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Distribution of graminoids in open habitats in Tajikistan and Kyrgyzstan

Sebastian Świerszcz[1,2,3], Grzegorz Swacha[4], Małgorzata W. Raduła[5], Sylwia Nowak[3]

1 *Polish Academy of Sciences Botanical Garden – Center for Biological Diversity Conservation in Powsin, Warszawa, Poland*
2 *Franciszek Górski Institute of Plant Physiology, Polish Academy of Sciences, Kraków, Poland*
3 *Institute of Biology, University of Opole, Opole, Poland*
4 *Botanical Garden, University of Wrocław, Wrocław, Poland*
5 *Institute of Agroecology and Plant Production, Wrocław University of Environmental and Life Sciences, Wrocław, Poland*

Corresponding author: Sebastian Świerszcz (sebastian.swierszcz@ob.pan.pl)

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Abstract

Aims: Landscapes of Middle Asia are exposed to human influence due to long-lasting pastoral tradition, and now are largely dominated by non-forest vegetation. Graminoids perform key ecosystem functions, and constitute an important feed source for livestock. We studied the distribution patterns of graminoids cover under climatic and grazing pressure gradients in different open vegetation types. **Study area:** Tajikistan, Kyrgyzstan. **Methods:** 1,525 vegetation plots representing five open vegetation types (mires, salt marshes, tall-forb communities, pseudosteppes and steppes) were extracted from the Vegetation of Middle Asia Database. We assessed the relative cover of graminoid species in each vegetation type. The importance of mean annual temperature, sum of annual precipitation, aridity and livestock density as drivers of relative cover of graminoids contribution patterns in the five vegetation types were explored with use of polynomial functions and commonality analysis. **Results:** Open ecosystems of Middle Asia are characterized by different graminoid contributions. The highest relative cover of graminoids was found for steppes, pseudosteppes and mires. Comparison of model fits for relationship between the graminoids cover, climatic parameters and livestock pressure indicated advantage of polynomial models. The best-fitting models for pseudosteppes were for mean annual temperature, Aridity Index and livestock density, for steppes mean annual temperature and Aridity Index, and for salt marshes mean annual temperature. For mires and tall-forb communities, the models showed a poor fit or no effect of the variables studied. **Conclusions:** Our study shows that climate and livestock pressure have an impact on the contribution of graminoids in open vegetation types, but a general pattern is difficult to describe. Ongoing climate change may influence the share of graminoids in salt marshes, steppes and pseudosteppes. Grazing (with a common effect of climatic factors) is the most important factor influencing graminoids contribution on pseudosteppes, confirming the secondary origin of this vegetation type.

Taxonomic reference: The nomenclature of the vascular plants follows Plants of the World Online (POWO 2022) and problematic taxonomic issues were based on The World Flora Online (WFO 2022). Nomenclature of *Stipa* spp. follows Nobis et al. (2020).

Keywords

aridity, climate, *Cyperaceae*, grassland, hot-spot, *Juncaceae*, Kyrgyzstan, Middle Asia, open habitat, *Poaceae*, steppe, Tajikistan

Introduction

Graminoids are a major component of open habitats across the world, particularly wetlands and grasslands (Gibbson 2009; Bragina et al. 2018; Nowak et al. 2020a). Graminoids include vascular plants with a grass-like morphology from three groups: grasses (*Poaceae*), sedges (*Cyperaceae*) and rushes (*Juncaceae*). *Poaceae*, as one of the most species-rich family worldwide, includes around 11,500–12,000 taxa classified to about 770–780 genera (Christenhusz and Byng 2016; Soreng et al. 2017). The second most abundant family of graminoids, *Cyperaceae*, includes approx. 5,500 species within about 90 genera (Christenhusz and Byng 2016). The most common group are sedges, represented mainly by the genus *Carex*, which are found in many types of habitats, often as dominants or co-dominants (Spalink et al. 2018). At high altitudes, e.g. the Pamir Plateau, the Tibetan Plateau and the Himalayas, open vegetation is dominated by cold-resistant sedge species such as *Kobresia* spp. creating dense, low mats (Miehe et al. 2009; Vanselow 2011). Vegetation types dominated by species from *Kobresia* or *Carex* are used as winter pastures because they store more nutrients in the cold season, and maintain the nutritional value for livestock longer than other graminoids, e.g. grasses (Vanselow 2011). The third graminoid group, *Juncaceae*, is less numerous and includes about 460 species within eight genera (Christenhusz and Byng 2016). The most species-rich genus is *Juncus*, with the majority of the species growing sparsely in wetland habitats.

Many grasses, sedges and rushes are effective colonisers, making them cosmopolitan (Spalink et al. 2016; Linder et al. 2018; Martín-Bravo et al. 2019). Grass-dominated ecosystems cover 31–43% of the earth's surface (Gibbson 2009). Colonisation of new areas and habitats is facilitated by dispersal and establishment ability, broad environmental tolerance and ecological competitiveness of the species (Scheiter et al. 2012; Linder et al. 2018). They are often exposed to extreme environmental conditions such as drought and high salinity and various disturbances, e.g. intensive herbivory (Coughenour 1985; Gibbson 2009; Borer et al. 2019). Graminoids are intensively used as forage for livestock (Linder et al. 2018). In the course of evolution, graminoids have developed several features that allow them to endure harsh conditions. For example, traits allowing to tolerate drought, which are also useful in adapting to grazing resistance, include basal meristems, rapid growth, high shoot density, nutrient storage and rapid transpiration (Coughenour 1985). Saline and wet habitats promote plants with lower requirements for mechanical support characterized by long rhizomes and short stature (Dolezal et al. 2019).

Due to its unique floristic richness, most of the territory of Tajikistan and Kyrgyzstan is recognized by Conservation International as a biodiversity hotspot – Mountains of Central Asia (Mittermeier et al. 2011). The diverse landscape, extreme climate and varied habitat conditions shape the biogeography of Middle Asia (Nowak et al. 2020a; Wagner et al. 2020), offering a high diversity of plants and vegetation types (Stanyukovich 1982). The landscape of Middle Asia is dominated by open habitats with a high contribution of graminoids as a consequence of thousands of years of pastoralism. Steppes are the most prominent biome in Middle Asia, divided into three types: high altitude arid steppes (Nowak et al. 2018), mountain steppes of semi-arid areas, and dry, thermophilous steppes of montane and subalpine belts (Nowak et al. 2016b, 2018, 2020a). The most abundant plant group of the Middle Asian steppes is *Poaceae*. Examples of prominent grass genera in the steppe vegetation are *Agropyron*, *Avena*, *Bromus*, *Elymus*, *Elytrigia* and *Stipa* (Nowak et al. 2020a) and the most diverse genus is *Stipa* with 76 species and subspecies. Contrary to the steppes, pseudosteppes are secondary grassland types that have replaced natural thermophilous open woodlands and scrub vegetation, as a result of clearing and subsequent grazing of the herb layer (Świerszcz et al. 2020; Nowak et al. 2022b). Mesophilous grasslands ranging from the lowlands to the alpine belt form a distinct vegetation type, in which numerous graminoid species occur. At high elevation in the alpine belt, graminoid vegetation is often dominated by *Kobresia* species (Nowak et al. 2020a). Graminoids are also core species in fen and spring communities, as well as littoral vegetation (Nowak et al. 2014, 2016a). A distinct vegetation type are salt marshes, which develop on lake shores at high altitudes but also in the colline and foothill belts along rivers, springs and artificial leakages, under harsh saline conditions (Nowak et al. 2020a). In areas of deforestation of juniper woods, tall-forb communities dominated by dicotyledonous perennials with a variable proportion of graminoids develop (Nowak et al. 2020b).

