

Classification of tall-forb vegetation in the Pamir-Alai and western Tian Shan Mountains (Tajikistan and Kyrgyzstan, Middle Asia)

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Abstract

Aims: To complete the syntaxonomic scheme for tall-forb vegetation of the montane and alpine belts in the Pamir-Alai and western Tian Shan Mountains in Tajikistan and Kyrgyzstan with some remarks on its environmental predictors. **Study area:** Middle Asia: Tajikistan and Kyrgyzstan. **Methods:** A total of 244 relevés were sampled in 2013–2019 using the seven-degree cover-abundance scale of the Braun-Blanquet approach. These were classified with a modified TWINSPAN algorithm with pseudospecies cut-levels 0%, 5% and 25%, and total inertia as a measure of cluster heterogeneity. Diagnostic species were identified using the phi coefficient as a fidelity measure. NMDS was used to explore the relationships between the distinguished groups. **Results:** Our classification revealed 19 clusters of tall-forb vegetation in Middle Asia. Among others we found forb communities typical for Tian Shan, western Pamir-Alai, forb-scrub vegetation of Pamir-Alai, dry tall-forbs and typical forbs of the alpine belt. A total of eight new tall-forb associations and five communities were distinguished. The forb vegetation of Middle Asia has been assigned to the class *Prangetea ulopterae* Klein. The main factors differentiating the species composition of the researched vegetation are elevation, mean annual temperature, sum of annual precipitation and inclination of the slope. **Conclusions:** The paper presents the first insight into the comprehensive classification of the alpine forb vegetation in Middle Asia and fosters progress in explaining the relationship of boreo-temperate and Mediterranean-like (Irano-Turanian) vegetation in western Asian and central Asian subregions of the Irano-Turanian phytogeographical region.

Taxonomic references: The nomenclature of the vascular plants follows generally Cherepanov (1995) and for *Bromus* spp. The Plant List (2020) Version 1.1. <http://www.theplantlist.org/>.

Syntaxonomic references: The names of syntaxa are used in accordance with Ermakov (2012), Gadghiev et al. (2002) and Nowak et al. (2018).

Abbreviation: NMDS = Non-metric Multidimensional Scaling.

Keywords

Alpine vegetation, forb, Middle Asia, Pamir-Alai, phytogeography, *Prangetea ulopterae*, shiblyak, syntaxonomy

Introduction

Tall-forb vegetation is known to be one of the most prominent and species-rich communities, particularly in mountainous landscape (Kočí 2001). The communities of the class *Mulgedio-Aconitetea* are natural tall-grass, tall-forb, or krummholz (shrubberies) vegetation with a well developed, often luxuriant herb layer. In the newest classification, the shrubby krummholz is excluded and incorporated into *Betulo carpaticae-Alnetea viridis* (Mucina et al. 2016). All these prominent vegetation types of the mountainous landscapes occur at varying elevations, mainly from lower montane to the high alpine belt. Its range covers a vast area from western and northern Europe to southern Siberia (Hilbig 1995; Ermakov et al. 2000). However, towards the south such hygrophilous vegetation gradually gives way to the more thermophilous and drought-tolerant tall-forb communities of the Irano-Turanian region. Middle Asia, as in the case of chasmophytic, steppe and forest vegetation (Nowak et al. 2017a, 2018, 2020a), stretches on the borderland of these different, although closely related, types of vegetation. Distinct communities are formed here, particularly in the relatively moist and nutrient rich habitats of the Afghano-Turanian subregion *sensu* Kameilin (2010). This subregion supports a species rich and abundant vegetation with a dominance of tall forbs, mainly from the *Apiaceae* (*Ferula*, *Mediasia*, *Prangos*) and *Polygonaceae* (*Aponogeton*, *Polygonum*, *Rheum*) families. For this type of tall-forb vegetation, in the northern Iran, the class *Prangetea ulopterae* was coined (Klein 1987).

In the long history of research on the vegetation of Middle Asia, mainly in Tajikistan, vegetation similar to the *Prangetea* class was defined in very different ways. Firstly, it was recognized as “forb meadows” (Korovin 1934), subtropical steppes or semi-savannas (Rubtsov 1952; Ovchinnikov 1957), communities of *Prangos* and *Ferula* (Golovkova 1959) or the “ephemeroid” vegetation (Agakhanyanz and Yusufbekov 1975). Ovchinnikov (1971) proposed the name “yuganniki” for *Prangos pabularia* communities (*Prangos* in Tajik language is *yugan*) and kamolniki (scree forbs) for *Ferula* spp. vegetation. Additionally, Pavlov (1967, 1980) introduced the term “umbeliferniki” for *Apiaceae* species (alternative name *Umbelliferae*) dominated vegetation.

In the Pamir-Alai, in central Tajikistan, the first notes on the composition and distribution of *Apiaceae* dominated communities were published by Goncharov (1936). His research was focused on the vegetation of *Feruleto-Prangosetum*, *Polygoneto-Prangosetum* and *Artemisio-Feruletum* with prominent contribution of *Ferula kokanica*, *F. jaeschkeana*, *P. pabularia*, *Polygonum coriarium* and *Artemisia persica*. Additionally, from the Hissar Mountains, namely the Varzob River Valley, the community of *Prangos pabularia-Ferula jaeschkeana* was mentioned (Ovchinnikov 1971). Less frequently, the communities of *Prangetea ulopterae* were noted from the Eastern Pamir, some of which may be scree vegetation. It is also worth mentioning the works of Agakhanyanz

(1966) who reported the vegetation of *Ferula grigoriewii* (as *Feruleta grigorjewii*) and *Prangos pabularia* (as *Prangoseta pabulariae*).

Representation of *Prangetea ulopterae* can be observed not only in Pamir-Alai but also in western Tian Shan. These areas are in close proximity to juniper groves and occur as a forb rich undergrowth dominated by *Prangos pabularia*, *Ferula tenuisecta*, *F. tschimganica*, *F. pallida*, *F. prangifolia* and *Rheum maximowiczii*. This vegetation occurs mainly in upper montane and alpine belts at an elevation of 1,500–2,800 m a.s.l. (Pavlov 1980). Recently, the work of Wagner (2009) gives some important insights and shows nine distinct plant communities belonging to meadow-forb vegetation (e.g. *Dactylis glomerata-Karatavia kultiassovii* and *Nepeta mariae-Aconogonon coriarium*) in the Aksu-Jabagly Nature Reserve in the western Tian Shan. Other pasture vegetation communities were revealed in the research of Borchardt et al. (2011), where they proposed a variation of tall-forb communities (*Aconogonon coriarium-Prangos pabularia-Galium aparine* and *Ligularia thomsoni-Dactylis glomerata* communities). However, these studies did not aggregate the communities into higher-level units and rationalise them with the known orders and classes. Understandably, the hierarchical system of all Middle Asian grasslands is challenging to the vegetation ecologist, despite being crucial for communication and application in conservation (De Cáceres et al. 2018).

This paper presents the first attempt to classify the tall-forb vegetation in the Pamir-Alai and south-western Tian Shan Mountains and to relate it to steppe and alpine meadow communities. We aimed at addressing the following questions during our study: (1) What is the diversity of tall-forb vegetation of the montane and alpine zones in the Pamir-Alai and south-western Tian Shan Mountains? (2) What are the environmental and habitat requirements of the described plant communities? (3) What is the species composition and structure of the vegetation plots? and (4) Which species have important diagnostic value for the described communities?

Study area

The vegetation survey was conducted in an area of ca. 350,000 km² located in the central part of Middle Asia (the Pamir-Alai in Tajikistan, and western and central Tian Shan in Kyrgyzstan, Figure 1). Due to the considerable phytogeographical differences between Pamir-Alai and Tian Shan Mountains, the research aimed at examining the tall-forb vegetation of both areas, including Alai, Transalaian, Alichurian, Shachdarian, Shugnan, Sarikol, Yazgulem and Peter the First Ranges in Pamir-Alai and Trans-Ili Alatau, Kyungey Ala-Too, Terskey Ala-Too, Songkol, Fergana, Kyrgyz and the Chatkal Mountains in Kyrgyzstan. The mountainous character of the highland landscapes of Middle Asia makes this territory particularly suitable for different types of tall-forb communities.

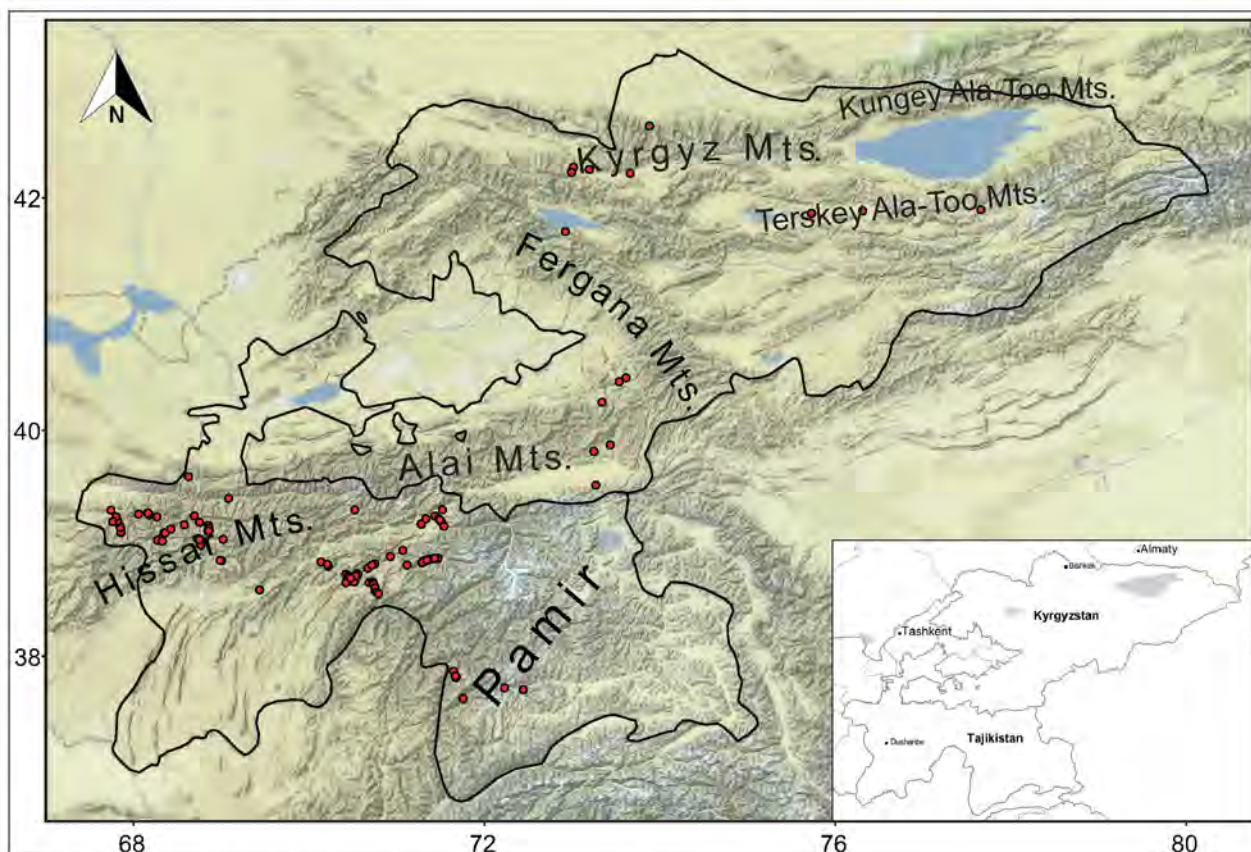


Figure 1. Study area and distribution of the vegetation plots ($n = 244$).

The vast alpine habitats of Middle Asia extend across a long elevational gradient. The studied sites were located between 1,300 and 3,500 m a.s.l. (mean 2,270) and within habitats that differ in terms of aspect, inclination, bedrock and particle size.

The study area is located between two main bioclimatic zones (the Irano-Turanian and Central Asiatic) and is additionally influenced by the Indo-Indochinese climate from the south and Euro-Siberian from the north. It is difficult to characterize the climatic conditions of the region, as it stretches across a transition zone between the Temperate and Irano-Turanian macrobioclimates. The first zone is characterized by a summer precipitation peak, whereas a winter precipitation peak and higher continentality are typical of the latter (Djamali et al. 2012). There are four main climatic regions within the research area (Latipova 1968; Narzikulov and Stanyukovich 1968; Safarov 2003):

(1) The warm, continental, Irano-Turanian region that includes the Fergana Valley. The surroundings of Jalalabad and Osh are characterized by winter precipitation that in March achieves its peak of 80 mm and an annual average of ca. 200–250 mm. The temperatures reach 20 °C in April and 34 °C from June to August. During these months, the precipitation is scarce, with 0–10 mm of rainfall per month. Snow and frost occur from December to February, with an average no lower than -3 °C and extreme values reaching -27 °C in some years.

- (2) The warm, humid, continental region that includes the Tian Shan and Pamir-Alai ranges. Average temperature in June in the colline and montane belts within this region is around 22 °C. In the alpine belt, the temperature drops to 10 °C. Annual precipitation ranges from about 500 mm on the northern slopes up to ca. 1000 mm on the southern.
- (3) The cold semi-arid region that includes the Issyk-Kul basin, central and western parts of the Alai Valley, and foothills and plateaus on the colline, montane and subalpine belts. These areas are clearly distinguished by lower precipitation, with an average ca. 200–400 mm per year. The distribution of rainfall during the year is similar to that in the temperate climate, with a maximum of 70 mm between May and July. The temperature exceeds 20 °C only in summer, and the annual average temperature is ca. 10 °C.
- (4) The cold desert climate region that includes the easternmost sections of the Alai Valley and the eastern Pamirian Plateau. This area is distinguished by significant aridity with less than 100 mm mean annual precipitation. Only in May and August does the average monthly precipitation exceed 20 mm. The yearly annual precipitation is slightly above 0 °C, with the minimum falling below -30 °C in January – February.

It is important to note that a multitude of local anomalies caused by orography, wind conditions and altitudinal differences occur within each of these regions (Figure 1).

