PRIMARY RESEARCH ARTICLE

Post-Soviet shifts in grazing and fire regimes changed the functional plant community composition on the Eurasian steppe

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Abstract

Globally, grasslands are shaped by grazing and fire, and grassland plants are adapted to these disturbances. However, temperate grasslands have been hotspots of land-use change, and how such changes affect interrelations between herbivory, fire and vegetation are poorly understood. Such land-use changes are widespread on the Eurasian steppe, where the dissolution of the Soviet Union in 1991 triggered the abandonment of cropland and pasture on globally relevant scales. Thus, to determine how relationships between plant functional composition, grazing and fire patterns changed after the Soviet Union dissolved, we studied a 358,000 km^2 region in the dry steppe of Kazakhstan, combining a large field dataset on plant functional traits with multi-scale satellite data. We found that increases in burned area corresponded to decreases in livestock grazing across large areas. Furthermore, fires occurred more often with high cover of grasses with high leaf dry matter content and thus higher flammability, whereas higher grazing pressure favoured grazing-tolerant woody forbs and ruderal plants with high specific leaf area. The current situation of low grazing pressure represents a historically exceptional, potentially non-analogue state. We suggest that the dissolution of the Soviet Union caused the disturbance regime to shift from grazer to fire control. As grazing and fire each result in different plant functional compositions, we propose that this led to widespread increases in grasses and associated changes in steppe plant community structure. These changes have potentially occurred across an area of more than 2 million km^2, representing much of the world's largest temperate grassland area, with globally relevant, yet poorly understood implications for biodiversity and ecosystem functions such as carbon cycling. Additionally, future steppe management must also consider positive implications of abandonment ('rewilding') because reverting the regime shift in disturbance and associated changes in vegetation would require grazing animals to be reintroduced across vast areas.

KEYWORDS
disturbance, grassland, Kazakhstan, land use, Landsat, livestock decline, MODIS, regime shift

1 | INTRODUCTION

While climate and soil are the main factors that govern the broad-scale distribution of grasslands, the two main disturbances that control biomass consumption and vegetation structure in grasslands are grazing and fire (Bond & Keeley, 2005; Hempson et al., 2015). The interplay of both disturbance factors, referred to as 'pyric herbivory', is crucially important for creating and maintaining structural heterogeneity, a key factor of grassland biodiversity and functioning (Fuhlendorf et al., 2009). In natural grasslands, fires spread where herbivore pressure is low and fuel accumulates. As large grazers prefer freshly burned areas due to the higher nutritional value of the regrowth (Hempson et al., 2015), short-growing lawns are maintained for some time after a fire (Geremia et al., 2019) while fuel accumulates on unburned patches for future fires. Where these processes are balanced, a diverse mosaic of burned, grazed and old-growth patches is created (Fuhlendorf et al., 2009). Grasslands have been shaped by these processes for millennia, and plants have thus evolved a range of functional traits to cope with fire and grazing (Díaz et al., 2007; Keeley et al., 2011).

Nonetheless, naturally functioning grasslands are rare. In most of the world's grassland areas, grazing and fire patterns have been altered by humans (Archibald, 2016; Pausas & Keeley, 2014; Vannière et al., 2008), and over the past centuries much of the world's grasslands have been converted to cropland, especially in the temperate zone (Ramankutty & Foley, 1999) while the remaining grasslands are increasingly used as pastures (Ellis et al., 2013; Kuemmerle et al., 2013). In the late 19th century, the conversion of grasslands to cropland and the reduction of biomass fuel by grazing caused a strong decline in global biomass burning (Marlon et al., 2008). In fact, fire and grazing act as alternative agents that compete for biomass in grasslands (Bond & Keeley, 2005), as illustrated by the use of grazing as a fuel management tool (Davies et al., 2010). As attempts to restore 'pyric herbivory' suggest, the fire–grazing interplay shapes the structure and functional composition of grasslands (Fuhlendorf & Engle, 2004; Fuhlendorf et al., 2009). Yet, in many regions of the world, it remains poorly understood how changes in fires and grazing pressure interact and how these changes impact the functional composition of grassland vegetation.

We can start to understand the interplay of grazing and fire by analysing patterns in plant functional traits. On heavily grazed sites, plants must cope with repeated defoliation and trampling; thus, responses to grazing include a short, prostrate growth to avoid defoliation (Díaz et al., 2001), physical and chemical defences (e.g. Hartley & DeGabriel, 2016) or a short life cycle to ensure population survival (Díaz et al., 2007). Intensive grazing often suppresses tussock plants (Díaz et al., 2007) and favours annual plants and species with a high specific leaf area and high rate of regrowth. Plant responses to fire are diverse. Plants with high resprouting ability (e.g. grasses) have an advantage after fire by protecting buds belowground (Collins et al., 2012; Davies et al., 2012; Shryock et al., 2014; Spasojevic et al., 2010). Woody plants in fire-prone systems persist at the individual level due to resprouting or

at the population level by reseeding at long fire recurrence intervals (Clarke et al., 2013; Pausas & Verdú, 2005), but obligate seeding species usually decrease with frequent fires (Bowman et al., 2014; Pausas & Bradstock, 2007).

In grasslands, perennial grasses have a particularly high leaf dry matter content, thereby contributing to the accumulation of flammable biomass (Manea et al., 2015; Pausas et al., 2017; Simpson et al., 2016). Furthermore, due to various factors such as high fuel availability caused by fast regrowth of grasses after fire, higher litter accumulation and enhanced flammability of the dense grass swards, grass-dominated areas can show a high fire frequency in which fires spread over large areas (Bowman et al., 2014; Wragg et al., 2018). In contrast, where grassland vegetation is shaped by grazing, fires are suppressed, as grazers preferentially feed on grasses (Elson & Hartnett, 2017) and reduce overall fuel load. This results in a patchy vegetation structure that inhibits fire spread (Fuhlendorf et al., 2009; Hempson et al., 2015; Starns et al., 2019). Whereas grazers select plants based on nutritional value, fire favours flammable plants while suppressing fire-sensitive competitors (Bond & Midgley, 1995). As a result of the differing effects of fire and grazing disturbances on plant communities, changes in disturbance regimes should thus trigger profound turnover in plant functional trait composition and associated ecosystem properties in grasslands.

Knowledge on the impacts of large-scale changes in fire and grazing patterns on the functional composition and structure of grassland ecosystems is limited. In parts of Africa, abrupt declines in large herbivores have triggered widespread increases in savanna tree cover and major changes in vegetation structure (Daskin et al., 2016; Holdo et al., 2009). In temperate systems, fire suppression and increased grazing pressure can induce woody encroachment, which requires a targeted and sometimes drastic fire and grazing management to reverse or halt encroachment and restore a grass-dominated state (Briggs et al., 2005; Miller et al., 2017; Twidwell et al., 2016). Existing work from temperate grasslands, however, is heavily biased towards the North American prairies (e.g. Fuhlendorf et al., 2009), and changes in grazing and fire patterns across broader scales due to changes in land use remain rarely studied anywhere in the world.