About 9,300 vascular plant species have been described from the Middle Asia region (Khassanov 2015). The vascular flora of Kyrgyzstan consists of ca. 4,000 species (Lazkov and Sultanova 2014), of which about 10% are endemics (Lazkov and Umralina 2015). The families *Poaceae*, *Cyperaceae* and *Juncaceae* account for a total of 430 species, and among them 120 species are endemics or sub-endemics (21% of all graminoids; Lazkov and Sultanova 2014). The Tajik flora consists of ca. 4,300 species (see Nowak et al. 2020c), where approx. 30% are known as endemics (Nowak et al. 2011). In Tajikistan, 438 species belong to the *Poaceae*, *Cyperaceae* and *Juncaceae* families, 70 of them are endemics or sub-endemics (16% of all graminoids) and 133 are considered endangered at the national level (Nowak et al. 2020c). These numbers show how unique the flora of Middle Asia is, and how abundant graminoids are.

In terms of food and economic safety, Middle Asia is almost entirely dependent on livestock production. This region has a long tradition of pastoralism and since ancient times a whole human population consider its welfare with the quality of pasturelands and the number of livestock herds. Besides typical grasslands, there are also other vegetation types in Middle Asia such as tall-forb communities, mires, and salt marshes used for grazing in which graminoids are likely key contributors to biomass and diversity.

Thus, finding basic patterns of graminoid species abundance and distribution in different vegetation types in Middle Asia is of high importance. In this paper, we addressed three main questions: (1) How is graminoid species richness shaped in the open vegetation types of Tajikistan and Kyrgyzstan? (2) Is there a general pattern of graminoid occurrence in different open vegetation types? (3) How do climate and livestock density affect the proportion of graminoids?

Study area

The study was conducted within the administrative borders of Tajikistan and Kyrgyzstan (Figure 1). The landscape of the area is dominated by diverse open habitats, which are shaped by the strongly varied environment, landscape, and human activity, grazing of sheep, goats, cattle and horses in particular. The study area is mainly dominated by steppes and chasmophytic vegetation. However, hay meadows also contribute importantly to the landscape at intermediate altitudes (ca. 2,000–3,000 m a.s.l.). Alpine swards in subalpine and alpine belts are used as summer pastures, and *Kobresia* mats at the highest altitudes are used as winter pastures. Additionally, the wide terraces of lowland river valleys and floodplains of the alpine rivers offer suitable habitats for grassland development. Salt marshes develop under harsh saline conditions. The studied vegetation types differ considerably in terms of topographic and edaphic conditions as well as altitude.

The region is characterized by a very long elevational gradient ranging from 287 to 7,495 m a.s.l, which makes this territory particularly diverse in terms of climate, land relief and geomorphology. The geological profile is complex with a predominance of limestone, marble, dolomite, dolomitic shale, clay shale, phyllitic schist, siltstone, and argillaceous slates of Carboniferous, Cambrian, Silurian, and Early Cretaceous origin. However, the specific geological conditions of this region are still under study (Leven 1981; Budanov and Pashkov 1988; Lohr 2001).

The study area is difficult to characterize in terms of climatic conditions. The climate differs spatially in terms of its continentality, topographic complexity, and orography. However, according to Latipova (1968), Narzikulov and Stanyukovich (1968), and Safarov (2003), four main climatic regions can be distinguished. The study area is placed between two main biogeographic regions, Irano-Turanian and Central Asiatic, with climatic influences from the Indo-Indochinese region in the south and the Euro-Siberian region in the north. The specific conditions of the regions are as follows (Figure 1):

The warm and continental Irano-Turanian region (Fergana Valley and south-western Tajikistan) is characterized by low annual precipitation with the sum of ca. 200–250 mm, and the peak in March (ca. 80 mm). During the summer months (from June to August) the precipitation is scarce, with the sum of 0–10 mm per month. Snow and frost occur only in winter (from December to February). Temperatures strongly vary during the year; in the warmest