Methods

Data sampling and data analyses

In total, 244 relevés were collected in tall-forb vegetation of Tajikistan and southern Kyrgyzstan in all vertical belts of Pamir-Alai and the Tian Shan Ranges during seven successive vegetation seasons (2013–2019). The size of each sampled vegetation plot ranged from 4 m² to 50 m², but most were 10 m². In each plot, all vascular plant and cryptogam species were recorded using the seven-degree Braun-Blanquet cover-abundance scale (Westhoff and van der Maarel 1973). The sampled data represent broad ranges of habitats, elevations, aspects, and inclination. For each plot, geographical coordinates were measured using a GPSMAP 60CSx device with an accuracy of ±5 m and a WGS84 reference frame.

In the tables containing plot data (Suppl. material 1), both latitude and longitude are given in decimal scale.

Data were stored in the Vegetation of Middle Asia database (Nowak et al. 2017b) and analyzed in R (R Core Team 2020) and JUICE software (Tichý 2002). A modified TWINSpan analysis (Hill 1979; Roleček et al. 2009) provided an initial understanding of the data structure and resolution. The cover-abundance scale was transformed using the three-step interval scale with cut-off levels at 0%, 5% and 25%. As the plots were selected fairly objectively, we downweighted rare species using chord distance as a measure of cluster heterogeneity (Roleček et al. 2009). Taxa identified only at the genus level were omitted during the analysis. Diagnostic species were identified using the phi coefficient as a fidelity measure (Chytrý and Tichý 2003). Group size was standardised and the Fisher exact test ($p < 0.05$) applied. Species with a phi coefficient higher than 0.20 were considered diagnostic for a particular cluster (except that for communities of *Phlomis oreophila* and *Inula macrophylla* where we show only those with phi > 0.30 to shorten the list for the first twelve clusters, which seem to have outlier positions in the data. Diagnostic taxa for alliances were defined as those with a phi coefficient ≥ 0.15 in at least two clusters within this alliance (with the exception of one very distinct cluster). Species with a higher frequency than 40% were defined as constant, and those with a maximum cover value exceeding 20% as the dominant species of an individual cluster (plant community). For translation of the TWINSpan results into phytosociological associations, we chose the highest division that still yielded floristically well-characterized terminal clusters with their own diagnostic species (Dengler et al. 2005, Michl et al. 2010). These terminal clusters were considered as associations or plant communities, depending on the geographical range, certainty of taxonomic status of the diagnostic species, and recommendations of the International Code of Phytosociological Nomenclature (ICPN). The habitat profile and authors' field experience were used during the division to find comprehensive and ecologically interpretable results of classification.

To check the floristic-sociological classification and highlight the relationships between relevés and species, non-metric multidimensional scaling (NMDS) was performed (with downweighting of rare species, response data were log-transformed). Species cover values on the 7-degree Braun-Blanquet scale were transformed to a percentage scale (r, +, 1, 2, 3, 4, 5 to 0.1, 1, 5, 15, 37.5, 62.5 and 87.5 respectively). Differences in environmental factors (elevation, temperature, precipitation, inclination) and vegetation variables (cover herb and moss layer, species richness and Shannon diversity index) between groups were assessed using the Kruskal–Wallis rank sum test (function *kruskal.test*) with multiple comparison based on Dunn's test using the *dunnTest* function in the 'FSA' package (Ogle et al. 2018) in R. Climatic data were extracted from the Chelsea database version 1.2 (<http://chelsea-climate.org>; Karger et al. 2017).

The shortened synoptic table with the constancy of all diagnostic species is presented in Table 1. The full synoptic table is given in Supplementary material 2. All mentioned plant communities are arranged into an overview at the beginning of the description in the results section. We considered the spatial structure and environmental characteristics – mainly the elevation and precipitation – to be the habitats' most significant attributes.

The species nomenclature mainly followed Cherepanov (1995) and, in some exceptional cases (e.g. *Bromus* spp.), according to The Plant List (2020). The plant material collected during field studies was deposited in the Herbarium of Middle Asia Mountains, hosted in OPUN (University of Opole, Poland) and KRA (Jagiellonian University, Poland).

Results

General floristic features and relations between plant communities

The total number of taxa recorded in the whole data set (244 relevés) was 810 with only 18 exceeding 5% of constancy. The group of species with the highest frequencies includes plants typical of tall-forbs such as *Prangos pabularia* (99 occurrences), *Polygonum coriarium* (68), *Ferula kuhistanica* (65), *Scabiosa songarica* (60), *Ligularia thomsonii* (58), *Elaeosticta hirtula* (54), *Geranium regelii* (48), *Eremurus comosus* (45) and *Phlomis lehmanniana* (41). However, the most frequent species was *Poa bulbosa* (132), considered a typical steppe plant, but apparently having a wider ecological amplitude. Other typically grassland species were *Carex turkestanica* (73), *Plantago lanceolata* (53) and *Arenaria serpyllifolia* (52). The group of most frequent species includes also scree plants like *Galium spurium* subsp. *spurium* (84) and *Hypericum scabrum* (41). Despite the close similarity between tall-forbs and xeric shrubs, the latter group includes only few taxa in the data set, such as *Ephedra gerardiana*, *E. glauca*, *Rosa beggeriana*, *R. corymbifera* or *R. divina* which occur with low frequency. Much richer is the flora of scree with fre-

Group No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Frequency	
No. of relevés	14	4	17	17	10	17	17	7	2	1	36	4	17	14	13	4	4	17	29		
	Ligularia thomsonii-Geranion regelii										Scabiosa songaricae-Phlomidion lehmannianae										
	Poison alpine										Rheion maximowiczii										
<i>Koeleria macrantha</i>	29	75	175	4
<i>Ceratodon purpureus</i>	57	207	...	24	58	...	29	73	29	8	6	21
<i>Euphorbia alata</i>	21	200	3
<i>Adenophora himalayana</i>	21	200	3
<i>Kobresia capilliformis</i>	14	200	...	6	3
Community of <i>Allium hymenorhizum</i>																					
<i>Allium hymenorhizum</i>	7	75	175	4
<i>Euphorbia jaxartica</i>	...	75	175	3
<i>Pedicularis grigorjevii</i>	...	100	146	...	30	89	6	14	11
<i>Eremogone griffithii</i>	...	75	175	18	7	7
<i>Nepeta podostachys</i>	...	75	93	...	40	71	18	29	21	18	10	22
<i>Astragalus saratagus</i>	...	75	228	...	10	4
<i>Asyneuma argutum</i>	...	75	313	...	20	7	8	...	6	12
<i>Ferula ovina</i>	...	50	711	...	6	20	57	154	8	3	11
<i>Phlomis seravschanica</i>	...	50	150	...	10	7	4
<i>Rosa divina</i>	...	50	34	...	6	7	10	4,8	...	7
<i>Astragalus skarniakowii</i>	...	25	238	1
<i>Angelica ternata</i>	...	25	238	1
<i>Gypsophila cephalotes</i>	...	25	238	1
<i>Asperula pamirica</i>	...	25	238	1
<i>Polygonum coriarium</i>	...	100	104	59	74	18	70	107	71	93	59	7	12	43	23	...	29	21	...	68	
<i>Cousinia pannosa</i>	...	25	317	7	2
<i>Cousinia outchashensis</i>	...	25	306	12	8	3
<i>Lomatocarpa albomarginata</i>	...	25	200	6	3
Ass. <i>Feruletum sumbuli</i>																					
<i>Ferula sumbul</i>	59	16,7	10
<i>Hedysarum flavescens</i>	21	138	...	29	379	10	3	7	13
<i>Ephedra intermedia</i>	41	34	6	3	9
<i>Thalictrum kuhistanicum</i>	65	22,5	12	10	24	21	15	24
<i>Asyneuma attenuatum</i>	24	22	4
<i>Euphorbia transoxana</i>	29	217	5
<i>Astragalus kabadianus</i>	12	311	2
Ass. <i>Heraclietum lehmannianii</i>																					
<i>Heraclium lehmannianum</i>	7	...	6	65	157	18	10
<i>Euphorbia lamprocarpa</i>	24	84	4
<i>Ranunculus brevirostris</i>	7	41	164	6	9
<i>Mentha asiatica</i>	7	47	30	10
<i>Trifolium pratense</i>	6	71	34,2	18	6	20
<i>Carum carvi</i>	7	47	29,5	24	5,5	8	15
<i>Cousinia pseudarctium</i>	59	201	20	18	29	71	103	...	25	41	8,7	...	38
<i>Nepeta cataria</i>	18	22,5	3
<i>Convolvulus arvensis</i>	35	30	6	...	43	15	25	65	7	...	37
<i>Dactylis glomerata</i>	6	59	26,5	71	10,9	7	...	50	38



Group No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Frequency
No. of relevés	14	4	17	17	10	17	17	7	2	1	36	4	17	14	13	4	4	17	29	
	Poion										Scabiosa songaricae-Phlomidion lehmannianae									
	alpinae																			
	Ligularia thomsonii-Geranion regelii										Rhizon maximowiczii									
<i>Allium elatum</i>				24	29						3			7				6		7
<i>Cynoglossum viridiflorum</i>				18	31															3
<i>Lithospermum officinale</i>				18	31.5										8				10	7
<i>Poa pratensis</i>	43			76	30.1	40	65	16	100		11			7	23	50	75	35	3	56
Ass. Eremuretum kaufmannii																				
<i>Eremurus kaufmannii</i>					40	47.9							6						3	6
<i>Dictamnus angustifolius</i>					50	31.5					6			14	8					10
<i>Lonicera nummularifolia</i>					20	30.5								8						3
<i>Restella albertii</i>					20	17.2														2
<i>Poa ursulensis</i>	25				80	18.9	71	17.8	6		3		24	14	8			6	14	35
<i>Artemisia dracunculus</i>	29	25	24	6	80	14.9	12		100			6			31			12	3	29
<i>Paeonia intermedia</i>					40	37.7	29	19.8							23	4.4				12
<i>Iris haagiiana</i>					30	34.4														4
<i>Astragalus nuciferus</i>					30	33.2					3									5
Ass. Anthriscidetum glacialis																				
<i>Anthriscus glacialis</i>						59	4.4													10
<i>Elytrigia repens</i>				12		47	51.4	6										29		16
<i>Draba huetti</i>	7					29	40.1				14							6		12
<i>Picris nuristanica</i>			12	6		35	39.9												7	11
<i>Crepis darvazica</i>						53	35.1													9
<i>Leonurus turkestanicus</i>						41	30.8							14				6		10
<i>Oberna wallichiana</i>						65	30.5							7				6		14
<i>Tanacetum pseudochillia</i>			6			35	26.8				14							18		15
<i>Euphorbia sarawshchanica</i>						53	26.4				3			14	8			18	7	18
<i>Astragalus aksuensis</i>						41	28.3													7
<i>Anemonastrum protractum</i>	7					24	24.8													5
<i>Rumex nepalensis</i>						35	24.4													6
<i>Asyneuma baldshuanicum</i>						29	22.8													5
<i>Phleum pratense</i>				12		41	31.9													9
<i>Pedicularis algae</i>			6			53	31.1								15			6		13
<i>Polygonum hissaricum</i>						18	30.8											12	5	5
<i>Ligularia alpigena</i>	21	9.5			10	29	30.5							7						10
<i>Nepeta formosa</i>						35	30.4							7						7
Community of Cousinia batalinii and Euphorbia pamirica																				
<i>Euphorbia pamirica</i>				6															21	11
<i>Cousinia batalinii</i>							71	42.4												12
<i>Eremopoa persica</i>				12		41	43.4	14						50	16.9			12	3	17
<i>Tulipa dasystemon</i>							12	29.1			3									3
<i>Astragalus lasiosemius</i>							24	24.7						14						10
<i>Platatherum sagalanum</i>							47	26.4						14						11
<i>Ephedra Gerardiana</i>							24	24.7						7						9
<i>Lappula badachschanica</i>							41	26.4												7
<i>Artemisia rutifolia</i>		50	16.4	6			41	23.8							15			6	3	16



Group No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Frequency	
No. of relevés	14	4	17	17	10	17	17	7	2	1	36	4	17	14	13	4	4	17	29		
Poion alpinae											Scabiosa songaricae-Phlomidion lehmanniana										
Ligularia thomsonii-Geranium regelii											Rheion maximowiczii										
<i>Cirsium badkhanicum</i>				18		12				100	423										6
<i>Dracocephalum diversifolium</i>										100	169										1
<i>Thalictrum isopyroides</i>						6				100	652			8							3
<i>Gentianella turkestanorum</i>	21	655								100	314										4
<i>Cotoneaster nummularioides</i>										100	355	14	28	7							7
<i>Berberis heterobotrys</i>										100	325	25									4
<i>Thymus proximus</i>	14	116			10					100	207			15	3						6
<i>Artemisia santalinifolia</i>			6			6	14			100	232	50	177								10
Ass. Eremuretum stenophyllido-comosif																					
<i>Exochorda karolkowii</i>											28	369									10
<i>Eremurus comosus</i>	50					6	57	84	100	153	69	349	6	7		50		12	17		45
<i>Rosa ovczinnikovii</i>			24	6							56	297	6	57	25			29	45	127	53
<i>Ferula transiliensis</i>											33	376									12
<i>Colutea paulsenii</i>											25	262									9
<i>Rosa papavi</i>					10						39	263	12								21
<i>Berberis nummularia</i>											19	343									8
<i>Eremurus stenophyllus</i>				6							64	317				25		6			26
Community of Inula macrophylla																					
<i>Inula macrophylla</i>				6							3	100	976								7
<i>Microthlaspi perfoliatum</i>				6							39	50	671		8	25					19
<i>Convolvulus pseudocantabrica</i>											3	100	616								5
<i>Bromus oxodon</i>			12		10	12	6			100		100	344	36	18			12			19
<i>Stubendorffia orientalis</i>						6						50	554					6			4
<i>Serratula lyratifolia</i>												75	457								3
<i>Delphinium biternatum</i>												50	476		8						7
<i>Eremurus tianschanicus</i>												50	424								2
<i>Gallium pamirolaicum</i>	36	148			10	6						50	351					6	7		15
<i>Stipa caucasica</i>			6								6	50	948								11
<i>Astragalus sieversianus</i>											3	75	348		8	25					9
<i>Carex turkestanica</i>	21				40	6	14				39	100	238	71	113	14	23	50	18	83	73
<i>Eremurus turkestanicus</i>												50	317								2
<i>Artemisia ferganensis</i>												50	337								2
<i>Eulophus ferganensis</i>												50	304								2
<i>Astragalus alopecias</i>												50	304								2
<i>Perovskia abrotanoides</i>												50	304								2
<i>Artemisia glanduligera</i>												50	304								2
<i>Spiraea hypericifolia</i>												50	201		8						4
<i>Haplophyllum acutifolium</i>												50	322								3
<i>Silene brahucica</i>			6									50	274	18	37	14					12
<i>Stipa kazachstanica</i>												50	248								2
<i>Spiraea pilosa</i>												50	248								2
<i>Tulipa bifloriformis</i>												50	248								2
<i>Achnatherum caragana</i>												50	268	18	59						5

