.e. periods of a high probability of ignition.

In Kazakhstan, where the largest steppe fires occur (Fig. S3), annual mean air temperature increased by ca. 2 °C with a strong increase in extreme temperatures in the period between 1941 and 2011, whereas there was only a weak decreasing trend in precipitation (Salnikov et al. 2015). More recently, in 1980 to 2015, temperatures increased especially in the western part, whereas precipitation increased over most of Kazakhstan (Schierhorn et al. 2020).

Across Kazakhstan, the total area burned per year was significantly negatively correlated with precipitation, soil moisture and relative humidity. It was positively correlated with the frequency of hot days during the burning season, from June to September (Xu et al. 2021). These results stem from simple annual correlations. However, the study period, from 1997 to 2016, covers both the rise and decline of the intensive fire regime and might therefore hint to some climatic influence independent of land use. In the Russian steppes, in addition to a lack of grazing, the increase in fire area in the 1990s was correlated with high temperatures in August leading to drought and high availability of dry biomass, but associations were much weaker than those with grazing parameters (Dubinin et al. 2011).

For the period 2002 to 2016, there was a statistically significant interaction of climate and land use (Hao et al. 2021): burned area decreased where precipitation increased, but this was moderated by livestock density. The area burned was unaffected by grazing intensity in dry years, but in wet years with high amounts of biomass, higher grazing intensity was associated with less burned area.

In summary, the steppe fire regime seems to have been fuel-limited in Soviet times due to higher livestock density, but became somewhat more sensitive to climate after number of native and domestic ungulates collapsed in the early 1990s. Such patterns have also been observed elsewhere, e.g. in the Western Mediterranean Basin (Pausas & Fernandez-Muñoz 2012).

5. Fire impacts on ecosystem properties

5.1 Vegetation and plant communities

The collapse of wild and domestic ungulate populations in the early 1990s resulted in the build-up of massive amounts of fuel across the Kazakh and Russian steppes (Fig. 2): Tall-growing stands of highly flammable grasses developed, together with thick litter layers, a condition that allows ignition and rapid fire spread (Simpson et al. 2016; Pausas et al. 2017). The resulting increase in fire size and frequency on abandoned pasture and cropland, led to a decline of annuals, woody forbs and dwarf shrubs (especially *Artemisia* spp., Freitag et al. 2021). Vast, homogenous expanses of grass developed, dominated by often only one or two species, especially *Stipa lessingiana, S. sareptana, S. capillata, Agropyron cristatum* and *Leymus ramosus*, peaking in the early 2000s when the fire regime was most intense. Grasses recover quickly on burned areas in comparison to forbs, due to increased post-fire nutrient mobilisation (Gabbasova et al. 2019), and litter accumulates within a few years (Dusaeva et al. 2019). The cycle of fast grass and litter recovery, new ignition and vegetation homogenisation has likely led to a feedback loop on the steppes that allows large, grassy areas to persist (cf. Bowman et al. 2014).

Grass encroachment, structural and functional simplification and declining plant species richness at high fire frequency were also observed across the western Eurasian steppes, e.g. in Crimea (Kobechinskaya & Andreeva 2018), the Volga area (Ryabinina 2018; Ilyina et al. 2021) and the southern Ural steppes (Anilova et al. 2011; Dusaeva et al. 2019). Grass encroachment supresses the establishment of woody plants in the forest steppe (Khanina et al. 2018; Ilyina et al. 2021).

The resistance, resilience and temporal stability of vegetation structure and plant community composition at different fire frequencies has not been studied extensively. On abandoned cropland restoring back into steppe, in the absence of grazing and following grass encroachment, fire might delay restoration to steppe plant communities (Brinkert et al. 2016).

In the more productive Ukrainian steppes, the cover of vascular plants recovered within a year, whereas the cover of mosses and plant litter remained sparse for four years (Polchaninova et al. 2019).

In the dwarf shrub-dominated semi-deserts of Kazakhstan, recovery trajectories seem to differ from the grassy steppes: species richness and α- diversity of plants were twice as high in the first three years after fire compared to controls that had not burned for at least 35 years, but declined again from year 8 to 30 (Lednev et al. 2021). Here, fire disturbance creates vegetation heterogeneity, as a dense, closed sagebrush canopy is removed by fire, allowing for colonization of annuals and seed germination from the soil seed bank (Lednev et al. 2021).

5.2 Soil properties, carbon stocks and biomass

The change from a grazing-dominated to a fire-driven regime had likely important implications also for soil, biomass and carbon stocks. Fire promotes bare ground, resulting in an increase in topsoil temperature amplitude and transpiration. Soil moisture is reduced during the first three years after steppe fires (Pavleichik & Myachina 2016; Pavleichik et al. 2020), e.g. up to 30% in the 0–30 cm soil layer in the Orenburg region of Russia (Galaktionova & Vasilchenko 2019). This affects the movement and chemistry of soil solutions: Soluble salts, carbonates, and sulfate concentrations increase in the upper layer of the soil profile, with phosphorus and potassium contents returning to the level at control sites three years after a steppe fire (Galaktionova & Vasilchenko 2019). Grass litter burns almost completely, but restores 3–4 years after fire (Dusaeva 2022). Similar recovery times in soil characteristics, i.e. humus, black carbon, pH, and soluble salts were found in the dry steppe of Southern Ukraine (Morgun & Ushacheva 2008). In the Trans-Urals area of Russia, fire effects were restricted to the uppermost horizon of 0–5 cm soil depth, where soil pH, organic carbon, nitrogen, plant available phosphorous and potassium, and exchangeable base cations such as sodium and calcium increased (Gabbasova et al. 2019). These effects were still visible two years after fire. Enzyme activity declined after fire but restored within less than a year. In summary, fire leads to short-term fertilization effects, allowing fast and dense regrowth of grasses.

