

Halophytic vegetation and adjoining plant communities in Middle Asia (Pamir-Alai and western Tian Shan)

Halophytenvegetation und angrenzende Pflanzengesellschaften in Mittelasien (Pamir-Alai und westlicher Tian Shan)

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Abstract

In this paper, we complete the syntaxonomical scheme for halophytic vegetation and adjoining plant communities of the lowland, montane and alpine zones in the Pamir-Alai and western Tian Shan in Tajikistan and Kyrgyzstan with some remarks on its environmental predictors. A total of 217 relevés were sampled in 2014–2019 using the seven-degree cover-abundance scale of the Braun-Blanquet approach. Modified TWINSpan was used to classify plant communities based on species composition. The cover-abundance scale was transformed using the four-step interval scale with cut-off levels at 0%, 5% and 25%. Diagnostic species were identified using the *phi* coefficient as a fidelity measure. Non-metric Multidimensional Scaling (NMDS) was used to explore the relationships between the distinguished groups. A total of five halophytic or subhalophytic grasslands, five halophytic thermophilous scrub communities, three hypersaline alluvial temporary flooded swards, and one riparian scrub community were distinguished in the study area, grouped in four orders. Four plant communities have been established as new associations: *Knorringietum sibiricae*, *Puccinellietum pamiricae*, *Carici physodis-Zygophylletum gontscharovii* and *Zygophylletum ferganensis*. The *Taraxacion murgabici* is described as new alliance of high-altitude halophytic vegetation in arid environments. The hypersaline alluvial temporary flooded swards were included in a new order – the *Psylliostachyetalia spicato-leptostachyae*. The main factors differentiating the species composition of the researched vegetation seem to be: the share and number of annual vs. perennial species, coverage of shrub layer, number and share of Irano-Turanian plants, mean annual temperature, and altitudinal position. This is the first time we have initiated research on halophytic vegetation in Middle Asia. However, further geobotanical studies in this part of the world are needed, because the syntaxonomical position of some of the distinguished communities still remains vague.

Keywords: halophytes, Middle Asia, saline habitats, salt-marshes, solonchak, solonetz, syntaxonomy

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Halophytic vegetation extends across the globe and is distributed from equatorial mangroves to polar shorelines (KAPLER 2019). Though not particularly rich in species, the saline habitats harbour approx. 1% of unique, specialised terrestrial plant species that can flourish in unique and conservationally important biotopes (ROZEMA & FLOWERS 2008). Halophyte habitats have always been regarded as model ecosystems for displaying clear and comprehensible patterns reflecting the varying affinities of species and plant communities to dominant environmental factors, in this case soil salinity. Despite the taxonomic problems related to a number of hardly identifiable cryptic taxa occurring in halophytic communities, chiefly from the cosmopolitan family of the *Chenopodiaceae* (HERNÁNDEZ-LEDESMA et al. 2015), an increasing number of synthetic phytosociological works has emerged in recent years in continental Asia (e.g. GOLUB et al. 2001, RUKHLENKO 2011, LYSENKO 2014, MEṬRAK et al. 2017).

Several factors may be responsible for the formation of saline habitats. Soil salinisation may be an effect of natural processes (primary soil salinisation) or a consequence of human activity (secondary salinisation; VENGOSH 2014). The former occurs when evaporation exceeds precipitation, which leads to the salt being deposited in upper soil layers rather than leached. Hence, primary soil salinisation by the occurrence of salt and gypsum containing sedimentary strata applies particularly to arid and semi-arid climatic zones (VENGOSH 2014). Secondary salinisation is a result of agricultural land use, such as heavy irrigation, insufficient drainage, or road de-icing by salting (HAMIDOV et al. 2016). Halophytes thrive in Central Asia thanks to the combination of both primary and secondary soil salinisation, and occur here in a number of different ecosystems, ranging from lowlands to the high plateaus of the Pamir. In Tajikistan, saline habitats stretch from the lower reaches of the Syr Darya and Amu Darya Rivers (350–500 m a.s.l.) to the colline and foothill belts of the Mogoltau, Aktau, Babatag and Zeravshan ranges (600–1800 m a.s.l.) and further up to the Pamir highlands (3700–4400 m a.s.l.). The most important habitats for this vegetation are subsaline and saline semi-deserts, semi-natural meadows and pastures bordering creeks, springs and freshwater lakes, and temporarily inundated salt marshes. Typical halomorphic soils of these lands are solonchaks and solonetz, and in seasonally flooded flatlands, the takir (takyr). Halophytic vegetation invades anthropogenic habitats only locally in badly managed irrigated fields or the sediment ponds of the mining industry (see KAPLER 2019). A striking example of salt-bearing geological strata is the ‘salt mountain’, Hodzha-Mumin Mt., where soil formation is virtually absent due to strong soil erosion. Such areas also offer diverse habitats, and endemic halophytes, such as *Olgaea chodshamuminensis* and *Echinops chodshamumini*, might have evolved there (RAHIMOV & MAMADJONOV 2015).

In the Pamir-Alai (Tajikistan) and western Tian Shan (Kyrgyzstan) regions – regarded as global biodiversity hotspots (MITTERMEIER et al. 2006) – halophytic vegetation remains poorly investigated. It was almost completely neglected in recent studies on vegetation classification in the former Soviet Union (e.g. STANYUKOVICH 1982, MIRKIN & NAUMOVA 2012). In Tajikistan, some types of halophytic phytocenoses, such as the community of *Haloxylon aphyllum*, were mentioned but included in desert vegetation (STANYUKOVICH 1982). In recent years, the research of MEṬRAK et al. (2017) conducted on the halophytic vegetation of eastern Pamir was based on the collection of several dozens of relevés; however, only partially in typical saline habitats. Within the flora of Tajikistan (RASULOVA 1991), ca. 120 species (2.8%) are salt-bushes and about 260 (ca. 6.1%) have been reported as herbaceous species from salt-marshes (NOWAK et al. 2020). Some of them probably occur in

semi-deserts or patchy steppes, but there is no detailed data on the share of salt-adapted species in these habitats. Within the flora of saline habitats, 36 species endemic to Tajikistan were reported – among others, *Asparagus ferganensis*, *Calligonum santoanum*, *Halothamnus seravschanicus*, *Salsola vvedenskyi* and *Taraxacum schugnanicum*. Several of them, such as *Anabasis pelliotii*, *Limonium ovczinnikovii* and *Sophiopsis micrantha*, are critically endangered at the global scale (NOWAK et al. 2020).

Despite being crucial for communication and application in conservation, the establishment of a hierarchical system of all halophytic vegetation for Central Asia remains a challenge (DE CÁCERES et al. 2018). Hence, this paper presents the authors' attempt to classify the halophytic vegetation in the Pamir-Alai and western Tian Shan and to relate it to mire, meadow and semi-desert communities. We have aimed at addressing the following questions during our study: (1) Which halophytic plant communities can be distinguished in the Pamir-Alai and western Tian Shan? (2) Which species have important diagnostic value for the described syntaxa? (3) What is the species composition and vegetation structure of the saline habitats of the Pamir-Alai and western Tian Shan regions? Furthermore, we outlined the basic habitat conditions of the described plant communities.

2. Study area

The vegetation survey was conducted in an area of ca. 200,000 km² located in the Pamir-Alai (Tajikistan) and western Tian Shan (southern and eastern Kyrgyzstan) in the central part of Middle Asia (Fig. 1a). Due to considerable phytogeographical differences between these two main mountain ranges in Middle Asia, the research includes halophytic vegetation and adjoining plant communities of both regions. Saline habitats of eastern Middle Asia, extend across a long elevational gradient. The studied sites were located between 300 and 4200 m a.s.l. (mean 1500). In the lowlands, saline habitats occur mainly within the Amu Darya and Syr Darya River floodplains, and are mostly associated with heavy irrigation or insufficient drainage which led to the secondary salinization. On the other hand, harsh climatic conditions and prevailing groundwater supply of the wetlands create saline habitats in the Pamir.

It is difficult to characterise the climatic conditions, because the region is located between two main bioclimatic zones of the Irano-Turanian region with Central Asiatic climate influenced by Indochinese climate from the south and Euro-Siberian from the north. Unlike the Mediterranean region, the study area is characterised by a shift in rainfall peak to the spring months and additionally higher continentality (DJAMALI et al. 2012). There are four main types of climatic zones within the research area:

(1) the warm, continental, Irano-Turanian climate in the Fergana Basin. The surroundings of Jalalabad and Osh (Fig. 1b) are characterised by winter precipitation that achieves its peak in March and April with up to 50 mm and a yearly average of ca. 350 mm. The average daily temperatures rise up to 25 °C in June to August. During these months the precipitation is scarce, with 15–25 mm per month. Snow and frost occur from December to February with averages not below -3 °C and with extreme values of -27 °C in some years;

(2) the warm humid, continental climate in the Tian Shan and Pamir-Alai ranges. In this area the average temperature in June is around 22 °C in the colline and montane zones and drops to 10 °C in the alpine belt. The lower limit of perpetual snow in the western Tian Shan is at 3000–3300 m a.s.l. Annual precipitation ranges here from about 500 mm on the northern slopes to ca. 1000 mm on the southern;

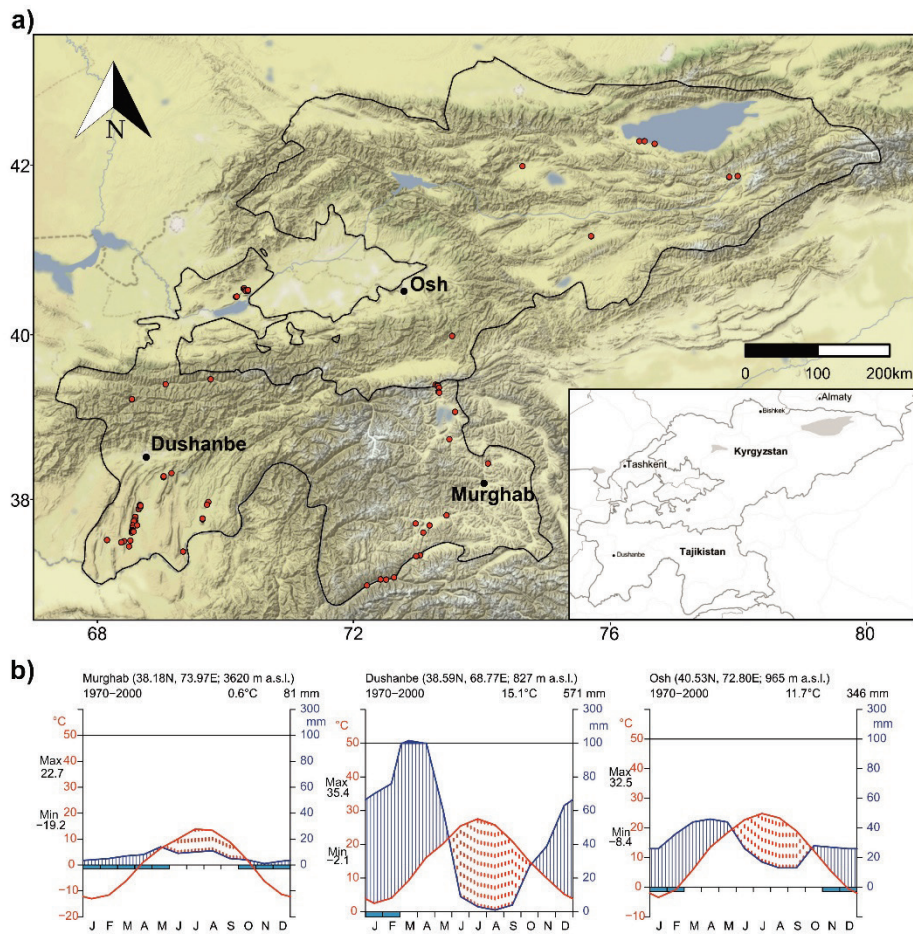


Fig. 1. a) Study area and spatial distribution of relevés ($n = 217$) and **b)** climate diagrams for temperature (red line) and precipitation (blue line) for Murghab, Dushanbe and Osh. Values on the top-right of diagrams represent the averaged value of mean temperature and annual precipitation along the whole period. Values in black on the y₁ axis represent the maximum and minimum temperature along the whole period.