Group No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Frequency	
No. of relevés	14	4	17	17	10	17	17	7	2	1	36	4	17	14	13	4	4	17	29		
	Ligularia thomsonii-Geranion regelii										Scabiosa songaricae-Phlomidion lehmannianae										
	Rheion maximowiczii										Rheion lehmannianae										
Poion alpinae																					
<i>Alyssum calycinum</i>											3	75	74.8			50	13.7		12	24	19
<i>Carex pachystylis</i>											6	50	25.3		15				18	17	20
<i>Scutellaria przewalskii</i>	7											50	24.8								3
<i>Dianthus tetralapis</i>							6					50	24.8	7	8					3	6
<i>Hyalolaena trichophylla</i>												25	22.8								1
<i>Leptorhabdos parviflora</i>											8	50	22.5	13	14					10	15
<i>Impatiens parviflora</i>				12	10			14			19	50	21.9		15						15
Ass. Stipetum marginalicae																					
<i>Carex dimorphotheca</i>	7					35	11.6	12					59	66.6	8				50		22
<i>Stipa marginalica</i>													65	61.1							11
<i>Astragalus mucidus</i>													76	47.1						10	16
<i>Scabiosa songarica</i>						6					25	75	74	33.9	43	25			29	66	60
<i>Allium barszewskii</i>			12			6	18				22	25	53	31.3	29	8			18	17	38
<i>Astragalus krauseanus</i>													59	28.3					12		12
<i>Cousinia mulgedifolia</i>													41	23.3					6	7	10
<i>Ferula violacea</i>													18	24.6							4
<i>Astragalus filicaulis</i>					10						8		24	20.5						3	9
<i>Poa bulbosa</i>			24	47	50	35	29	29	100		64	75	100	20.3	43	69	100	100	76	6.8	132
Ass. Lathyretum mulkaki																					
<i>Lathyrus mulkak</i>														29	40.7						4
<i>Lophanthus elegans</i>							6							21	24.5						4
<i>Iris darwasica</i>											3			36	27.6						6
<i>Nepeta algae</i>														14	20.9						3
Ass. Potentillo orientalis-Eremuretum fuscii																					
<i>Eremurus fuscus</i>															54	55.4					7
<i>Veronica arguteserrata</i>				12											38	37.8					7
<i>Eremurus brachystemon</i>					10										31	37.3					5
<i>Scorzonera tadshikorum</i>															15	38.1				7	4
<i>Gymnospermium albertii</i>						40	39.8				3				54	31.3					13
Ass. Hordeo bulbosi-Astragaletum retamocarpi																					
<i>Astragalus retamocarpus</i>													6								5
<i>Hypericum perforatum</i>				29	19.2	6					36			7					25	24	30
<i>Medicago rigidula</i>										17	16.3								100	107.6	10
<i>Hordeum bulbosum</i>				18						31	25								100	49	24
<i>Aegilops triuncialis</i>															75	61.6					3
<i>Crepina vulgaris</i>										19					75	39.1			6	3	13
<i>Buglossoides arvensis</i>										25					50	34.3					11
<i>Ferula gigantea</i>															50	28.7					2
<i>Medicago orbicularis</i>															50	33.7					2
<i>Rochella cardiosepalata</i>				6	10	12				17			18		14				100	59.6	38
<i>Elaeosticta allioides</i>										14			41	30	7				100	30.1	21
<i>Vicia angustifolia</i>										11									50	29.2	10
<i>Tragopogon capitatus</i>															50	21.6					2



Group No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Frequency	
No. of relevés	14	4	17	17	10	17	17	7	2	1	36	4	17	14	13	4	4	17	28		
	Rheion maximowiczii										Scabioso songaricae-Phlomidion lehmanniana										
	Ligulario thomsonii-Geranion regelii										Scabioso songaricae-Phlomidion lehmanniana										
Poion alpinae																					
<i>Tulipa subquaquefolia</i>										3						50	24			3	
<i>Pseudohandelia umbellifera</i>																50	18,4			3	
<i>Elaeosticta hirtula</i>			24	10	18	12				33		24		14		100	32,7		59	1,8	41
<i>Echium biebersteinii</i>				6												50	14,3			3	
<i>Medicago denticulata</i>										3						25	2,8			2	
Ass. Eremuretum robusti																					
<i>Eremurus robustus</i>						24	2,8								15			53	40,5	10	
<i>Phlomis arctifolia</i>													7					29	30,6	14	
<i>Vicia tenuifolia</i>			29	35	12,7	24						25			8	25		41	30,5	21	
<i>Cousinia umbrosa</i>					30	6,8	18								15	25		41	16,1	17	
Ass. Phlomidio lehmanniana-Onobrychidetum grandis																					
<i>Phlomis lehmanniana</i>					10	12					28	12	14			50		24		62	
<i>Onobrychis grandis</i>										3		12	21							45	
All. Ligulario thomsonii-Geranion regelii																					
<i>Ligularia thomsonii</i>	29		65	59	70	22,5	94	24,9		100				7				24		7	
<i>Geranium regelii</i>	86	32,3	50	47	11	41	3,6	40		100	6,8			15				6		48	
<i>Centaurea ruthenica</i>			25	35	13,7		10	6					64	15				12		30	
<i>Galium turkestanicum</i>	43	31,5			29	9,7	20	6		100								6		19	
<i>Myosotis alpestris</i>							30	11,9		53	27,1									12	
<i>Potentilla sericea</i>			75	20,3				53	26,5											12	
<i>Linum olgae</i>	21	18,8	25		10															6	
<i>Fritillaria regelii</i>						24	1,5							15	7,7					6	
All. Rheion maximowiczii																					
<i>Plantago lanceolata</i>				59	7,1		18			100	37,6				31	75	33,3	25		53	
<i>Ferula kokanica</i>							53	24,7		29				71	32,8	16,2		6		36	
<i>Rheum maximowiczii</i>							35	29,1				25		43	24,6					23	
<i>Poterium polygamum</i>											50									18	
<i>Bunium badachschanicum</i>							24	20,6												4	
All. Scabioso songaricae-Phlomidion lehmanniana																					
<i>Ferula kuhistanica</i>				18			53	11,8			22		18	43	15	50		59	18,4	66	
<i>Gentiana olivieri</i>					10	24				25			35	15,7		50		12		34	
<i>Rumex paulsenianus</i>			6	12	10	6			100	7,8								41	7,1	7	
<i>Solenanthes circinnatus</i>			6	12	10	24	3,9											29	6,8	3	
<i>Poterium lasiocarpum</i>				24	9,7			29	13,8		3							18	8,4	10	
<i>Rochelia peduncularis</i>							12						6	7						17	
<i>Onobrychis baldshuanica</i>											8		12	16,1						5	
O. Ferulo kuhistanicae-Prangetalia pabulariae																					
<i>Prangos pabularia</i>					50	6	35			47		50	100	24,5	71	23		53		83	
<i>Origanum tyttanthum</i>				18					50		64	50		21	38			6		14	
<i>Potentilla transcaspica</i>				12	10	29				3			6		8	50		50		7	

quent representatives including *Rochelia cardiosepala*, *Polygonum paronychioides*, *P. polycnemoides*, *Rheum maximowiczii* or *Poterium polygamum*. Additionally, a number of thermophilous shrubs were detected with *Lonicera nummulariifolia*, *Cousinia batalinii*, *Cerasus verrucosa* or *Crataegus remotilobata* as the most frequent. There are also species originating in juniper woods, such as *Juniperus seravschanica* or *Lonicera olgae*. It is worth noticing that the species list of the tall-forb vegetation of Middle Asia also includes a number of taxa of open, ruderal habitats (e.g. *Convolvulus arvensis*, *Potentilla orientalis*), meso-

representative of the *Prangetea ulopterae* known from Iran, we defined five communities (e.g. *Phlomoidetum kaufmannianae* and *Eremuretum stenophyllido-comosi*) and include them in the newly coined alliance *Rheion maximowiczii*. The last group, shown on the left part of the TWINSpan diagram, covers the mesophilous tall-forb communities of the western Pamir-Alai Mountains with very distinct communities such as *Feruletum sumbuli*, *Heracleetum lehmannianii*, *Eremuretum kaufmannii* and *Anthriscidetum glacialis*. They are included in the new alliance *Ligulario thomsonii-Geranium regelii*.

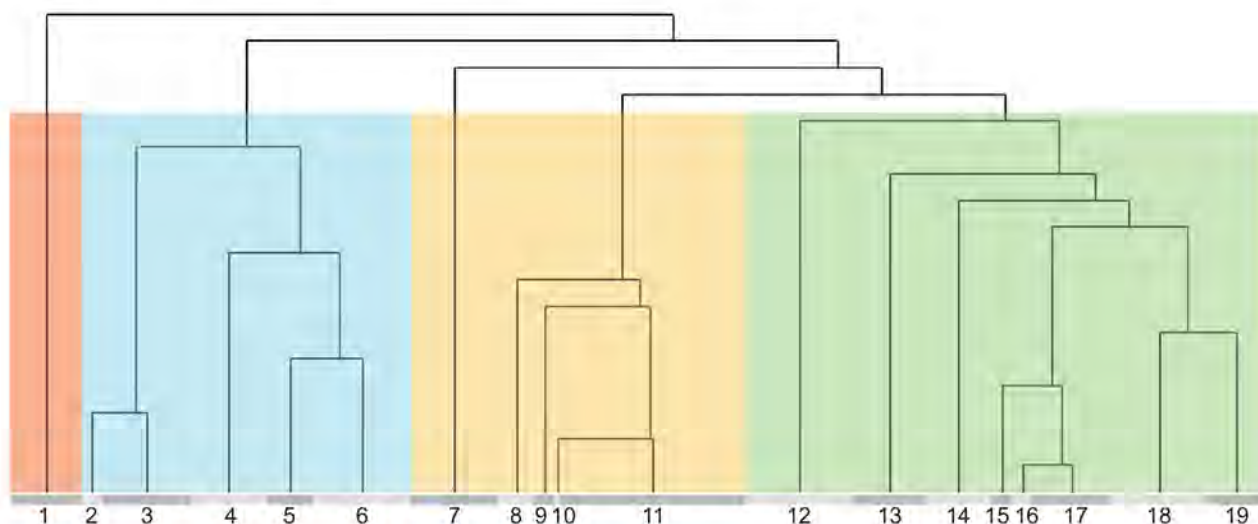


Figure 2. Dendrogram illustrating the assignment of relevé groups identified by TWINSpan to particular syntaxonomic units (see Syntaxonomic synopsis). The different background colors refer to alliances: red – *Poion alpinae*, blue – *Ligulario thomsonii-Geranium regelii*, orange – *Rheion maximowiczii* and green – *Scabioso songaricae-Phlomoidion lehmanniana*.

philous forests (*Impatiens parviflora*, *Asyneuma argutum*, *A. baldshuanicum*) or steppes (*Gentiana olivierii*, *Bunium persicum* or *Hordeum bulbosum*).

As a result of the TWINSpan classification, three main groups at the alliance level have been distinguished within the tall-forb vegetation (Figure 2). Additionally, one group was assigned to alpine meadows and left rankless for further studies (comm. *Phlomoides oreophila*). The NMDS diagram clearly showed a distinction between three main tall-forb types and vegetation classified as alpine meadows (Figure 3). The most diverse alliance includes dry tall-forb communities of the subhumid zone of the eastern Irano-Turanian region, which occur within the complex of vast pasturelands (steppes and pseudosteppes). This group (*Scabioso songaricae-Phlomoidion lehmanniana*) includes the highest number of distinct communities with typical tall-forbs (e.g. *Eremuretum robusti* or *Phlomoidion lehmanniana-Onobrychidetum grandis*) or communities transitional towards grasslands (e.g. *Stipetum margelanicae* or *Potentillo orientalis-Eremuretum fuscii*). A very distinguishable type of tall-forb vegetation in Middle Asia are the communities on scree-like habitats. They inhabit gentle slopes with deep, nutrient-rich soil, but are covered by rock debris. In this type of tall-forb vegetation, repre-

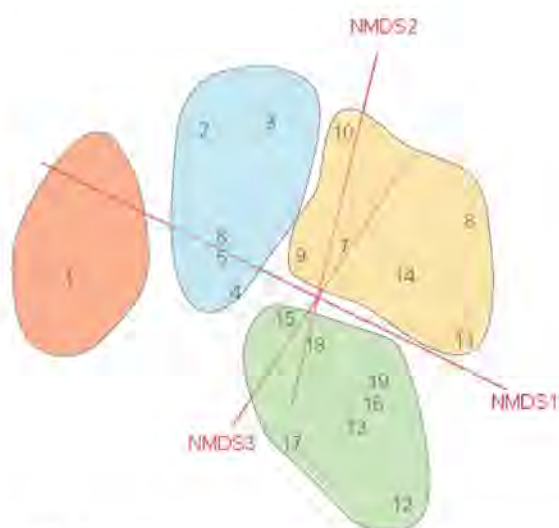


Figure 3. NMDS ordination of tall-forb communities in the Pamir-Alai and western Tian-Shan Mountains. The different envelopes colors refer to alliances: red – *Poion alpinae*, blue – *Ligulario thomsonii-Geranium regelii*, orange – *Rheion maximowiczii* and green – *Scabioso songaricae-Phlomoidion lehmanniana*. Numbers on ordination refer to centroids of clusters (see Syntaxonomic synopsis).



Classification of the vegetation units

As a result of our classification analysis, 19 well-defined plant communities were distinguished according to species composition (Figure 2). As our study pioneers research in the area, we chose not to apply any refinements in the classification by moving some relevés between clusters using iterative relocation methods or deletion of any outliers. With insufficient field experience to identify atypical or fragmentary stands, we believe that our approach is the most justified. Distribution maps of all tall-forb types within the study area are presented in Figure 4. Environmental and vegetation parameters are presented in Figure 5 and photographs of selected communities are presented on Figures 6 and 7.