Regular fires cause gaseous losses of carbon and nitrogen, with an estimated global average carbon loss of 18% under repeated grassland fires (Pellegrini et al. 2022). For the western Eurasian steppe belt, the recent decline in fire disturbance was predicted to result in carbon gains (Pellegrini et al. 2023). However, combustion-related carbon losses can partly be offset by the accumulation of pyrogenic carbon, with 8 to 17% in Chernozems and Kastanozems of southern Russia (Rodionov et al. 2006). The highest concentrations of pyrogenic carbon are found in a depth of over 50 cm, illustrating the important role of social, burrowing rodents that move carbon from the surface (where it is sensitive to combustion in during subsequent fire, Czimczik & Masiello 2007), to deeper soil layers. Direct carbon losses, accumulation of black carbon, and changes in bioturbation due to fire-induced declines of burrowing mammals (see 6.1) will have influenced the carbon cycle on the steppes during over the past 40 years, but the contributions of each effect remain largely unstudied.

5.3 Fodder quality

Feather grass *Stipa* spp. has a high fodder value in spring when leaves exhibit a high palatability and high nutrient contents. From June onwards, the nutritional value rapidly decreases due to high lignin and leaf dry matter content (Freitag et al. 2021; Koshkina et al. 2023) and the allocation of leaf nutrients such as N and P to the root system. The dominance of *Stipa* over large areas in the 2000s has likely reduced fodder quality, also because annual and biennal species declined where *Stipa* expands (Brinkert et al. 2016). As these ruderals have a high specific leaf area and high seed and leaf nutrient contents they have a high palatability and fodder quality. The currently observed recovery in wild and domestic ungulates (see 4.1) might therefore increase fodder quality in previously ungrazed areas, at least at moderate stocking densities.

6. Fire impacts on faunal biodiversity

6.1 Vertebrates

Small, social, herbivorous, burrowing mammals play an important role as ecosystem engineers in most grassland systems of the world (Davidson et al. 2012). A high fire frequency between 2000 and 2015 had a negative effect on the occurrence and abundance of Bobak Marmot *Marmota bobak* (Koshkina et al. 2020) and Yellow-ground Squirrel *Spermophilus fulvus* (Koshkina et al. 2023), and the latter species recovered in population density with progressing time after fire. The dense, homogenous grassy swards that dominate in areas of frequent fire (cf. 5.1) make movement difficult, decrease fodder palatability and plant nutrient contents and obstruct views, which increases predation risk by e.g. Steppe Eagles *Aquila nipalensis* foxes (Koshkina et al. 2023). In Mid-day Gerbils *Meriones meridianus*, the effects of pasture abandonment, including a fire-triggered shift to grass dominance, led to a population crash

(Tchabovsky et al. 2016). In birds, species richness and abundance were negatively related to high fire frequency, fire area and extent in 2009 to 2017 on moderately and ungrazed steppe, i.e. the steppe types with the highest fire frequency. There were more species with decreased abundance than those reaching higher abundances at high levels of fire disturbance. Fire legacy effects were detectable for at least eight years (Bhagwat et al. 2024). In contrast, bird responses were positively related to high burn frequency in semi-deserts (Bhagwat et al. 2024), as birds here might have profited from a higher heterogeneity in vegetation where fires occur (Lednev et al. 2021). Mechanisms behind negative responses to high fire frequency include habitat loss, e.g. in the globally threatened Great Bustard *Otis tarda* in the Russian forest steppe (Collar et al. 2017), and burning of nests in the globally threatened Steppe Eagle *Aquila nipalensis* as well as declines in small mammals, their main prey (Pulikova et al. 2021).

6.2 Invertebrates

The post-Soviet increase in fire disturbance was associated with a delince of specialist steppe invertebrate species and a reorganization of communities (Nemkov & Sapiga 2010): In the Russian steppes, the abundance of Tenebrionid and Carabid beetles did not change with increasing fire disturbance, but specialist species were replaced by generalists. The abundance of Curculionid beetles, Heteroptera, Spiders, Woodlice and Myriapods showed a strong decrease directly after fire suggesting negative effects of high fire frequency. An increase in fire size meant that there were less refugia left for these taxa in the period of frequent burning (Nemkov & Sapiga 2010). In meadow steppes of Russia, richness and activity density of ground-dwelling beetle species increased in the second post-fire year, while that of spiders decreased (Polchaninova et al. 2016). A comparison of burned and unburned steppe in eastern Ukraine suggested a decrease in abundance, but an increase in richness in spider communities immediately after fire, but also identified species that occur exclusively on burned sites. In the year after fire, diversity differences disappeared, but abundances remained lower at burned sites (Prokopenko & Savchenko 2013). Where fire intensity increased in the post-Soviet period, species richness decreased threefold after fire, but had recovered almost entirely after three years. Fire effects were positive for species preferring bare ground, but negative for litter dwellers and rare, range-restricted species (Polchaninova 2015). After a recovery period of five years, spider communities had largely reached pre-fire abundance, diversity and community composition, whereas abundance and diversity of ground-dwelling beetle communities remained significantly different from pre-fire communities with regard to trophic guild ratios and dominance structures (Polchaninova et al. 2019).

In summary, intensifying fire regimes have led to a taxonomic, functional and structural homogenisation of plant communities and vegetation. Animal communities at lower trophic levels (insects and spiders) seem to be impacted directly by fire, but often recover quickly, although changes in community composition occur. Small mammals and birds seem to suffer from intensifying fire regimes indirectly through vegetation homogenization. However, responses are often species specific and the available evidence is rather scarce, generalization therefore difficult.