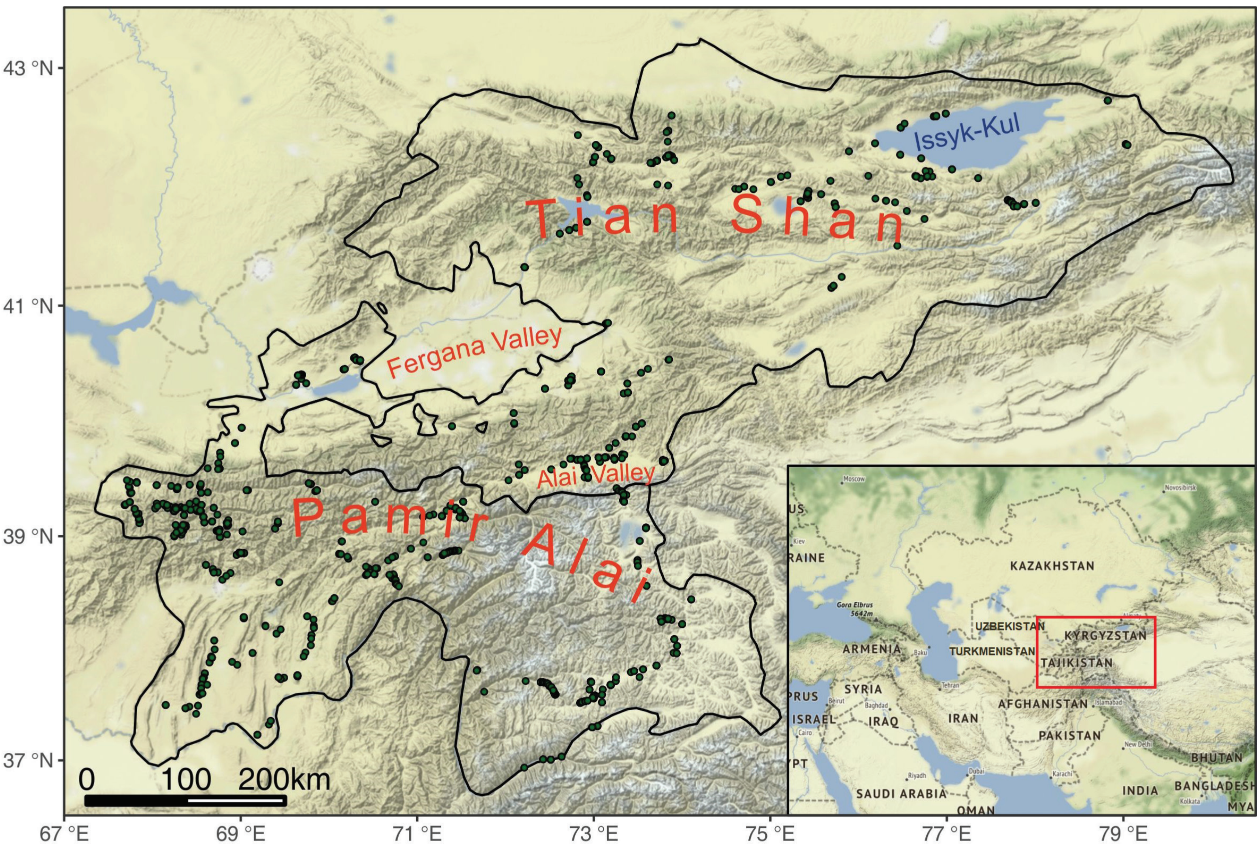

Figure 1. Distribution of plots in the study area (n = 1,525).

months, they reach from 20°C (May) to 34°C (June, July, August). In winter, the mean temperature is no lower than -3°C with extreme values reaching -27°C in some years.

The warm, humid and continental region includes the Tian Shan and Pamir-Alai ranges. The sum of annual precipitation ranges from ca. 500 mm in northern slopes to ca. 1000 mm in southern slopes. In June, the mean temperature in colline and montane belts reaches ca. 22°C while in alpine belts, it reaches up to 10°C.

The cold, semi-arid region includes the Issyk-Kul basin, central and western parts of the Alai Valley, as well as foothills and plateaus in the colline, montane and subalpine belts. The area is characterized by low precipitation, with the sum of ca. 200–400 mm per year. The precipitation reaches a peak of 70 mm per month in spring (from May to July). The annual mean temperature is ca. 10°C, it exceeds 20°C only in the summer months.

The cold and arid climate region includes the easternmost sections of the Alai Valley and the eastern Pamirian Plateau. The sum of annual precipitation is extremely low and does not exceed 100 mm. Only in May and August the monthly sum of precipitation is ca. 20 mm. The annual mean temperature is slightly above 0°C, with a minimum of ca. -30°C from January to February.

Methods

Vegetation data preparation

The primary source of data was the Vegetation of Middle Asia database (Nowak et al. 2017; GIVD ID: AS-00-003) containing 4,649 vegetation plots (relevés) stored in TURBOVEG (Hennekens and Schaminée 2001). Plots that were previously classified as natural or semi-natural vegetation of open habitats were extracted. We removed plots with a shrub layer > 50% and also those that are not typically used for grazing. At this stage, we obtained a data set representing five types of vegetation (Table 1; Figure 2). Because of the low number of records from meadows in our database (26 vegetation plots), they were excluded. The plant identification was based on the ten-volume flora of Tajikistan (Ovchinnikov 1957, 1963, 1968, 1975, 1978, 1981; Chukavina 1984; Kochkareva 1986; Kinzikaeva 1988; Rasulova 1991) and the ten-volume study of the flora of the former Soviet part of the Middle Asia (Conspectus Florae Asiae Mediae; Kovalevskaya 1968–1993).

Table 1. Number of plots for each open vegetation type (n = 1,525).

Vegetation types	Number of plots	Plot size range (m²)
Mires	489	2–30
Tall-forb communities	168	10
Pseudosteppes	150	10
Salt marshes	191	10–100
Steppes	527	10–30

The final data set consisted of 1,525 vegetation-plot records of open habitats (Table 1). Plots were sampled from 2006 to 2019 in Tajikistan and Kyrgyzstan (Figure 1). Each plot contains a full list of vascular plant species recorded in a plot, often also a list of bryophytes, and estimates of the cover-abundance of species in each layer in the Braun-Blanquet or percentage scale. For each plot, geographical coordinates were measured using a GPSMAP 60CSx device with an accuracy of ± 5 m, and the WGS84 reference frame. In the case when the Braun-Blanquet scale was used, we transformed to the percentage scale (r: 1%, +: 2%, 1: 3%, 2: 13%, 3: 38%, 4: 63%, 5: 88%). Then we calculated the relative cover of each species within each plot. Relative cover was calculated by dividing the cover of each species by the total vegetation cover of all species in the plot. To determine the relative cover of graminoids, we summed the relative cover of each species in this group in the plot.

Environmental variables

We assessed the importance of mean annual temperature, sum of annual precipitation, aridity, and livestock density (surrogate of grazing intensity) as drivers of the relative cover of graminoids. Mean annual temperature and sum of annual precipitation are two key climate factors that determine plant distribution (Whittaker 1975). Aridity and grazing are factors that promote species with grazing resistance traits (Coughenour 1985; Milchunas et al. 1988).

Based on the coordinates, we derived the mean annual temperature and the sum of annual precipitation from the CHELSA dataset, with a resolution of 0.00833 decimal degrees (30 arc sec; Karger et al. 2017a, 2017b). Global Aridity Index (hereinafter referred to as Aridity Index) was obtained from the Global-PET geospatial dataset available on the CGIAR-CSI GeoPortal (Zomer et al. 2022). Aridity Index values are unitless and decrease with more arid conditions (Zomer et al. 2022). Livestock density data were obtained from the Gridded Livestock of the World database at a spatial resolution of 0.083333 decimal degrees (approximately 10 km at the equator) (GLW v3.1; Gilbert et al. 2018). For this study, we selected population densities (the average number of animals per km^2) of the most common and influential livestock species: sheep, goats and cattle combined.

Statistical analyses

All statistical analyses were performed in R environment (R Core Team 2022). The relative cover (%) of all graminoids in the plots as well as of *Poaceae*, *Cyperaceae* and *Juncaceae* was presented by density curves computed by weighted kernel density smoothing functions using 'ggridges' package (Wilke 2021).