Syntaxonomic synopsis

Mesic mown and grazed subalpine meadows and pastures on fertile soils

Class: *Molinio-Arrhenatheretea* Tx. 1937

1. Order: *Poo alpinae-Trisetetalia* Ellmauer et Mucina 1993

1.1. Alliance: *Poion alpinae* Gams ex Oberd. 1950

1.1.1. Community of *Phlomoïdes oreophila* (cluster 1)

Irano-Turanian thermophilous, mesic tall-forb communities of the western Pamir-Alai and Tian Shan Mountains

Class: *Prangetea ulopterae* Klein 1987

2. Order: to be described

Forb rich mesophilous tall-forb communities of the western Pamir-Alai Mountains

2.1. Alliance: *Ligulario thomsonii-Geranion regelii* Nowak et al. all. nov. prov.

2.1.1. Community of *Allium hymenorhizum* (cluster 2)

2.1.2. *Feruletum sumbuli* Nowak et al. 2015 (cluster 3)

2.1.3. *Heracleetum lehmannianii* Nowak et al. ass. nov. prov. (cluster 4)

2.1.4. *Eremuretum kaufmannii* Nowak et al. ass. nov. prov. (cluster 5)

2.1.5. *Anthriscidetum glacialis* Nowak et al. 2020 ass. nov. prov. (cluster 6)

Scree-like tall-forb communities of the eastern Irano-Turanian region

2.2. Alliance: *Rheion maximowiczii* Nowak et al. all. nov. prov.

2.2.1. Community of *Cousinia batalinii* and *Euphorbia pamirica* (cluster 7)

2.2.2. *Phlomoïdetum kaufmanniana* Nowak et al. ass. nov. prov. (cluster 8)

2.2.3. *Eremostachyetum tadshikistanicae* Nowak et al. 2016 (cluster 9)

2.2.4. Community of *Senecio saposchnikovii* (cluster 10)

2.2.5. *Eremuretum stenophyllido-comosi* Nowak et al. ass. nov. prov. (cluster 11)

Dry tall-forb communities of the subhumid zone of the eastern Irano-Turanian region

2.3. Alliance: *Scabioso songaricae-Phlomoïdion lehmanniana* Nowak et al. all. nov. prov.

2.3.1. Community of *Inula macrophylla* (cluster 12)

2.3.2. *Stipetum margelanicae* Nowak et al. 2016 (cluster 13)

2.3.3. *Lathyretum mulkaki* Nowak et al. ass. nov. prov. (cluster 14)

2.3.4. *Potentillo orientalis-Eremuretum fusci* S. Świeraszcz et al. 2020 (cluster 15)

2.3.5. *Hordeo bulbosi-Astragaletum retamocarpi* S. Świeraszcz et al. 2020 (cluster 16)

2.3.6. Community of *Ferula kuhistanica* (cluster 17)

2.3.7. *Eremuretum robusti* Nowak et al. ass. nov. prov. (cluster 18)

2.3.8. *Phlomoïdo lehmanniana-Onobrychidetum grandis* Nowak et al. ass. nov. prov. (cluster 19)

Mesic mown and grazed subalpine meadows and pastures on fertile soils

1.1.1. Community of *Phlomoïdes oreophila* (cluster 1)

Diagnostic species: *Alchemilla bungei*, *Astragalus alpinus*, *Aulacospermum simplex*, *Caragana jubata*, *Cerastium tianschanicum*, *Festuca alatavica*, *Geranium regelii*, *Myosotis asiatica*, *Pedicularis ludwigii*, *Phlomoïdes oreophila*, *Poa alpina*, *Thalictrum foetidum*, *Valeriana dubia*, *Veronica porphyriana*
Constant species: *Geranium regelii*, *Phlomoïdes oreophila*
Dominant species: *Phlomoïdes oreophila*

Floristic and habitat characteristics: We recorded plots of this association in the alpine belt of Kyrgyz and Talas Ranges in Kyrgyzstan (Figure 4). It was found between 2,100 and 3,500 m a.s.l. (mean approx. 2,750, Figure 5a). It occupies gently sloping mountains on a vast territory making up the sheep pastures. It grows on fertile, deep and well hydrated soils, often with a close relationship to mire vegetation with *Primula auriculata*, *P. olgae*, or the alpine windswept mats of *Kobresia pamiroalaica*. The plots have dense cover and a typical forb luxuriance with the average vegetation cover over 90% (Figure 5d). The association is fairly species rich, with a mean of 26 species per plot (ranging from 13 to 37; Figure 5f). The community is intensively grazed by sheep and sporadically goats. Due to scarce sampling we left this community rankless and plan to collect supplementary data from pasturelands of Kyrgyzstan.

Irano-Turanian thermophilous, mesic tall-forb communities of the Pamir-Alai and Tian Shan Mountains

For the eastern territories of the Irano-Turanian region, a distinct group of communities within the forb vege-

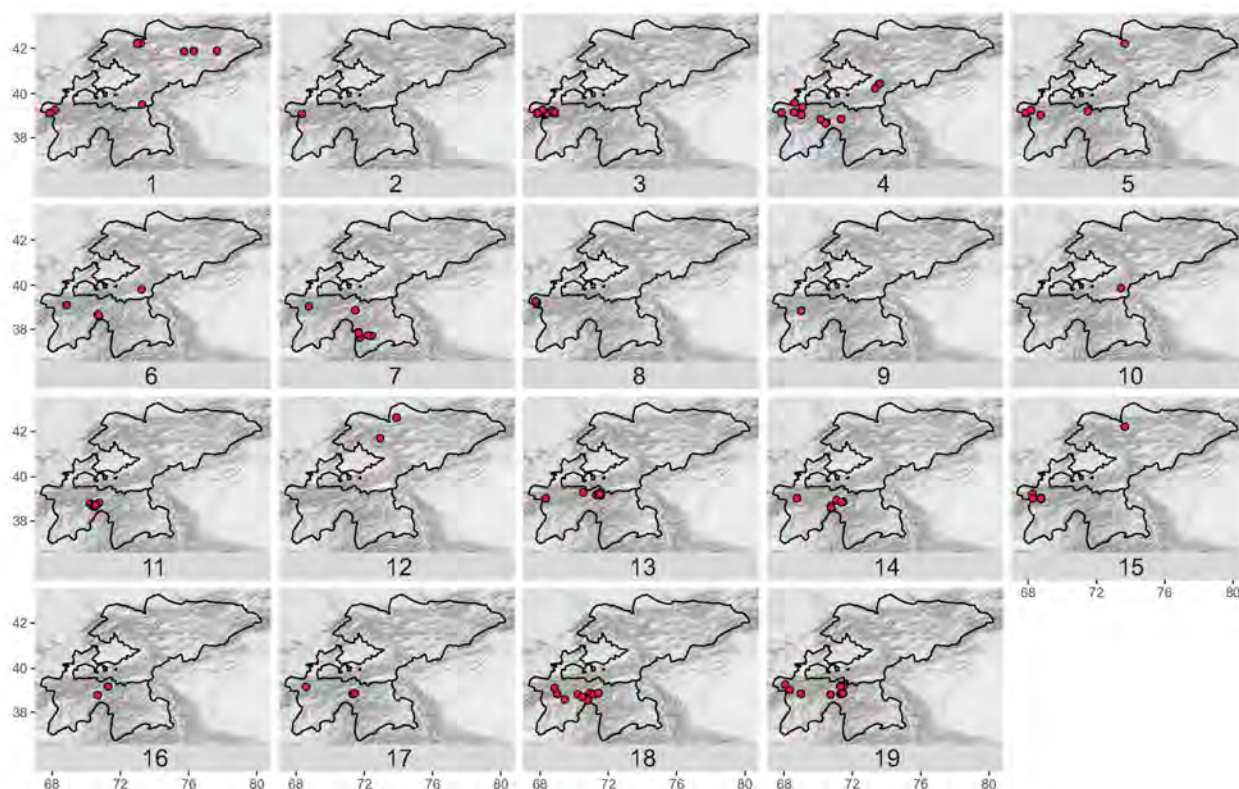


Figure 4. Distribution of relevés assigned to the particular vegetation units ($n = 244$). The name of syntaxon (1–19) are written in the Syntaxonomic synopsis.

tation of *Prangetea ulopterae* Klein 1978 dominated by typical Middle Asian species such as *Prangos pabularia*, *Ferula kuhistanica*, *F. kokanica*, *Aponogeton coriarium* and *A. songaricum* should be defined. This type of vegetation occurs throughout the Pamiro-Alai and the western and southern Tian Shan. It inhabits fertile soils, mainly in the alpine belt. They vary according to the type of habitat, in particular in the inclination of the slope and the presence of stones in the substrate. In particular, the forb vegetation of the *Rheion* alliance occupies places with the topsoil covered with unstable rocks, creating a characteristic “fertile scree” vegetation. This tall-forb vegetation is most often used extensively as pastures for sheep and goats, less often for horses and yaks.

Forb rich mesophilous tall-forb communities of the western Pamir-Alai Mountains

2.1. Alliance: *Ligularia thomsonii*-*Geranium regelii* Nowak et al. all. nov. prov.

These tall-forb communities grow mainly in the alpine belt of the western Pamir-Alai ranges on deep and humid fertile soils with calcareous bedrock. They form a luxuriant vegetation on slopes and flat lands. Only *Heracleetum lehmannianii* is apparently restricted to river sides and occasionally slope water outflows. The composition of this vegetation is clearly determined by large forbs, with the high share of *Geranium* sp., *Phlomoides* sp., *Polygonum* sp., *Eremurus* sp., *Anthriscus* sp. and *Nepeta* sp.

Diagnostic taxa: *Ligularia thomsonii*, *Centaurea ruthenica*, *Fritillaria regelii*, *Geranium regelii*, *Galium turkestanicum*, *Myosotis alpestris*, *Potentilla sericea*

2.1.1. Community of *Allium hymenorhizum* (cluster 2)

Diagnostic species: *Allium hymenorhizum*, *Lomatocarpa albomarginata*, *Angelica ternata*, *Asperula pamirica*, *As-tragalus saratagiensis*, *A. skorniakowii*, *Asyneuma argutum*, *Cousinia outichaschensis*, *C. pannosa*, *Eremogone griffithii*, *Euphorbia jaxartica*, *Ferula ovina*, *Gypsophila cephalotes*, *Nepeta podostachys*, *Pedicularis grigorjevii*, *Phlomoides seravschanica*, *Polygonum coriarium*, *Rosa divina*

Constant species: *Allium hymenorhizum*, *Eremogone griffithii*, *Nepeta podostachys*, *Pedicularis grigorjevii*, *Polygonum coriarium*

Dominant species: *Allium hymenorhizum*, *Linum olgae*

Floristic and habitat characteristics: The stands of *Allium hymenorhizum* occur in different habitats in terms of environmental conditions, particularly humidity. It generally prefers organic, well watered soils, sometimes in contact with typical fens, but generally inhabits slopes with typical tall-forb, meadow-like or even grassy vegetation across the whole Tajikistan. Due to this uncertainty and the small sample number, we leave this community rankless. Patches of this vegetation were found in the alpine belt at the average elevation of ca. 2,800 m a.s.l. (between 2,700 – 2,850 m a.s.l., Figure 5a). It inhabits gently slopes with 5° to 15° inclination (average 11°) and northern aspects. The plots were moderately rich in species with the average of

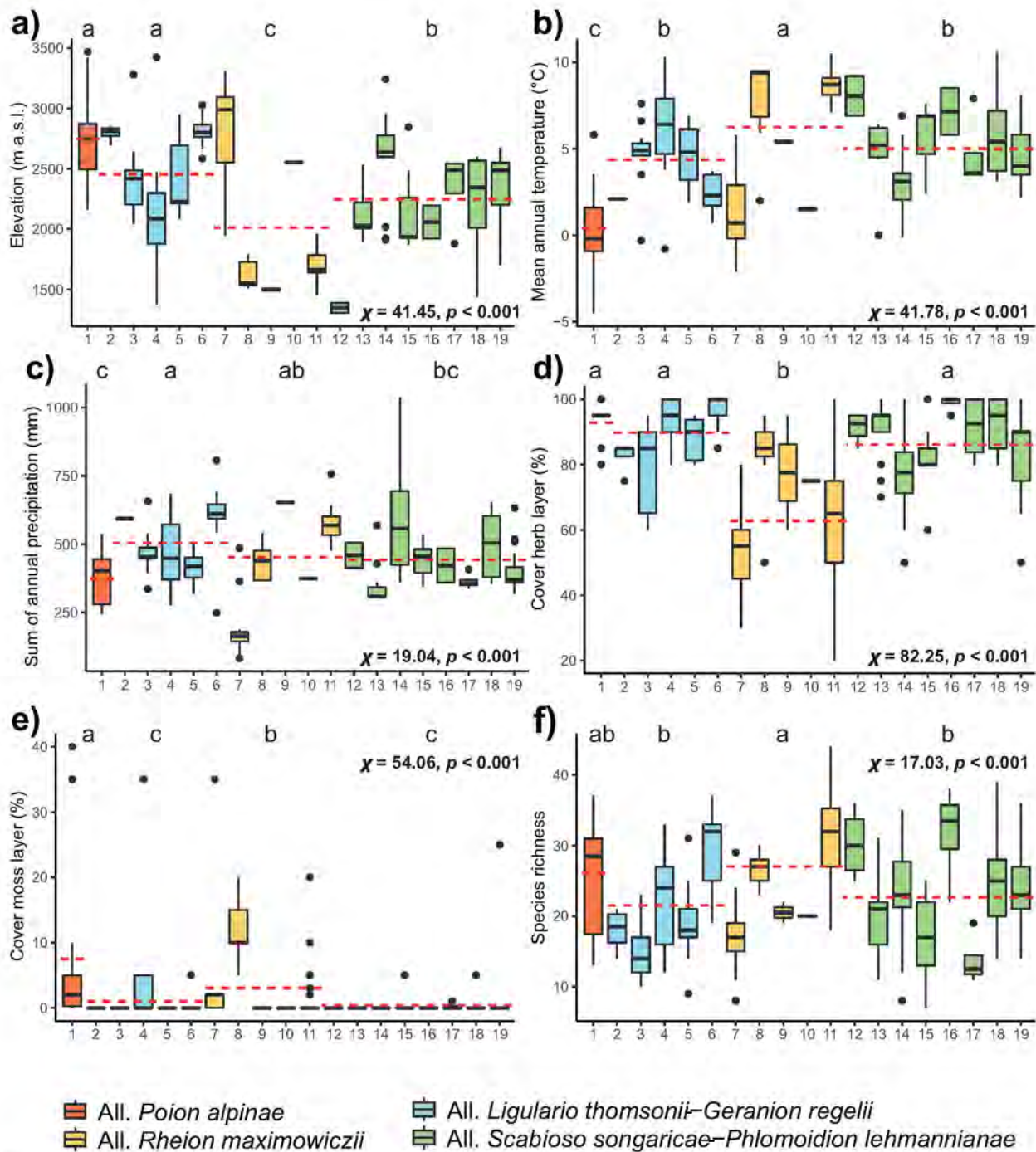


Figure 5. Boxplots showing median (line), quartiles, outliers and the range of (a) elevation, (b) mean annual temperature, (c) sum of annual precipitation, (d) cover of herb layer, (e) cover of moss layer and (f) species richness for particular syntaxonomic units. Red line indicates mean values of alliances. The values of χ^2 and p for statistical tests for vegetation groups are shown. Different letters indicate significant differences among the alliances. The abbreviations of the syntaxonomic units are explained in the Syntaxonomic synopsis.

ca. 18 taxa per plot (ranging from 14 to 21; Figure 5f). The community has high vegetation cover reaching up to 85% (Figure 5d). This tall-forb vegetation is extensively grazed by sheep and, sporadically, goats.