Abb. 1. a) Untersuchungsgebiet und Lage der Aufnahmeorte ($n = 217$); **b)** Klimadiagramme von Murghab, Dushanbe und Osh mit Temperatur (rote Linie) und Niederschlag (blaue Linie). Die Werte oben rechts geben die durchschnittlichen Jahresmittelwerte für Temperatur und Niederschlag während des Erhebungszeitraums 1970–2000 an. Die Werte in schwarz neben der linken y-Achse bezeichnen die Maximum- und Minimum-Temperaturen im Erhebungszeitraum.

(3) the cold semi-arid climates of the Issik-Kul basin, central and western parts of the Alai Valley and foothills and plateaus at the colline, montane and subalpine belts. These areas are clearly distinguished by lower precipitation with an average of ca. 200–400 mm per year. The distribution of the rainfall during the year is similar to the temperate climate with the maximum in May–July (up to 70 mm). The temperatures exceed values of 20 °C only in summer with an annual average of ca. 10 °C;

(4) the cold desert climate of the easternmost sections of the Alai Valley and eastern Pamirian Plateau. Unlike the west Pamir or Tian Shan ranges, this area is distinguished by significant aridity with less than 100 mm mean annual precipitation (Fig. 1b). Only in May and August does the average monthly rainfall exceed 20 mm. The average yearly temperature slightly exceeds 0 °C with minima far below -30 °C in January - February (LATIPOVA 1968, NARZIKULOV & STANYUKOVICH 1968, SAFAROV 2003).

However, because of elevation amplitude, orography and wind conditions within all these zones a lot of local anomalies occur.

3. Methods

We conducted the research in the years 2014–2019. Altogether, 217 relevés were collected in the Pamir-Alai (195 relevés) and western Tian Shan (22 relevés). The size of each plot was generally 10 m² for herbaceous and 100 m² for shrubby vegetation. In each relevé all vascular plant species and mosses were recorded using the seven-degree cover-abundance scale of the Braun-Blanquet approach (WESTHOFF & VAN DER MAAREL 1973).

We stored the data in the Vegetation of Middle Asia database (NOWAK et al. 2017) and analysed in R (R CORE TEAM 2020) and JUICE software (TICHÝ 2002). Modified TWINSpan (HILL 1979, ROLEČEK et al. 2009; Fig. 2) was used to classify plant communities based on species composition. The cover-abundance scale was transformed using the four-step interval scale with cut-off levels at 0%, 5% and 25%. As the plots were selected fairly objectively, we downweighted rare species using the chord distance as the measure of cluster heterogeneity (ROLEČEK et al. 2009). Plant species determined only to the genus level were excluded from the analysis (*Orobanch* sp., *Taraxacum* sp.). Diagnostic species were identified using the *phi* coefficient as a fidelity measure (CHYTRÝ et al. 2002). Group size was standardised, and the Fisher exact test ($p < 0.05$) was applied. Species with a *phi* coefficient higher than 0.20 were considered diagnostic for a particular cluster. Diagnostic taxa for alliances were defined as those with a *phi* coefficient ≥ 0.15 in at least two clusters within this alliance. Species with a higher frequency than 50% were defined as constant, and those with a maximum cover value exceeding 30% 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 characterised terminal clusters with their own diagnostic species (DENGLER et al. 2008, MICHL et al. 2010). These terminal clusters were considered as associations or plant communities depending on the geographical range and certainty of taxonomic status of the diagnostic species. During the division the habitat profile and authors' field experience were used as to find the comprehensive and ecologically interpretable results of classification. For descriptions of new associations, the International Code of Phytosociological Nomenclature (ICPN; THEURILLAT et al. 2021) was adhered to. The type relevés are given in the description of the discussed associations. All mentioned syntaxa were arranged into a syntaxonomic overview at the beginning of the description in the Results section and in a synoptic table (Supplement S1). When establishing a new association, we follow the recommendation 7A of the ICPN (THEURILLAT et al. 2021), i.e. we left the community rankless when the diagnostic species exhibit a fairly wide geographical range and occur in the limits of their distribution within the study area. Furthermore, if the taxonomic position of the diagnostic species for the community was unresolved or vague, we also decided to define this type of vegetation as rankless. In addition, we refrained from defining the association when the species with the highest fidelity were observed as having wider ecological amplitude in the field studies but not documented in the data set. Moreover, we did not apply any refinements in the classification by moving some relevés between clusters using some iterative relocation methods or deletion of any outliers because of the pioneer character of our research.

In order to assess the floristic relationships among the vegetation types non-metric multidimensional scaling (NMDS) based on Euclidean distance was performed using the function *metaMDS* in the *vegan* package (OKSANEN et al. 2019). Floristic data prior to the analysis were Hellinger-transformed.

The final ordination was run with 999 random starts with the use of two dimensions (stress value = 0.083). Environmental and vegetation parameters were passively projected post-hoc onto the ordination to explore their associations with each vegetation type using the function *envfit* with 999 permutations in the *vegan* package (OKSANEN et al. 2019). Mean annual temperature and the sum of annual precipitation were extracted from the WorldClim database (FICK & HIJMANS 2017). We determined the medians and SD of the measured environmental and vegetation parameters (altitude, temperature, precipitation, species richness per plot, Shannon diversity index, share of therophytes, cryptophytes, phanerophytes and phytogeographical elements in each relevé) for all communities. The differences between syntaxonomical classes in relative cover of measured environmental and vegetation parameters were assessed using Kruskal–Wallis rank sum test (function *kruskal.test*) with multiple comparison using Dunn's test, which was executed using the *dunnTest* function of the *FSA* package (OGLE et al. 2018) in R.

Distribution maps of all types of halophyte vegetation within the study area are presented in Supplement E1. Environmental and vegetation parameters are shown in Supplement E2. The plant communities are depicted on photographs (Fig. 5 and 6).

The nomenclature of the vascular plants follows generally CHEREPANOV (1995) and for *Bromus* spp. THE PLANT LIST (2013). The names of syntaxa are used in accordance with RUKHLENKO (2011), GOLUB et al. (2001) and LYSENKO (2014).

4. Results

4.1 Classification of the vegetation units

Our classification analysis resulted in the delimitation of 15 clusters (Figs. 2 and 3, Supplement S1). Four of them were well-defined in terms of species composition and have been described as new associations. Other clusters that were clearly separated by the clustering algorithm were left as rankless communities or had been previously described in the literature (RUKHLENKO 2012a, b). We refrained from the description of clusters 2 and 13, which represent vegetation with a dominance of *Suaeda acuminata* and *Hordeum turkestanicum*, respectively. The first community was found only on sandy hills and dunes as well as gravelly substrates on slopes and road verges on the southern shore of the Issik-kul Lake in Kyrgyzstan. Due to the fact that the algorithm assigned only two relevés to this cluster, its position is uncertain, and therefore we decided not to present this community in the synopsis and figures. The group from high-altitude desert saline habitats with three plots dominated by *Hordeum turkestanicum* and the additional contribution of taxa typical for alpine meadows, such as *Agrostis alba*, *Alopecurus pratensis*, *Ligularia alpigena*, *Poa alpina*, and *Trifolium pratense* was also left without description due to insufficient sampling. However, we retained all clusters in the original TWINSPAN dendrogram with the original numbering of clusters.

The NMDS run for all samples revealed relationships between distinct plots and groups along the two most significant gradients of the ordination (Fig. 3). The most influential discriminant factor is altitude. It clearly separates the high-altitude habitats of the *Taraxacion murgabici* alliance. Phytocoenoses, preferring the lowland and colline locations that are distributed mainly in Western Pamir-Alai, are concentrated in the left part of the graph. They form two main distinct groups according to species richness and shrub contribution (Figs 3, 4e, f, Supplement S1). The species-rich communities of hypersaline alluvial temporary flooded habitats in the semi-desert and desert zones (*Sphenopodo-Climacopteretum glaberrimae*, *Cephalorhizum popovii* and *Aeluropus littoralis-Salsola leptoclada* communities),

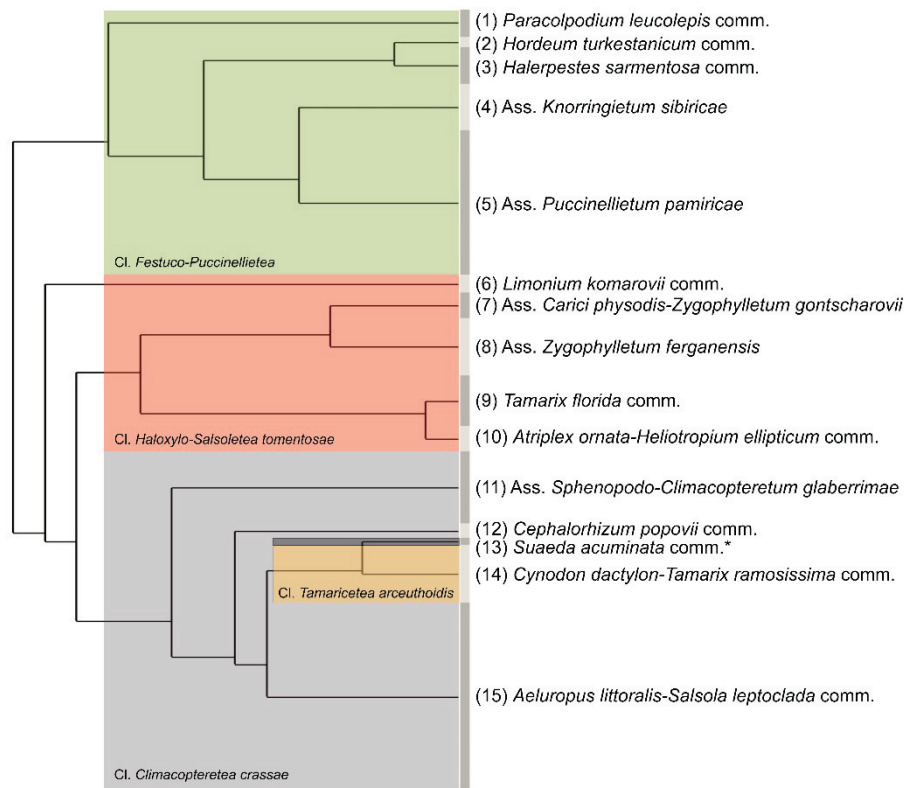


Fig. 2. TWINSPAN classification diagram for the whole data set of 217 relevés. The numbers represent the cluster numbers, while the width of the bars is proportional to the number of relevés originally assigned to the clusters. Note that clusters 2 and 13 contain only 2–3 relevés and were not included in the hierarchical system and description of the communities.

Abb. 2. TWINSPAN-Klassifikationsdendrogramm für den kompletten Datensatz aus 217 Aufnahmen. Die Zahlen beziehen sich auf die Nummern der Vegetationseinheiten, die Strichbreite ist proportional zur Zahl der Aufnahmen in der Gruppe. Beachte, dass die Gruppen 2 und 13 nur 2–3 Aufnahmen enthalten und nicht in die Beschreibung und syntaxonomische Bewertung der Gesellschaften einbezogen wurden.

typical for solonchak soils, are grouped in the bottom part of the NMDS graph. The upper left side of the diagram is occupied by the fairly heterogeneous group of thermophilous scrub vegetation on hypersaline solonetz and solonchak soils of the arid zones of southern Middle Asia. This heterogeneity results from differences in habitat conditions, mainly intensity of grazing (strong influence in the lowest elevations on *Atriplex ornata-Heliotropium ellipticum* and *Limonium komarovii* vegetation). The soil substrate also has a considerable effect and makes the *Tamarix florida* community distinct, as it occurs on wet solonchaks in wide river valleys. This community resembles the typically river-bed shrubs of *Tamaricetea arceuthoidis* reported in south-western Asia, namely the *Cynodon dactylon-Tamarix ramosissima* community. However, as it is still poorly investigated, it needs to be studied further and supported by additional data.