We used linear models to explore the effects of the mean annual temperature, sum of annual precipitation, Aridity Index and livestock density for the patterns of graminoid

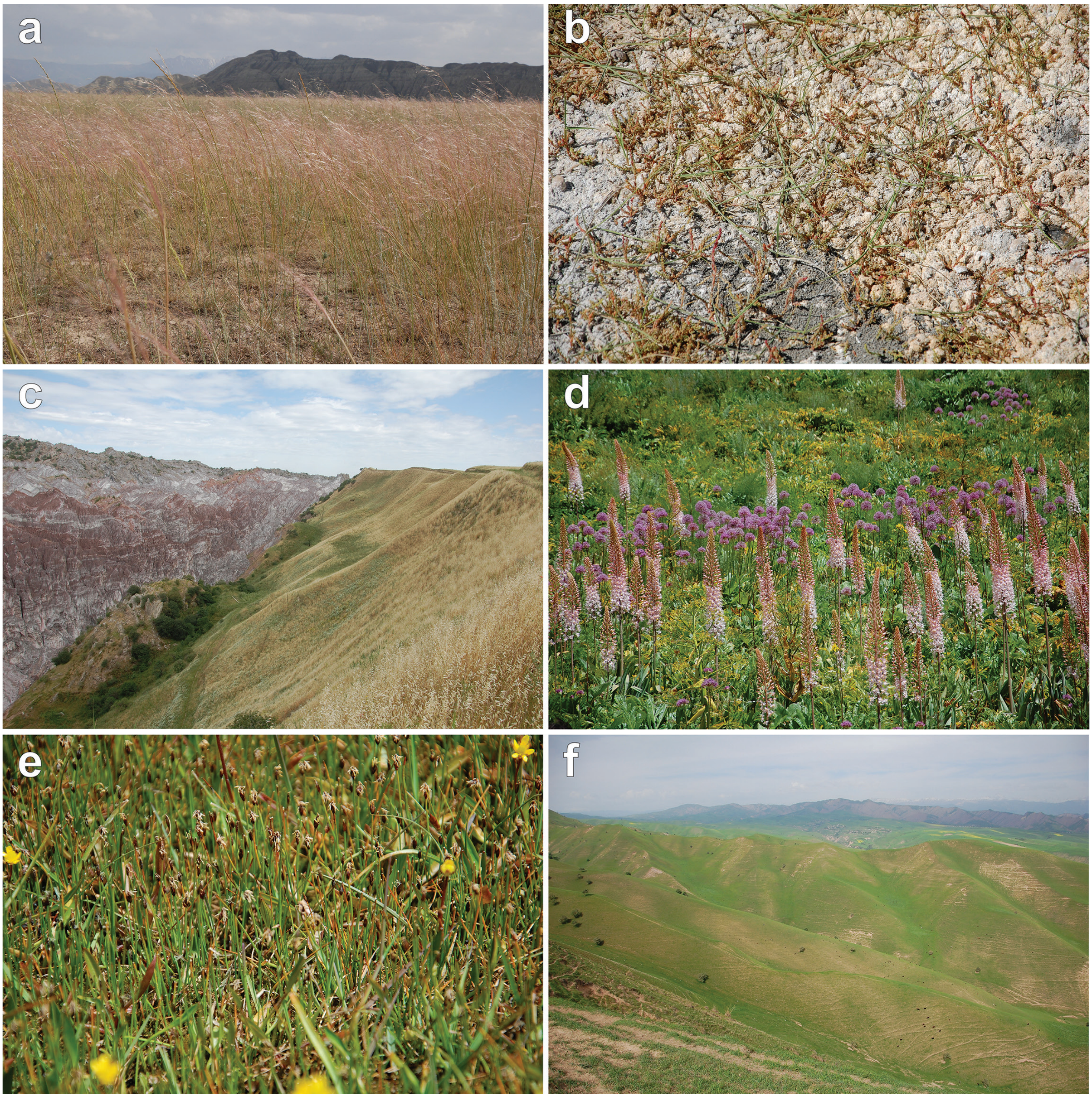

Figure 2. Photos of the open vegetation types: (a) steppe (Kosh-Dobo, Kyrgyzstan), (b) salt marsh (Zoogvand, Tajikistan), (c) pseudosteppe (on the right site of the photo; Khoja Mumin Mt. near Vose, Tajikistan), (d) tall-forb community (near Rabot, Tajikistan), (e) mire near Jelondy (Tajikistan) and (f) overgrazing – one of the main human-driven threats to grasslands in Middle Asia leading to land degradation.

abundance in open habitats. We performed linear models and evaluated the relevance of a quadratic term (polynomial) to account for potential curvilinear relationships. We built models for each vegetation type and explanatory variable separately. The best model among the linear and quadratic ones was evaluated by their coefficient of determination (R^2) and root mean-squared error (RMSE) with the *compare_performance* function in the R package 'performance' version 0.8.0 (Lüdecke et al. 2021). Results of linear and polynomial models performance are presented in Suppl. material 1.

Additionally, we used commonality analysis to find the most important factors influencing the contributions of relative cover of graminoids. To do this, we decomposed the variance of R^2 into unique and common effects of predictors. Unique effects indicate how much variance is uniquely accounted for by a single predictor and common effects indicate how much variance is common to a predictor set (Ray-Mukherjee et al. 2014). The sum of unique and common effects (total) represents the total contribution of a predictor to the dependent variable irrespective of collinearity with other variables (Prunier et al. 2015). Commonality analysis was conducted with *commonalityCoefficients* function in 'yhat' package (Nimon et al. 2008).

Results

In total, we recorded 255 graminoid species within all vegetation types. Graminoid-richest vegetation types were steppes (136 species – 53.3% of the total graminoid flora) and pseudosteppes (94 species – 36.9% of the total graminoid flora) (Table 2). Lower number of graminoid species was recorded in mires (77), salt marshes (74) and tall-forb communities (57). The observed number of shared species between vegetation types and the proportion of the observed species varied between the pairs of vegetation types (Table 2). The highest number of shared species was found for steppes and pseudosteppes, steppes and tall-forb communities, and pseudosteppes and tall-forb communities. Mires and salt marshes had the lowest number of shared graminoid species among all pair-wise comparisions. The most common species were *Calamagrostis pseudophragmites* and *Poa bulbosa* (Suppl. material 2).

The highest relative cover of graminoids was found for steppes (median: 47.8%), mires (median: 43.06%) and pseudosteppes (median: 39%). However, a particular density peak cannot be distinguished because the relative cover of graminoids is evenly distributed along the entire range within these vegetation types (Figure 3a). The distribution of the relative cover of *Poaceae* is similar to the distribution of relative cover of all graminoids (Figure 3b) indicating the apparent dominance of species from this family. The only exception was mires, where *Cyperaceae*