2.1.2. *Feruletum sumbuli* Nowak et al. 2015 (cluster 3)

Diagnostic species: *Astragalus kabadianus*, *Asyneuma attenuatum*, *Ephedra intermedia*, *Euphorbia transoxa-*

na, *Ferula sumbul*, *Hedysarum flavescens*, *Thalictrum kuhistanicum*

Constant species: *Ferula sumbul*, *Hedysarum flavescens*

Dominant species: *Ferula sumbul*, *Hedysarum flavescens*

Floristic and habitat characteristics: *Ferula sumbul* is an endemic plant of the western Pamir-Alai occurring in Tajikistan preferably in the Zeravshan and Funn Ranges (Nowak et al. 2020a). Occasionally, it occurs in forest openings and alpine meadows, but forms the com-

munity in the valley bottoms, particularly often in sites with coarse blocks of rocks from eroded rock walls (Figure 6a). The association was described as the forb community from scree aprons in Fann Mountains (Nowak et al. 2015; Figure 4). Its stands are distributed in the alpine belt within the range of elevations from 2,050 to 3,300 m a.s.l. (Figure 5a). It prefers limestone bedrock and alkaline soil substrates. Patches of this association were found on relatively gentle slopes (foothills of large block screes) with a mean inclination of approx. 10°. The association inhabits different slopes with northern, southern and western aspects. It is characterized by a dense forb cover up to 95% (mean close to 80%, Figure 5d) and a negligible moss contribution. The richness of vascular plant species is moderate, with an average of 15 species and a maximum of 23 per plot (Figure 5f).

2.1.3. *Heracleetum lehmannianii* Nowak et al. ass. nov. prov. (cluster 4)

Diagnostic species: *Allium elatum*, *Carum carvi*, *Convolvulus arvensis*, *Cousinia pseudarctium*, *Cynoglossum viridiflorum*, *Dactylis glomerata*, *Euphorbia lamprocarpa*, *Heracleum lehmannianum*, *Lithospermum officinale*, *Mentha asiatica*, *Nepeta cataria*, *Poa pratensis*, *Ranunculus brevirostris*, *Trifolium pratense*

Constant species: *Cousinia pseudarctium*, *Heracleum lehmannianum*

Dominant species: *Cousinia pseudarctium*, *Heracleum lehmannianum*

Floristic and habitat characteristics: This distinct association is formed by the endemic *Heracleum lehmannianum* of Middle Asia distributed across all of Pamir-Alai and western Tian Shan (Nowak et al. 2020a). *Heracleetum lehmannianii* mainly occurs along mountain rivers and streams, rarely inhabiting water outflows on slopes (Figure 6b). The vegetation has been recorded in the Zeravshan, Hissar, Hazratishoh and Western Pamir Ranges (Figure 4). The association prefers deep, well watered soils with small gravel ingredients. The phytocoenosis has a fairly wide altitudinal amplitude across montane and alpine belts and inhabits the range between 1,500 and 3,500 m a.s.l. (mean approx. 2,000; Figure 5a). Patches of this vegetation inhabit mainly flat land, but sometimes they can be found on relatively steep slopes, up to 30° (mean approx. 15°), where it prefers the northern aspects. Total cover of the herb layer is very high, often reaching 100% (Figure 5d). Only occasionally, whether in *Heracleum lehmannianum* or *Cousinia pseudarctium* stands, does it have sparser cover, but never below 80%. The vegetation is moderately rich in species relative to the average of 22 species per plot. However, some patches can consist of up to 33 or have as few as 12 species per plot (Figure 5f). The moss layer has inconsiderable value, however in some sites close to fen vegetation it can reach up to 35% (Figure 5e). The association is clearly a vicariant one of the Caucasian stands of *Heracleum mantegazzianum* or *H. sosnovskyi* and Alborz hogweeds like *H. persicum*.

2.1.4. *Eremuretum kaufmannii* Nowak et al. ass. nov. prov. (cluster 5)

Diagnostic species: *Artemisia dracunculus*, *Astragalus nuciferus*, *Dictamnus angustifolius*, *Eremurus kaufmannii*, *Iris hoogiana*, *Lonicera nummulariifolia*, *Paeonia intermedia*, *Poa urssulensis*, *Restella albertii*

Constant species: *Artemisia dracunculus*, *Ligularia thomsonii*, *Prangos pabularia*

Dominant species: *Eremurus kaufmannii*, *Prangos pabularia*

Floristic and habitat characteristics: This is typical alpine tall-forb vegetation of the Pamir-Alai Range. *Eremurus kaufmannii* occurs in northern Tajikistan and northern Afghanistan forming its own association on gentle slopes in the alpine pastureland zone (Ovchinnikov 1963). The patches of this remarkable vegetation were noted in the Zeravshan and Hissar Mountains (Figure 4) at the elevation of ca. 2,400 m a.s.l. (ranging between 2,100 and 2,850; Figure 5a). They occur on gentle slopes from 10° to 40° (mean ca. 20°) inclination and preferably at a northern aspect. The total cover of the vegetation was approx. 90% on average (ranging between 80 and 95%; Figure 5d). This tall-forb vegetation is moderately rich in species having from 9 to 31 species per plot (mean ca. 19; Figure 5f). This type of forb, dominated by the decorative *Eremurus kaufmannii*, is very spectacular in the pasture landscape of alpine meadows (the plant itself is poisonous to stock animals, Figure 6c). The tall, ornamental *Eremurus* is a prominent feature in the landscape of the high Pamir-Alai mountains, especially after the first passage of sheep herds.

2.1.5. *Anthriscidetum glacialis* Nowak et al. ass. nov. prov. (cluster 6)

Diagnostic species: *Anemonastrum protractum*, *Anthriscus glacialis*, *Astragalus aksuensis*, *Asyneuma baldshuanicum*, *Crepis darvazica*, *Draba huetii*, *Elytrigia repens*, *Euphorbia sarawschanica*, *Leonurus turkestanicus*, *Ligularia alpigena*, *Oberna wallichiana*, *Pedicularis olgae*, *Phleum pratense*, *Picris nuristanica*, *Polygonum hissaricum*, *Rumex nepalensis*, *Tanacetum pseudachillea*

Constant species: *Anthriscus glacialis*, *Ferula kuhistanica*, *Geranium regelii*, *Ligularia thomsonii*

Dominant species: *Anthriscus glacialis*, *Ferula kuhistanica*

Floristic and habitat characteristics: *Anthriscus glacialis* is a widely distributed alpine species across the whole Pamir-Alai and western Tian Shan Ranges (Chukavina 1984). We recorded the stands of this species mainly in the central section of the Darvaz Range around the Hoburobot Pass (Figure 4). It grows on nutrient rich, deep, nitrophilous soils within a pastureland complex with intensive grazing (Figure 6d). Stands of this vegetation were recorded in the upper alpine belt between 2,500 and 3,000 m a.s.l. elevation (mean ca. 2,800 m; Figure 5a). The association prefers gentle slopes or flat plots in the vast pasturelands, sometimes in close vicinity to villages (so called "letovki" – summer huts) with mean inclination of approx. 12° (ranging from

5° to 25°. It occurs preferably at western and south-western aspects. The herb layer is particularly luxuriant and reaches on average close to 100% cover (Figure 5d). *Anthriscidetum glacialis* includes from 19 to 37 species, approx. 30 per plot (Figure 5f). It is intensively grazed and very sporadically mowed (patches in villages neighbourhood).

Scree like tall-forb communities of the eastern Irano-Turanian region

Alliance: *Rheion maximowiczii* Nowak et al. **all. nov. prov.**

This tall-forb vegetation mainly grows in the montane and subalpine belts on gravelly scree-like slopes, with the soil often covered by coarse rocky debris. Therefore, apart from the typical tall-forb species, there are many scree plants such as *Tetrataenium olgae* or *Senecio saposchnikovii*. The soil profile is relatively deep and nutrient rich, however in some cases it is almost completely covered with unstable rock debris. In Middle Asia, communities of this type occur across the Pamir-Alai and western Tian Shan Ranges, and is particularly frequent in Zeravshan, Vanch, Rushan, Hissar, Alai and Fergana Mountains. Plots of the phytocoenoses were sampled at elevation between 1,500 and 3,300 m a.s.l. (mean approx. 2,000; Figure 5a). They inhabit slopes with an inclination of 3°-45° (average 25°). This tall-forb alliance is rich in species with an average of 27 per plot (ranging from 8 to 44; Figure 5f). The herbaceous layer varies from 20% to 100%, with an average of ca. 65% (Figure 5d). The vegetation forms luxuriant stands (Figures 6e, 7e, f) with a number of dominant species that are endemic to Middle Asia (e.g. *Rheum maximowiczii*, *Bunium badachschanicum*, *Phlomooides tadschikistanica*). As in other *Prangetea ulopterae* vegetation, large *Apiaceae* species are highly represented (e.g. *Ferula kokanica* or *F. transiliensis*). Patches of this vegetation can withstand periodic drought of habitats during hot summer.

Diagnostic taxa: *Bunium persicum*, *B. badachschanicum*, *Eremurus stenophyllus*, *Ferula kokanica*, *Plantago lanceolata*, *Poterium polygamum*, *Rheum maximowiczii*

2.2.1. Community of *Cousinia batalinii* and *Euphorbia pamirica* (cluster 7)

Diagnostic species: *Acantholimon parviflorum*, *Artemisia rutifolia*, *Astragalus lasiosemius*, *Bunium badachschanicum*, *Cousinia batalinii*, *Ephedra gerardiana*, *Eremopoa persica*, *Euphorbia pamirica*, *Kudrjaschevia allotricha*, *Lappula badachschanica*, *Linaria sessilis*, *Piptatherum sogdianum*, *Rheum maximowiczii*, *Scariola orientalis*, *Tetrataenium olgae*, *Tulipa dasystemon*

Constant species: *Ferula kokanica*

Dominant species: *Cousinia pseudarctium*, *Ferula kokanica*
Floristic and habitat characteristics: *Cousinia batalinii* is an endemic plant of the Hissar and Darvaz Ranges, and occurs only sporadically in the Western Pamir (Rasulova 1991). The second of the two main diagnostic species,

Euphorbia pamirica, is distributed almost across the same area. It grows in the Hissaro-Darvaz geobotanical region, but is also rarely found in the West and East Pamirs (Ovchinnikov 1981). The community forms a scree-like vegetation, however is rich in species with considerable cover in the herb layer. Plots of this vegetation were noted in the alpine belt at an elevation of 1,950 to 3,300 (average approx. 2,850 m a.s.l.; Figure 5a). The patches were recorded on slopes with an inclination of 10°-45° (average 35°), preferably at south-western and southern aspects. The total cover of herbs was approx. 55% (ranging from 30% to 80%; Figure 5d) and the plots consisted of 8 to 29 species per plot (mean approx. 17; Figure 5f). This is one of the most scree-like vegetation types of *Prangetea ulopterae*, and because of its internal heterogeneity we decide to leave it rankless.

2.2.2. *Phlomooidetum kaufmanniana* Nowak et al. **ass. nov. prov. (cluster 8)**

Diagnostic species: *Alcea nudiflora*, *Anisantha tectorum*, *Boissiera squarrosa*, *Bromus danthoniae*, *Bunium persicum*, *Crambe kotschyana*, *Crepis pulchra*, *Eremurus soogdianus*, *Erodium cicutarium*, *Lindelofia macrostyla*, *Nardurus krausei*, *Neurotropis kotschyana*, *Papaver pavoninum*, *Perovskia virgata*, *Phlomooides kaufmanniana*, *Piptatherum kokanicum*, *Scandix stellata*, *Scrophularia scabiosifolia*, *Taeniatherum crinitum*, *Valerianella ovczinnikovii*, *Bryum caespiticium*, *Encalypta vulgaris*, *Pohlia nutans*, *Tortula muralis*

Constant species: *Perovskia virgata*, *Phlomooides kaufmanniana*, *Bryum caespiticium*, *Encalypta vulgaris*, *Pohlia nutans*

Dominant species: *Phlomooides kaufmanniana*

Floristic and habitat characteristics: *Phlomooides kaufmanniana* is a narrowly distributed forb species of the western Pamir-Alai. Its stands were found only in a few valleys in the Zeravshan and Turkestan Mountains in Tajikistan (Kochkareva 1986). It has been noted in the montane belt at an elevation of approx. 1,500 – 1,800 m a.s.l. (average approx. 1,630; Figure 5a). This vegetation prefers western aspects with a moderate inclination of about 5°-35° (average approx. 15°, Figure 7e). The cover of the herb layer ranges from 50 to 95%, with a mean of 80% (Figure 5d). Mosses were observed within plots with a mean cover of ca. 12% (Figure 5e). Plots include from 23 to 30 species, with an average of approx. 26 per plot (Figure 5f).