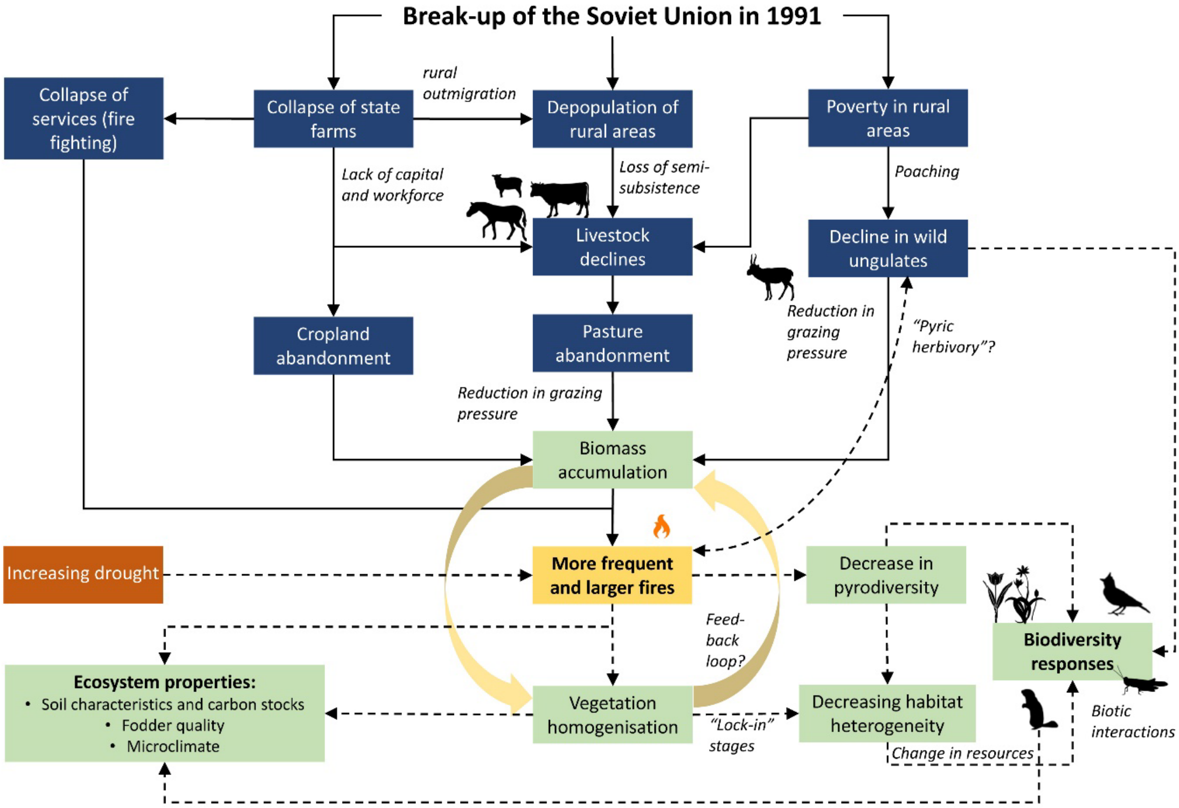

Figure 3: Processes, outcomes (boxes) and potential drivers (in italics) of increasing fire disturbance due to post-Soviet land abandonment between ca. 1995 and 2005 that persist across parts of the Eurasian steppe until today. Solid lines connect patterns that are supported by published evidence. For those linked by dashed lines, evidence is either scarce or hypothetical. Boxes in blue summarize socio-economic processes and outcomes, those in green biodiversity responses and ecosystem responses.

7. Discussion

We provide evidence that a period of extremely rapid decline in wild and domestic ungulates, caused by the collapse of the Soviet Union, triggered a regime shift towards a strong increase in fire disturbance on the Eurasian steppe during the second half of the 1990s, that persisted for at least ten years until recovery in livestock and increasing grazing pressure started controlling fire again. Fire regimes were additionally affected by increasing aridity and changes in precipitation, but likely only after changing land use allowed fuel to accumulate. This shift had largely negative consequences for ecosystem functioning, with vegetation homogenisation, biodiversity loss and community reorganization. We here outline important research gaps that our review identified, and suggest future research directions.

7.1 Baselines: historical fire regimes

Current fire management should operate from baselines informed by historical fire regimes (Gillson et al. 2019). Paleoecological evidence suggests that fire has been an integral part of the Mongolian steppes since the early Holocene (Leys et al. 2018), but a lack of charcoal remains points to fire suppression by a long grazing history, dating back at least to 1200, perhaps to 6000 years BP (Umbanhowar et al. 2009). Holocene fire disturbance levels are less clear for the Eurasian steppes, as the global charcoal database does not contain data from this ecoregion (Leys et al. 2018). Charcoal concentrations from the Russian forest steppe suggest a high fire frequency ca. 13,000 to 8,000 years BP (Lukanina et al. 2022). In the mountain steppes of Armenia, peaks of charcoal concentrations coincided with high grass pollen, peaks of low charcoal concentrations with high Chenopodiaceae pollen concentrations (Cromartie et al. 2020). Chenopodiaceae indicate grazed (and therefore fire-suppressed) steppe. A decline in Poaceae and an increase in Chenopodiaceae pollen since 4200 years BP (Cromartie et al. 2020) could point to early fire suppression, coinciding with the development of animal husbandry and mobile pastoralism on the Eurasian steppe (Hanks 2010). However, periods of abundant pollen grazing indicators and high charcoal concentrations overlapped in the Russian forest steppe (Lukanina et al. 2022).

In the 18th and 19th century, anecdotal evidence from narrative accounts of explorers and ethnographs suggests that fire was used by Kazakh, Nogai and Kalmyk tribes for pasture management and tactical warfare across the Eurasian steppes (Smelansky et al. 2015). Reports from the 1920s indicate that fire intensity increased during the period of Stalin's collectivisation and sedentarization of nomads, with associated famine and massive human outmigration to Mongolia and China (Kerven et al. 2021). This caused a collapse in livestock numbers in the same order as the post-Soviet changes we describe here (Kerven et al. 2021), but the consequences for fire regimes are unknown. The later Soviet period between 1950 and

1980 was characterized by low fire frequency and small fire size due to strict fire suppression and high grazing levels (Smelansky et al. 2015).

Taken together, fire regimes of the Eurasian steppes over the past centuries, but also on geological time-scales, seem understudied. More research on charcoal deposition seems necessary to establish fire intensity baselines. The results could then serve to model the effects of different fire regimes on the steppe ecosystem.

7.2 Understanding fire-grazing interactions for restoration and rewilding

Across the steppes of Russia and Kazakhstan, millions of hectares of cropland and pasture remain abandoned (Lesiv et al. 2018). For vast areas, it is still unclear when and to what extent land use will return due to a lack of infrastructure and ongoing human outmigration (Baumann et al. 2020). Here, considerable potential for ecosystem restoration and rewilding exists (Baumann et al. 2020). Currently, 'passive rewilding' (du Toit and Petorelli 2019), i.e. the absence of human restoration interventions, prevails on abandoned land. We have shown here that the continued lack of grazing and the associated intensification of fire regimes has likely had negative ecosystem consequences. It might therefore be more desirable to follow two potential pathways to rewilding: i) a reintroduction of large herbivores to their native range with management tapering out over time ('active rewilding' *sensu* du Toit and Petorelli 2019), ii) an expansion of traditional livestock grazing systems into abandoned pasture areas that mirror grazing intensity and patterns of native grazers (partial restoration).