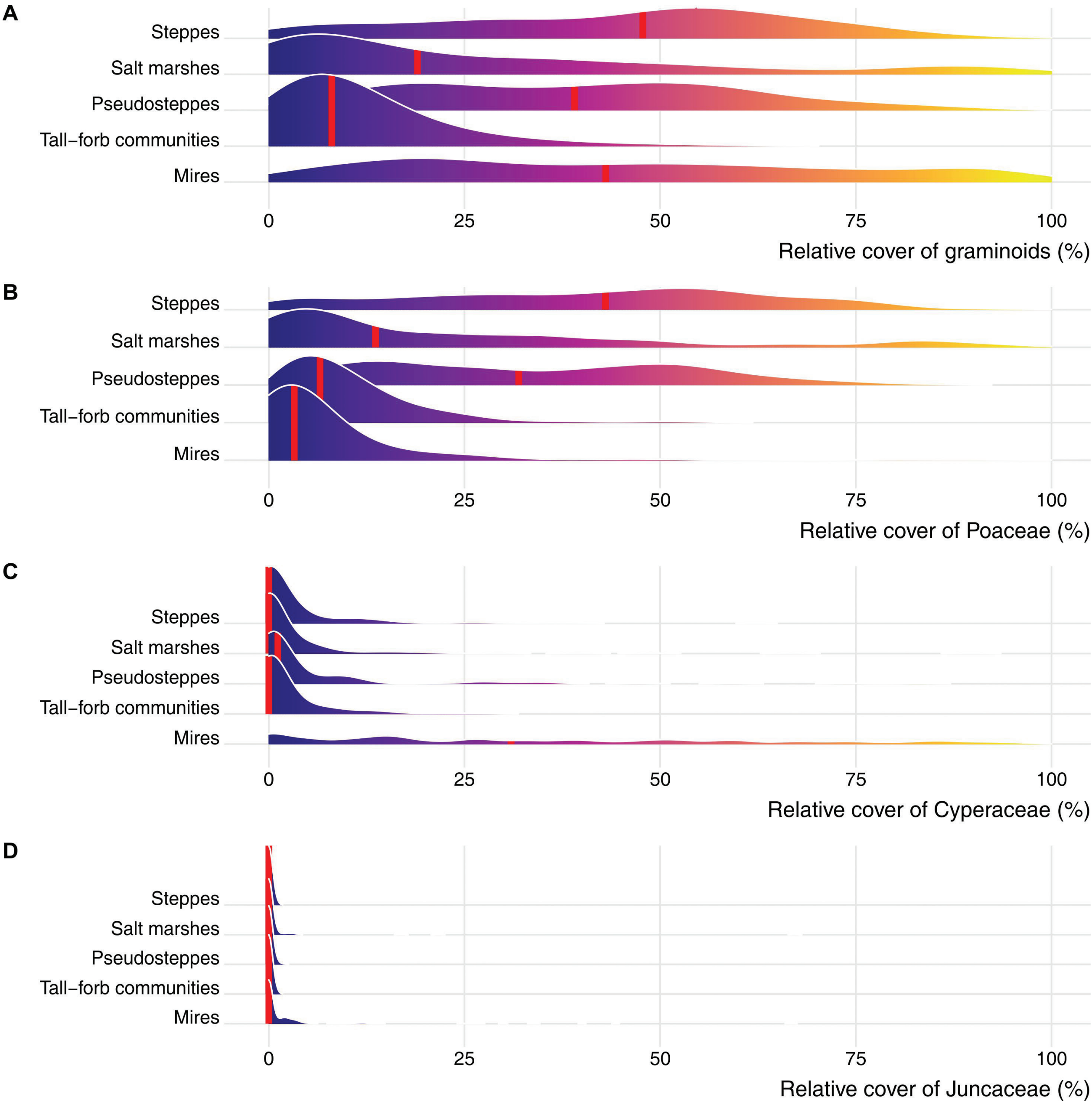

Figure 3. Density curves representing the distribution of relative cover (%) for all graminoids together (a) and split by family (b, c, d) within open habitat types at plot level. The vertical red line shows the median value of relative graminoid cover within each vegetation type. On the y-axis, the distributions are represented by relative values with the maximum density of each group standardized to 1.

were dominating, with a median relative cover of 31% (Figure 3c). The relative cover of *Juncaceae* was lowest in all vegetation types (Figure 3d).

Model comparison showed that polynomial models provided a better fit for the relationship between graminoid relative cover and predictor variables (Table 3). The model of mean annual temperature showed a significant pattern of the relative cover of graminoids for salt marshes, pseudosteppes and steppes with the best fit and high unique effect for salt marshes (R^2 = 0.32 and 65.3% of the regression effect; Table 3). The relative cover of graminoids increased in pseudosteppes, and decreased in salt marshes with increasing mean annual temperature. The effect of the mean annual temperature in steppes was hump-shaped with the highest values of graminoids between ca. 0 and 10°C (Figure 4).

The model showed that sum of annual precipitation had statistically significant effect on all vegetation types, although with a low model fit (R^2 = 0.05–0.1; Table 3). The effect of this variable in pseudosteppes and tall-forb communities was negative and in salt-marshes and steppes was positive. The highest unique effect of this factor was found in tall-forb communities (68.4%). No clear pattern was found for mires (Figure 4). The models of Aridity Index and domestic animal pressure measured by livestock density showed a statistically significant effect on the relative cover of graminoids in all vegetation types except tall-forb communities (Table 3).