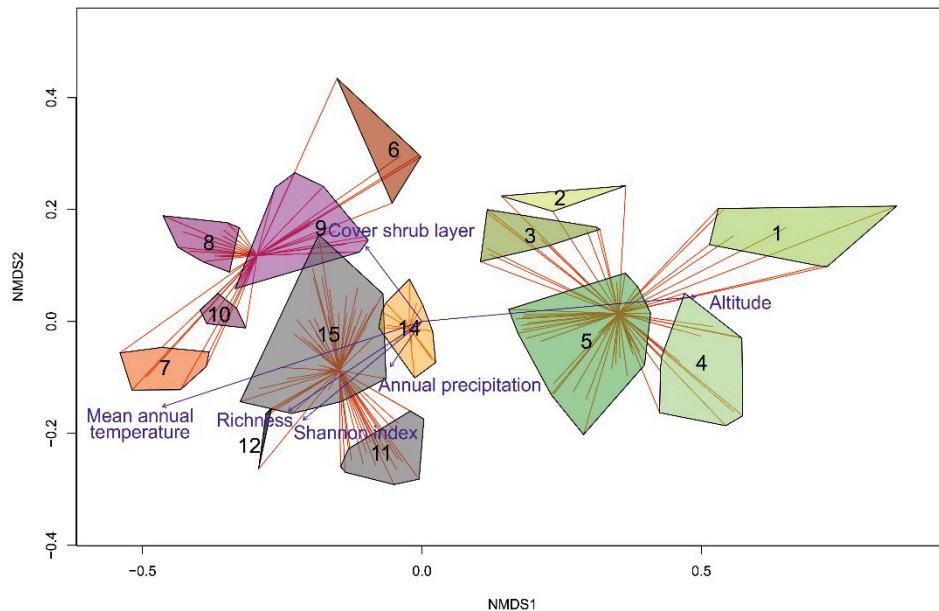


Fig. 3. NMDS ordination of halophytic communities in the Pamir-Alai and western Tian Shan. Red spider diagrams represent four classes of halophytic vegetation: *Festuco-Puccinellietea* (1, 3–5; green hulls), *Haloxylo-Salsoletea tomentosae* (6–10; purple and brownish hulls), *Climacopteretetea crassae* (11, 12, 15; grey hulls) and *Tamaricetea arceuthoidis* (14; orange hull). Arrows indicate environmental variables and only significant ones are shown ($p < 0.05$). The ordination was run with the use of two dimensions with stress value = 0.083. The names of syntaxon (1–15) are written in Supplement S1.

Abb. 3. NMDS-Ordinationsdiagramm (zwei Dimensionen, Stresswert 0,083) der Halophytengesellschaften des Pamir-Alai und des westlichen Tian Shan. Rote Spinnennetze repräsentieren die Bandbreite von vier Klassen der Halophytenvegetation: *Festuco-Puccinellietea* (1, 3–5; grün hinterlegt), *Haloxylo-Salsoletea tomentosae* (6–10; violett und braun), *Climacopteretetea crassae* (11, 12, 15; grau) und *Tamaricetea arceuthoidis* (14; orange). Pfeile bezeichnen Umweltvariablen (nur signifikante aufgenommen, $p < 0,05$). Namen der Syntaxa 1–15 wie in Beilage S1.

4.2 Syntaxonomical synopsis

A. High altitude arid halophytic graminoid communities

Class: *Festuco-Puccinellietea* Soó ex Vicherek 1973

Order: *Artemisietalia pauciflorae* Golub et Karpov in Golub et al. 2005

Alliance: *Taraxacion murgabici* S. Świerszcz et al. 2021

Paracolpodium leucolepis community (cluster 1)

Hordeum turkestanicum community (cluster 2)

Halerpestes sarmentosa community (cluster 3)

Ass. *Knorringietum sibiricae* S. Świerszcz et al. 2021 (cluster 4)

Ass. *Puccinellietum pamiricae* S. Świerszcz et al. 2021 (cluster 5)

B. Halophytic thermophilous scrub vegetation on dry solonetz and solonchak soils in arid zones of southern Middle Asia

Class: *Haloxylon-Salsoletea tomentosae* Akhani 2004 (provisional)

Order: ???

Alliance: ???

Limonium komarovii community (cluster 6)

Ass. *Carici physodis-Zygophylletum gontscharovii* S. Świerszcz et al. 2021 (cluster 7)

Ass. *Zygophylletum ferganensis* S. Świerszcz et al. 2021 (cluster 8)

Tamarix florida community (cluster 9)

Atriplex ornata-Heliotropium ellipticum community (cluster 10)

C. Hypersaline alluvial temporary flooded swards in the semi-desert and desert zones on solonchak soils in the Irano-Turanian region

Class: *Climacopteretea crassae* Akhani 2004 ex Świerszcz et al. 2021

Order: *Psylliostachyetalia spicato-leptostachyae* Świerszcz et al. 2021

Alliance: *Climacopterion lanatae* Berdiev et Golub in Golub 1995

Ass. *Sphenopodo-Climacopterium glaberrimae* Rukhlenko 2014 (cluster 11)

Cephalorhizum popovii community (cluster 12)

Aeluropus littoralis-Salsola leptoclada community (cluster 15)

D. Riparian scrub communities of saline and subsaline alluvial habitats along mainly intermittent rivers

Class: *Tamaricetea arceuthoidis* Akhani et Mucina 2015

Order: *Elaeagno turcomanicarum-Tamaricetalia ramosissimae* Akhani et Mucina 2015

Alliance: *Agropyro fragilis-Tamaricion ramosissimae* Golub in Barmin 2001

Cynodon dactylon-Tamarix ramosissima community (cluster 14)

4.3 Description of the communities

A. High altitude arid halophytic graminoid communities

Alliance: *Taraxacion murgabici* Świerszcz et al. **all. nov.**

Nomenclatural type: *Puccinellietum pamiricae* S. Świerszcz et al. 2021

Diagnostic species: *Taraxacum murgabicum*, *Glaux maritima* (= *Lysimachia maritima*), *Carex pseudofoetida*

Distribution and ecology: The phytocoenoses of the *Taraxacion murgabici* alliance were recorded in the eastern Pamir-Alai Mts. and south-western Tian Shan. They probably also occur in Tibet, north Pakistan and north Afghanistan at the highest plateaus. The communities of the *Taraxacion murgabici* occupy saline habitats in wet locations in the semi-desert zone of Central Asia, mainly between (2800–) 3500–4500 m a.s.l. The phytocoenoses of the alliance are typical vegetation in continental climate and extremely harsh conditions. They are poor in species and have scarce vegetation cover.

***Paracolpodium leucolepis* community (cluster 1)**

Diagnostic species: *Cerastium pusillum*, *Paracolpodium leucolepis* (= *Colpodium leucolepis*, = *C. altaicum*), *Trollius komarovii* (= *Hegemone micrantha*), *Ranunculus pseudohirculus* (= *R. longicaulis* var. *pseudohirculus*), *Taraxacum jashikkuliense*, *Valeriana minuta*

Constant species: *Paracolpodium leucolepis*

Floristic and habitat characteristics: Plots of this community were recorded in the highest reaches of the Dzhilusu Valley in the Terskey Ala-Too Mts. in Kyrgyzstan with a continental, very cold but humid climate (Supplement E1). This vegetation occupies flat, muddy terraces along water courses with scarce organic matter content. The plots have sparse and patchy physiognomy with an average vegetation cover of ca. 35%. The association is not species-rich with a mean of approx. 5 species per plot (Supplement E2). As the community has a transitional character between typical halophyte vegetation and high altitude wetlands, a number of mires taxa were spotted within the plots (e.g. *Carex orbicularis* or *Trollius komarovii*). The community of *Paracolpodium leucolepis* is extensively grazed by yaks and occasionally goats. We decided to leave this community rankless, as we spotted it in one valley only.

***Halerpestes sarmentosa* community (cluster 3)**

Diagnostic species: *Blysmus compressus*, *Carex pseudofoetida*, *Glaux maritima*, *Halerpestes sarmentosa*, *Hygroamblystegium varium*, *Juncus heptopotamicus*, *J. turkestanicus*, *Lotus krylovii*, *Philonotis fontana*, *Poa supina*, *Potentilla anserina*, *Puccinellia hackeliana*, *Veronica anagalloides*

Constant species: *Halerpestes sarmentosa*

Floristic and habitat characteristics: During the research, several plots of the community were recorded across the alpine belt of the Pamir-Alai and Tian Shan (Supplement E1). The community forms dense mats around shallow ponds with saline water. Sometimes, after seasonal flooding, it has a buoyant character similar to that formed by *Ranunculus natans*. It often inhabits sites frequently trampled by ungulate herds despite being fairly useless for grazing. The plots of the *Halerpestes sarmentosa* community were moderately rich in species (ca. 10 species per plot; Supplement E2), but the richest if only the group of the highest halophyte vegetation is considered (*Taraxacum murgabicae*). This is probably because it occupies the lowest section of the alpine belt (mean approx. 1800 m a.s.l.). This type of vegetation is characteristic of wastelands only sporadically grazed by cattle, sheep and goats. As *Halerpestes sarmentosa* is a species with a wide range and has been reported to be a diagnostic taxon for different syntaxa, we left this community rankless (see MIRKIN & NAUMOVA 2012).

***Knorringietum sibiricae* S. Świerszcz et al. ass. nov. (cluster 4, Fig. 6e)**

Diagnostic species: *Ajania tibetica*, *Atriplex pamirica*, *Carex pseudofoetida*, *Dilophia salsa*, *Oxytropis boguschii*, *Knorringia sibirica* (= *Polygonum sibiricum* var. *thomsonii*, *P. pamiricum*, *Knorringia pamirica*), *Puccinellia humilis*, *Taraxacum murgabicum*

Constant species: *Knorringia sibirica*

Floristic and habitat characteristics: This species-poor xerohalophytic vegetation occupies the most arid habitat in the highlands of Eastern Pamir (Supplement E1) with close contact to the mesic communities of *Puccinellia pamirica* and typical marsh species: *Carex*

pseudofoetida, *Blysmus rufus* and *Triglochin maritimum*. It often occupies hyperhalophytic sites with gravelly or sandy substrates along tiny brooks and rivulets. Patches of this vegetation were found in the high alpine belt with a mean elevation of approx. 4000 m a.s.l. The plots were very poor in species (mean ca. 5) but with a high cover of ca. 50% on average (Supplement E2). The *Knorringietum sibiricae* has no importance for the human economy. It is sporadically grazed on by yaks and sheep.

Typus relevé: (relevé number 28 in Supplement E3: 09 July 2018; Markansu: 39.31556 N; 73.33305 E; 3979 m a.s.l.; relevé area 10 m²; species richness: 7; species: *Knorringia pamirica* 2, *Puccinellia humilis* 2, *P. pamirica* 1, *Neotorularia humilis* (*Braya humilis*, *Torularia humilis*) +, *Dilophia salsa* +, *Taraxacum murgabicum* 2, *Ajania tibetica* +.

***Puccinellietum pamiricae* S. Świerszcz et al. ass. nov. (cluster 5, Fig. 6b–d)**

Diagnostic species: *Chenopodium iljinii*, *Oxytropis lehmanni*, *Puccinellia pamirica*, *Saussurea faminziniana*

Constant species: *Puccinellia pamirica*

Floristic and habitat characteristics: *Puccinellietum pamiricae* is closely related to the above-mentioned association; however, it occupies more mesic habitats and has a greater share of typical mire vegetation. It also withstands droughts and extremely xeric periods. It was found to be a common type of halophilous vegetation in the highlands of Eastern Pamir with a considerable share in the vegetation in the vicinity of seasonal ponds, along brooks and streams (Supplement E1). It is a species-poor community with ca. 5 species on average per plot and a plant cover of ca. 50% (Supplement E2). The average elevation of the recorded plots was ca. 3700 m a.s.l. This vegetation is sporadically used as a poor pasture for sheep and goats.