Yet, a 'natural experiment' of large-scale and abrupt changes in fire and grazing patterns in temperate grasslands began upon the dissolution of the Soviet Union. During the 1990s, the former Soviet Union faced the most sudden and most widespread land-use change in the 20th century in the northern hemisphere (Ramankutty & Coomes, 2016). In particular, after the Soviet Union dissolved in 1991, the state farm system collapsed, which led to rural outmigration and large-scale abandonment of agricultural land (Kurganova et al., 2014). In parallel, livestock numbers declined drastically (Kamp et al., 2011; Robinson & Milner-Gulland, 2003). Grazing by private-owned livestock is now concentrated in areas close to intact settlements (Kerven et al., 2016a; Robinson et al., 2017) such that the declines in livestock left behind large areas of abandoned pastures, especially in more remote areas with deserted rural settlements (Dara, Baumann, Freitag, et al., 2020).

The collapse in livestock numbers and the associated increase in plant biomass likely caused an increase in fires on the steppes of Russia and Kazakhstan (Dara, Baumann, Hölzel, et al., 2020; Dubinin et al., 2011), which have recently become a global fire hotspot (Archibald et al., 2013). These are the same areas where overall grazing pressure has decreased massively (Dara, Baumann, Freitag, et al., 2020). Yet, there is substantial heterogeneity in both fire and grazing trends across the region (Hilker et al., 2014; Loboda et al., 2012), and it is poorly understood how regional-scale changes in grazing and fire patterns translate into changes in the functional composition of steppe vegetation and how this affects ecosystem processes such as carbon and nitrogen cycling (e.g. Jones et al., 2019; Pellegrini et al., 2018).

Results from other grassland areas such as the comparatively well-studied North American prairies cannot easily be transferred to the Eurasian steppe, as the steppe has a much longer history of domestic livestock grazing (Hanks, 2010). Furthermore, while C4 grasses dominate the North American prairies and subtropical/tropical grasslands, C3 grasses dominate the Eurasian steppe. As recent research has highlighted that the Kazakh steppe has faced widespread increases in burned area (Dara, Baumann, Hölzel, et al., 2020) and large-scale declines in grazing pressure (Dara, Baumann, Freitag, et al., 2020), here we combine these novel data sources with a large dataset of field-sampled vegetation, plant traits and soil data to determine the following:

1. the spatial relationships between changes in grazing and fire patterns across very large scales on the Eurasian steppe and
2. the impact of changing grazing and fire patterns on the functional composition of plant communities of the Eurasian steppe.

2 | MATERIALS AND METHODS

2.1 | Study area and grazing history

Our study area in central northern Kazakhstan spans from the dry steppe in the north to the semi-desert in the south (358,000 km^2, Figure 1). The climate is continental semi-arid. Annual precipitation amounts to about 200 mm in the south and 300 mm in the north. Mean temperatures range from −17°C in January to 22°C in July. Dominant soils are humus-rich Chernozem and Kastanozem and alkaline Solonetz soils. The vegetation is dominated by perennial plants, such as tussock grasses (*Stipa* spp., *Festuca valesiaca* and *Agropyron cristatum*) and wormwood (*Artemisia* spp.). While the northern steppes are richer in herbs, larger areas in the south are also covered by alkaline and salt-tolerant plants such as *Atriplex cana* or *Anabasis salsa*.

The Kazakh steppe has a long history of grazing and nomadic pastoralism. While large megafauna such as steppe bison (*Bison priscus*) went extinct in the early Holocene, wild horse (*Equus ferus*) and Kulan (*Equus hemionus*) persisted in small numbers until the 19th century. Today, Saiga Antelope (*Saiga tatarica*) is the last wild herbivore that ranges the Kazakh steppe (Pushkina & Raia, 2008). Between 3,200 and 2,300 BP and about 2,000 years after horse domestication, nomadic pastoralism developed (Hanks, 2010). Until the 1930s, pastoralists moved up to 700 km between summer pastures in the steppe in the north and semi-desert in the south. Collectivization between 1930 and 1933 forced the Kazakh people into sedentarization, after which 1.5 million Kazakh died in a famine and livestock numbers declined by 80% (Robinson & Milner-Gulland, 2003). After 1940, livestock numbers recovered and even exceeded numbers before collectivization. Soviet state and collective farms managed the livestock in a semi-nomadic
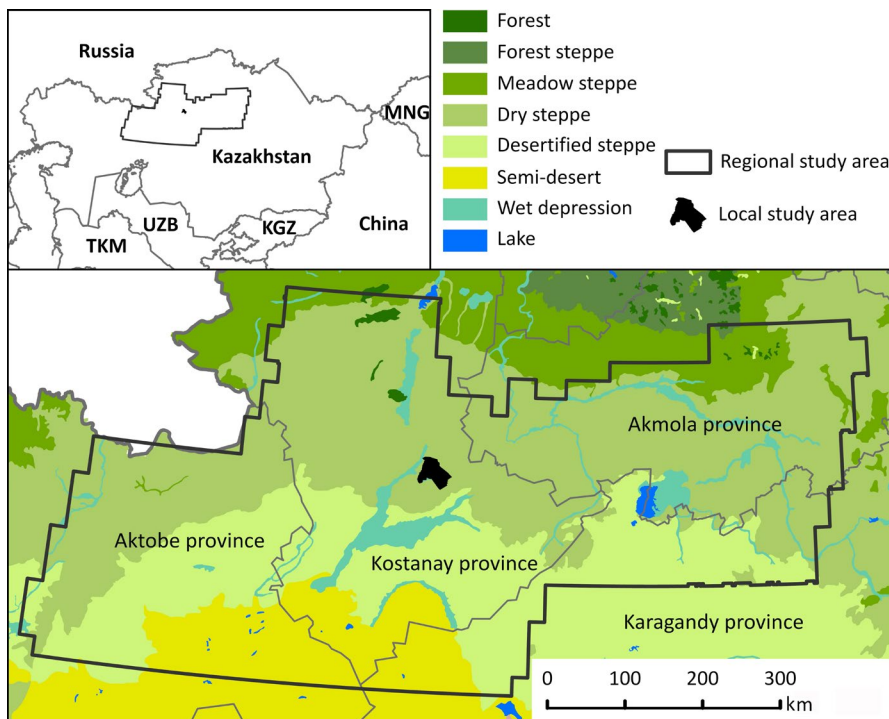
FIGURE 1 Overview of the location of the study area. We analysed fire and grazing patterns at the regional scale in four provinces in northern Kazakhstan, which span ecozones from the meadow steppe in the north to the semi-desert in the south. Especially in the Akmola province, large parts of the northern dry steppe zone consist of active or abandoned cropland. On the local scale, we analysed effects of fire and grazing on plant functional traits. Country name abbreviations in the top left refer to Kyrgyzstan (KGZ), Mongolia (MNG), Turkmenistan (TKM) and Uzbekistan (UZB). Ecozone data used with permission of the UNEP-GEF-WWF project Econet Central Asia

way, which partly reflected the movements in pre-Soviet times between summer and winter pastures (Robinson & Milner-Gulland, 2003).