Large efforts towards active rewilding are already being made in Kazakhstan. Saiga antelopes have recovered from an all-time low of ca. 30,000 animals in 2002 to a population of ca. 1.9 million in 2023 due to better protection (Krivosheyeva 2023). Depleted and extinct large herbivores such as Kulan *Equus hemionus* and Przewalski's horse *Equus przewalski* are reintroduced (Kaczensky et al. 2021). In contrast, the future of free-ranging livestock production is unclear across the steppes, and livestock systems might intensify, with free-ranging grazing systems transitioning to feedlot-based production (Dara et al. 2020a).

It seems timely to study the implications of these various strategies in an integrated fire management approach: Assessing detrimental and benign effects of fire, weighting benefits and risks and responding appropriately and effectively based on predefined objectives Wollstein et al. 2022). Acknowledging the strong fire-grazing interaction in the system, this could be implemented through the lens of "pyric herbivory" (Fuhlendorf et al. 2009): Herbivores prefer nutrient-rich and palatable biomass, which is available after a certain time has passed after fire. Animals move to find patches with optimal foraging conditions, and, through their grazing, affect the build-up of new biomass, which in turn affects ignition probability.

Land management strategies should therefore i) quantify the scale and spatio-temporal pattern (incl. pyrodiversity, see section 3 above) of pyric herbivory with the help of remote-sensing data on fire and tracking data on wild and domestic herbivores; ii) quantify ecosystem resilience, i.e. determine recovery times and baselines, quantify potential feedback loops (see 5.1.), and establish grazing levels to halt these; iii) develop scenarios of varying fire frequencies, grazing intensity levels and their interactions that maximize biodiversity, ecosystem functions, and fodder quality for livestock and, iv) integrate Protected Areas into rewilding strategies as a strict prohibition of grazing has led to increased fire activity (Pavleichik & Chibilev 2018).

7.3 Climate change impacts on fire regimes

Our review suggests that climate change has been affecting fire regimes on the Eurasian steppe, but likely only after fuel accumulation due to declining grazing pressure. Several future scenarios seem plausible: A further recovery of wild and domestic grazers would reduce fuel loads, therefore minimizing the impact of climate on fire regimes. In contrast, a stagnation of agricultural reclamation would mean a continued high load of flammable biomass on abandoned cropland and pasture.

A stronger than global mean warming trend is predicted for Central Asia until the end of the century, with increasing drought in summer, but also increasing spring and summer precipitation (Jiang et al. 2020). Drought events are predicted to become more frequent, with longer duration, higher severity and intensity (Guo et al. 2022). Current and future climate change patterns are highly variable across the steppes (Schierhorn et al. 2020). This already translates into variable regional change in vegetation cover, the area of green and the area of photosynthetically active vegetation (Lewinska et al. 2023). Given this large number of potential levers of biomass availability, flammable vegetation development and fire weather, predictions of future fire regimes are difficult: for the Eurasian steppes, they range from an expert-based likelihood of < 50% of *any* regime shift by 2100 (Sayedi et al. 2024) to a prediction of 3 % to 13 % increase in burned area by 2080 (Zong et al. 2020).

Adaptive fire management on the steppes would therefore benefit from the consideration of interacting climate change and land-use scenarios, and more regionalized efforts to model the effects of predicted climate change. Ideally, this would also be combined with a spatial assessment of ignition risk: most fires in the area are of anthropogenic origin (Smelansky et al. 2015, Nemkov & Sapiga 2010), and this is driven by socio-economic developments such as recolonization of recultivated areas, or continued outmigration.

7.4 Armed conflict

In addition to socio-political shocks such as the collapse of the Soviet Union, warfare and armed conflict can affect land-use decisions and trajectories (Yin et al. 2019, Olsen et al. 2021). The exact consequences of conflict for land use (Baumann & Kuemmerle 2016), fire regimes and biodiversity (Hanson 2018) are poorly understood, but there is evidence that warfare impact overruled climate in controlling fire regimes along the Silk Road in China and Central Asia over the past 2000 years (Zhang et al. 2023). The Russian war against Ukraine since February 2022 has resulted in an increase in fires, and warfare concentrates in the steppe ecozone. War-related land abandonment has affected ca. 8% of the cropland in 2022 alone (He et al. 2023), led to biomass accumulation and provides fuel for fire. Ignition happens through shelling and artillery combat. In 2023, over 40% of the fires were on grassland (including abandoned cropland), mostly in the steppe ecozone (Tomchenko et al. 2023). In July 2022, more than 100,000 ha were burning (Yailymov et al. 2023), incl. repeated, large fires in Protected Areas in the steppe zone. In contrast to Kazakhstan and parts of Russia, only tiny, fragmented steppe grasslands remain in Ukraine due to widespread transformation into cropland (Fig. S5). The change in fire regimes in natural grasslands will therefore have a disproportionately large effect on ecosystems and biodiversity at the westernmost part of the steppe zone, which merits more research on potential consequences. This is even more important as the war effects will add to the long-term legacies of the collapse of the Soviet Union, and therefore provide a perspective on linked, legacy-driven fire disturbances.

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Data and code availability

All bibliographic data, livestock and fire data as well as Google Earth Engine and R-scripts to reproduce the analyses and figures are available at https://doi.org/10.5281/zenodo.12609025.