2.2.3. *Eremostachyetum tadshikistanicae* Nowak et al. 2016 (cluster 9)

Diagnostic species: *Achillea biebersteinii*, *Amoria repens*, *Geranium divaricatum*, *Hedysarum denticulatum*, *Medicago sativa*, *Phlomooides canescens*, *P. tadshikistanica* (*Eremostachys tadshikistanica*), *Ranunculus muricatus*, *Trichodesma incanum*

Constant species: *Amoria repens*, *Phlomooides tadshikistanica*, *Plantago lanceolata*

Dominant species: *Phlomooides tadshikistanica*

Floristic and habitat characteristics: *Phlomooides tadshikistanica* is an endemic species of the Hissar, Darvaz and Ak-tau ranges in the western Pamir-Alai (Kochkareva 1986). This community has been characterised in our previous work devoted to scree vegetation on montane and colline belts (Nowak et al. 2016b), but it is also presented here as we found two additional plots representing this association in the Darvaz Mountains (Figure 4). They were located at an elevation of 1,500 m a.s.l. (Figure 5a) on a steep scree exposed to the south and with an inclination of 45° (Figures 5a, 7f). The average herb layer cover was approx. 80%. Plots were moderately rich with 19 or 22 species per plot (Figure 5f).

2.2.4. Community of *Senecio saposchnikovii* (cluster 10)

Diagnostic species: *Anaphalis racemifera*, *Artemisia santolinifolia*, *Berberis heterobotrys*, *Cirsium badakhschanicum*, *Cotoneaster nummularioides*, *Dracocephalum diversifolium*, *Gentianella turkestanorum*, *Senecio saposchnikovii*, *Thalictrum isopyroides*, *Thymus proximus*

Constant species: *Senecio saposchnikovii*

Dominant species: *Senecio saposchnikovii*

Floristic and habitat characteristics: The only patch of vegetation supporting *Senecio saposchnikovii* was noted in the Alai range close to the Uch-tube village (Figure 4). It occurs on steep, loose scree at an elevation of approx. 2,500 m a.s.l. (Figure 5a), with the soil underlying gravel. The community grows on the exposed western slopes with an inclination of approx. 35°. The vegetation was relatively abundant with 75% cover of the herb layer (Figure 5d) and was composed of 20 plant species (Figure 5f). This very distinct community is left rankless until additional patches are surveyed.

2.2.5. *Eremuretum stenophyllido-comosi* Nowak et al. ass. nov. prov. (cluster 11)

Diagnostic species: *Berberis nummularia*, *Colutea paulsenii*, *Exochorda korolkowii*, *Rosa ovczinnikovii*, *R. popovii*, *Eremurus comosus*, *E. stenophyllus*, *Ferula transiliensis*, *Poterium polygamum*

Constant species: *Eremurus comosus*

Dominant species: *Rosa ovczinnikovii*; *Eremurus comosus*

Floristic and habitat characteristics: This is one of the most frequent communities of the scree-like forbs of the Eastern Irano-Turanian subregion, however it can also occur in gentle sloping or flat pastures with negligible rock debris. The association has been recorded mainly in the Hissar Mountains (e.g. Mayhura Valey) and Darvaz Mountains (e.g. Obikhingou Valley; Figure 4). *Eremurus stenophyllus* is a typical Irano-Turanian element distributed from Iran to Central Asia, but *E. comosus* is considered an endemic plant of the western Pamir-Alai Mountains (Ovchinnikov 1963). The community forms distinct stands on large areas within the montane belt (Figure 6e). The association's plots have been found at an elevation between 1,450 and 2,000 m a.s.l. (average approx. 1,700 m; Figure 5a). They main-

ly inhabit south-eastern and southern slopes, with varying inclinations from 5° to 40° (average approx. 23°). The association is characterized by a varied herb cover, ranging between 20 and 100% (approx. 60% on average, Figure 5d). Between 18 and 44 vascular plant species were recorded in each relevé, with an average of 32, which positioned this tall-forb association as one of the most speciose (Figure 5f).

Tall-forb communities of the subhumid zone of the eastern Irano-Turanian region

2.3.2. Alliance: *Scabioso songaricae-Phlomooidion lehmanniana* Nowak et al. all. nov. prov.

This tall-forb vegetation forms luxuriant stands mainly in montane and subalpine belts on gentle slopes with nutrient rich soil and negligible rock debris. The only exception is the association of *Lathyretum mulkaki* growing occasionally almost on pure screes, but then creating species impoverished stands. Patches of this vegetation are found in micromosaic situations with other vegetation, mainly thermophilous shrubs (shiblyak) or scree vegetation and alpine pastures. In Middle Asia, the communities of this type occur across all of Pamir-Alai and western Tian Shan Mountains, and are particularly frequent in the Darvaz, Hissar, Peter the First, Vanch, Alai and Fergana Mountains. The plots comprising this phytocoenoses were sampled at an elevation between 1,300 and 3,250 m a.s.l. (mean approx. 2,200; 5a). They inhabited slopes with an inclination of up to 55° (average approx. 20°). This tall-forb vegetation is rich in species with an average of 23 per plot (ranging from 7 to 39; Figure 5f). The cover of herbaceous layer is much higher than in the previous alliance (*Ligularia thomsonii-Geranium regelii*) and differs from 50% to 100% reaching the average of ca. 85% (Figure 5d). The vegetation forms dense stands (Figures 6f, 7a-d, g) with a number of distinct, prominent Middle Asian species (e.g. *Eremurus robustus*, *E. fuscus*, *E. brachystemon*, *Lathyrus mulkak*, *Phlomooides lehmanniana*, *P. tadshikistanica*). As in other *Prangetea ulopterae* vegetation the large *Apiaceae* species have considerable representation, e.g. *Prangos pabularia*, *Ferula gigantea*, *F. kuhistanica* or *F. violacea*.

Diagnostic taxa: *Gentiana olivieri*, *Onobrychis baldshuanica*, *Phlomooides lehmanniana*, *Poterium lasiocarpum*, *Rumex paulsenianus*, *Inula macrophylla*, *Rochelia peduncularis*, *Soleanthus circinnatus*

2.3.1. Community of *Inula macrophylla* (cluster 12)

Diagnostic species: *Artemisia ferganensis*, *A. glanduligera*, *Astragalus alopecias*, *A. sieversianus*, *Bromus oxyodon*, *Carex turkestanica*, *Convolvulus pseudocantabrica*, *Delphinium biternatum*, *Eremurus tianschanicus*, *E. turkestanicus*, *Eulophus ferganensis*, *Galium pamiroalaicum*, *Inula macrophylla*, *Microthlaspi perfoliatum*, *Perovskia abrotanoides*, *Serratula lyratifolia*, *Spiraea hypericifolia*, *Stipa caucasica*, *Stubendorffia orientalis*

Constant species: *Bromus oxyodon*, *Carex turkestanica*, *Convolvulus pseudocantabrica*, *Galium pamiroalaicum*,



Inula macrophylla, *Prangos pabularia*, *Serratula lyratifolia*, *Stubendorffia orientalis*

Dominant species: *Bromus oxyodon*, *Carex turkestanica*, *Inula macrophylla*, *Prangos pabularia*, *Stubendorffia orientalis*

Floristic and habitat characteristics: Stands of *Inula macrophylla* are relatively common in the Pamir-Alai, however it seems that the species is only a contributor to other vegetation types. It is widespread in the whole of Middle Asia and occurs also in the Tarbagatai Mountains in Kazakhstan (Kinzikaeva 1988). We recorded only a few plots dominated by this plant in the Fergana and Talas in Kyrgyzstan (Figure 4) at the elevation of 1,300 to 1,400 m a.s.l. (average 1,350 m, Figure 5a) on deep, nutrient rich soil overlying limestone bedrock (Figure 6f). This community inhabits relatively steeply descending slopes with a mean inclination of approx. 30°, with a preference for northern aspects. It is characterized by a very dense herb cover which often reaches 100% (average close to 90%, Figure 5d). The richness of vascular plant species was high, with an average of 30 species and a maximum of 36 per plot (Figure 5f).

2.3.2. *Stipetum margelanicae* Nowak et al. 2016 (cluster 13)

Diagnostic species: *Allium barsczewskii*, *Astragalus filicaulis*, *A. krauseanus*, *A. mucidus*, *Carex dimorphothea*, *Cousinia mulgediifolia*, *Ferula violacea*, *Poa bulbosa*, *Scabiosa songarica*, *Stipa margelanica*

Constant species: *Artemisia persica*, *Carex dimorphothea*, *Poa bulbosa*, *Prangos pabularia*, *Scabiosa songarica*, *Stipa margelanica*

Dominant species: *Prangos pabularia*, *Stipa margelanica*

Floristic and habitat characteristics: This association was previously proposed after field studies conducted in the northern Pamir-Alai (Nowak et al. 2016a), but with additional data it is presented again here. *Stipetum margelanicae* has the intermediate character and is a kind of steppe vegetation with a significant share of forb plants. It has been found in the alpine belt within an altitudinal range between 1,900 and 2,200 m a.s.l. (mean approx. 2,100; Figure 5a). Patches of this vegetation inhabit gentle slopes (average inclination of approx. 15°) and only sporadically were found on steeper descents of up to 40°. It prefers south-eastern and eastern aspects. The total cover of herb layer is relatively high and ranges from 70% to 100% (mean approx. 90%; Figure 5d). The vegetation is moderately rich, with 13 to 31 species per plot (mean ca. 20; Figure 5f).

2.3.3. *Lathyretum mulkaki* Nowak et al. ass. nov. prov. (cluster 14)

Diagnostic species: *Iris darwasica*, *Lathyrus mulkak*, *Lophanthus elegans*, *Nepeta olgae*

Constant species: *Cousinia pseudarctium*, *Ferula kokanica*

Dominant species: *Cousinia pseudarctium*, *Ferula kokanica*, *Lathyrus mulkak*

Floristic and habitat characteristics: This tall-forb vegetation (Figure 7a) occurs mainly in the Darvaz and Hissar Mountains in the alpine belt with relatively high precipitation (up to 1,000 mm yearly). It is closely related to scree communities in terms of habitat conditions, however the floristic composition positioned it within the *Scabioso songaricae-Phlomooidion lehmanniana* alliance. Documented plots occupied steep slopes at the alpine elevations in the Western Pamir-Alai Mountains (Figure 4). They were noted at ca. 1,900 to 3,250 m a.s.l. with a mean of ca. 2,600 m (Figure 5a), mainly at southern and southwestern aspects with an inclination of 10° to 55° (mean approx. 30°). The number of vascular plant species ranges from 8 to 35 with a mean of 23 (Figure 5f). The average cover of the herb layer was moderate when compared to other forb vegetation of Middle Asia, ranging from 50 to 100%, average approx. 75%. (Figure 5d).

2.3.4. *Potentillo orientalis-Eremuretum fuscii* S. Świercz et al. 2020 (cluster 15)

Diagnostic species: *Eremurus brachystemon*, *E. fuscus*, *Gymnospermium albertii*, *Scorzonera tadshikorum*, *Veronica arguleserrata*

Constant species: *Eremurus fuscus*

Dominant species: *Eremurus brachystemon*, *E. fuscus*, *Ferula kokanica*, *Gymnospermium albertii*

Floristic and habitat characteristics: This association was described from the alpine belt of the western Pamir-Alai as intensively grazed grassland vegetation (Świercz et al. 2020). During the current research, additional plots of this vegetation were found in Central Tajikistan as well as in the Kyrgyz and Talass Mountains in Kyrgyzstan (Figure 4). This association prefers vast open habitats in the alpine pastureland zone between 1,850 and 2,500 m a.s.l. (mean approx. 2,100; Figure 5a). It develops on gentle slopes with an average inclination of approx. 20°. *Potentillo orientalis-Eremuretum fuscii* appears indifferent to slope or exposure, but often occurs at southern or north-western aspects (Figure 7d). The total cover of the herb layer is high and ranges between 80 and 100% (average approx. 83%; Figure 5d). The species richness is moderate with 7 to 25 species per plot (average 17; Figure 5f).

2.3.5. *Hordeo bulbosi-Astragaletum retamocarpi* S. Świercz et al. 2020 (cluster 16)

Diagnostic species: *Aegilops triuncialis*, *Astragalus retamocarpus*, *Buglossoides arvensis*, *Crupina vulgaris*, *Echium biebersteinii*, *Elaeosticta allioides*, *E. hirtula*, *Ferula gigantea*, *Hordeum bulbosum*, *Hypericum perforatum*, *Medicago denticulata*, *M. orbicularis*, *M. rigidula*, *Pseudohandelia umbellifera*, *Rochelia cardiosepala*, *Tragopogon capitatus*, *Tulipa subquinquefolia*, *Vicia angustifolia*

Constant species: *Astragalus retamocarpus*, *Carex turkestanica*, *Ferula kuhistanica*, *Medicago rigidula*, *Poa bulbosa*