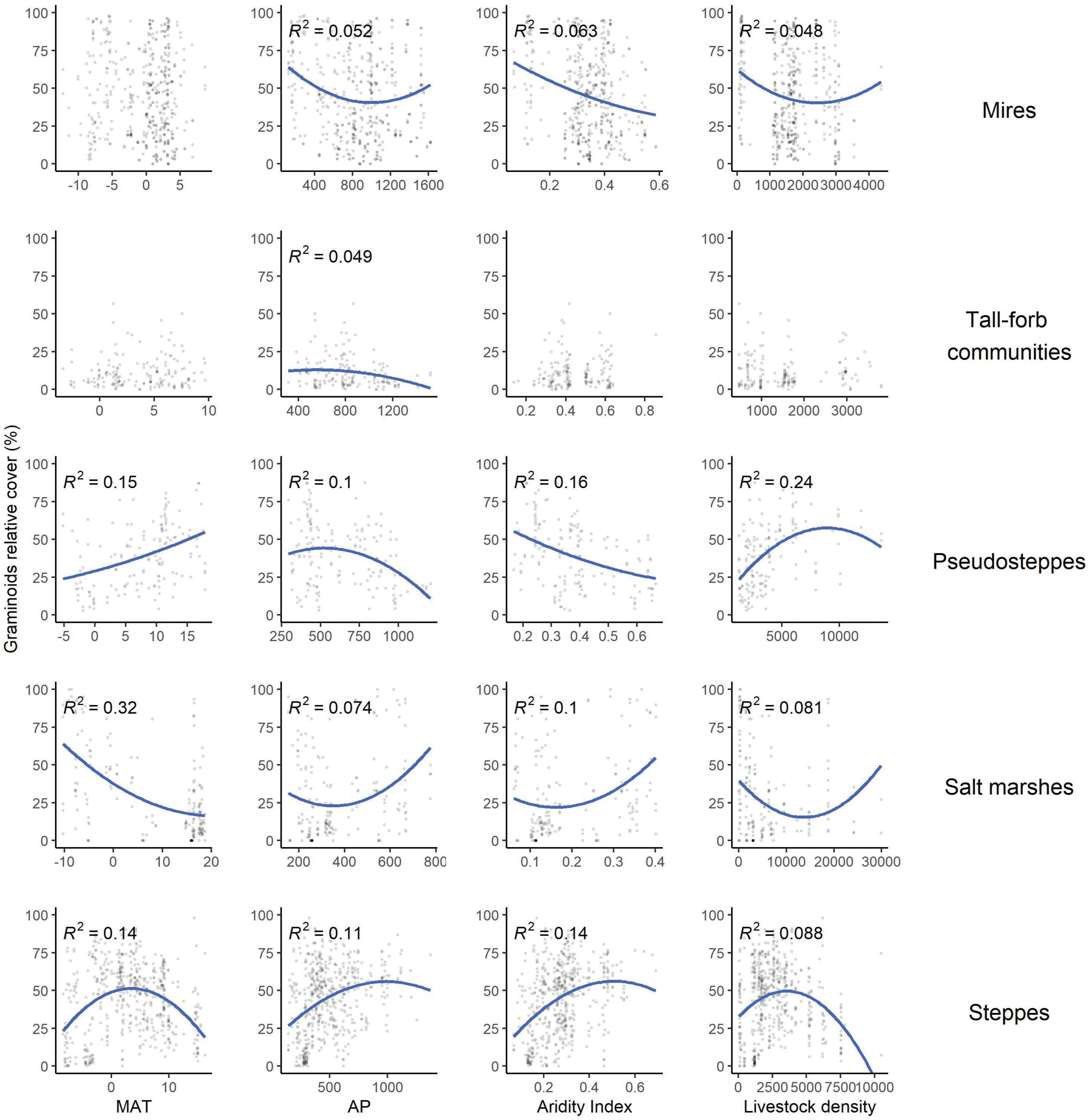

Figure 4. The relationship between graminoids relative cover and mean annual temperature (MAT), sum of annual precipitation (AP), Aridity Index and livestock density for open vegetation types in Tajikistan and Kyrgyzstan. Lines are predictions of fitted polynomial models (for a comparison of linear and polynomial models see Suppl. material 1). Only significant models at $p < 0.05$ level are shown.

Table 2. Graminoid species cumulative number in each open vegetation type and the quantitative proportion of graminoids in relation to the graminoid flora (255 species). Grey-shaded cells show the number and percentage value (in brackets) of shared graminoid species between pairs of vegetation types. The darker the cell, the higher the number of shared graminoid species between pairs of vegetation types.

Total graminoid species richness = 255	Mires	Tall-forb communities	Pseudosteppes	Salt marshes	Steppes
Mires	77 (30.2)	10 (3.9)	24 (9.4)	22 (8.6)	13 (5.1)
Tall-forb communities		**57 (22.4)**	41 (16.1)	15 (5.9)	40 (15.7)
Pseudosteppes			**94 (36.9)**	30 (11.8)	61 (23.9)
Salt marshes				**74 (29)**	26 (10.2)
Steppes					**136 (53.3)**

Table 3. Results of the polynomial regression models and commonality analysis for the effect of mean annual temperature, sum of annual precipitation, Aridity Index and livestock density on graminoids relative cover for open vegetation types. The significant values are shown in bold. Commonality analysis output represents a unique, common and total contribution of each predictor variable to the regression effect. The proportion of variance explained by the predictor is presented in parenthesis as a percentage of R^2.

Explanatory variable	F	p-value	R^2	Commonality analysis		
				Unique	Common	Total
Mires						
Mean annual temperature	1.20	0.303	0.005	0.001 (0.8%)	0.004 (5.8%)	0.005 (6.6%)
Sum of annual precipitation	**13.30**	**< 0.001**	**0.052**	0.003 (4.6%)	0.016 (22.3%)	0.019 (27%)
Aridity Index	**16.23**	**< 0.001**	**0.063**	0.033 (46.2%)	0.028 (39.9%)	0.061 (86.1%)
Livestock density	**12.25**	**< 0.001**	**0.048**	0.003 (4.8%)	0.025 (35%)	0.028 (39.7%)
Tall-forb communities						
Mean annual temperature	0.82	0.441	0.010	0.003 (5.4%)	0.005 (9.7%)	0.008 (15.2%)
Sum of annual precipitation	**4.26**	**0.016**	**0.049**	0.037 (68.4%)	0.003 (6%)	0.04 (74.3%)
Aridity Index	1.16	0.316	0.014	0.013 (25.1%)	-0.002 (-2.8%)	0.012 (22.3%)
Livestock density	0.88	0.417	0.011	0.004 (7.7%)	-0.004 (-7.3%)	0.0002 (0.4%)
Pseudosteppes						
Mean annual temperature	**13.31**	**< 0.001**	**0.153**	0.029 (11.1%)	0.123 (46.4%)	0.152 (57.5%)
Sum of annual precipitation	**8.55**	**< 0.001**	**0.104**	0.004 (1.5%)	0.07 (26.6%)	0.074 (28.1%)
Aridity Index	**14.40**	**< 0.001**	**0.164**	0.045 (17%)	0.116 (43.9%)	0.161 (60.9%)
Livestock density	**22.69**	**< 0.001**	**0.236**	0.02 (7.4%)	0.152 (57.4%)	0.172 (64.9%)
Salt marshes						
Mean annual temperature	**43.51**	**< 0.001**	**0.316**	0.239 (65.3%)	0.068 (18.6%)	0.307 (83.9%)
Sum of annual precipitation	**7.56**	**< 0.001**	**0.074**	0.001 (0.2%)	0.044 (11.9%)	0.044 (12.1%)
Aridity Index	**10.91**	**< 0.001**	**0.104**	0.004 (1.2%)	0.078 (21.2%)	0.082 (22.4%)
Livestock density	**8.25**	**< 0.001**	**0.081**	0.031 (8.4%)	-0.003 (-0.8%)	0.028 (7.6%)
Steppes						
Mean annual temperature	**43.02**	**< 0.001**	**0.141**	0.0001 (0.1%)	0.001 (0.4%)	0.001 (0.5%)
Sum of annual precipitation	**33.03**	**< 0.001**	**0.112**	0.013 (9.6%)	0.085 (63.3%)	0.098 (73%)
Aridity Index	**42.06**	**< 0.001**	**0.138**	0.036 (26.6%)	0.083 (62.1%)	0.119 (88.6%)
Livestock density	**25.31**	**< 0.001**	**0.088**	0.001 (0.7%)	0.0002 (0.1%)	0.001 (0.8%)

The best-fitted models for Aridity Index were found for pseudosteppes (R^2 = 0.16) and steppes (R^2 = 0.14). The highest unique effect of Aridity Index was found for mires (46.2%), however the highest common effect for this factor was recorded for steppes (62.1%) and pseudosteppes (43.9%). In pseudosteppes and mires relative cover of graminoids decreased with increasing Aridity Index (and therefore increasing moisture availability, see the Methods), and in steppes and salt marshes, relative cover of graminoids increased with increasing Aridity Index (Figure 4). For livestock density, the best-fitted model was found for pseudosteppes (R^2 = 0.24). However, the unique effect of livestock density is relatively low (7.4%), but the common effect with other factors is the highest among all the open vegetation types analysed (57.4%). The highest graminoids relative cover values on pseudosteppes was found at a density of ca. 9,000 animals per km^2. Similar hump-shape pattern was found for steppes with the highest graminoids relative cover values at a density of ca. 4,000 animals. On the other hand, for salt marshes and mires we found a U-shaped pattern with the lowest relative cover of graminoids at level of ca. 1,500 and 2,500 domestic animals per km^2 respectively (Figure 4).