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SUPPLEMENTARY ONLINE MATERIAL

Review

Collapse and recovery of livestock systems shape fire regimes on the Eurasian steppe: a review of ecosystem and biodiversity implications

Johannes Kamp, Tejas Bhagwat, Norbert Hölzel, Ilya Smelansky

Supplementary figures S1 to S5

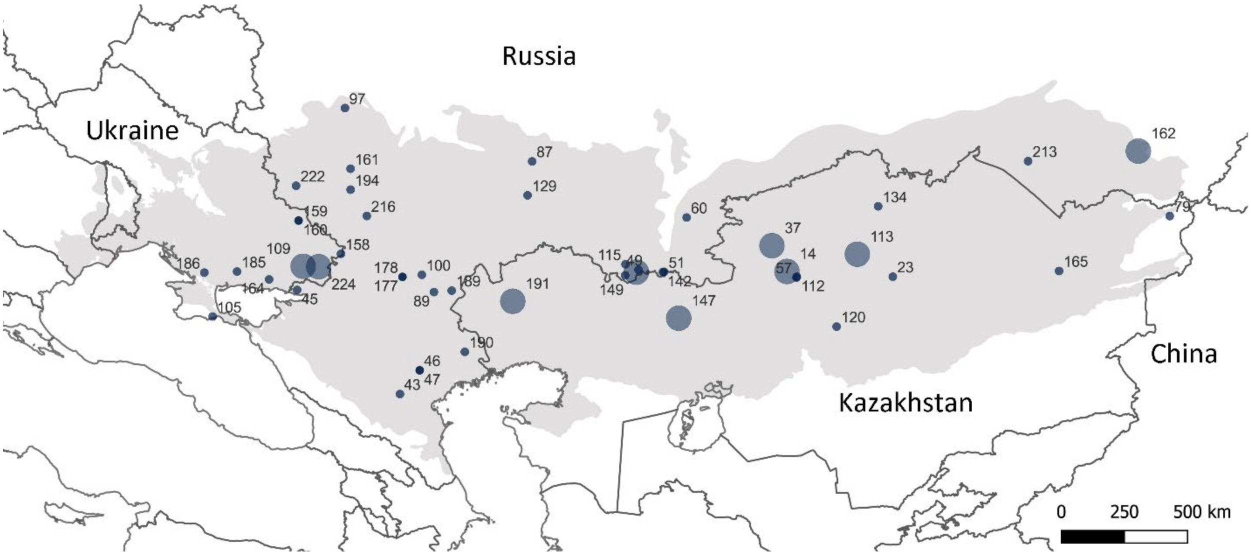

Figure S1: Study region comprising the Eurasian steppes and adjacent semi-desert ecotones. Numbers refer to published case studies from which information was used in the review and correspond to the list of references provided as data table. Large circles indicate studies that were conducted over larger areas, e.g. an entire province. Map projection: EPSG 3576, tilted -35°.

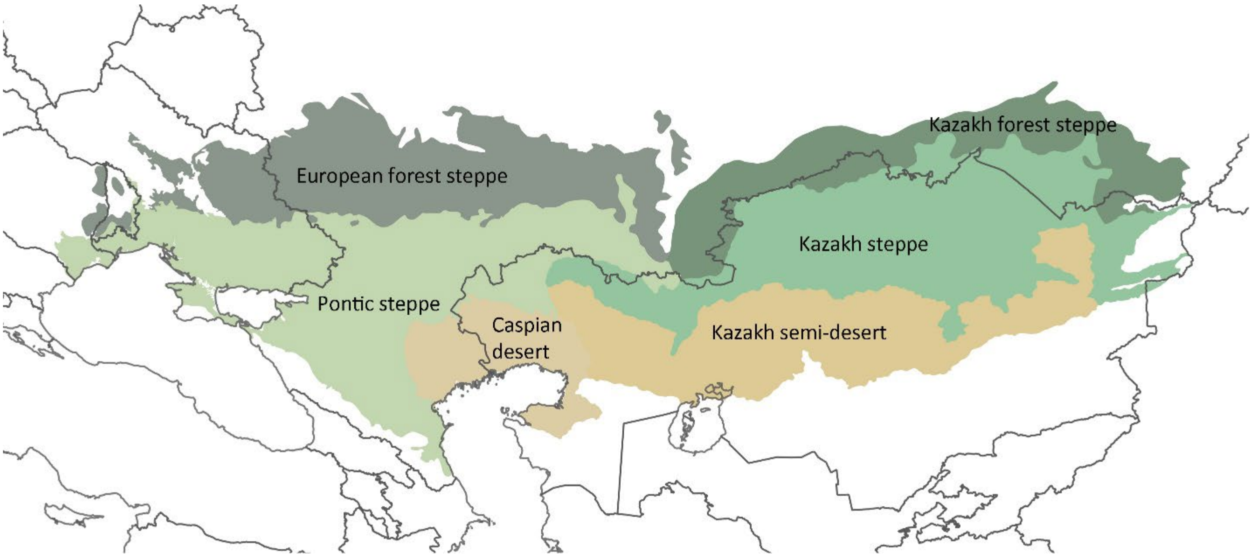

Figure S2: Summarized major ecoregions in the study region, based on the finer delineation in Olson et al. (2001) that separates Altai montane forest steppe, East European forest steppe, Kazakh forest steppe, South Siberian forest steppe, Kazakh steppe, Kazakh upland, Pontic steppe, Altai steppe and semi-desert, Caspian Lowland desert and Kazakh semi-desert.

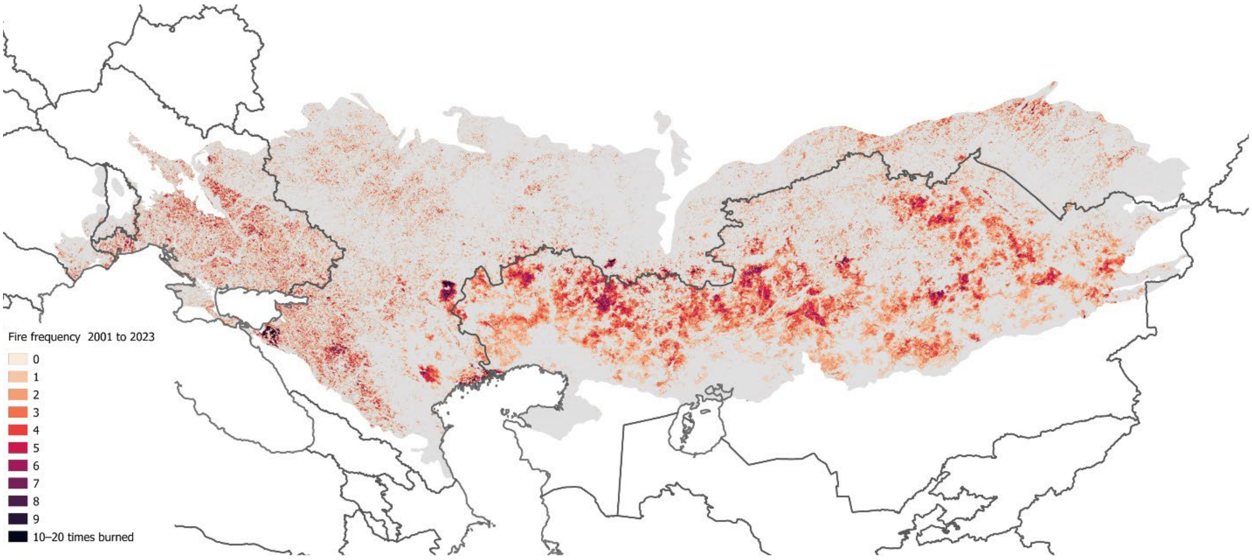

Figure S3: Fire frequency 2001–2023, calculated from the MODIS burned area product (MCD64A1, Collection 6, see below for details).