However, after 1990, livestock numbers plummeted. Sheep numbers dropped from 33 million animals in 1992 to 8.7 million in 1999 and cattle from 9.5 million to 4 million animals (FAO, 2020). Horse and goat numbers declined less, but overall numbers are low compared to sheep and cattle. Since 2010, the numbers have begun to recover but are currently stagnant at less than 50% of the 1992 numbers. Today, most livestock is owned privately and kept in the vicinity of settlements year-round. In the dry steppe, cattle and sheep (sometimes including small numbers of goats in mixed herds) are mostly herded by local shepherds, while semi-wild horses roam unattended.

2.2 | Regional-scale livestock grazing and fire data

We used a spatial grazing pressure dataset for 1990 and 2015 from our own previous work (Dara, Baumann, Freitag, et al., 2020). Grazing probability was derived from a binary random forest classifier using several spectral indices based on Landsat imagery at 30 m resolution. The resulting maps were averaged across 3-year periods centred on 1990 and 2015 (Landsat Imagery available from the U.S. Geological Survey). Grazing probability was highly correlated with field-based data on grazing intensity (e.g. dung counts). We also used existing data on active and abandoned rural settlements and livestock stations from our own previous work (Dara, Baumann, Hölzel, et al., 2020) as a proxy for livestock distribution and compared the intactness of this livestock infrastructure to fire patterns (see Appendix S1).

To assess fire patterns, we used two complementary, satellite-based maps of burned area and fire frequency. First, we derived fire frequency (i.e. number of fires detected per 500 m pixel) and time since last fire from the MODIS burned area raster product (Roy et al., 2005) for the period 2000–2015. Second, to assess changes in burned area between Soviet times and today, we used burned area maps from our own previous work (Dara, Baumann, Hölzel, et al., 2020). Burned area was derived from Landsat imagery at 30 m resolution and summed across 3-year periods centred on the years 1990 and 2015. While the MODIS-based maps have the advantage of higher temporal resolution

and thus higher detectability of active fires, the Landsat-based analyses extend back to the Soviet period and include smaller fire scars. The Landsat-based maps in Dara, Baumann, Hölzel, et al. (2020) represent the most detailed remote sensing burned area dataset for the region, but they could not be derived continuously due to missing Landsat imagery. The maps had an overall accuracy of 96% for 2015, and fire patterns showed a high overlap with the MODIS data.

2.3 | Field data on plants

We collected field data on plant communities and soil characteristics on 204 plots in a study area near the village Stepnyak (1,018 km^2, 50.78°N, 65.06°E). We used a stratified randomized sampling design to cover the gradients of grazing intensity and fire frequency. We classified areas closer than 4 km to settlements as potentially grazed and other areas as potentially ungrazed based on livestock tracking data (Kamp et al., 2012). We classified all ungrazed areas as 'unburned' (no fires in 2000–2015 based on MODIS fire frequency data), 'rarely burned' (1–2 fires) and 'frequently burned' (>2 fires). We excluded wetlands and active or abandoned arable fields. We randomly placed 70 plots in the grazed strata and 50 plots each in the three ungrazed (unburned, rarely burned and frequently burned) strata, with a minimum distance of 500 m between plots. We could not access some plots, which decreased the final sample size to 66 plots in the grazed, 45 plots in the unburned, 45 plots in the rarely burned and 48 plots in the frequently burned strata (see Appendix S2 for an overview of the study area).

At each plot, the same two observers recorded the cover of all vascular plants and agreed on an estimate of the percentage cover for each species in a 10 m × 10 m quadrat from mid-May until mid-June 2016. Nomenclature follows Czerepanov (1995). We collected field data on plant functional traits that we assumed to relate to fire and grazing (Díaz et al., 2007; Shryock et al., 2014; Simpson et al., 2016; Table 1). In each plot, we measured the plant height of four individuals of each species that had at least 1% cover. Material for the leaf trait measurements was collected in the surrounding of the study area, in Kostanay province, in 2016. We arbitrarily collected fully developed leaves of at least four adult individuals per species.

TABLE 1 Overview of the plant functional traits used in the analyses. For height and leaf measurements, plants harvested across the study area were used (cf. Section 2)

Trait	Units/categories	Ecological meaning[a]
Canopy height	Maximum height of photosynthetic active leaves (cm)	Competitive advantage for light
Specific leaf area	Leaf area per dry mass (mm^2/mg)	Related to potential relative growth rate
Leaf dry matter content	Leaf dry mass per fresh mass (mg/mg)	Related to leaf life span and leaf toughness
Growth form	Dwarf shrub, herbaceous forb, woody forb, graminoid	Integrates physiological differences and life history, for example vulnerability of woody plant parts to fire
Life cycle	Annual/biennial, perennial	Representing population persistence and related to stress regime

[a]After Pérez-Harguindeguy et al. (2013).

Categorical whole-plant traits were assigned in the field or derived from Czerepanov (1995). For 92 of the 178 recorded species, a full set of traits was available. We restricted the trait-based analyses to 198 plots, for which the cover of species with trait information accounted for at least 80% of the total cover (Pérez-Harguindeguy et al., 2013).

As an indicator of grazing intensity, we counted dung piles of sheep, goat, cattle and horses (which are visible for about two grazing seasons) along a strip transect of 100 m length and 2 m width, centred on each plot (Brinkert et al., 2016). We recorded evidence of recent fires (e.g. the presence of charcoal in grass tussock bases) at each plot, and, where fire evidence was found but the plot was not classified as burnt in the MODIS product, we corrected fire frequency and time since fire using Bing/Google Earth images. On these high-resolution images, burnt areas are easily visible due to their dark colours that often change at sharp borders.

At each plot, we extracted soil samples of 3 cm diameter from two depths: 5–30 cm (3 cores) and 30–60 cm (1 core). Samples were mixed, air-dried and sieved to 2 mm. We measured pH in 5–30 cm depth in a 1:2.5 soil/distilled water solution and assessed sand content by sieving 10 g soil of depth 5–30 cm to 62 μm diameter. Soil electric conductivity—a measure of soil alkalinity—was measured in a 1:10 soil/distilled water solution and averaged over the two depth layers because we assumed soil electric conductivity to be more variable in depth.

2.4 | Regional-scale analysis

To analyse how changes in fire and grazing relate to each other at the regional scale—and thus to estimate the area over which these changes might have impacted plant communities—we relied on high-resolution maps of changes in livestock distribution and fire frequency and extent. For the purpose of our analyses, we aggregated all these maps to a common resolution of 3×3 km^2 (i.e. the Landsat-based, 30 m resolution grazing and burned area maps for 1990 and 2015). We calculated average grazing probabilities and the proportion of burned area within 3×3 km^2 cells for 1990 and 2015. Similarly, we also averaged MODIS fire frequency data within the 3×3 km^2 cells. Because we assumed patterns to be different in active or abandoned cropland due to different factors controlling fuel availability and structure, we restricted the maps to 3 km cells with at least 50% grassland. We determined the proportion of stable grassland (representing dry and desert steppe plant communities, see Figure 1) for each cell using a Landsat-based land-cover change map (Baumann et al., 2020). This land-cover change map had an overall accuracy of 86.3%.