Typus relevé: (relevé number 39 in Supplement E3: 25 July 2016; Markansu: 39.39583 N; 73.31138E; 3842 m a.s.l.; relevé area 10 m²; species richness: 6; species: *Puccinellia pamirica* 3, *Plantago coronopus* +, *Carex pseudofoetida* +, *Taraxacum murgabicum* +, *Bryum argenteum* 2.

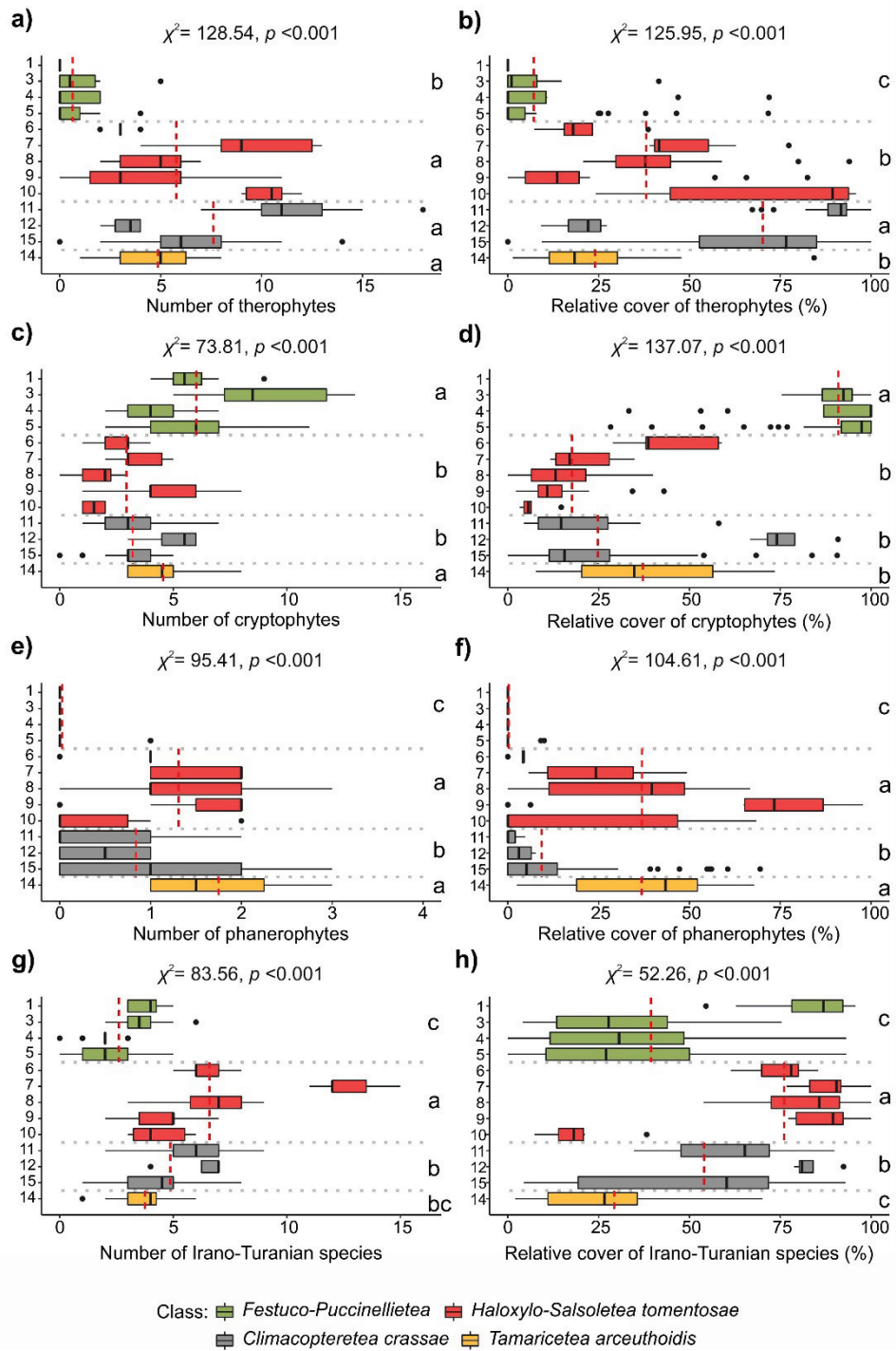
B. Halophytic thermophilous scrub vegetation on hypersaline solonetz and solonchak soils of arid zones of southern Middle Asia

***Carici physodis-Zygophylletum gontscharovii* S. Świerszcz et al. ass. nov. (cluster 7, Fig. 5e)**

Diagnostic species: *Amberboa turanica*, *Arnebia obovata*, *Artemisia eremophila* (= *Seriphidium eremophilum*), *Carex physodes*, *Climacoptera brachiata*, *Cymatocarpus popovii* (= *C. heterophyllus*), *Echinops knorringianus*, *Erodium oxyrhynchum* (= *E. oxyrhynchum* subsp. *oxyrhynchum*), *Lachnoloma lehmannii*, *Lappula mogoltavica*, *Lolium subulatum*, *Meniocus linifolius* (= *Alyssum linifolium*), *Salsola montana*, *Sisymbrium subsplenescens*, *Strigosella scorpioides*, *Tanacetopsis santoana*, *Ziziphora tenuior*, *Zygophyllum gontscharovii*

Constant species: *Zygophyllum gontscharovii*

Floristic and habitat characteristics: This community has a typical shrubby physiognomy and sparse cover (Fig. 4f). It occupies gentle slopes with northern and eastern expositions in south-western Tajikistan and in Syr Darya River Valley (Supplement E1). It prefers typical



solonetz soils and occurs in colline and foothill belts. The association is moderate in species richness and diversity; however, if compared to other halophytic vegetation, it is one of the richest (Supplement E2). We found 16 species per plot on average. The vegetation cover is scarce and generally does not exceed 20% in herbaceous and 15% in shrub layer. Grazing is rather uncommon, and during the winter and early spring this vegetation is sporadically used by sheep and goats. Additionally, it is used as a source of brushwood.

Typus relevé: (relevé number 98 in Supplement E3: 19 May 2019; Rabat: 40.45621 N; 70.17938 E; 726 m a.s.l.; relevé area 10 m²; species richness: 18; species: *Zygophyllum gontscharovii* b 3, *Carex physodes* 1, *Erodium oxyrrhynchum* 1, *Lachnoloma lehmannii* 1, *Meniocus linifolius* 1, *Strigosella scorpioides* 1, *Amberboa turanica* +, *Arnebia obovata* +, *Artemisia eremophila* +, *Cymatocarpus popovii* +, *Eremopyrum distans* +, *Koelpinia linearis* +, *Lappula mogoltavica* +, *Lolium subulatum* +, *Roemeria refracta* +, *Schismus arabicus* +, *Strigosella strigosa* +, *Tanacetopsis santoana* +.

***Zygophylletum ferganensis* S. Świerszcz et al. ass. nov. (cluster 8, Fig. 5a)**

Diagnostic species: *Anabasis truncata*, *Astragalus spinescens*, *Echinops nanus*, *Ephedra strobilacea*, *Girgensohnia oppositiflora*, *Reaumuria turkestanica*, *Salsola turkestanica*, *Silene glaucescens*, *Strigosella strigosa* (*Malcolmia strigosa*), *Zygophyllum ferganense*

Constant species: *Zygophyllum ferganense*

Floristic and habitat characteristics: This is one of the most thermophilous communities of shrubby continental halophyte vegetation in Middle Asia distributed in the Fergana Basin in the colline belt (average altitude ca. 500 m a.s.l., Supplement E1). The community develops on deep hypersaline solonetz on hilly lands. The community is rather species-poor with an average of ca. 9 plants per plot. The main blooming season is in spring between March and May. Similarly to the former association, the coverage both in the herb and shrub layer

Previous page (vorherige Seite):

Fig. 4. Boxplots showing number and relative cover of different life-form species (**a, b** – therophytes; **c, d** – cryptophytes; **e, f** – phanerophytes), **g**) number and **h**) relative cover of Irano-Turanian species for clusters with median (line), quartiles, outliers and the range of data. Red line indicates mean values of each class of halophytic vegetation. The values of χ^2 and p for statistical tests for vegetation groups are shown. Different letters indicate significant differences among classes. The numbers on y axis correspond to the cluster numbers. Vegetation types: (1) *Paracolpodium leucolepis* comm., (3) *Halerpestes sarmentosa* comm., (4) *Knorringietum sibiricae*, (5) *Puccinellietum pamiricae*, (6) *Limonium komarovii* comm., (7) *Carici physodis-Zygophylletum gontscharovi*, (8) *Zygophylletum ferganensis*, (9) *Tamarix florida* comm., (10) *Atriplex ornata-Heliotropium ellipticum* comm., (11) *Sphenopodo-Climacopterium glaberrimae*, (12) *Cephalorhizum popovii* comm., (15) *Aeluropus littoralis-Salsola leptoclada* comm., (14) *Cynodon dactylon-Tamarix ramosissima* comm.

Abb. 4. Boxplots mit Median (Linie), Quartilen, Ausreißern und den Datenbereichen. Gezeigt wird die Artenzahl und Deckung verschiedener Lebensformen (**a, b** – Therophyten; **c, d** – Kryptophyten; **e, f** – Phanerophyten), sowie **g**) Anzahl und **h**) relativen Deckung irano-turanischer Arten in den Vegetationseinheiten, jeweils mit den statistischen Werte zu χ^2 und p . Rote Linien geben Mittelwerte für jede Vegetationsklasse an. Verschiedene Buchstaben geben signifikante Unterschiede zwischen Klassen an. Die Nummern entlang der y-Achse beziehen sich auf die Pflanzengesellschaften. Vegetationstypen s. o.

is not considerable, at ca. 15–20% on average (Supplement E2). The shrubby vegetation of *Zygophyllum ferganense* is rarely used as a spring pasture for goats but often used as a source of brushwood.

Typus relevé: (relevé number 55 in Supplement E3; 19 May 2019; Rabat: 40.55517 N; 70.29313 E; 511 m a.s.l.; relevé area 10 m²; species richness: 11; species: *Zygophyllum ferganense* b 2, *Astragalus spinescens* 1, *Echinops nanus* +, *Girgensohnia oppositiflora* +, *Lactuca glaucifolia* +, *L. undulata* +, *Lycium ruthenicum* +, *Peganum harmala* +, *Salsola micranthera* +, *S. pestifera* (= *S. kali* subsp. *ruthenica*) +, *Strigosella strigosa* (= *Malcolmia strigosa*) +.

***Tamarix florida* community (cluster 9, Fig. 5d)**

Diagnostic species: *Chaenorhinum spicatum*, *Climacoptera turcomanica*, *Halostachys belangeriana*, *Limonium otolepis*, *Orobanche mongolica*, *Polygonum equisteiforme*, *Rumex halacsyi* (*R. dentatus* subsp. *halacsyi*), *Tamarix florida*

Constant species: *Halostachys belangeriana*, *Tamarix florida*

Floristic and habitat characteristics: This community was found in only one area – around the village of Rabat in the Syr Darya River Valley (Supplement E1). It occupies extensive muddy or moderately sandy alluvials of the river near the Lake Oksukon. It forms a dense thicket with up to 85% of shrub cover (Supplement E2) and the domination of *Tamarix florida* and *Halostachys belangeriana*. The community is moderately rich in species with an average of 10 taxa per plot. Herbs take advantage of clearings heavily grazed by cattle, the most dominant including *Limonium otolepis*, *Climacoptera turcomanica* and *Cynodon dactylon*.