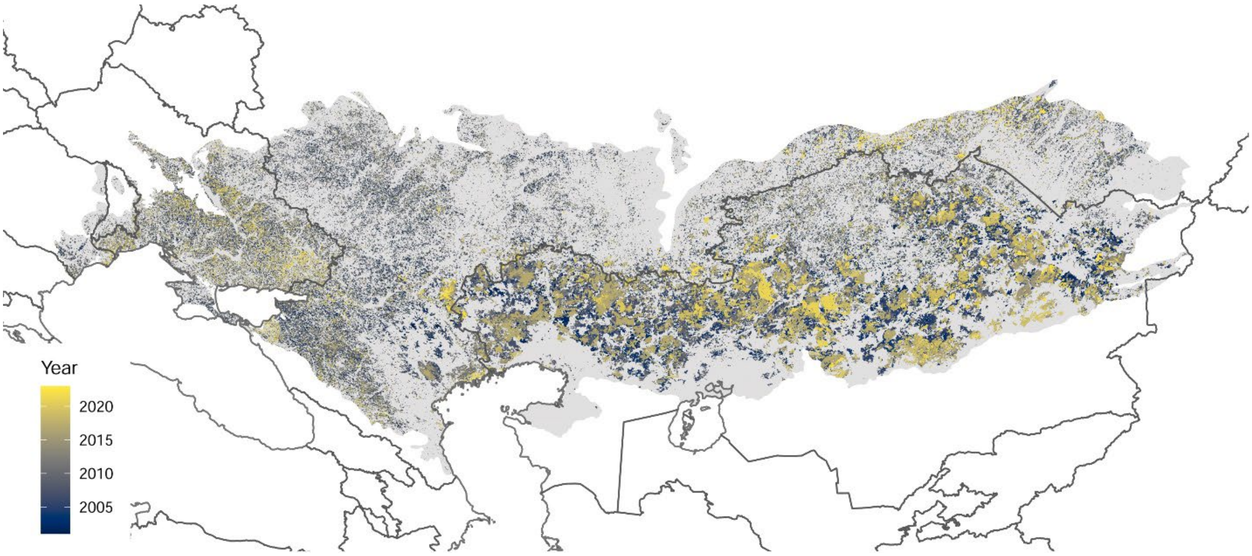

Figure S4: Time since last fire for the period 2001–2023, calculated from the MODIS burned area product (MCD64A1, Collection 6, see below for details).

Figure S5: Used and abandoned cropland (not pasture) across the study region in ca. 2016, plotted from open access data in Lesiv et al. (2018). Brown = active cropland, green = abandoned cropland. Note that cropland abandonment was far less widespread in Ukraine compared to Russia and Kazakhstan, and that less uncultivated steppe vegetation remains in Ukraine. This has implications for fire regimes (cf. main text).

Supplementary Text S1: Methods

1. Literature review

We conducted a systematic review, largely following guidance by Foo et al. (2021). We outline the steps in the following.

Question formulation

After several rounds of iterative scoping searches and mapping of the literature, we arrived at three main questions, that we maintained as central for the review:

- How have fire regimes changed across the Eurasian steppe in the period 1990 to 2020?
- What were the drivers of observed changes?
- How do grassland fires, and changes in fire regimes, affect biodiversity and ecosystem services?

Scoping search and literature mapping

We first conducted a scoping search on Web of Science with a relatively broad string, using the main focal terms combined with the geographical scope of our review:

> *fire AND (steppe OR grassland OR semi-desert) AND (Kazakh* OR Russia* OR Siberia* OR Ukraine*)*

As this returned many papers on fire in geological history, we added the exclusion term "*NOT (Holocene OR glacial)*" before searching again. We set time period for papers to 01/01/1990–23/11/2023, the day of the search, as we were mostly interested in recent changes, and those that occurred due to the massive political and societal change triggered by the collapse of the Soviet Union in 1991.

We received 166 results. These were downloaded as BibTex file (incl. abstracts), cleaned, filtered for stop-words and visualized with bar-charts (e.g. most common journals, authors and number of publications by year) and a word-cloud using R package "wordcloud" 2.6 (Fellows et al. 2018). "Forest" was the most common term returned, as research on forest fires dominates in Siberia, and grassland fires have received relatively little information. However, excluding "forest" from the search resulted in a loss of 80% of the papers, including those that dealt with "forest steppe", which was of interest to us. We therefore decided to filter papers on forest fires manually later. After removing general terms such as "fire", "steppe" and "burning", we manually categorized the word-cloud terms into three categories: “drivers”, “ecosystem properties” and “biodiversity”.

Table S1: Categorization of common terms from the word cloud into drivers, ecosystem properties and processes and biodiversity

Drivers	**Ecosystem properties and processes**	**Biodiversity**
Climate	Carbon	Plants
Dynamics	Soil	Community
post-Soviet	Vegetation	Larch
Land-use	Emissions	Pine
Grazing	Aboveground	Arthropods
Permafrost thaw	Biomass	Fauna
Management	Degradation	Birds
History	Tree	
Trends	Litter	
Protected	Organic matter	
Drought	Buds	
Pyrogenic	Seed bank	
Disturbance	Seeds	
Cropland	Nitrogen	
Restoration	Woody	
Shrub encroachment		

Literature search

Based on our scoping, we developed the final search terms. Our initial screening suggested that major drivers of fire patterns and change therein were climate and land use, that most studied ecosystem processes were related to soil, vegetation, biomass and soil organic carbon, and that biodiversity featured only with rather general terms.