Using these data, we first derived bivariate overlay maps of grazing versus fire indicators. Next, we performed an analysis of the spatial association between these parameters using the local indicator of spatial association (LISA) framework as implemented in GeoDa version 1.14.0 (Anselin et al., 2006); particularly, we used LISA to identify the direction and strength of local associations between Landsat-based grazing probability and burned area in 1990 and 2015 (and the 2000–2015 MODIS fire frequency). As a measure of local spatial association between grazing and fire indicators, we calculated Moran's *I*, a local

version of a global spatial correlation coefficient, for each cell using the eight surrounding cells in the grid (i.e. Queen's contiguity weight, first order; see Appendix S3 for comparisons with second and third orders). This yielded four clusters of spatially significant associations: high–high (high grazing probability—high fire frequency), low–low, low–high and high–low. The significance of associations here was tested using a Monte-Carlo permutation test ($N = 999$, significance level = 0.05).

2.5 | Local-scale analysis: Relationship between fire and grazing and changes in plant communities

All local-scale analyses were done in R 4.0.1 (R Core Team, 2020). We used generalized linear models (GLMs) to explore relationships between grazing intensity, grazer distribution and fire frequency for the 204 vegetation plots. We modelled grazing intensity (density of dung piles from field data) as a function of distance to settlement (incl. livestock stations) with negative binomial error distribution ($\theta = 2$) and fire frequency as a function of grazing intensity assuming Poisson errors. To test for thresholds of grazing intensity below which fire frequency would strongly increase, we conducted a segmented regression based on the aforementioned model. We used an iterative fitting procedure to estimate threshold location and a break in the grazing intensity parameter estimate in the *segmented* package (Muggeo, 2017) and selected the best-performing model based on AIC.

To examine gradients in the functional community composition, we performed a principal component analysis (PCA) on plant traits using the *vegan* package (Oksanen et al., 2019). We calculated community-weighted means of each trait weighted by the log-transformed species cover using the *FD* package (Laliberté & Legendre, 2014) and scaled all traits to zero mean and unit standard deviation. We correlated time since fire, fire frequency, grazing intensity (density of dung piles from field data) and soil properties (soil electric conductivity, pH, sand content) post-hoc with the PCA axis scores. Significance of correlations was tested with permutation tests ($N = 4,999$). To gain insight into gradients of species composition, we also carried out an analogous detrended correspondence analysis on species cover estimates (see Appendix S4).

To reveal effects of fire and grazing on traits, we fitted GLMs for each trait separately. Because substantial variance of fire frequency was explained by grazing intensity, we used the response scale residuals of fire frequency predicted by grazing (see analysis above) in our trait-GLMs; thus, we removed collinearity among predictors and disentangled the effects of fire and grazing on traits. We log-transformed grazing intensity and soil electric conductivity and scaled all predictors to zero mean and unit standard deviation. We modelled the cover sums of growth forms as a function of grazing intensity, residual fire frequency and soil electric conductivity (the key soil parameter revealed by the PCA analyses, see Section 3) using the *glmmTMB* package (Brooks et al., 2017) and beta family error distribution. As the beta distribution does not allow for zeros, we linearly transformed all cover values according to $\text{cover}^* = \frac{\text{cover}(N-1) + \frac{1}{2}}{N}$, where N is the number of observations (Douma & Weedon, 2019). We inspected

the residuals using the *DHARMa* package (Hartig, 2020) to ensure appropriate model specification. Because visual inspection of the dwarf shrub model residuals suggested a quadratic relationship to soil electric conductivity and excess zeros, we added a quadratic term and explicitly modelled a zero-inflation component with the full set of predictors instead of transforming the cover values. We corrected *p* values of the growth form models according to Hochberg (1988) to account for multiple testing. Using the same set of predictors, we modelled the community-weighted mean of height with Gamma errors and log-link, and the community-weighted means of leaf dry matter content and specific leaf area assuming Gaussian errors.

3 | RESULTS

### 3.1 | Regional-scale patterns of post-Soviet changes in grazing and fire

Our regional-scale analyses revealed that between 1990 and 2015 grazing pressure had decreased and burned area had increased strongly across vast areas (Figure 2a,c). Analysing the local spatial association of grazing and fire as well as the changes in these patterns over the study period using the LISA analysis showed marked and heterogeneous spatial patterns in spatial associations. In 1990, 31% of the grid cells showed significant negative associations between high levels of grazing (measured via grazing probability) and low levels of burning

(measured via burned area; i.e. high–low cluster, Figure 2b), whereas only small areas were assigned to clusters of significant associations of high levels of burning and low or high levels of grazing (low–high = 5% and high–high 3%, respectively). This had changed drastically in 2015. The widespread declines in grazing pressure between 1990 and 2015 (Figure 2c) led to a remarkable increase in significant associations between low levels of grazing and low levels of burning (Figure 2d, 21%), mostly at the expense of high–low areas in 1990 (17%). Burned area generally increased (Figure 2c), as did significant associations of low levels of grazing and high levels of burning, as well as high levels of grazing and high levels of burning (9% and 8%, respectively, Figure 2d). The spatial patterns and associations between MODIS fire frequency (2000–2015) and grazing probability (2015) showed overall similar patterns to the Landsat analyses (Figure 2e,f). However, the MODIS fire frequency captured additional fires before 2014 in the western part of the study area (Figure 2e), and those areas of high fire frequency showed significant associations to low grazing probability in 2015 (Figure 2f).

3.2 | Local relationships between grazing, fire and plant functional community composition

Our fieldwork highlighted strong relationships between fire, grazing and distance to human settlements. At distances further from settlements, grazing intensity (the number of dung piles per 100 m × 2 m transect) strongly declined and fire intensity increased (Table 2; Figure 3a).