Discussion

Graminoids are not always the dominant group in broadly-defined grasslands of Tajikistan and Kyrgyzstan

Grasslands are generally described as vegetation dominated by graminoids, which typically have > 25% coverage (Dengler et al. 2014). Referring to the definition of Allen et al. (2011) the vegetation of grassland is broadly considered because a variety of plant groups are present including grasses, legumes and other forbs, with no or scarce occurrence of woody plants. The results of our research showed that the analysed types of vegetation, which can be broadly classified as grasslands (steppes, pseudosteppes, mires, salt marshes and tall-forb vegetation), are characterized by different proportions of graminoids (Figure 2). It is not surprising that the highest proportion of graminoids was recorded in steppes, mires and pseudosteppes. These are vegetation types that are shaped by the livestock grazing. The area of Middle Asia is characterized by long pastoral tradition, which for many years influenced the formation of plant communities consisting of grazing tolerant species (Wesche and Treiber 2012; Spengler et al. 2014). In grassland vegetation occurring in Tajikistan and Kyrgyzstan, species from *Poaceae* dominate or constitute a significant share. An important component of steppe vegetation are species from the genus *Stipa* (Wesche and Treiber 2012); in this study 33 *Stipa* taxa (species and subspecies) were found within the study area. Pseudosteppes are secondary grassland types developed in habitats primarily dominated by shrublands. This vegetation type occurs in lowlands (Figure 2c), in the southern regions of Middle Asia characterized by relatively high annual precipitations and high temperatures (Świerszcz et al. 2020). Similarly to steppes, they are characterized by a constant and significant share of species from the *Poaceae*, including the most frequently recorded *Poa bulbosa*. Also, some pseudosteppes are characterized by a higher frequency and cover of annual species, e.g. *Aegilops triuncialis*, *Avena sterilis* subsp. *ludoviciana*, *Bromus lanceolatus*, or *Vulpia persica* (Suppl. material 2).

The vegetation type with the highest proportion of graminoids are mires, which occur mostly in the mountainous areas of Middle Asia. Harsh environmental conditions at high elevational zones together with an intensive grazing promote species from the *Cyperaceae*. An increasing abundance of *Cyperaceae* representatives with increasing altitude was also found in the Himalayas (Dolezal et al. 2019). However, despite analogous relationships in the proportion of graminoids in the altitudinal gradient our results do not show any clear pattern in sedges-dominated mires related to elevation (data not shown).

Salt marshes and tall-forb vegetation had a low contribution of graminoids (median relative coverage < 25%, Figure 3). Halophytic vegetation is quite diverse in terms of dominant plant groups: from graminoid-dominated communities with *Aeluropus littoralis* or *Puccinellia* spp. (Świerszcz et al. 2021) to vegetation with a negligible share of graminoids, e.g. communities dominated by stem succulent C_3 chenopods of the genera *Salicornia*, *Halopeplis*, and *Suaeda* (Akhani 2004). Our study showed that the number of graminoid species is relatively low in salt marshes of Middle Asia (74 taxa; Suppl. material 2); however, they are used as pasture, mostly in the harsh conditions of the Pamirs (Świerszcz et al. 2021). Tall-forb communities are also characterized by a low graminoid abundance. They are dominated by tall forbs, such as species from the Apiaceae (e.g. *Prangos pabularia*, *Ferula kuhistanica*, and *Heracleum lehmannianii*; Nowak et al. 2020b). Similar results were obtained by Wagner (2009) in meadow-forb vegetation in the western Tian Shan, where non-graminoid species dominate while only 19 graminoid species were recorded. The low number and contribution of graminoids in tall-forb vegetation can be explained by their close relationship with juniper forests, xerophytic shrubs, or screes in which graminoids occur with low abundance (Nowak et al. 2020b, 2022a; Świerszcz et al. 2022). Moreover, tall-forb communities are used as pastures, but grazing animals use sward selectively because the vegetation includes tasteless or even poisonous species (e.g. *Prangos pabularia*, species of the genus *Ferula*). This phenomenon causes a strong growth and dominance of these plants and simultaneously inhibits the growth of grasses and sedges (Figure 2d).

Effects of climatic factors on the abundance of graminoids

Grasslands in Middle Asia, despite having similar physiognomy, show high variation in species composition (Wesche and Treiber 2012). Grasslands, similarly to other vegetation types, change along environmental gradients in relation to climatic variables such as precipitation, temperature, and aridity. The altitudinal gradient influences the structure, phenology and species composition of grasslands in this strongly mountainous region (Wagner et al. 2020).

Steppes are typical grassland vegetation and constitute an important feature of the diverse landscape in Middle Asia. Our study showed strong response of graminoids relative cover to climatic gradients in these steppes. We observed a sharp decrease of graminoids at low average annual temperatures at altitudes above 3,000 m a.s.l. (own observations). With the increasing altitude and harsher environmental conditions, graminoids are replaced by resilient semi-desert taxa adapted to high elevations, e.g. *Artemisia skorniakovii*, *Astragalus chomutowii* or *Braya pamirica* (Nowak et al. 2018; Świerszcz et al. 2020). Low proportion of graminoids is also noted in the more thermophilic steppes in the colline and montane belts, where the vegetation may consist mainly of dwarf shrubs (Nowak et al. 2016b). A possible explanation for this may be that the graminoids involved in the formation of the steppe vegetation have a long life span and are less resistant to aridity and low annual precipitation. The opposite pattern was found for pseudosteppes, where a higher contribution of graminoids was recorded in a more arid environment. Pseudosteppes develop in zones with high average temperatures with dry periods during the summer, when the entire grasslands sesonally dry up (Guarino et al. 2020). High precipitation in spring and autumn and dry summers promote periodically drought-tolerant species that increase in abundance seasonally. Due to arid climatic conditions, high livestock pressure, and soil erosion, the vegetation has a greater contribution of graminoids, especially annual grasses, e.g. *Avena sterilis* subsp. *ludoviciana*, *Bromus lanceolatus*, and *Vulpia persica* (Suppl. material 2; Świerszcz et al. 2020). This secondary vegetation within the shrubland zone (Figure 2c) is similar to the thermo-mesomediterranean grasslands occurring in the Mediterranean Region (San Miguel 2008; Guarino et al. 2020; Świerszcz et al. 2020).