We developed two final search strings. The first one contained country name, grassland terms, fire terms and a variety of terms on potential drivers of changing fire regimes. The second one was identical, but the driver terms were replaced with terms on biodiversity and ecosystems properties. For both search terms, we first compared several combinations of increasing complexity based on their hit rate (precision, percentage of relevant records), and the miss rate (the percentage of known relevant records that are not found in the search), and the total number of records retrieved. We used 20 relevant papers known to us from previous research (50% with involvement of first author JK) to establish miss rates for different combinations of search terms. When a balance between precision and miss rate was reached, and the total number of records stabilized at between 170 and 200, we decided to use these search terms as the final strings for Web of Science:

> (*Kazakh* OR Russia OR Siberia OR Soviet) AND (grassland OR steppe OR forest steppe OR semi-desert) and (fire OR wildfire or burn*) AND (climate OR land use OR grazing OR pasture OR abandonment OR herbivor*) NOT (Holocene OR glacial)*

and

> *(Kazakh* OR Russia OR Siberia OR Soviet) AND (grassland OR steppe OR forest steppe OR semi-desert) and (fire OR wildfire or burn*) AND (biodiversity OR ecosystem service* OR bird* OR mammal* OR insect* OR arthropod OR plant* OR vegetation OR biomass OR nutrient* OR carbon OR soil) NOT (Holocene OR glacial)*

The first string resulted in 109 found papers, the second one in 137. Adding “change” or “dynamics”, and removing “forest” or “boreal” decreased the number of results, but increased omission errors. Removing the first part of the search string, the geographical names, increased the number of search results to over 6,000, but with an estimated 90% originating from research in North America and Australia. We downloaded results for both search terms as BibTex files (incl. abstracts). We combined them and deleted duplicates in R package revtools 0.4.3 (Westgate 2019). This resulted in 148 papers in the combined dataset, suggesting again that some search saturation had been reached.

We screened the abstracts using function “screen_abstracts” in package revtools, we then excluded papers from the dataset that concerned studies not conducted in our defined study area, not during the chosen study period, or studies for which the title or abstract suggested no relevance for our review. We retained all other papers (n = 58) that seemed informative to answer our initial questions.

Due to known biases and inadequacies (Gusenbauer & Haddaway 2020), we did not use google scholar as a primary search engine, but conducted an additional search, because we assumed that google scholar would pick up additional useful references. We used the same search strings as for the Web of Science search (see above), and stopped after the first 200 papers retained by google scholar, as results were becoming hardly relevant afterwards with regard to our inclusion criteria (see above). We retained, using the abovementioned filter criteria, 131 papers.

To obtain references that were missed so far, we used a backward search to download the reference lists of the selected papers, and a forward search to identify papers that cited selected, important papers. We used the R package citation chaser (https://estech.shinyapps.io/citationchaser/, Haddaway et al. 2022) to generate citation networks, and identify especially influential papers (characterized by a high number of citations in the field and a high centrality). We identified 54 additional papers that were considered useful for the review, including papers that were found using citation chaser, and those that were found using manual screening of the reference lists of published, influential papers.

After the completion of the Web of Science search, the google scholar search and the backward-forward search, we again deleted duplicates using R package revtools. We screened the abstracts of these papers and retained again only those that i) met our filter criteria with regard to study region and study period, and ii) were considered informative for answering the main questions of the review. We obtained a total of 229 papers, of which 143 were retained.

Because ignoring sources in languages other than English can lead to bias in meta-analyses (Amano et al. 2021), and because in Russia and Kazakhstan, Russian is still the *lingua franca* in research, we also searched the standard scientific Russian-language search engine http://www.elibrary.ru for papers in Russian. As this search engine cannot easily accommodate long search strings, we used simple combinations of two terms for (steppe) fire (степные й пожар or палы) and the major topics of this review, namely: динамика (dynamics), мониторинг (monitoring), биоразнообразие (biodiversity), почва (soil), климат (climate), землепользование (land-use), залежы (abandoned fields), скот (livestock), пастбище (pasture), растительность (vegetation) and экосистема (ecosystem). This resulted in 89 hits that were all screened and checked for useful information. We retained 23 of these papers that passed the abovementioned filter criteria.

In a final step, we screened the full-text of the 229 English-language and 23 Russian-language papers, and identified a total of 106 papers that contained useful information to answer our research questions. We extracted information from those papers that used scientific methods and did not consider more anecdotal reports. The BibText files documenting the search process and the final list of papers screened are available as online archive at https://doi.org/10.5281/zenodo.12609025.

2. Change-point analysis

We were interested to illustrate trends and changepoints therein of cropland area, livestock numbers (an indicator of grazing pressure) and total area burned. Since the hotspot of large, frequent fires emerging in the late 1990s was nearly exclusively within the borders of Kazakhstan (Fig. S3, S4), we downloaded and plotted the annual number of cattle, sheep and horses as well as the area sown for wheat and fodder crops across Kazakhstan from KazStat (Bureau of National statistics, Agency for Strategic planning and reforms of the Republic of Kazakhstan), accessed via https://stat.gov.kz/. For some provinces, livestock data was not available before 2000, we therefore sourced these data from the database in Hankerson et al. (2019). We also estimated the cumulated total annual area burned across the steppe ecozones of Kazakhstan (forest steppe, steppe and semi-desert), i.e. the part of the study region (cf. Fig. S2) that was situated in Kazakhstan (see below). We identified changepoints in positive or negative trends of the land-use variables and total area burned using change point analysis in R package mcp (Lindeløv 2020). This approach uses regression with one or multiple change points (mcp) between generalized and hierarchical linear segments, based on Bayesian inference. We used this method, as plots of the raw data suggested that the number of changepoints and the form of the regression line segments between them were relatively straightforward to define. Based on visual inspection and our prior knowledge, we defined three models:

- Model 1 was used for all land-use variables except horse numbers and had two changepoints. It started with an intercept-only segment assuming initial stability, followed by two joined linear segments that mirrored the period of post-Soviet decline and more recent recovery in cropland area and livestock numbers: Model1 = list(y ~ 1, ~0 + year, ~0 + year)
- Model 2 was used for horse numbers. Specifications were identical with that of model 1, but the third segment was assumed to be quadratic, allowing for a faster increase in horse number in the recovery period: Model2 = list(y ~ 1, ~0 + I(year^2), ~0 + I(year^2))
- Model 3 was used for burned area and had only one changepoint to avoid overfitting, and based on prior knowledge from the sources used for the literature review. It started with an intercept-only segment assuming initial stability and a disjoined second segment to accommodate the very rapid increase in burned area and the subsequent slower decrease: Model3 = list(y ~ 1, ~ 1 + year).