FIGURE 2 Overlays of grazing probability and fire patterns (left column) and significant spatial associations between both (right column), calculated using local indicators of spatial association (LISA) and Moran's local *I*. (a) Grazing probability was highest and burned area lowest around 1990, when (b) large areas were assigned to clusters of significant association of high grazing and low burned area (*p* < .05). (c) Grazing probability decreased across the whole study area and the burned area increased markedly by 2015, yielding previously largely absent clusters of low grazing and low burning, as well as and large areas of low grazing and high burning (d). Notably, clusters of high grazing and high burning also occurred, suggesting that factors other than a decline in grazing pressure might explain increased burning there (such as discontinued fire management). Burned area in 2015 was a robust estimate, as spatial patterns and local associations overlap with patterns of fire frequency in 2000–2015 (e, f). To focus on patterns in grassland, 3 km cells with less than 50% grassland were removed (see Section 2)
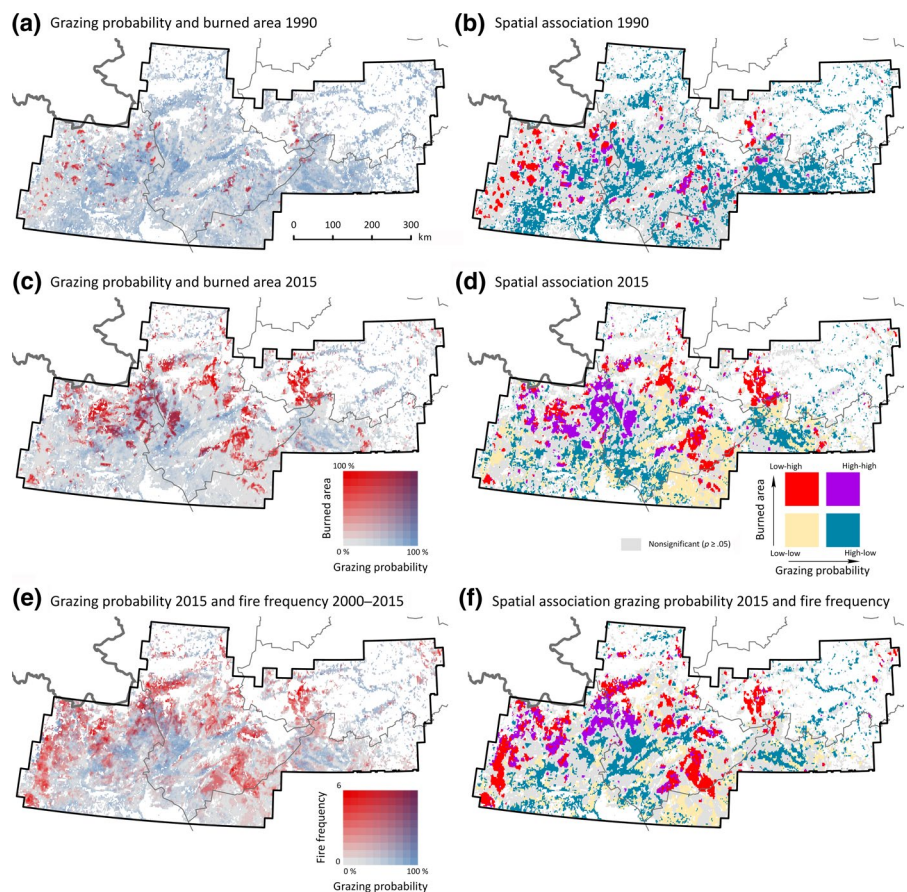
TABLE 2 Generalized linear model parameters for the effects of distance to settlement on grazing intensity (number of dung piles per 100 m × 2 m transect) and grazing intensity on fire frequency (number of fires from 2000 to 2015) at the 204 vegetation plots. Grazing intensity was modelled with negative binomial distribution and log-link. Fire frequency was modelled as Poisson distributed with log-link including a breakpoint with an associated segmented regression term. Fire frequency decreased nonlinearly with grazing intensity until a threshold of four dung piles per area (threshold SE = 1.8, see Figure 3). Above this breakpoint, the segmented term is added such that fire frequency decreases less with grazing intensity

	Estimate	SE	z value	p
Grazing intensity (df = 202, pseudo-R^2 = .87)				
Intercept	2.70	0.13	21.5	<.001
Distance to settlement	−0.18	0.02	−11.4	<.001
Fire frequency (df = 200, pseudo-R^2 = .60)				
Intercept	0.79	0.07	11.1	<.001
Grazing intensity	−0.35	0.08	−4.4	<.001
Segmented term	0.23	0.10	2.4	.015
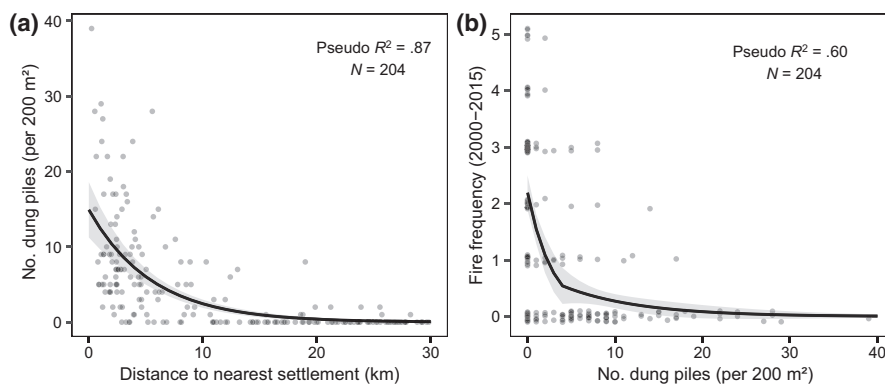
FIGURE 3 (a) Grazing intensity (number of dung piles per strip transect) decreased strongly with distance to nearest village or permanent livestock station in the local study area and (b) fire frequency (number of fires in 2000–2015 from MODIS data) decreased nonlinearly with grazing intensity. Fire frequency decreased rapidly until a threshold of four dung piles per 200 m^2 strip transect (SE = 1.8) and decreased less at higher grazing intensities. Plots show observed data and predicted values ±1.96 × SE (grey area) from a GLM with negative binomial distribution (a) and Poisson error distribution (b) and log-link. Note that some vertical jitter was added to panel b

At distances beyond 10 km from a settlement, we detected virtually no signs of grazing. Fire frequency decreased strongly with increasing grazing intensity, but exhibited a threshold in the response at four dung piles per 200 m^2 (threshold standard error = 1.8, Table 2). Adding a breakpoint to the regression model significantly improved model performance (ΔAIC = −1.97, ANOVA p = .05, breakpoint segmented term p = .015). We observed an average fire frequency of 2.2 times in the period 2000–2015 at plots with zero grazing intensity, which decreased to a fire frequency of 0.5 at the threshold. The breakpoint suggests that at higher grazing intensities above four dung piles per 200 m^2, fire frequency decreased significantly less with grazing intensity than below the threshold (Figure 3b; Table 2).