The contribution of graminoids in salt marshes also varied along climatic gradients. The highest graminoid cover was found on sites with a low mean annual temperature, high precipitation and less arid conditions. Middle Asian salt marshes vary according to geobotanical regions. In south-western Tajikistan and in the Ferghana Valley salt vegetation inhabits e.g. shallow ponds and around riverbeds. The most common graminoid species is *Aeluropus littoralis*, however, it does not make a significant contribution to the vegetation. The high-elevation salt marshes in the Eastern Pamir are different. The vegetation is shaped by extremely harsh conditions and is species poor. However, a common feature of graminoid species found in salt marshes, as in steppes, is their longevity and low resistance to soil drought. Many vegetation patches are dominated by graminoids adapted to the high salt content in the soil, e.g. species of the genus *Puccinellia* (Nowak et al. 2020a).

Although our results show some patterns in the proportions of graminoids with regard to precipitation and the Aridity Index in mires, the models show a poor fit. The lack of a clear climatic gradient may be due to the fact that sedges are the main component of this type of vegetation (Spalink et al. 2018; Martín-Bravo et al. 2019). Mires are hydrogenic habitats, fed mainly by seeping groundwater (Nowak et al. 2016a), thus they buffer the surplus of water supplied by rainfall. However, the highest share of graminoids in this type of vegetation, mainly species from *Cyperaceae*, is recorded in the driest areas (with low Aridity Index values). In the case of Middle Asia, such conditions prevail mainly in high altitudes of the Pamir Mountains, where long-rhizomatous graminoids typical for high alpine vegetation are promoted (Dolezal et al. 2019). Also, aridity facilitates the development of other plant features, e.g. grazing-resistance traits (Adler et al. 2004). These features, combined with resistance to cold, radiation, drought and strong wind are very important from the point of view of livestock production, especially as winter pastures (Göbel et al. 2019; Can et al. 2020).

Tall-forb communities are not typical graminoid vegetation. In most cases, graminoids do not dominate in these communities, although there is great variability within this type of vegetation (Nowak et al. 2020b). However, bioclimatic variables studied poorly explained patterns of graminoids contribution. This may be explained by plant species composition in tall-forb communities, which depends on specific microclimatic and soil conditions, not examined in this study. For example, Central European tall-forb communities with a high abundance of graminoids are associated with acidic soils and/or excessive depositions of atmospheric nitrogen (Świerkosz and Reczyńska 2022).

Grazing-induced changes in graminoids abundance

The vegetation cover of open habitats in Tajikistan and Kyrgyzstan is strongly affected by livestock grazing, which resulted in changes in graminoid abundance. However, our study shows that not all analysed vegetation types respond to grazing in terms of graminoid contribution. We obtained the best-fitted model for pseudosteppes, where the proportion of graminoids increases with increasing livestock density to the highest point of all vegetation types analysed. The results confirm that pseudosteppes are a secondary vegetation type created after the cutting of pistachio groves (Nowak et al. 2022b). Intensive grazing, mainly by sheep and goats, results in the appearance of a high abundance of species resistant to grazing (e.g. *Poa bulbosa*, *Carex pachystylis*, *Cynodon dactylon*) and characterized by animal-induced diaspore dispersal (e.g. *Aegilops triuncialis*, *Avena sterilis* subsp. *ludoviciana*, *Taeniatherum caput-medusae* subsp. *crinitum*; Suppl. material 2). Many of them are ephemeral species (Toderich et al. 2013) also resistant to aridity and high temperatures. Milchunas et al. (1988) showed that arid conditions promote grazing resistance traits. It appears that semi-natural pseudosteppes are associated with a long evolutionary history of grazing, strongly linked to climatic conditions (e.g. seasonally dry soils; Guarino et al. 2020). Similar relationships have been confirmed in other parts of the world, e.g. the Patagonian steppes of southern Argentina (Adler et al. 2004; Guarino et al. 2020). On the other hand, in the steppes, which are characterized by similar vegetation physiognomy and land use type, according to our results, the variation in relative graminoid cover is mainly related to climatic conditions. Grazing has a much smaller effect on their share of patches in the vegetation; moreover, grazing intensification may lead to a reduction in the proportion of graminoids at the expense of other grazing-tolerant species, e.g. species of the genus *Astragalus* (= *Tragacantha*, *Astracantha*).

Conclusions

Our study shows that the largest number of graminoid species is associated with steppes, which are the most common vegetation type in Middle Asia. However, there is no universal pattern for graminoid distribution along the climatic and grazing gradient, but such relationships were found for particular vegetation types. Strong but not consistent relationships were found in steppes, pseudosteppes and salt marshes. These differences result mainly from biogeographic features of the study area. But it is important to bear in mind that current and upcoming climate change may contribute to the potential extinction of some graminoid species, including endemics (Vintsek et al. 2022). Grazing showed to be the strongest variable influencing the proportion of graminoids in pseudosteppes, pointing to their anthropogenic origin. The mountainous landscape and the history of human activity, especially grazing by sheep, cattle and horses, create favourable habitats for various types of graminoid communities. It is worth noting that major changes in open ecosystems are related to expanding human and livestock populations, resulting in pastures that are often overgrazed, which can lead to more serious problems related to soil erosion, among others (Figure 2f). As Middle Asia is an area where the human food and economic safety is largely depended on grazing animals, research on group of plants is necessary and should be continued, also for vegetation types important for grazing but not covered by our analyses (e.g. alpine meadows, *Kobresia* mats). The knowledge about relative cover patterns of graminoids and their underlying factors increases our understanding of ecological patterns in the open vegetation of Middle Asia.

Data availability

Primary data are stored in the Vegetation of Middle Asia database (http://www.givd.info/ID/AS-00-003) (Nowak et al. 2017).

Author contributions

S.Ś. planned the research. S.Ś., G.S, and S.N. collected part of the field data. S.Ś. prepared the final dataset, performed statistical analyses and led the writing. G.S., M.R., and S.N. critically revised and edited the manuscript.

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E-mail and ORCID

Sebastian Świerszcz (Corresponding author, sebastian.swierszcz@ob.pan.pl), ORCID: https://orcid.org/0000-0003-2035-0035
Grzegorz Swacha (grzegorz.swacha@uwr.edu.pl), ORCID: https://orcid.org/0000-0002-6380-2954
Małgorzata W. Raduła (malgorzata.radula@upwr.edu.pl), ORCID: https://orcid.org/0000-0002-9578-6135
Sylwia Nowak (snowak@uni.opole.pl), ORCID: https://orcid.org/0000-0003-2867-9839

Supplementary material

Supplementary material 1
Comparison of models performance used in our study
Link: https://doi.org/10.3897/VCS.95767.suppl1

Supplementary material 2
A list of graminoid species recorded in the study area
Link: https://doi.org/10.3897/VCS.95767.suppl2