***Atriplex ornata*-*Heliotropium ellipticum* community (cluster 10)**

Diagnostic species: *Alhagi canescens*, *Atriplex ornata*, *Chenopodium botrys*, *Chrozophora hierosolymitana* (= *Ch. tinctoria*), *Eremopyrum triticeum*, *Gastrocotyle hispida*, *Heliotropium ellipticum*, *Hyoscyamus pusillus*, *Salsola pestifera*, *Tribulus terrestris*

Constant species: *Heliotropium ellipticum*

Floristic and habitat characteristics: This community differs from the former in its substrate conditions. It inhabits sandy sediments in the Syr Darya River Valley in northern Tajikistan (Supplement E1). It has a sparse herbaceous cover of ca. 20% on average and a sporadic shrub layer built by *Lycium ruthenicum*. It is a community with moderate species richness (mean number of ca. 12 taxa, Supplement E1). Similarly to the former vegetation type, it has a clear share of semi-desert species (e.g. *Peganum harmala*, *Schismus arabicus* and *Tribulus terrestris*) and plants from nitrogen-rich, degraded habitats (e.g. *Chenopodium botrys* and *Descurainia sophia*). The community is grazed by cattle in spring and early summer.

Several relevés from the Zeravshan Mts. fall into the group of thermophilous scrub halophytic vegetation. They are dominated by *Limonium komarovii* and *Camphorosma lessingii*, a species endemic to western Pamir-Alai. This community occupies the weathering slopes of the Zeravshan Mts. with a high level of salt. Since we found it only in the surroundings of the Sorvoda settlement, we leave it rankless.

C. Hypersaline alluvial temporary flooded swards in the semi-desert and desert zones on solonchak soils in Irano-Turanian region

Class: *Climacopteretea crassae* Akhani 2004 ex Świerszcz et al. cl. nov.

Nomenclatural type: *Psylliostachyetalia spicato-leptostachyae* Świerszcz et al. 2021

This class was originally coined for annual therophytes with prevailing succulent plants with a C4 metabolism (AKHANI 2004). Because it was proposed as provisional without assigning the nomenclatural type according to the Code, it has to be validated (art. 5 ICPN; THEURIL-LAT et al. 2021).

The vegetation of the *Climacopteretea crassae* consists mainly of chenopod species with the domination or frequent occurrence of *Suaeda arcuata*, *S. altissima*, *S. aegyptiaca*, *Climacoptera* spp., *Petrosimonia glauca*, *Halanthium rarifolium*, *Atriplex tatarica*, *Bienertia cycloptera* or *Cornulaca monacantha*. The vegetation prefers moderately to strongly saline habitats in the lowlands of the Irano-Turanian region. It prefers river shores, salty depressions (sabkha) or inundated plains with clay or loamy-clay substrates (AKHANI et al. 2003). It tolerates natural disturbances, like floodings, or anthropogenic disturbances such as trampling or heavy grazing. In relation to *Thero-Salicornietea*, the vegetation inhabits more saline and drier habitats. The communities of the *Climacopteretea crassae* occur frequently in close relation with *Tamaricetea*, *Salicornietea fruticosae* or *Haloxylon-Salsolitea* vegetation (AKHANI 2004).

Order: *Psylliostachyetalia spicato-leptostachyae* Świerszcz et al. ord. nov.

Nomenclatural type: *Climacopteron lanatae* Berdiev et Golub in Golub 1995

Diagnostic species: *Aeluropus littoralis*, *Limonium reniforme*, *Salsola leptoclada*, *Atriplex tatarica*, *Climacoptera transoxana*

Distribution and ecology: The order includes phytocoenoses characterised by a high share of salt tolerant annual plants (Fig. 4a, b) of an Irano-Turanian distributional range (Fig. 4h). They form ephemeral vegetation on solonchak or sometimes solonetz soils and also on anthropogenic habitats. The main diagnostic species of the order are *Psylliostachys leptostachya* in the eastern part of the province and *P. spicata* in the western part. Some of the typical species of this syntaxon are endemic to Tajikistan and Middle Asia, e.g. *Heliotropium olgae*, *Lachnoloma lehmannii*, *Cephalorhizum popovii*, but the majority have wide distribution ranges.

Phytocoenoses assigned to this order occur across the Irano-Turanian province – in Iran, the Caspian Basin, Turkmenistan, Uzbekistan, Kazakhstan, Tajikistan and Kyrgyzstan. The major part of their vertical range lies in the lowland, colline, and only occasionally montane belts, from 200 up to 1600 m a.s.l. Communities of the new order develop on flat lands such as pond basins, saline pans, pool sides, fields and gentle slopes. They are mainly made up of *Climacoptera* spp., *Salsola* spp., *Petrosimonia* spp., *Gamanthus* spp. and other chenopods. A number of the taxa are adjusted to continental hot climate with a C4 metabolic cycle. The vegetation of *Psylliostachyetalia spicato-leptostachyae* is used extensively as a winter-spring pasture mainly for cattle and goats.



Fig. 5. Photos of the halophytic vegetation belonging to the **a)** *Zygophylletum ferganensis* near Asht in the Fergana Basin Gate; **b)** *Aeluropus littoralis-Salsola leptoclada* community near Obi-kiik in southern slopes of Aktau Mts; **c)** typical phytocoenosis of *Sphenopodo-Climacopteretum glaberrimae* Rukhlenko 2014 with domination of *Psylliostachys ×myosuroides* near Sambuli; **d)** the community of *Tamarix florida* near Rabat in Syr Darya Valley; **e)** *Carici physodis-Zygophylletum gontscharovii* near Samgar in northern Tajikistan; **f)** *Cynodon dactylon-Tamarix ramosissima* community in Vaksh Valley in south-western Tajikistan (Photos: A. Nowak, 2010–2019).

Abb. 5. Fotos der Halophytenvegetation: **a)** *Zygophylletum ferganensis* nahe Asht im Ferghanatal; **b)** *Aeluropus littoralis-Salsola leptoclada*-Gesellschaft bei Obi-kiik am Südhang der Aktau-Berge; **c)** typischer Bestand des *Sphenopodo-Climacopteretum glaberrimae* mit Dominanz von *Psylliostachys ×myosuroides* nahe Sambuli; **d)** *Tamarix florida*-Gesellschaft nahe Rabat im Syr Darya-Tal; **e)** *Carici physodis-Zygophylletum gontscharovii* bei Samgar im nördlichen Tadschikistan; **f)** *Cynodon dactylon-Tamarix ramosissima*-Gesellschaft im Vaksh-Tal im südwestlichen Tadschikistan (Fotos: A. Nowak, 2010–2019).

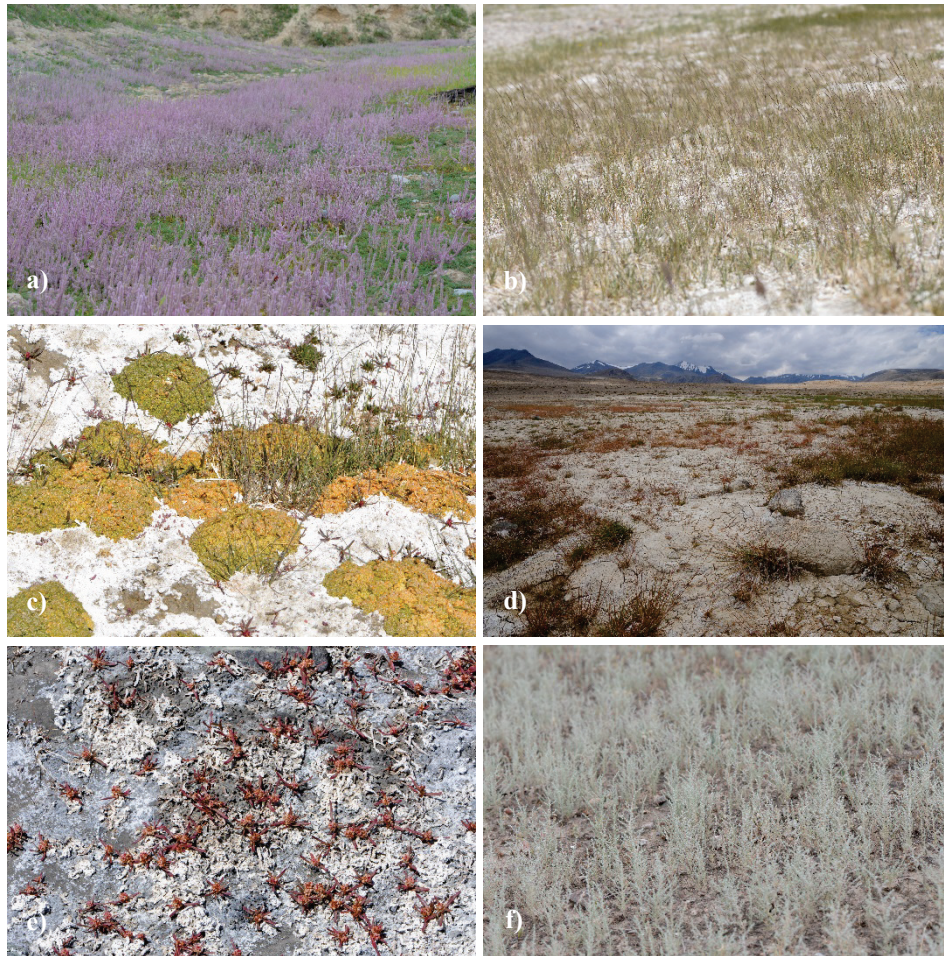


Fig. 6. Photos of the halophytic vegetation belonging to the: **a)** community with domination of *Psylliostachys leptostachya* and *suworowii* on salt marshes near Vose in southern Tajikistan; **b)** Typical *Puccinellietum pamiricae* on the salty pans near Alichur in the Pamir; **c)** the high mountain salt marsh vegetation of *Puccinellietum pamiricae* with domination of *Dilophia salsa*; **d)** *Puccinellietum pamiricae* near Kara-kul Lake in the Eastern Pamir along the lake shore; **e)** *Knorringietum sibiricae* near Alichur in Eastern Pamir; **f)** typical phytocoenosis of *Climacopteretea crassae* with domination of *Salsola leptoclada* near Hudzhant in Mogol-tau Mts (Photos: A. Nowak, 2010–2019).

Abb. 6. Fotos zur Halophytenvegetation. **a)** Von *Psylliostachys leptostachya* und *P. suworowii* dominierte Vegetation in Salzmarschen bei Vose im südlichen Tadschikistan; **b)** Typisches *Puccinellietum pamiricae* auf Salzpflanzen nahe Alichur im Pamir; **c)** Hochgebirgs-Salzrasen des *Puccinellietum pamiricae* dominiert von *Dilophia salsa*; **d)** *Puccinellietum pamiricae* am Ufer des Sees Kara-kul im östlichen Pamir; **e)** *Knorringietum sibiricae* bei Alichur im östlichen Pamir; **f)** typischer Bestand der *Climacopteretea crassae*, dominiert von *Salsola leptoclada*, bei Hudzhant im Mogol-tau-Gebirge (Fotos: A. Nowak, 2010–2019).

***Sphenopodo-Climacopteretum glaberrimae* Rukhlenko 2014 (cluster 11, Fig. 5c)**

Diagnostic species: *Frankenia pulverulenta*, *Galium decaisnei*, *Halimocnemis mollissima*, *Herniaria hirsuta*, *Microcephala lamellata*, *Plantago coronopus*, *Psylliostachys leptostachya*, *P. ×myosuroides*, *Sagina micropetala*, *Spergularia maritima* (= *S. marginata*), *S. microsperma*, *Sphenopus divaricatus*, *Strigosella stenopetala*, *Tetradiclis tenella*, *Veronica campylopoda*, *Vulpia hirtiglumis* (= *V. villosa*).

Constant species: *Frankenia pulverulenta*, *Plantago coronopus*, *Psylliostachys leptostachya*, *P. ×myosuroides*

Floristic and habitat characteristics: The plots of the association were found in lowland and colline zones of subhumid and warm locations in the surroundings of south-western Tajikistan and the Fergana Valley (Supplement E1). The ephemeral vegetation, composed mainly of annual plants (Fig. 4a, b), occupies flatlands along rivers, gentle slopes, and even ruderal sites, such as sediment ponds or ditches. This is one of the richest types of halophytic vegetation with 14 species per plot on average. It has a patchy physiognomy with an average herb cover of ca. 50% (Supplement E2). This community is used mainly for grazing by cattle and goats.