The PCA of plant traits revealed pronounced differences in the functional composition of plant communities. The main gradient along PCA axis 1 summarized 42% of the variance in community-weighted means. Axis 1 separates communities with higher proportions of dwarf shrubs, woody forbs, as well as annual and biennial plants from communities with high proportions of graminoids (Figure 4). Axis 2 summarized 24% of
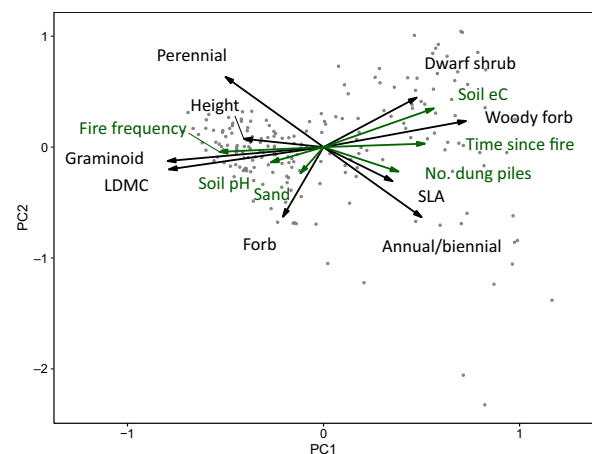
FIGURE 4 Principal component analysis of functional community composition. The first two PCA axes display 66% of the variance in community-weighted mean plant functional traits (N = 198, grey points). Black arrows indicate traits, while green arrows indicate environmental variables fitted post-hoc onto PCA axes scores. Arrow length is proportional to loadings on (traits) and correlations with (environmental variables) the PCA axes, respectively

FIGURE 5 Effects of grazing intensity (no. of dung piles per strip transect), fire frequency and soil electric conductivity on plant functional traits. Due to the collinearity between fire frequency and grazing intensity, the response scale residuals of fire frequency after correcting for the effect of grazing intensity on fire frequency were used. Each row refers to one GLM, and plots show the predicted regression line of fixed effects ±1.96 × SE (grey area) conditioned on mean values of the other predictors. Dots show observed covers and community-weighted mean trait values, respectively
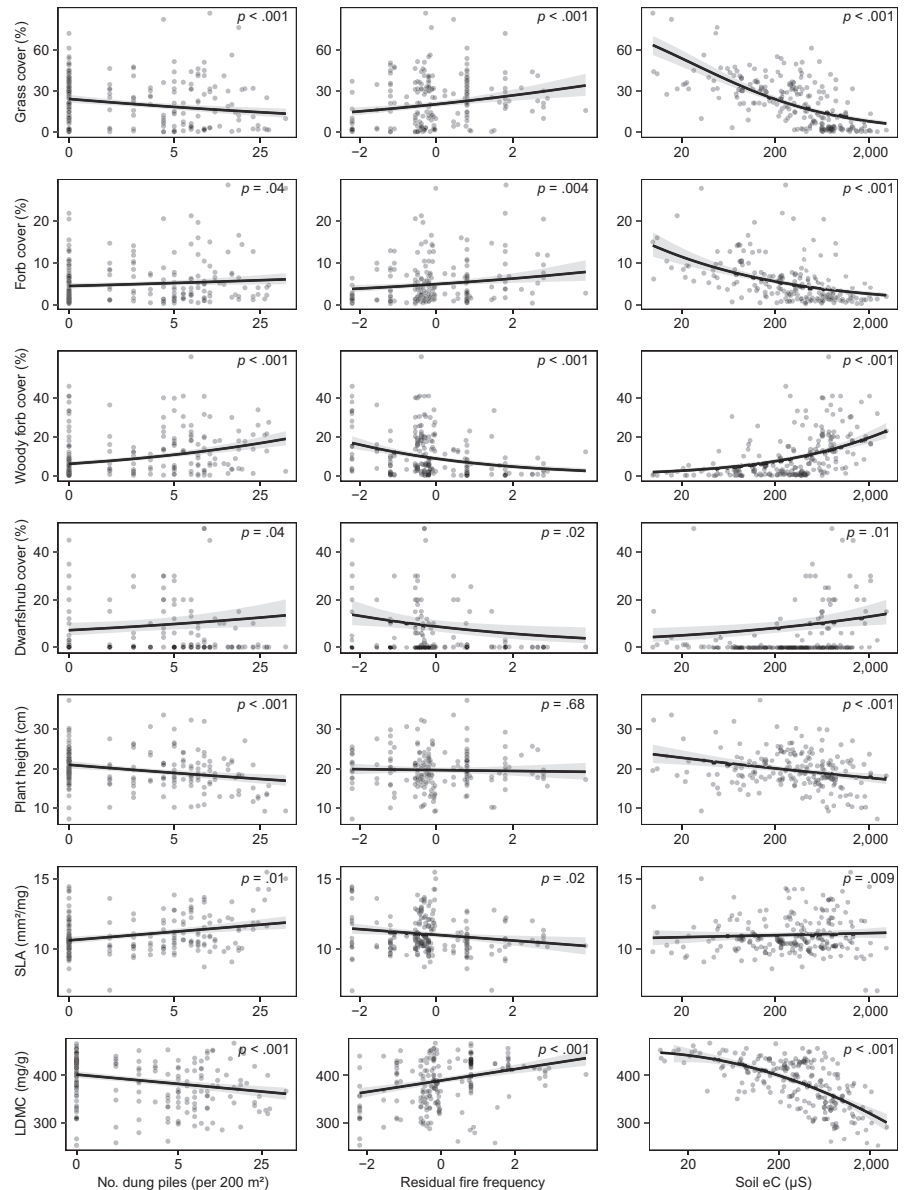
the trait variation and separates perennial dwarf shrubs from annual or biennial plants and herbaceous forbs. All environmental parameters were significantly correlated with the PCA axis scores ($p < .001$, see Table S2). High fire frequency ($r = .53$) and less time since fire ($r = .52$) were correlated with high cover of graminoids and high leaf dry matter content at low values on axis 1 (Figure 4). On the opposite side of the axis, grazing intensity (number of dung piles) was associated with higher proportions of woody forbs, annual and biennial plants, and a higher specific leaf area ($r = .44$). Soil electric conductivity was associated with functional composition ($r = .66$): high soil electric conductivity was correlated with higher cover of dwarf shrubs and woody forbs and lower leaf dry matter content. Soil pH ($r = .30$) and soil sand content ($r = .26$) were much less correlated with the PCA axes, but were rather associated with higher grass cover (soil pH) and higher herbaceous forb cover (sand content, Figure 4).

The GLMs that related vegetation parameters (i.e. growth form covers and trait means) to fire frequency, grazing intensity and soil electric conductivity revealed further insights into the sources of variation in the composition of plant functional communities. Most importantly, fire correlated with increased grass cover with high leaf dry matter content. The cover of woody forbs and dwarf shrubs decreased with increasing fire frequency, as measured by the residuals of the variable, while graminoid cover increased (Figure 5; Table 3). The community-weighted mean of leaf dry matter content increased with increasing fire frequency. Additionally, the probability of observing zero dwarf shrub (i.e. the zero-inflation component) increased slightly with fire frequency, but uncertainty in the effects on dwarf shrub cover was highest compared to other growth forms due to the high proportion of predicted zero cover (Table 3).