Dominant species: *Astragalus retamocarpus*, *Ferula kuhistanica*, *Poa bulbosa*

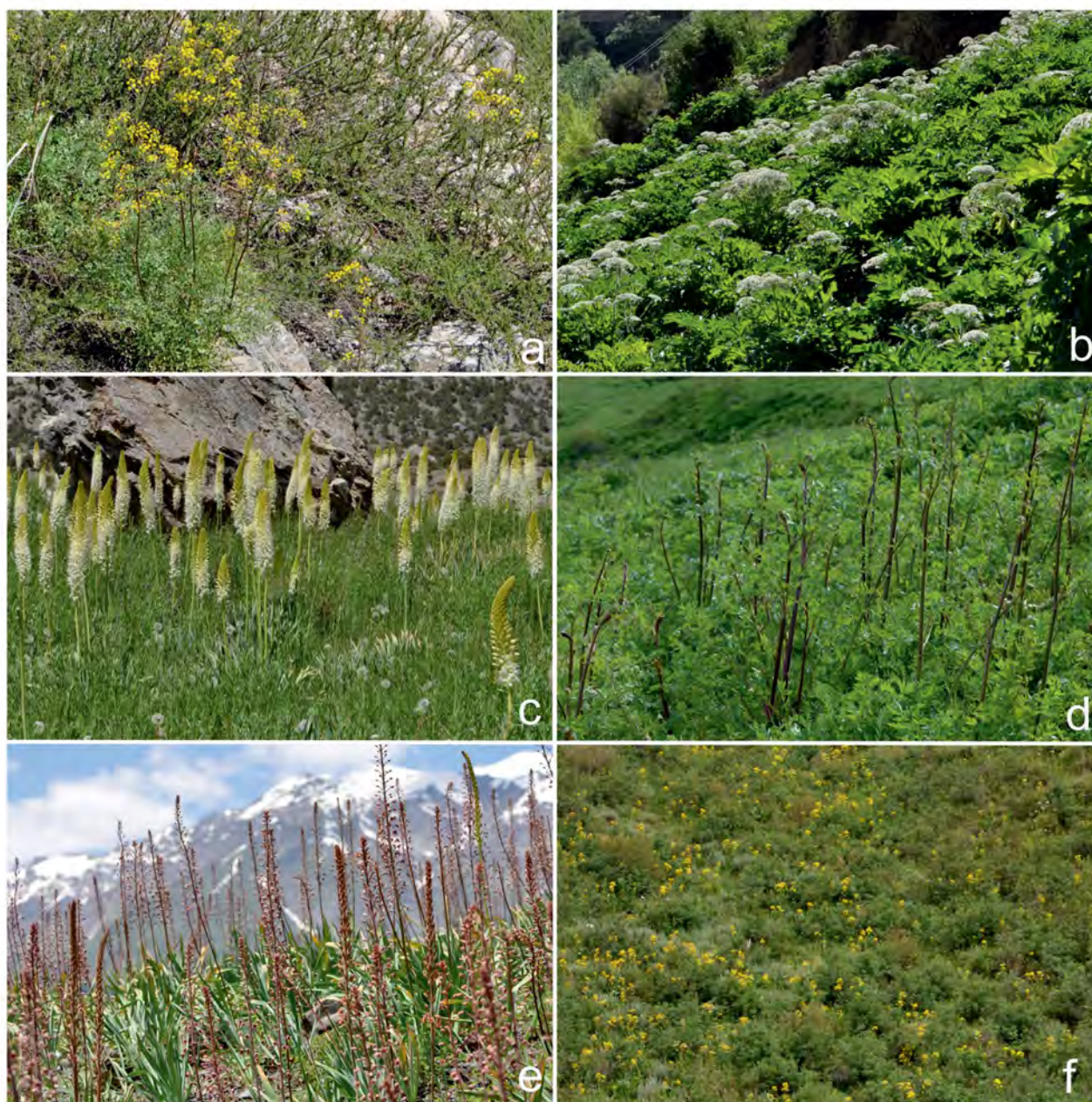


Figure 6. Photographs of the tall-forb vegetation belonging to: a – *Feruletum sumbuli* in the Haf-kul Valley in the Funn Mts, Western Pamir-Alai; b – *Heracleetum lehmannianii* on the slope water outflow in Haf-kul Valley, Western Pamir-Alai, approx. 1,850 m a.s.l.; c – *Eremuretum kaufmannii* in the Kuli-kalon Plateau in Funn Mountains, approx. 3,400 m a.s.l.; d – *Anthriscidetum glacialis* near the Hoburobot Pass in Darvaz Mountains, approx. 3,500 m a.s.l.; e – *Eremuretum stenophyllido-comosi* in Mayhura Valley in Hissar Mountains, approx. 2,650 m a.s.l.; f – community of *Inula macrophylla* near Chilishtak Village in Darvaz Mountains, approx. 1,450 m a.s.l.

Floristic and habitat characteristics: This is another association that was described from the montane belt of south-western Pamir-Alai as the pseudosteppe vegetation (Świerszcz et al. 2020). A few additional plots of this vegetation were found in Peter the First Range (Figure 4) in the alpine pastureland zone between 1,900 and 2,200 m a.s.l. (mean approx. 2,050; Figure 5a). It was recorded on gentle slopes with an average inclination of approx. 14° at western or southern aspects. As in other grasslands or forb-dominated vegetation, the density of vegetation was very high and the noted cover of herbs was close to 100% (Figure 5d).

The average species richness was also one of the highest, with 30 species per plot (ranging from 22 to 38, Figure 5f).

2.3.6. Community of *Ferula kuhistanica* (cluster 17)

Diagnostic species: -

Constant species: *Ferula kuhistanica*

Dominant species: *Cousinia pseudarctium*, *Ferula kuhistanica*, *Potentilla orientalis*, *Rochelia cardiosepala*

Floristic and habitat characteristics: *Ferula kuhistanica* is one of the most frequent species in tall-forb vegetation

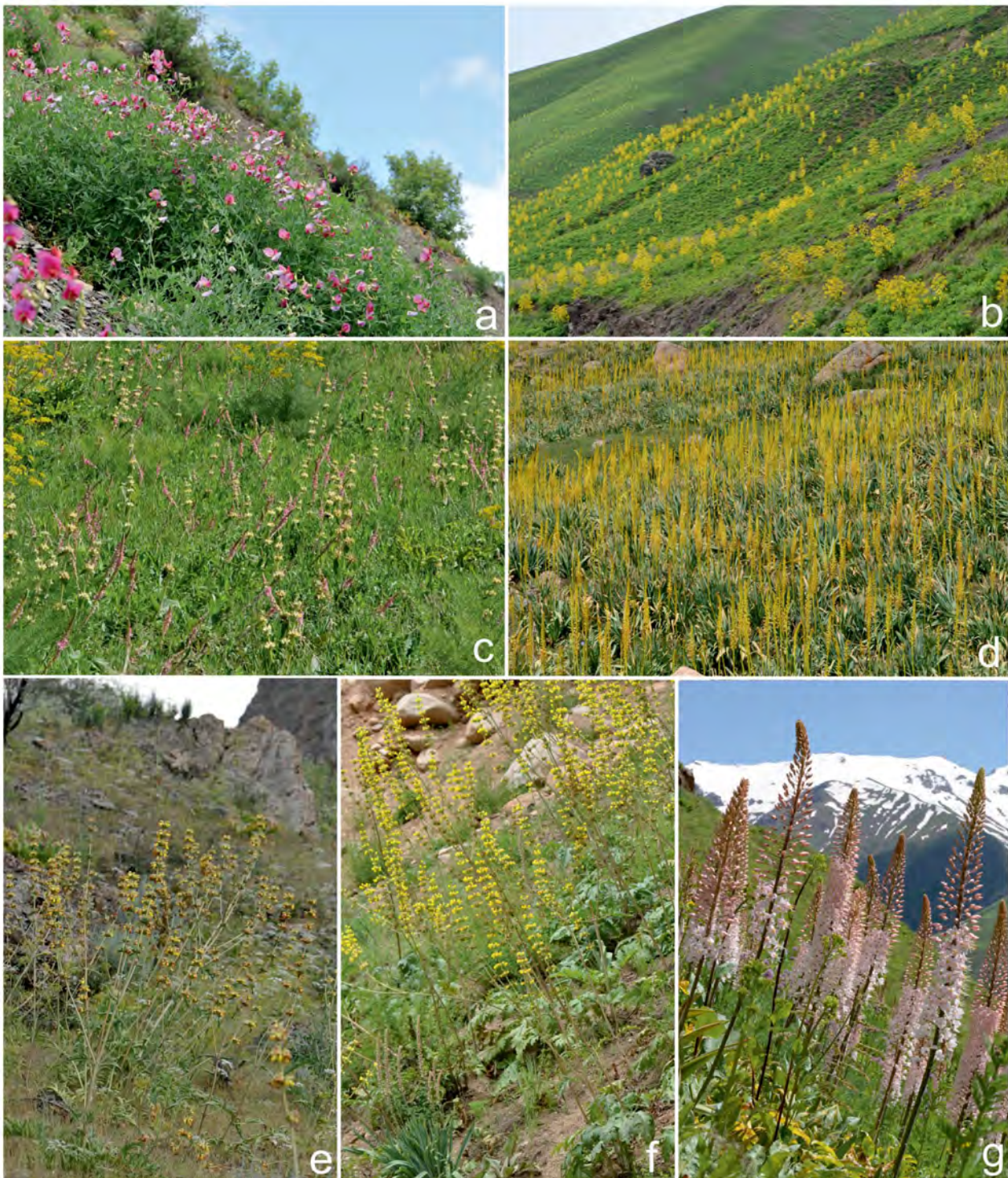


Figure 7. Photographs of the tall-forb vegetation belonging to: a – *Lathyretum mulkaki* near the Anzob Pass in Hissar Mountains, approx. 3,100 m a.s.l.; b – community of *Ferula kuhistanica* near the Hoburobot Pass in Darvaz Mountains, approx. 3,600 m a.s.l.; c – *Phlomoido lehmannianae*-*Onobrychidetum grandis* in the Obikhingou River Valley near Roha, approx. 3,200 m a.s.l.; d – *Potentillo orientalis*-*Eremuretum fuscii* in Talas Mts, Kyrgyzstan, approx. 2,700 m a.s.l.; e – *Phlomoidetum kaufmannianae* near Mogien in Funn Mountains, approx. 1,600 m a.s.l.; f – *Eremostachyetum tadshikistanicae* in Darvaz Mountains, approx. 1,500 m a.s.l.; g – *Eremuretum robusti* near Rabot, Darvaz Mountains, approx. 2,750 m a.s.l.

in the Pamir-Alai, contributing to almost all communities growing on nutrient rich, deep soils of higher montane and alpine belts. Cluster 17 was separated by the algorithm as

probably the central community within the alliance with no diagnostic species. A few plots of the community were found in the Darvaz and Peter the First ranges (Figure 4)

in heavily grazed pasturelands which possibly impoverished the community affecting floristic composition (Figure 7b). Thus, we only mention this group for consistency without giving a detailed floristic description.

2.3.7. *Eremuretum robusti* Nowak et al. ass. nov. prov. (cluster 18)

Diagnostic species: *Cousinia umbrosa*, *Eremurus robustus*, *Phlomooides arctifolia*, *Vicia tenuifolia*

Constant species: *Eremurus robustus*, *Ferula kuhistanica*, *Prangos pabularia*

Dominant species: *Cousinia pseudarctium*, *Eremurus robustus*, *Phlomooides arctifolia*, *Prangos pabularia*

Floristic and habitat characteristics: This is one of the most spectacular tall-forb vegetation types in Pamir-Alai (Figure 7g), with the main occurrence on the humid slopes of the Hissar, Darvaz, Hazratishoh and Peter the First Ranges (Figure 4). It forms tall stands in the upper montane and alpine belts within an altitudinal range between 1,500 and 2,600 m a.s.l. (average approx. 2,250 m; Figure 5a). It grows on flat, deep, well-watered soils in wide river valleys or occasionally, on gentle slopes with an inclination up to 25°. However, it always occurs in a moist, deep and fertile soil substrate, at no particular aspect. *Eremuretum robusti* is a luxuriant, rich vegetation with between 14 and 39 species within the sampled plots (average approx. 25, Figure 5f). The association is characterized by a relatively high total cover of herb layer. In many cases it reached 100%, with the average over 90% (Figure 5d). It is one of the most eminent tall-forb vegetation types of Middle Asia.

2.3.8. *Phlomooides lehmanniana*-*Onobrychidetum grandis* Nowak et al. ass. nov. prov. (cluster 19)

Diagnostic species: *Onobrychis grandis*, *Phlomooides lehmanniana*

Constant species: *Ferula kuhistanica*, *Phlomooides lehmanniana*, *Poa bulbosa*, *Prangos pabularia*

Dominant species: *Ferula kuhistanica*, *Phlomooides lehmanniana*, *Prangos pabularia*

Floristic and habitat characteristics: This association is one of the most widespread in Central Tajikistan, mainly in the Darvaz, Peter the First and Hissar Ranges (Figure 4). It also has some outliers in the Zeravshan, Turkestan and western Pamirian Mountains. The Pamir-Alai is an exclusive occupancy area of *Phlomooides lehmanniana*, an endemic of these mountains (Figure 7c). The association patches inhabit moderately fertile slopes within the upper montane and alpine belts, between ca. 1,700–2,700 m a.s.l. (mean ca. 2,400 m; Figure 5a). Phytocoenoses were noticed on flat lands in a wide valley, as well as on relatively steep slopes, up to 45° (average approx. 17°) and southerly aspects. The particular plot of *Phlomooides lehmanniana*-*Onobrychidetum grandis* consisted of 14 to 36 species (average 24, Figure 5f). The total herb cover ranged from 50% to 100% (average 84%) (Figure 5d) in a particular plot.

Discussion

The origin of the tall-forb vegetation in Middle Asia

Because paleoecological and palynological data are limited and incomplete for Middle Asia, the history of vegetation is insufficiently explained and due to past misunderstandings (see Zhilin 1989) can be misleading. However, based on palaeoflora data from the Turan (Turgay flora) region, the Russian palaeoecologists presented interesting hypotheses about the development of vegetation of large umbel communities (see Klein 1988). From the lower Miocene, significant variations in climate caused the replacement of broadleaf turgay forests (ancestor of today's chernoles – *Juglans regia* and *Platanus orientalis* stands), first by the paleoshiblyak (= preshiblyak) and later by steppes and deserts. In vast areas the dense broadleaf forests gave way to sclerophyllous and xerophytic formations often with patchy physiognomy. Preshiblyak was a sparse tree and shrub “paleoformation”, very xerophilic, considered to be the ancestral to the current thermophilous shiblyak and juniper grooves. Besides numerous woody species, there was a luxuriant herb layer that included representatives of today's typical tall-forb taxa such as *Prangos*, *Ferula*, *Rheum* and *Polygonum*. Due to strong climatic stress, preshiblyak became a stage of prompt radiation for many genera like e.g. *Malus*, *Rosa*, *Crataegus*, *Amygdalus*, *Ficus* etc. One prominent taxon that has benefited from these changes was *Ferula*, particularly species from the subtribe *Ferulinae* (*Ferula*, *Dorema*, *Leutea*; Panahi 2019). During the Pliocene-Pleistocene transition, not only was there a progressive reduction of broad-leaf forests, but also further fragmentation of the shiblyak for the benefit of ephemeroid formations of umbels. Kamelin (1967) suggests that, during the Pleistocene, the complex of semi-savannas with high grass (Himalayan-type prairies introduced by Korovin) spread widely and adapted perfectly to the post-Pliocene xerothermic period, with an ephemeroid-type development rhythm. This complex was derived from the preshiblyak, which reduced further in the Pleistocene and transformed in its upper limits into thermophilic forests of *Junipers*. The latter, after their felling and thinning by man, gave way to communities of large umbellifers. The natural species composition of this vegetation was poor and the structure sparse, which in the gaps allowed room for the development of a rich undergrowth. Moreover, it is supposed that the vegetation of large umbels evolved after the anthropogenic impact of the pastoral culture in Central Asia which replaced juniper groves and shiblyak orchards (Klein 1988). As the pastoralism in Tajikistan and Kyrgyzstan has a very long tradition (Dakhshleyger 1980; Mirzabaev et al. 2016), the species pool and surface of the pastures and meadows is fairly high. The impacted, loose character of both descendant vegetation types of preshiblyak harbor in the gaps more than 1,300 typical tall-forb species only in the territory of Tajikistan, including ca. 30 *Ferulas*, four *Pran-*

gos and many other *Apiaceae* (Nowak et al. 2020b). Many of these are endemic plants of the country (Nowak et al. 2011) and at the same time due to considerable changes in agriculture economy of Tajikistan, are facing serious threat (Nowak et al. 2020b).