***Aeluropus littoralis-Salsola leptoclada* community (cluster 15, Fig. 5b)**

Diagnostic species: *Aeluropus littoralis*, *Climacoptera transoxana*, *Cressa cretica*, *Parapholis incurva*, *Salicornia europaea*, *Salsola leptoclada*, *Suaeda paradoxa*

Constant species: *Aeluropus littoralis*, *Salsola leptoclada*

Floristic and habitat characteristics: This fairly common vegetation inhabits flat seasonally inundated lands in the warm zones of southern Middle Asia (Supplement E1). Sometimes it occurs on wet soils on gentle slopes in the foothills of the Ak-tau and Baba-tag Mts. but not higher than 600 m a.s.l. This vegetation type is species-poor with a mean number of plants per plot at no more than 10. However, as many plants are abundant, the total cover of herbaceous layer can exceed 80% with an average ca. 60% (Supplement E2). The group has a rather heterogeneous character with plots dominated by *Aeluropus littoralis* as well as by therophytes like *Salicornia europaea* on wet soils and *Salsola leptoclada* on drier substrates (Fig. 4b). These co-occurring variants of the group convinced us that further study is required for it to be decisively assigned to a rank.

Additionally, within the ephemeral vegetation of halophytes in thermophilous lowlands, the community of *Cephalorhizum popovii* (cluster 12) was distinguished by the TWINSPAN algorithm (Fig. 2). Unfortunately, we found only four plots in one location on the Hodzha-Mumin salt mountain (Supplement E1), in a small eroded ephemeral water tank, which is why we leave this community rankless.

D. Riparian scrub communities of saline and subsaline alluvial habitats along mainly intermittent rivers

***Cynodon dactylon-Tamarix ramosissima* community (cluster 14, Fig. 5f)**

Diagnostic species: *Alhagi kirghisorum*, *Artemisia stenocephala*, *Cynanchum sibiricum* (= *C. acutum* subsp. *sibiricum*), *Cynodon dactylon*, *Elaeagnus angustifolia*, *Erianthus ravennae* (= *Saccharum ravennae*), *Limonium reniforme*, *Medicago lupulina*, *Tamarix ramosissima*

Constant species: *Cynodon dactylon*, *Tamarix ramosissima*

Floristic and habitat characteristics: This community was found mainly in south-western Tajikistan (Supplement E1). It inhabits the edges of canals, ditches, river valleys and intermittent watercourses; it was also found on escarpments with seeping water. It is a typical thicket community with a moderate number of species (12 on average) occurring in lowlands (Supplement E2). Gallery forest taxa (e.g. *Erianthus ravennae*, *Elaeagnus angustifolius*) contribute to the plots, as the *Tamarix* thicket is sometimes a successional stage before the *Populus pruinosa* stands. The bushy community is often grazed by cattle and reveals an increased share of species adapted to trampling and grazing e.g. *Lagonychium farctum* (= *Prosopis farcta*), *Hordeum geniculatum* (= *H. marinum* subsp. *gussoneanum*), *Amoria fragifera* (= *Trifolium fragiferum*).

5. Discussion

5.1 The layout and relations of annual ephemeral vegetation of halophytic pans and lowland river valleys to the neighbouring regions

The pioneer ephemeral habitat of herbaceous vegetation is spread mainly in the south-western Pamir-Alai foothills. Here, they occupy the salt pans of seasonal pools or the gentle slopes of river valleys. They are sporadically grazed by cattle, goats and sometimes sheep, however mainly as a winter pasture.

The vegetation of annual succulent halophytes was reported from tidal mud flats and edges of irregularly flooded saline inland waters from the whole of Eurasia. For the continental centre of Asia, the *Camphorosmo-Salicornietalia* Borhidi 1996 vegetation dominated by annual succulents on solonchak and solonetz soils of inland salt pans has been established (GOLUB et al. 2001). For the temporarily wet halophytic vegetation on solonchak soils, the *Suaedion acuminatae* Golub et Tsorbadze in Golub 1995 corr. Lysenko et Mucina 2015, a Sarmatian vegetation of annual succulent halophytes, has been proposed. In northern Iran, the class *Climacopteretea crassae* was coined for annual therophytic, succulent plants, mainly of a C4 metabolism. These Chenopod communities inhabit more saline and drier habitats than the *Thero-Salicornietea* (AKHANI 2004). Thorough analyses of our relevés (particularly clusters 11 and 15) convinced us to include this vegetation in the *Climacopteretea crassae*. Apart from the presence of C4 species, such as *Climacoptera turcomanica* and *C. transoxana*, the main reason behind this is the share of typical Irano-Turanian taxa e.g. *Gamanthus gamocarpus*, *Galium decaisnei*, *Garhadiolus papposus*, *Halimocnemis mollissima*, *Salsola leptoclada* and others (Fig. 4h). Around half of the vegetation cover have their ranges confined to this phytogeographical province.

Additionally, a number of semi-desert taxa contribute to this vegetation, e.g. *Aristida heymanii* (= *A. adscensionis*), *Capparis herbacea*, *Strigosella scorpioides*, *Salsola pestifera* and *Schismus arabicus*. It is possible that separate plots, located close to river currents or in the centre of seasonal lakes in northern Middle Asia, have more similarities to the *Thero-Salicornietea*, but this should be thoroughly studied, particularly in Uzbekistan. It is worth mentioning that similar vegetation type (under the name of *Climacopterideta varia*) was reported in this country based on research conducted in desert saline habitats with the application of the dominant-species approach (AKZHIGITOVA 1973). In recent decades, two associations dominated by species of *Climacoptera* and *Petrosimonia* (*Petrosimonia-Climacopteretum glaberrimae* and *Sphenopodo-Climacopteretum glaberrimae*) were described in south-eastern Turkmenistan with similar habitats as in SW Tajikistan (RUKHLENKO 2012a).

Analysing the plots from south-western Pamir-Alai, we also took a closer look at *Aeluropetea* vegetation. This type of vegetation was proposed for hypersaline alluvial temporary flooded swards in the semi-desert and desert zones of Central Asia, Middle East and the Ural River Valley (GOLUB et al. 2001). The physiognomy and management of this meadow-like vegetation make it similar to the vicariant syntaxon of the west European *Scorzonero-Juncetea gerardii*. However, the significant difference between our communities and those reported from the Artek River Valley is that the share of hemicryptophytes is negligible in Tajikistan-Kyrgyzstan vegetation (Fig. 4c, d). Besides the phytogeographical differences, this is probably due to less intensive grazing in Middle Asia and occasional usage of the plots as weak winter pastures. Apart from *Aeluropus littoralis*, the number of plants with high forage value is scarce.

Cluster 11 has a great share of *Frankenia pulverulenta*, a typical Irano-Turanian and Mediterranean taxon that occupies different saline habitats throughout southern Eurasia. It is included in the diagnostic taxa group of *Frankenietalia*. This Atlantic-Mediterranean winter annual vegetation occurs in disturbed saline habitats and inland saline badlands and is included in the class *Saginetea maritimae* (MUCINA et al. 2016). Communities of this class typically occupy small disturbed sites within large stands of the *Juncetea maritimi*, often characterised by some sand deposition. Due to strong disturbance in part of our samples, some of them are similar to this type of vegetation, however this should be considered an anthropogenic influence. Tajikistan has no marine habitats and is completely landlocked. Disturbance caused by ungulates, flooding, and man-made damage makes the physiognomy of some plots resemble the species composition of *Saginetea maritimae*, however they ought to be excluded from this Atlantic and Mediterranean halophytic vegetation.

Despite cluster 11 falling slightly apart from cluster 15 on the TWINSPAN dendrogram (Fig. 2), suggesting that these two associations are somewhat dissimilar, the ordination diagram shows quite clearly that they are not so distant (Fig. 3). Cluster 11 comprises relevés of an ephemeral character with a development peak in the spring. The most important seasons to communities from cluster 15 are late summer and autumn, and they often keep their physiognomy and fructescence until the end of December.

There are clear similarities between our plots and those reported in South Turkmenistan and Iran (AKHANI 2004; RUKHLENKO 2014). A number of species are shared between different communities, with the *Frankenia pulverulenta*, *Limonium reniforme*, *Tetradiclis tenella*, *Spergularia microsperma*, *Climacoptera glaberrima* (= *C. turcomanica*), *Sphenopus divaricatus*, *Psylliostachys* spp., *Plantago coronopus* and others. This type of temporal, seasonally inundated halophytic vegetation should be included in a separate order – *Psylliostachyetalia spicato-leptostachyae* – with diagnostic *Psylliostachys spicata*, *P. ×myosuroides* and *P. leptostachya* to highlight its Irano-Turanian character. This vegetation thrives on flat hypersaline pans along lakeshores and lowland rivers and can also develop on anthropogenic sites.

GOLUB (1995) defined the *Climacopteretum transoxanae* with the presence of *Halocnemum strobilaceum*, *Halostachys caspica*, *Aeluropus littoralis*, *Suaeda turkestanica*, *Strigosella brevipes*, and *Sphenopus divaricatus*. It was classified in *Aeluropodion littoralis* meadow solonchaks in Turkmenistan (GOLUB 1995). However, the cover of our vegetation (10–20%) does not resemble the salt meadows of Turkmenistan. Cluster 15 is the most similar to this community, but in our opinion it ought to be assigned to *Climacopteretea* rather than *Aeluropetea*.

5.2 The arrangement of scrub halophytic vegetation and its relation to other Irano-Turanian plant communities of saline habitats

The continental hypersaline scrub vegetation on the margins of the inland saline lakes of Eastern Europe and Central Asia has been included in the *Kalidietea* Mirkin et al. ex Rukhlenko 2012. In the desert lands of the Irano-Turanian province, this vegetation was assigned to *Kalidietalia foliati* Golub et al. 2001 and reported from the north-western outskirts of the Irano-Turanian province (MUCINA et al. 2016). Salt-tolerant shrubby succulent species were proposed as the diagnostic group of taxa. These included species of *Kalidium* spp. (e.g. *K. caspicum*), *Salsola* spp. (e.g. *S. lanata*, *S. transoxana*, *S. turcomanica*, *S. arbuscula*, *S. dendroides*, *S. orientalis*), *Petrosimonia* spp. (e.g. *P. glauca*, *P. oppositifolia*, *P. sibirica*), *Karelinia caspia* and *Halocnemum strobilaceum* (LYSENKO 2014, RUKHLENKO 2012b). Although this species set is quite similar to the floristic composition of our plots, the habitat conditions are not completely the same. This is probably due to the fact that the communities from Russia and Turkmenistan (Volga and Atrek River Valleys) were sampled from temporarily inundated solonchak soils. That is why we consider our plots, at least from the groups 7 and 8, as more comparable to the *Haloxylon-Salsolitea tomentosae* Akhani 2004 – hypersaline scrubs on solonetz soils. This assignment is supported by its close relation to desert steppe vegetation and subhalophytic *Anabasis* communities that were also reported in Iran in close vicinity to vegetation stands of the *Haloxylon-Salsolitea* (AKHANI 2004). Several plants typical for this subsaline habitat were also observed in our plots (*Alhagi canescens*, *Anabasis truncata*, *Salsola montana*, *Echinops knorringianus*, *Schismus arabicus* and *Menicocus linifolius*). In addition, *Haloxylon aphyllum* contributes to our plots. We need further sampling to adjust the hierarchical system within this group; at this stage of the research, this is quite problematic, as the group is considerably heterogeneous. Besides shrubby vegetation, it includes plots dominated by herbaceous plants on drier sand deposits within the river valleys, which can be related to a psammo-halophytic vegetation. Additionally, the community of *Limonium komarovii* is comprised of rather steppe-like vegetation and can be shifted to the class of desert steppes *Artemisietea lerchiana*.