Grazing affected many plant traits in the opposite way that fire did. Graminoid cover and plant height decreased with grazing

	Estimate	SE	z value	p
Grass cover (df = 193, pseudo-R^2 = .49)				
Intercept	−1.36	0.06	−22.5	<.001
No. dung piles	−0.22	0.06	−3.9	<.001
Residual fire frequency	0.21	0.05	4.0	<.001
Soil eC	−0.68	0.05	−12.5	<.001
Herbaceous forb cover (df = 193, pseudo-R^2 = .35)				
Intercept	−2.97	0.06	−51.1	<.001
No. dung piles	0.10	0.05	2.0	.04
Residual fire frequency	0.15	0.05	3.0	.004
Soil eC	−0.41	0.04	−9.2	<.001
Woody forb cover (df = 193, pseudo-R^2 = .58)				
Intercept	−2.32	0.07	−34.7	<.001
No. dung piles	0.39	0.05	7.4	<.001
Residual fire frequency	−0.40	0.06	−6.4	<.001
Soil eC	0.57	0.06	9.7	<.001
Dwarf shrub cover (df = 189, cor. R^2 = .16)				
Conditional model				
Intercept	−2.35	0.15	−15.4	<.001
No. dung piles	0.21	0.10	2.1	.04
Residual fire frequency	−0.27	0.11	−2.5	.02
Soil eC	0.27	0.10	2.7	.01
Zero-inflation model				
Intercept	0.29	0.15	1.9	.07
No. dung piles	−0.30	0.15	−2.0	.07
Residual fire frequency	0.37	0.16	2.4	.07
Soil eC	−0.23	0.15	−1.5	.12
Plant height (df = 192, pseudo-R^2 = .15)				
Intercept	2.98	0.02	183.4	<.001
No. dung piles	−0.07	0.02	−3.9	<.001
Residual fire frequency	−0.01	0.02	−0.41	.68
Soil eC	−0.07	0.02	−3.9	<.001
SLA (df = 193, pseudo-R^2 = .11)				
Intercept	11.0	0.09	120.2	<.001
No. dung piles	0.39	0.09	4.3	<.001
Residual fire frequency	−0.24	0.09	−2.6	.009
Soil eC	0.08	0.09	0.8	.41
LDMC (df = 192, pseudo-R^2 = .58)				
Intercept	389.3	3.0	131.0	<.001
No. dung piles	−12.3	2.4	−5.2	<.001
Residual fire frequency	14.2	2.3	6.1	<.001
Soil eC	−35.0	2.7	−13.2	<.001
Soil eC^2	−5.06	1.9	−2.7	.007

TABLE 3 Generalized linear model parameters for the effects of grazing intensity, fire frequency and soil electric conductivity on growth form covers and community-weighted mean functional traits. The residuals of fire frequency were used as predictors after correcting for the effect of grazing intensity, and all predictors were scaled to zero mean and unit standard deviation. As no pseudo-R^2 is defined for zero-inflated models, the squared Pearson correlation coefficient for predicted and observed covers (cor. R^2) is given for the dwarf shrub model

intensity, whereas the community-weighted mean of specific leaf area increased (Figure 5, see also PCA, Figure 4). Soil electric conductivity affected traits in a similar way as grazing intensity did, but it had strong negative effects on grass and herbaceous forb cover and on leaf dry matter content. Soil electric conductivity was the most influential variable in explaining the variation in plant functional trait means compared to the similarly strong effects of fire and grazing (Table 3).

4 | DISCUSSION

Because grassland vegetation is adapted to grazing and fire, any changes in these disturbance regimes should have profound impacts on the functional composition of plant communities. The temperate grasslands of the former Soviet Union have been a global hotspot of land-use change since 1990, yet how these land-use changes have impacted the interrelations of grazing, fire and grassland vegetation remains poorly understood. Our regional-scale analysis highlights the massive extent by which disturbances have changed, and it reveals widespread and significant associations between declining grazing pressure and increasing burning, likely as a result of the build-up of biomass fuel in areas where grazing ceased. Here, we illustrate that at the local scale, grazing and fire had divergent effects on plant functional community composition, suggesting that as a result of decreased grazing and increased burning, vegetation changed towards an increase in grasses. This suggests that the dissolution of the Soviet Union and the subsequent rural exodus of people led to (a) major shifts in disturbance regimes, from grazing-dominated to fire-dominated, across large areas; and (b) a major, yet fairly linear turnover in the functional composition of steppe plant communities. Given the large areas over which grazing declined in post-Soviet times and the vast extents over which fires have recently intensified in Central Asia (Dara, Baumann, Hölzel, et al., 2020; Mouillot & Field, 2005), our findings suggest far-reaching changes in steppe ecosystems' functionality, with possible consequences for carbon and nitrogen cycling (Jones et al., 2019; Pellegrini et al., 2018).

4.1 | Post-Soviet collapse of the livestock sector and its effects on steppe fires

Between 1990 and 2015, grazing pressure decreased significantly over vast areas, and over this time the number of areas with significant associations between low grazing pressure and high burning doubled in the study area. Formerly grazed areas around abandoned livestock stations also exhibited the highest levels of burning (Appendix Figure S4), suggesting that after grazing ceased in these areas, biomass fuel accumulated. At the local scale, fire frequency responded nonlinearly to grazing intensity. Specifically, we found that fires were largely suppressed in grazed areas, and that when the grazing intensity fell below a threshold of four dung piles per 200 m^2 ($SE = 1.8$), fire frequency started to increase sharply. This nonlinear relationship between the two disturbance types helps to explain why the incidence of fires rapidly increased after the post-Soviet livestock collapse in the 1990s (Dara, Baumann, Hölzel, et al., 2020; Mouillot & Field, 2005). Furthermore, our local-scale data suggest that even low levels of grazing can reduce fires, due to the consumption of fuel and the creation of gaps in the vegetation of grazed areas (Hempson et al., 2015; Johnson et al., 2018). This finding is in line with results from nearby Kalmykia in southern Russia, where increased burning was also best explained by decreasing grazing pressure (Dubinin et al., 2011).

However, several factors other than changes in grazing can explain the increase in burning, as we still found some areas with positive associations between high levels of grazing and high levels of burning. First, climatic changes could be responsible for the observed increases in burned area (Daniau et al., 2013; Pausas & Paula, 2012). High precipitation in spring or in previous years could have increased fuel loads, and drought periods could have created extraordinarily flammable conditions around the year 2015. Perhaps increased fuel loads due to higher precipitation led to slightly higher fire frequency in the northern part of the study area. However, burned area estimates for 2000 were even slightly higher than for 2015, and no trends in temperature or precipitation can easily explain the increases since 1990 (Dara, Baumann, Hölzel, et al., 2020), neither is the recovery of vegetation associated with the climatic gradient (Dara, Baumann, Freitag, et al., 2020). Second, rural depopulation alongside discontinued fire management could be a major cause for the increases in grassland fires in the region (Dara, Baumann, Hölzel, et al., 2020). In this situation, any fires used to remove crop residues from fields or any fires caused by accidental ignitions (e.g. near roads) will likely remain un-extinguished. This is especially likely in wet depressions, where accessibility is low, and the high fuel availability is weakly controlled by grazing pressure.

4.2 | Diverging responses of functional plant community composition to fire and grazing

Our analyses revealed that fire and grazing have distinct effects on plant functional traits, which, in the context of increased fires and livestock collapse, suggest significant ecological changes in the steppe plant communities. We highlight potential increases in grass cover (mainly abundant *Stipa* spp.) and associated increases in leaf dry matter content due to an increase in fire frequency. Compared to the situation in Soviet times, the flammability of steppe vegetation is now likely higher, as leaves have a lower leaf moisture content and litter accumulates (cf. Simpson et al., 2016).