When analyzing the origin of tall-forb vegetation in Middle Asia, it is worth noting the ecological affiliation of species that they share with closely related vegetation types. It is clearly evident that in terms of floristic similarity, the closest vegetation type is xerophytic shrubs (so called Rosaria and Efedrovniki – 185 common species), followed by thermophilous shrubland (so called shiblyak – 161 species), broad-leaved forests (141), Juniper grooves (127) and screes (104). These commonalities imply that the most important process for the formation of the species composition was aridization and the formation of xeric and thermophilous shrub and thicket vegetation.

It can therefore be summarized that after development of the main genera and species in the Eocene, the increase in occupancy area during the forest transition into sparse forb-forest vegetation of preshiblyak achieved compositional stability and allowed further expansion in shiblyak and juniper forest gaps during the Oligocene and Pliocene. This, along with progressive aridization and cooling of the climate, further developed the tall-forb communities dominated by umbels to reach their probable peak in the Holocene. It was only the intensive pastoral economy in the 20th century that initiated the process of degeneration of this vegetation and its change into intensively managed pastures or pseudosteppes. This should be one of the important concerns in regard to grazed tall-forb vegetation, as the long history of pastoralism (reaching 8000 years) and the grassland management in the region is no longer beneficial, but currently strongly impacting the vegetation cover in Middle Asia, including forbs (Mirzabaev et al. 2016). Sheep, goats, horses, yaks, cows and camels increase in numbers and combined with climate changes are an increasing threat to plant cover (Dakhshleyger 1980, Mirzabaev et al. 2016).

Comparisons of the Middle Asian tall-forb vegetation to the surrounding areas

Due to the high rate of Pamir-Alai endemism, the very distinct and typically Irano-Turanian vegetation of *Prangetea ulopterae* does not share many taxa with the plots documented in Iran. The only common species occurring in Middle Asia that were defined as diagnostic for the class are *Hypericum scabrum*, *Ferula ovina*, *Lappula microcarpa* and *Scariola (=Lactuca) orientalis* (Klein 1987, 1988), the last being more characteristic for scree vegetation rather than tall-forb. However, the list of other species known to have the ecological optimum in this vegetation and occurring in both areas (Iran and Middle Asia) is longer. Examples are e.g.: *Cotoneaster nummularia*, *Berberis integerrima*, *Lonicera nummularifolia*, *Thalictrum sultanbadense*. Additionally, there are many genera common in both regions with the most prominent *Cousinia*, *Geranium*, *Hel-*

ichrysum, *Isatis*, *Eryngium*, *Crepis*, *Cephalaria*, *Onosma*, *Rheum* and the richest *Astragalus* (Klein 1987). Despite this, all plant communities that were defined from Iran apparently have a different set of species and distinct habitat requirements (*Nepetum fissae*, *Salvietum hypoleuca* and *Helichrysetum oligocephali*).

Furthermore, the ancient Babylon territory lies in a former area of ancient Mediterranean vegetation. In the mountains of Helgurd-dagh in eastern Iraq, Hadač and Agnew (1963) described a number of pasture communities, including *Corydaleto-Prangetum ferulaceae* in the cones and aprons of rocky walls, *Prangeto-Astragaletum tragacanthae*, *Aethionemeto-Astragaletum tragacanthae* and *Rheum ribis*. They were documented only by few relevés and sometimes not all taxa were identified at the species level. Nevertheless, it is clear that this type of vegetation is closely related to its physiognomy and species composition of dominating plants of *Prangetea* known from Iran and Middle Asia. However, also in this case there are no common species and closer habitat similarities. The same holds true for the vegetation dominated by *Prangos pabularia* found in the mountains of Kopet-Dagh in southern Turkmenistan (Herrnstadt and Heyn 1977).

The overlap between Irano-Turanian tall-forb and scree vegetation and its relation to Juniper grooves

In this dry, semi-arid zone, the distinction between tall-forb vegetation dominated by *Apiaceae* and the scree vegetation, which can also be dominated by species of *Ferula*, *Prangos* or *Tetrataenium*, is not clear (Nowak et al. 2020a). Despite physiognomic similarities, the vegetation with the domination of *Apiaceae* species can be significantly different in species composition, abundance and habitat preferences. Only in Tajikistan do many *Apiaceae* species inhabit areas other than tall-forb habitats. Examples include meadows and pastures (e.g. *Ferula foetida*, *F. tadshikorum*, *F. karatavica*), screes (e.g. *Ferula giorgiewii*, *F. ovina*, *F. foetidissima*, *F. koso-polianskyi*, *Tetrataenium olgae*) or rock habitats (e.g. *Ferula bucharica*, *F. botschanzevii*, *F. lithophila*, *F. tschimganica*, *F. ugamica*, *Kafirnighania hissarica*, *Zeravshania regeliana*; see Nowak et al. 2020a). Thus, the separation of the nutrient poor scree, fertile pasture and meadow and nutrient rich habitats of tall-forb vegetation in Middle Asia requires thorough analyses, a large data base and fine resolution in this complex of phytogeographical boundaries. The Miocene aridization did not only influence the nutrient rich woody or shrubby vegetation but also left its mark on rock, scree and grassland communities. Species of the genus *Ferula* entered various habitats and are still found there today. Therefore, the name “umbeliferniki” for all tall-forb vegetation is inappropriate. In our case, out of 19 communities, only 5 are dominated by large umbels.

The suggested close relationship between tall-forb vegetation of Middle Asia to juniper groves also requires a detailed analysis as it is questionable when considering the

share of common species. As mentioned above, Klein (1988) suggests after Ovchinnikov (1971) that *Prangetea ulopterae* in Middle Asia originated from the Turgay flora and the ancient Mediterranean vegetation. At the beginning of the lower Miocene, significant variations in climate and gradual aridization caused the replacement of broad-leaf turgay forests by the paleoshiblyak. Palaoshiblyak is considered to be the ancestor formation for *Apiaceae* dominated stands as well as juniper groves (Kamelin 1967; Ovchinnikov 1967, 1971; Pavlov 1980). Additionally, Kamelin's (1967) opinion is that in the upper limits of prashiblyak, due to natural (xerophitisation, climate changes in Pleistocene) and anthropogenic (pastoral culture) factors, the shrubby formation was fragmented and in the patchy mosaic the *Apiaceae* began to expand and developed into today's thermophilous tall-forb communities. However, the number of common species, which may reveal the relationship of the two plant formations, is relatively small. Even typical deciduous forests (*Juglans regia* and *Platanus orientalis* stands) share more common taxa with tall-forb vegetation, not to mention the xerophytic and thermophilous shrubs. It is also worth noting that juniper forests themselves are not a homogenous formation. Apart from the typically thermophilic ones dominated by *Juniperus seravschanica*, there is also a zonal belt in the upper montane (sometimes up to 3,500 m a.s.l.) of *J. turkestanica* and *J. semiglobosa*. These two distinct belts have relatively different species composition and supposedly dissimilar relationship to tall-forb vegetation. It is still questionable whether the thermophilous *J. seravschanica* groves are more closely related to typical *Prangetea ulopterae* than they are to *J. turkestanica* stands, which themselves may be closer to alpine tall-forbs with *Anthriscus glacialis* or *Eremurus* spp.

The vegetation complex of xerothermophilous scrubs and Irano-Turanian tall-forbs extends far west, into the mountains of Armenia, the Caucasus and the mountains of Turkey. The recognition of links between the *Prangetea* vegetation and other thermophilous vegetation, e.g. the fringe vegetation of *Geranietea sanguinei* known from south-eastern Europe and Western Asia needs to be resolved. Particularly interesting is the relationship to xerophilous fringe and tall-forb vegetation of the Illyrian, Dinaric and Balkan Peninsula zone, which include a number of *Apiaceae* species (e.g. *Ferulago campestris*, *Laserpitium siler*, *Selinum silaifolium*) and reflects apparent habitat similarities (in *Dictamno albi-Ferulagion galbaniferae* and *Lathyro laxiflori-Trifolion velenovskiyi*; Mucina et al. 2016). As the tall-forb vegetation of the Irano-Turanian region are less hygrophilous and occupy not so fertile deep soils (as compared to the *Mulgedio-Aconitetea* vegetation known from the temperate zone), it is likely that there are also relationships and similarities to the steppe vegetation of *Festuco-Brometea* (e.g. *Stipion korshinskyi* Toman, 1969) and also with Middle Asian steppes (*Cleistogenetea squarrosae* Mirkin et al. ex Korotkov et al. 1991). In our data set, several plots were classified into the steppe vegetation with a high share of forb species (*Stipetum margelanicae*, *Hordeo-Astragaletum retamocarpi*). Additionally, some relationship to mesic mown and grazed meadows and pastures on fertile soils supporting *Poo alpinae-Trisetetalia* Ellmauer et Mucina 1993 should be investigated, especial-

ly if we considered the northern territories of Middle and particularly Central Asia. Towards the Altay and Siberia, the share of boreal species increases and the typical *Mulgedio-Aconitetea* vegetation prevails (Ermakov et al. 2000; Zibzeev and Nedovesova 2017; Heim and Chepinoga 2019). The definitive classification and characterization of the tall-forb communities require additional detailed survey in the montane and alpine belt of the whole Middle and Central Asia, particularly in the Tian Shan and Altay Mountains. Additionally, resolution of the Hindukush and Kopet-Dagh Mountains in relation to Middle Asian steppes and pseudosteppes (*Vulpio persicae-Caricion pachystylidis* Świeruszcz et al. 2020; see Nowak et al. 2017b; Świeruszcz et al. 2020), alpine swards and hay meadows (*Poo alpinae-Trisetetalia*), and boreo-temperate grasslands of *Molinio-Arrhenatheretea* meadows (mainly the steppe meadows of *Galietaalia veri* or mesic meadows of the continental forest-steppe zone *Caricimacrourae-Crepidetalia sibiricae*), is required.

Environmental features determining the floristic composition of communities

Despite considerable compositional differences between communities due to the great phytogeographic distinctiveness and high floristic richness of forb vegetation across Middle Asia, there are also other factors controlling its diversity. The longest gradient (NMDS1, Figure 3) of the tall-forb variability is apparently related to elevation. It clearly distinguishes communities from the highest locations, such as patches of *Phlomooides oreophila*, *Allium hymenorhizum* and *Anthriscidetum glacialis*, which prefers high-mountain habitats with cold and humid conditions. At the other extreme the vegetation of *Phlomooidetum kaufmanniana*, *Eremuretum stenophyllido-comosi* and community of *Inula macrophylla* are grouped. They prefer well drained substrates, warm and dry sites at colline and lower montane elevations. The pattern of vegetation types along the second ordination axis is less obvious. However, looking at its extreme it can be attributed to the fertility of the habitat. At one end (upper part of Figure 3), the communities of *Allium hymenorhizum*, *Cousinia batalinii* and *Euphorbia pamirica* and the association of *Feruletum sumbuli* are placed. They occupy less fertile, shallow, often stony soil substrates. The opposite extreme is occupied by phytocoenoses that prefer deep, fertile soils, rich in mineral and organic content. The examples of tall-forb associations that thrive in this habitat are luxuriant *Heracleetum lehmannianii*, *Hordeo bulbosi-Astragaletum retamocarpi*, *Eremuretum robusti* and the community of *Ferula kuhistanica*. Although hardly detectable, the third gradient is most likely related to the compactness and stability of the substrate. Vegetation of *Phlomooides oreophila* and *Ferula kuhistanica* as well as *Stipetum margelanicae* and *Phlomooidetum lehmanniana-Onobrychidetum grandis* grow on the stable, compact soils mainly on flatland or gentle slopes in the high alpine belt. The typical scree habitats are mainly occupied by communities such as *Phlomooidetum tadshikistanicae* or *Eremuretum stenophyllido-comosi* that occur in lower elevations mainly on southern slopes

with loose, unstable top soil. This vegetation is composed of species adapted to frequent disturbances caused by rolling stones and landslides, and to periodical drought. Disturbances due to land runoff are a critical factor for plant competitiveness and growing abilities and seem to be one of the most important drivers of vegetation variability in the stony landscapes of Middle Asia (Nowak et al. 2016b).

Conclusions

Our study has expanded the knowledge of the open habitat vegetation in the Pamir-Alai and western Tian Shan Mountains and contributed to the consistent hierarchical classification of tall-forb communities in the Irano-Turanian region (Nowak et al., 2020). The syntaxonomic position of some of the distinguished communities is still unclear, hence further research into floristic composition and habitat requirements for the vegetation of Middle Asia is required, especially in the communities originating from preshiblyak, i.e. thermophilous shrubs, xeric thickets and juniper woods.

Substantial areas of shrubby vegetation (both shiblyak and *Rosa-Ephedra* stands) in Middle Asia have been already degraded, and both climate warming and intensification of land use are serious threats for the biodiversity of grasslands in this region (Mirzabaev et al. 2016). This would also include the extremely species rich tall-forb.

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Data availability

All relevant data are within the paper and its Supporting Information files.

Author contributions

A.N., M.N. and S.S. planned the research, conducted the field sampling and identified the plant species. A.N. and S.S. performed statistical analyses. S.N. prepared the analytical tables, while all the authors participated in the writing of the manuscript and verification of plants in herbarium.

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Supplementary material

Supplementary material 1

The analytic table of tall-herb vegetation in the Pamir-Alai and western Tian Shan Mts. (Tajikistan and Kyrgyzstan, Middle Asia).

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Supplementary material 2

Full synoptic table with percentage frequency and fidelity values.

Link: <https://doi.org/10.3897/VCS/2020/60848.suppl2>