5.3 The distinct xerohalophytic vegetation of the high plateaus of the Eastern Pamir

As in the case of other types of vegetation (e.g. steppe, chasmophyte), the Eastern Pamir reveals an apparent distinctiveness regarding species composition of halophytic communities (ŚWIERSZCZ et al. 2020). This vegetation also differs considerably in terms of physiognomic and structural features. It is species-poor, with sparse vegetation cover, and inhabits the shores of alpine ponds, lakes, and brooks. It consists of species adapted to extremely harsh environments, with freezing winters, warm summers, and very low precipitation (ca. 100 mm per year). The most important species are *Halerpestes sarmentosa*, *Puccinellia pamirica*, *Suaeda olufsenii*, *S. paradoxa*, *Taraxacum murgabicum*, *Triglochin maritimum* and others including *Artemisia macrocephala*, *Dilophia salsa*, *Knorringia sibirica* and *Puccinellia humilis*. This strongly heterogeneous environment is also affected by a long history of pastoralism (stretching 8000 years back) and grassland management in the region (MIRZABAEV et al. 2016).

While sheep, goats, horses and cows prevail in the lower elevations, the high Pamirian plateau is grazed by yaks and camels during the summer, which promotes graminoid and rosette plants (e.g. *Hordeum turkestanicum*, *Knorringia pamirica*, *Puccinellia* spp.;

MIRZABAEV et al. 2016, VANSELOW et al. 2016). Despite the heterogenous bedrock conditions in the Eastern Pamir, the extremely harsh environment in valley bottoms – the most important habitat of this vegetation – causes a strong environmental filtering of the plant species. Additionally, the species scarcity in all types of vegetation (mires, semi-deserts, cryophilous steppes and halophytic vegetation) results in rather low dissimilarity between plots. In many cases, different vegetation occurs in a micro-mosaic pattern – in particular, mires and halophytic plots can be close neighbours, sharing a considerable part of the species set (e.g. MEṬRAK et al. 2017). Despite these close relations, the phytocoenoses of Pamirian highlands are notably different to the western Pamir-Alai vegetation and should probably be examined in relation to Tibetan and Western Himalayan communities in Pakistan (KHAN 2003, KHAN & QAISER 2006).

We describe a distinct alliance – the *Taraxacion murgabici* – for this type of halophytic vegetation. Communities of *Taraxacion murgabici* are typical halophytic vegetation on wet and mesic locations in the semi-desert zone of the highest belts (alpine and subnival) of Central Asia, mainly between 3000 and 4500 m a.s.l. They thrive in a strongly continental climate and extremely low precipitation which, like in other regions of the temperate zone, is mainly in summer. The semi-desert conditions of the arid Pamirian plateau convinced us to include the xerohalophytic vegetation of our study area in the saline steppes of the *Festuco-Puccinellietea* class (MUCINA et al. 2016). Despite the scarcity and sparse cover of vegetation, the clear dominance of *Puccinellia*, including an array of neoendemic taxa, shows apparent affinities to the cryophilous steppes of subsaline habitats of Tajikistan.

6. Conclusions

Our study sheds light on the halophytic vegetation in the mountainous region of Middle Asia and contributes to the consistent hierarchical classification of the vegetation in the region (NOWAK et al. 2016). The syntaxonomical position of some of the distinguished communities still remains unclear, hence further research on the halophytic vegetation of Middle Asia is required, especially on subhalophytic forb vegetation and meadows of the *Glycyrrhizetalia glabrae* and semi-desert or desert steppes of the *Artemisietea lerchianae*. The potential inclusion of other environmental factors and transitional zones between mires, steppes and semi-deserts into further studies would also be very valuable for a more detailed delimitation and description of the vegetation units. Halophytic vegetation does not provide any important economic services. Therefore, it is treated as needless wastelands or badlands, particularly in Eastern Pamir. However, under the changing climate, the conservation value of these sensible ecosystems has been stressed recently (JANSSEN et al. 2016), so it is of primary importance to recognise the diversity and richness of halophytic vegetation in the biodiversity hotspot of Middle Asia.

Erweiterte deutsche Zusammenfassung

Einleitung – Halophytenvegetation ist in allen Vegetationszonen der Erde verbreitet (KAPLER 2019). In Mittelasien ist die Halophytenvegetation noch wenig erforscht, und in Übersichten zur Vegetation im Gebiet der früheren Sowjetunion (s. STANYUKOVICH 1982, MIRKIN & NAUMOVA 2012) fehlt sie weitgehend. Im vorliegenden Beitrag klassifizieren die Autoren die Halophytenvegetation in einem Brennpunkt der globalen Biodiversität in Mittelasien (MITTERMEIER et al. 2006) – Pamir-Alai und westliches Tian Shan – und setzen sie in Beziehung zur Vegetation benachbarter Moore, Steppen und Halbwüsten. Die Autoren gehen folgenden Fragen nach: (1) Welche Halophytengesellschaften lassen

sich im Untersuchungsgebiet unterscheiden? (2) Welche Arten sind kennzeichnend für die beschriebenen Syntaxa? (3) Wie ist die Vegetationsstruktur der Salzstandorte, und welchen Standortbedingungen sind die beschriebenen Pflanzengesellschaften ausgesetzt?

Untersuchungsgebiet – Die Vegetationsdaten wurden in einem Gebiet von etwa 200.000 km² im Pamir-Alai (Tadschikistan) und im westlichen Tian Shan (Süd- und Ost-Kirgisistan) in Mittelasien erhoben (Abb. 1a). Die untersuchten Flächen an den Salzstandorten erstrecken sich über einen Höhengradienten zwischen 300 m und 4200 m Meereshöhe.

Methoden – Die Autoren führten die Untersuchungen in den Jahren 2014–2019 durch und fertigten 217 Vegetationsaufnahmen an. Die Größe der Aufnahmeflächen war 10 m² bei krautiger Vegetation und 100 m² bei Strauchvegetation. Alle Gefäßpflanzen- und Moosarten wurden erfasst und ihre Artmächtigkeit wurde mittels der 7-teiligen Braun-Blanquet-Skala geschätzt (WESTHOFF & VAN DER MAAREL 1973). Die Daten wurden in der Mittelasien-Vegetationsdatenbank hinterlegt (NOWAK et al. 2017) und in R (R CORE TEAM 2020) und in JUICE (TICHÝ 2002) analysiert. Die Pflanzengesellschaften wurden anhand ihrer Artenzusammensetzung klassifiziert mittels TWINSpan, modifiziert nach ROLEČEK et al. (2009; s. Abb. 2). Die Artmächtigkeitskala wurde auf drei Intervalle mit den Schwellenwerten 5 % und 25 % transformiert. Seltene Arten im Datensatz wurden herabgewichtet. Dabei wurde als Maß die Gruppen-Heterogenität verwendet (ROLEČEK et al. 2009). Diagnostische Arten wurden durch ihrer Treuemaße bestimmt (*phi*-Koeffizient; CHYTRÝ et al. 2002). Nach der Transformation der floristischen Daten (Hellingerabstand) wurden die floristischen Beziehungen zwischen den Vegetationseinheiten mittels nicht-metrischer multidimensionaler Skalierung (NMDS) eingeschätzt (*metaMDS* in *vegan*; OKSANEN et al. 2019). Umwelt- und Vegetationsparameter wurden nachträglich in die Ordination projiziert, um ihre Beziehungen zu den Vegetationseinheiten zu ermitteln (*envfit*, 999 Permutationen; OKSANEN et al. 2019). Die Autoren bestimmten die Mediane und die Standardabweichungen der Umwelt- und Vegetationsparameter (Meereshöhe, Temperatur, Niederschlag, Artenzahl pro Aufnahme, Shannon-Index, Anteile von Therophyten, Kryptophyten, Phanerophyten und pflanzengeografischen Elementen in den Aufnahmen) für alle Vegetationseinheiten (Abb. 4, Anhang E1).

Die Taxonomie der Gefäßpflanzen außer *Bromus* (hier THE PLANT LIST 2013) folgt CHEREPANOV (1995). Die Syntaxonomie ist abgestimmt mit RUKHLENKO (2011), GOLUB et al. (2001) und LYSENKO (2014).

Ergebnisse – Die Klassifikation der Vegetationsaufnahmen ergab 15 Gruppen (Abb. 2 und 3, Beilage S1). Vier floristisch besonders gut abgegrenzte Gruppen wurden als neue Assoziationen beschrieben. Die übrigen Gruppen wurden als ranglose Gesellschaften eingestuft, oder sie entsprechen bereits zuvor beschriebenen Assoziationen (RUKHLENKO 2012a, b). Im Einzelnen ließen sich unterscheiden: Hochgebirgs-Salztrockenrasen (*Paracolpodium leucolepis*-Ges., *Hordeum turkestanicum*-Ges., *Halerpestes sarmentosa*-Ges., *Knorringietum sibiricae*, *Puccinellietum pamiricae*); Strauchvegetation der ariden Zone Mittelasien auf hypersalinen Solonetz-Böden (*Limonium komarovii*-Ges., *Carici physodis-Zygophylletum gontscharovi*, *Zygophylletum ferganensis*, *Tamarix florida*-Ges., *Atriplex ornata-Heliotropium ellipticum*-Ges.); Irano-turanische Flutrasen der Halbwüsten- und Wüstenzonen auf hypersalinen Solontschak-Böden (*Sphenopodo-Climacopteretum glaberrimae*, *Cephalorhizum popovii*-Ges., *Aeluropus littoralis-Salsola leptoclada*-Ges.); Auengebüschvegetation auf (sub)salinen Schwemmböden entlang episodisch wasserführender Flussläufe (*Cynodon dactylon-Tamarix ramosissima*-Ges.).

Diskussion – Annuelle Sukkulentevegetation ist aus ganz Eurasien von unregelmäßig überfluteten Binnenlandsalzstellen und vom Wattenmeer bekannt. Sie ist im kontinentalen Inneren Zentralasiens durch die Ordnung *Camphorosmo-Salicornietalia* in Salztonebenen auf Solontschak- und Solonetz-Böden vertreten (GOLUB et al. 2001). Für die Vegetation auf zeitweise nassen Solontschak-Böden wurde der sarmatisch verbreitete Verband *Suaedion acuminatae* beschrieben. Im Norden Irans wurde die von C4-Pflanzen dominierte Klasse *Climacopteretea crassae* geprägt, die in trockeneren und stärker

salzigen Habitaten vorkommt als die *Thero-Salicornietea* (AKHANI 2004). Die Vorkommen der C4-Arten *Climacoptera turcomanica* and *C. transoxana*, vor allem aber der Anteil typisch irano-turanisch verbreiteter Taxa (*Gamanthus gamocarpus*, *Galium decaisnei*, *Garhadiolus papposus*, *Halimocnemis mollissima*, *Salsola leptoclada*; Fig. 4h) veranlasste uns, insbesondere die Vegetationseinheiten 11 und 15 zu den *Climacopteretea crassae* zu stellen. Zwei von *Climacoptera* und *Petrosimonia* dominierte Assoziationen (*Petrosimonio-Climacopteretum glaberrimae*, *Sphenopodo-Climacopteretum glaberrimae*) sind aus Südost-Turkmenistan beschrieben worden; ähnliche Standorte gibt es auch in Südwest-Tadschikistan (RUKHLENKO 2012a). Die Klasse *Climacopteretea crassae* war als provisorisch bezeichnet worden und ist damit nomenklatorisch ungültig (ICPN, art. 5, THEURILLAT et al. 2021); sie wird hier validiert und als ihr nomenklatorischer Typus wird die Ordnung *Psylliostachyetalia spicata-leptostachyae* beschrieben.