We observed high fire frequencies at high cover of perennial grasses, mainly represented by the tall- and dense-growing *Stipa* spp. Inversely, dwarf shrubs (e.g. *Atriplex cana*) and woody forbs (e.g. *Artemisia* spp., *Camphorosma monspeliaca*) are associated with low fire frequencies and alkaline soils with high electric conductivity. This suggests that, in our study system, woody plants are affected mainly by high fire frequencies (Haubensak et al., 2009). The build-up of fuels and associated high fire recurrence rates might be limited by the slow regrowth of dwarf shrub communities on alkaline soils. However, uncertainty in the response of dwarf shrubs to fire frequency is relatively high, perhaps in part due to the slow regrowth.

Grass-dominated plots were often found in areas of frequent fires, probably because grasses are able to resprout and quickly restore biomass (Davies et al., 2012). Grasses have been shown to more strongly promote fire spread than forbs (Wragg et al., 2018). Through an increased fuel connectivity and the high flammability of leaves with high leaf dry matter content, grasses foster fires and

construct their own niches at the expense of fire-intolerant herbs (Bond & Midgley, 1995; Pausas et al., 2017). The positive association between grasses and fire is squarely in line with findings from the North American prairies (Collins et al., 2012; Spasojevic et al., 2010); therefore, the response of grassy vegetation to fire might be similar in C4 grass prairies and the C3 grass-dominated Eurasian steppe. In both cases, the leaf traits of fire-tolerant grasses likely foster the high frequency and extent of fires (Pausas et al., 2017; Simpson et al., 2016).

The trait responses to grazing diverge from the responses to fire. High grazing intensities tended to decrease plant height and favour species with a high specific leaf area, which is associated with a high regrowth rate and nitrogen content (Pérez-Harguindeguy et al., 2013). This pattern is probably driven by annual species such as *Ceratocephala testiculata*, *Polygonum patulum* and *Poa bulbosa* because persistent seed banks and a fast growth rate are beneficial for colonizing gaps in grazed sites with repeated defoliation and intense trampling (Díaz et al., 2007). The negative relationship between grazing intensity and graminoid cover suggests that especially tussock grasses suffer from grazing due to trampling and preferred feeding. Perennial woody forbs such as *Artemisia* spp. seem to be less sensitive and indirectly profit from trampling and grazing disturbance because herbivores avoid these aromatic plants. In general, our results concur with global responses of traits to grazing (Díaz et al., 2007), showing that grazing favours ruderal annuals and trampling- and feeding-tolerant perennials rather than tall-growing grasses.

In addition to the effects of fire and grazing, soil properties also governed the functional composition of plant communities. Presumably controlled by topography, the soil electric conductivity—a measure of soil alkalinity—varied markedly in our study area, and in general more strongly affected traits than fire and grazing. Alkalinity also shapes the plant communities in the European part of the Eurasian steppe (Eliáš et al., 2013; Stevanović et al., 2016). Because our results demonstrate that plant communities in the dry steppe range from grass- and herbaceous forb-dominated communities to dwarf shrub- and woody forb-dominated communities along the alkalinity gradient, soil characteristics should be considered when investigating the effects of disturbance drivers on community composition.

4.3 | Large-scale changes in grassland composition and functioning?

Our results suggest that the Kazakh steppe has undergone a major shift in disturbance regimes. Regime shifts are triggered by changes in exogenous driver variables that have a determining role for the state of the system, which in grasslands can be precipitation or disturbances (Biggs et al., 2012; Ratajczak et al., 2018; Scheffer & Carpenter, 2003). Our analyses suggest that the sudden increase in fires on vast areas is at least partly the result of a nonlinear response to the decrease in grazing pressure. This may indicate a fire feedback

loop, where the increase in grasses under frequent fires increases the amount and flammability of biomass fuel (Bowman et al., 2014; Simpson et al., 2016). Our findings add evidence to the recent emergence of the region as a global fire hotspot, showing a twofold increase in burned area compared to pre-Soviet times and a threefold increase compared to Soviet times (Archibald et al., 2013; Mouillot & Field, 2005). Given that wild or domestic grazers have historically roamed the Kazakh steppe for thousands of years (Hanks, 2010; Robinson & Milner-Gulland, 2003), the current situation of low grazing pressure represents an exceptional, potentially non-analogue state.

The widespread changes in grazing and fire patterns across the steppe regions of the former Soviet Union and the distinct effects of fire and grazing imply significant ecological changes in steppe plant communities. Although our analysis highlights that under more frequent fires, there are potential increases in grass cover (mainly abundant *Stipa* spp.) and associated increases in leaf dry matter content, it is unclear how the vegetation changed over time to reach this point. For example, although our trait analysis suggests turnover in the functional composition, we do not know whether vegetation responded nonlinearly to the change in disturbances or even showed a regime shift of steppe vegetation. Further research is required both on the ecosystem-wide effects of the shift in disturbances on vegetation and on carbon and nutrient cycling (Jones et al., 2019; Pellegrini et al., 2018).

We suppose that to revert the regime shift in disturbance and associated changes in vegetation, it would be necessary to reintroduce grazing animals, wild (e.g. Saiga antelope or Kulan) and domestic, across vast areas of the Eurasian steppe. Grazing as a fuel management tool across large areas might suppress the spread and recurrence rates of fires (Johnson et al., 2018) and has been successfully tested in the US sagebrush steppe, a system similar to the Kazakh steppe (Davies et al., 2016). The restoration of free-range grazing systems would require large governmental investments into local infrastructure (e.g. transport facilities, stables and livestock watering) as well as the support of private and household farmers (Kerven et al., 2016b). Such an effort would also require measures to counteract the outmigration of the rural population, as the availability of shepherds is a major bottleneck to restore free-ranging herds. Governmental policies need to be adapted towards this aim. Furthermore, subsidies that support meat production in free-ranging livestock systems need to be prioritized over governmental help for feedlot-based systems (Hankerson et al., 2019), and financial incentives to restore depleted infrastructure (stables and wells, Kerven et al., 2016a) need to be available, and domestic meat markets strengthened. Rural areas need to be supported to prevent a further exodus of labour, incl. shepherds (Griewald et al., 2017).

5 | CONCLUSION

We have shown that large-scale land-use changes after the dissolution of the Soviet Union triggered shifts in grazing and fire patterns, and resulted

in changes in the functional composition of plant communities. These changes had important implications for Eurasian grassland ecosystem properties and happened on such a large scale that the overall implications (e.g. for carbon storage) might be globally relevant. The current 'hands-off' strategy on the Eurasian steppe has resulted in recovering bird populations (Kamp et al., 2011) and probably overall benefits for wildlife ('rewilding', Baumann et al., 2020), but ecosystem properties might have been affected in a negative way by pasture abandonment and rural outmigration. Therefore, future land management planning on the Eurasian steppe needs to consider both the retention of 'wild', undisturbed places (to harness the benefits of rural human outmigration), and the persistence of ecosystem services through prudent grazing management.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.