R package mcp uses WinBugs code and relies on Markov Chain Monte Carlo algorithms. We derived posterior distributions from three Markov chains with 9000 iterations each and used default priors. For details see Lindeløv (2020). We visually inspected the degree of mixing in trace-plots and assumed convergence if rhat values were 1.1 or lower (Table S2).

Table S2: Estimates for model of the changepoint models, separately for the five land-use variables and area burned. Mean is the posterior mean, lower and higher are the lower and higher quantiles of the highest-density posterior interval, Rhat is the is the Gelman-Rubin convergence diagnostic and n.eff is the effective sample size. Parameters as abbreviated as follows: cp_1 – changepoint at the end of the first segment, cp_2 – changepoint at the end of the second segment, int_1 – intercept in the year 1990, sigma_1 – a variance parameter initiated in the first segment, year_2 – the slope of variable year in segment 2, year_3 – the slope of variable year in segment 3.

	estimate for...	mean	LCrI	UCrI	Rhat	n.eff
Cattle numbers (million head)	cp_1	1993	1992	1993	1.0	103
	cp_2	1997	1997	1998	1.0	134
	int_1	9.61	9.22	9.99	1.0	322
	sigma_1	0.33	0.24	0.43	1.0	1858
	year_2	-1.29	-1.56	-1.07	1.0	57
	year_3	0.15	0.12	0.17	1.0	870
Sheep numbers (million head)	cp_1	1993	1992	1993	1.0	131
	cp_2	1997	1996	1997	1.0	136
	int_1	34.82	33.41	36.16	1.0	344
	sigma_1	1.17	0.86	1.51	1.0	2780
	year_2	-6.68	-7.67	-5.59	1.0	65
	year_3	0.46	0.39	0.53	1.0	893
Horse numbers (million head)	cp_1	1992	1991	1994	1.1	27
	cp_2	1998	1997	1998	1.0	50
	int_1	1.69	1.63	1.75	1.0	532
	sigma_1	0.06	0.05	0.08	1.0	2268
	year_2	-0.03	-0.04	-0.01	1.1	14
	year_3	0.00	0.00	0.00	1.0	114
Total sown (million ha)	cp_1	1993	1993	1994	1.0	93
	cp_2	1999	1998	1999	1.0	165
	int_1	34.88	34.08	35.72	1.0	345
	sigma_1	0.70	0.52	0.91	1.0	2269
	year_2	-3.22	-3.63	-2.84	1.0	57
	year_3	0.31	0.27	0.35	1.0	1068
Sown fodder crops (million ha)	cp_1	1993	1993	1994	1.0	94
	cp_2	1999	1999	2000	1.0	154
	int_1	11.14	10.79	11.46	1.0	332
	sigma_1	0.30	0.22	0.39	1.0	1825
	year_2	-1.41	-1.55	-1.25	1.0	73
	year_3	0.05	0.03	0.07	1.0	887
Burned area (million ha)	cp_1	2002	1994	2018	1.0	276
	int_1	3.58	0.76	6.65	1.0	778
	int_2	7.95	3.44	12.06	1.0	369
	sigma_1	3.74	2.66	4.87	1.0	1096
	year_2	-0.18	-0.51	0.11	1.0	475

3. Spatial fire patterns and pyrodiversity

We used freely available remote sensing data sets to identify and delineate current fire hotspots and describe trends in fire parameters and pyrodiversity. All spatial data were processed on the Google Earth Engine platform. We calculated two fire parameters across the entire study region: fire frequency, i.e. how often a certain pixel of our remote sensing layers burned in the period 2001 and 2023, and time since fire, i.e. the last year when a fire had been detected at a pixel. We calculated the metrics from the MODIS burned area product (MCD64A1, Collection 6 (Giglio et al. 2018; Boschetti et al. 2019). MODIS provides a burn date and burned area at a spatial resolution of 500 m on a monthly basis and is available only from 2001 onwards. We plotted the results as Fig. S3 and Fig. S4 using QGIS v 3.34.2. From the MODIS data, we also mapped the annual total burned area across that part of the study region that is situated in Kazakhstan (i.e. the fire hotspot *sensu stricto*) by summing up the area of all burned pixels per year (cf. main text, Fig. 1). As MODIS data reach back only until 2001, but as important changes in fire patterns happened from 1995 onwards, we additionally quantified the area burnt in the same area using advanced very high resolution radiometer (AVHRR) images, which have been suggested to detect steppe fires well (Dubinin et al. 2010). We used the FireCCILT11 product, which harnesses AVHRR data (resolution 0.05°, ca. 5 km).

We were also interested to explore patterns of **pyrodiversity** and change therein. We selected spatio-temporal diversity in fire frequency, because previous studies in the area have shown that both vegetation (Freitag et al. 2021) and higher trophic levels such as birds (Bhagwat et al. 2023) and mammals (Koshkina et al. 2023) react to fire frequency patterns. We overlaid a grid of 15 x 15 km onto the study region, a meaningful resolution for landscape-scale biodiversity responses on the largely homogenous steppe landscape.

We defined pyrodiversity as the Shannon diversity H´ of our MODIS-based fire frequency layer (Jones & Tingley 2022):

$$\boldsymbol{H}' = -\sum\nolimits_{i} \boldsymbol{p_i} * \ln \boldsymbol{p_i} \quad \text{with} \quad \boldsymbol{p_i} = \frac{\boldsymbol{n_i}}{\boldsymbol{N_i}}$$

Where p_i is the proportion of pixels of a certain fire class (1…n times burnt, 1…n years since fire of N total years) per each 15 km square. As we were interested in potential change in pyrodiversity, we also calculated the metric for the period of high fire activity 2001 to 2010, and for the more recent period of lower fire activity, 2011 to 2023.

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