Die kontinental-hypersaline Strauchvegetation an den Rändern von Binnensalzseen in Osteuropa und Zentralasien wird in der Klasse *Kalidietea* klassifiziert. In den Wüstengebieten der nordwestlichen Ausläufer der irano-turanischen Florenregion ist diese Vegetation durch die *Kalidietalia foliati* vertreten. Obwohl ihr Artenbestand dem unserer Probeflächen recht ähnlich ist, unterscheiden sich die Standortbedingungen, wohl weil die Gesellschaften der *Kalidietalia foliati* in Russland und Turkmenistan (Stromtäler von Wolga und Atrak) auf zeitweise überflutetem Solontschak nachgewiesen worden sind. Daher halten wir die Vegetation unserer Probeflächen, zumindest die der Vegetationseinheiten 7 und 8, als besser vergleichbar mit den *Haloxyl-Salsoletea tomentosae*, Gebüsch auf hypersalinem Solonetz. Diese Zuordnung wird unterstützt durch enge Beziehungen zur Wüstensteppenvegetation und zu subhalotoleranten *Anabasis*-Gesellschaften, die auch im Iran in unmittelbarer Nähe zur *Haloxyl-Salsoletea*-Vegetation vorkommen (AKHANI 2004). Weitere Erhebungen sind zur syntaxonomischen Klärung dieser sehr heterogenen Vegetation erforderlich, deren Gebüsch in den Flusstälern durchsetzt ist von krautdominierten Pflanzenbeständen auf trockeneren Sandablagerungen.

Wie auch andere Vegetationsformationen (Steppe, Felsvegetation; ŚWIERSZCZ et al. 2020) ist die Halophytenvegetation des östlichen Pamir floristisch und strukturell recht eigenständig. Sie ist artenarm, schütter und wächst an Ufern alpiner Seen, Teiche und Bäche. Die Arten sind angepasst an extrem harte Umweltbedingungen (strenge Fröste, heiße Sommer, Niederschläge um 100 mm pro Jahr) – und an jahrtausendelange Weidewirtschaft (MIRZABAEV et al. 2016). Wir beschreiben einen eigenen Verband – *Taraxacion murgabici* – für diese Halophytenvegetation an nassen bis frischen Standorten in der alpin-subnivalen Stufe (3000–4500 m Meereshöhe) Zentralasiens, klimatisch ausgeprägt kontinental mit geringen Niederschlagsmengen, die wie in anderen Gebieten der temperaten Zone vor allem auf den Sommer entfallen. Die Halbwüstenbedingungen des hochariden Pamir-Plateaus veranlassten uns, die xerohalotolerante Vegation unseres Untersuchungsgebietes in die Klasse der Salzsteppen *Festuco-Puccinellietea* zu stellen. Trotz der Kargheit der Vegetation zeigt die Dominanz von *Puccinellia*, mit einer Reihe von neoendemischen Taxa, auffällige Ähnlichkeiten zur Vegetation der kryophilen Steppen an subsalinen Standorten Tadschikistans.

Die vorliegende Untersuchung beleuchtet die Halophytenvegetation in Gebirgsregionen Mittelasiens und trägt zur Klärung syntaxonomischer Beziehungen bei (NOWAK et al. 2016). Die syntaxonomische Stellung einiger der unterschiedenen Gesellschaften bleibt unklar, weshalb weitere Forschung zur Halophytenvegetation Mittelasiens geboten ist.







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Author contributions

A.N., S.Š. and M.N. planned the research, A.N., M.N., S.Š., A.W., E.K. and S.N. conducted the field sampling and identified the plant species, S.Š. and A.N. performed the statistical analyses, S.N. prepared the synoptic and analytical table, while all the authors participated in the writing of the manuscript and verification of plant collections in the herbarium.

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Supplements

Supplement S1. Synoptic table of halophytic vegetation in the mountains of Middle Asia.

Beilage S1. Synoptische Tabelle der Halophytenvegetation in Gebirgen Mittelasiens.

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Distribution maps of all halophytic types within the study area.

Anhang E1. Verbreitung der Halophytengesellschaften im Untersuchungsgebiet.

Supplement E2. Boxplots showing median, quartiles, outliers and the range of environmental and vegetation parameters of clusters within different halophytic vegetation classes.

Anhang E2. Boxplots mit Median, Quartilen, Ausreißern und den Bereichen von Umwelt- und Vegetationsparametern in den Gruppen zu verschiedenen Vegetationsklassen.

Supplement E3. Analytic table of halophytic vegetation in the mountains of Middle Asia.

Anhang E3. Analytische Tabelle der halophytischen Vegetation in den Gebirgen Mittelasiens.

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Supplement S1. Synoptic table of halophytic vegetation in the mountains of Middle Asia.

1 – *Paracolpodium leucolepis* community; 2 – *Hordeum turkestanicum* community; 3 – *Halerpestes sarmentosa* community; 4 – *Knorringietum sibiricae*; 5 – *Puccinellietum pamiricae*; 6 – *Limonium komarovii* community; 7 – *Carici physodis-Zygophylletum gontscharovii*; 8 – *Zygophylletum ferganensis*; 9 – *Tamarix florida* community; 10 – *Atriplex ornata-Heliotropium ellipticum* community; 11 – *Sphenopodo-Climacopterum glaberrimae*; 12 – *Cephalorhizum popovii* community; 15 – *Aeluropus littoralis-Salsola leptoclada* community; 14 – *Cynodon dactylon-Tamarix ramosissima* community. The phi coefficient values (in superscript) in the table are multiplied by 100 and only shown when positive. Main values are species frequencies (in percentages). Letters after some species names indicate occurrence in shrub (b) and moss (d) layer.

Supplement E1. Übersichtstabelle der Salzvegetation in den Gebirgen Mittelasiens.

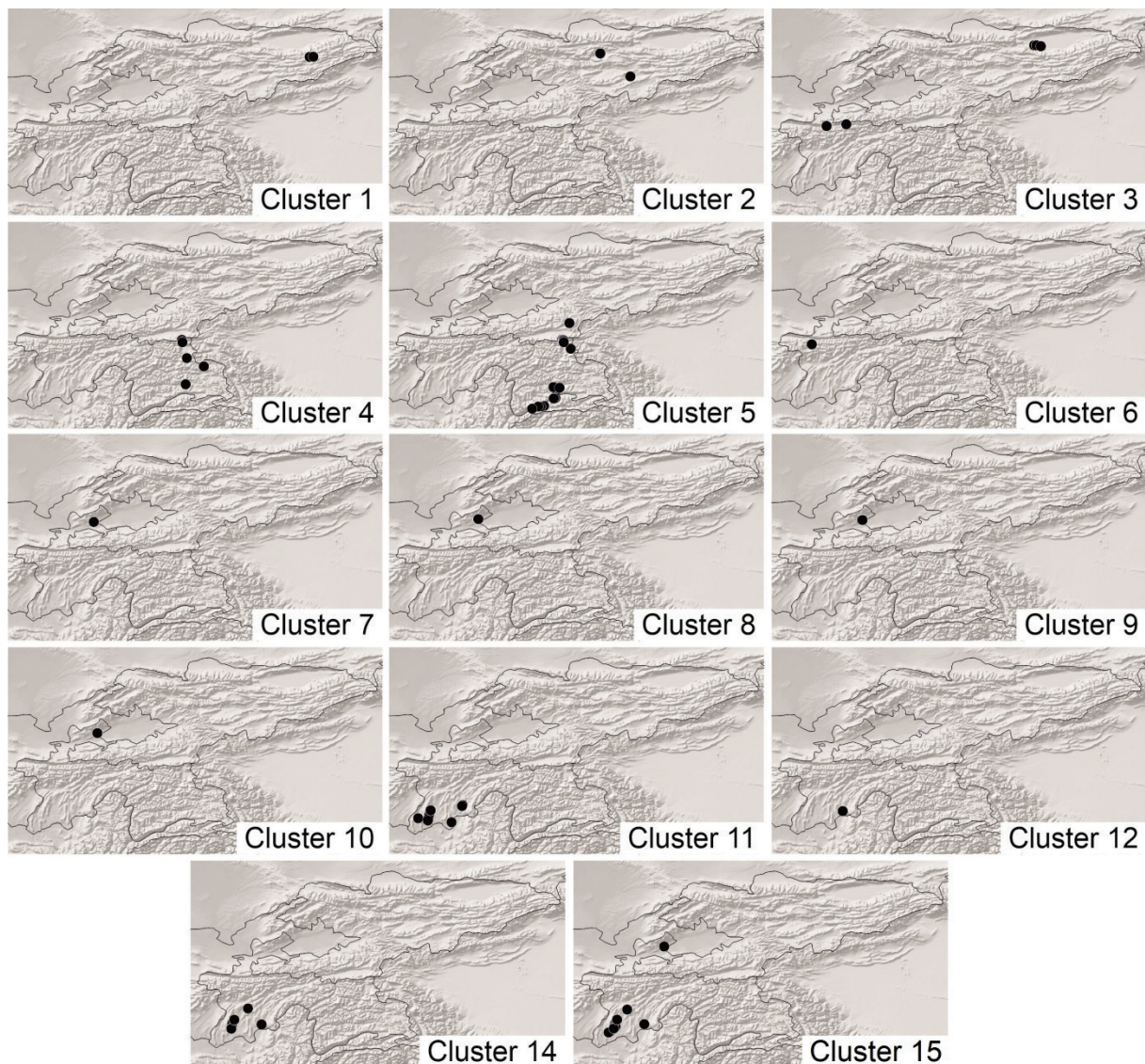
1 – *Paracolpodium leucolepis* community; 2 – *Hordeum turkestanicum* community; 3 – *Halerpestes sarmentosa* community; 4 – *Knorringietum sibiricae*; 5 – *Puccinellietum pamiricae*; 6 – *Limonium komarovii* community; 7 – *Carici physodis-Zygophylletum gontscharovii*; 8 – *Zygophylletum ferganensis*; 9 – *Tamarix florida* community; 10 – *Atriplex ornata-Heliotropium ellipticum* community; 11 – *Sphenopodo-Climacopterum glaberrimae*; 12 – *Cephalorhizum popovii* community; 15 – *Aeluropus littoralis-Salsola leptoclada* community; 14 – *Cynodon dactylon-Tamarix ramosissima* community. Die Werte der Phi -Koeffizienten (hochgestellt) in der Tabelle wurden mit 100 multipliziert und nur angezeigt, wenn sie positiv sind. Hauptwerte sind Stetigkeiten (in Prozent). Buchstaben nach einigen Artennamen weisen auf das Vorkommen in der Strauch- (b) und Mooschicht (d) hin.

Group No.	1	2	3	4	5	6	7	8	9	10	11	12	15	14
No. of relevés	8	3	10	13	40	5	7	16	15	6	20	4	52	16
Comm. Paracolpodium leucolepis														
<i>Paracolpodium leucolepis</i>	100 ⁷⁹
<i>Ranunculus pseudohirculus</i>	75 ⁴⁷
<i>Taraxacum jaschikkuliense</i>	50 ⁴²
<i>Trollius komarovii</i>	50 ³⁷
<i>Valeriana minuta</i>	38 ³²
<i>Cerastium pusillum</i>	50 ²⁷
Comm. Hordeum turkestanicum														
<i>Hordeum turkestanicum</i>	...	100 ⁸⁹	18
<i>Geranium collinum</i>	...	67 ⁷¹
<i>Ligularia alpigena</i>	...	67 ⁵⁷
<i>Oxytropis hirsutiusscula</i>	...	100 ⁵⁷	...	2
<i>Agrostis alba</i>	...	100 ³⁶	10
Comm. Halerpestes sarmentosa														
<i>Halerpestes sarmentosa</i>	50 ⁴	...	90 ⁷²	...	2
<i>Hygroamblystegium varium d</i>	50 ⁴⁴
<i>Puccinellia hackeliana</i>	31 ³⁹
<i>Potentilla anserina</i>	40 ³³
<i>Juncus turkestanicus</i>	30 ³¹
<i>Juncus heptopotamicus</i>	...	67 ¹⁴	40 ³⁰
<i>Philonotis fontana d</i>	40 ²⁹
<i>Poa supina</i>	30 ²⁶
<i>Veronica anagalloides</i>	20 ²¹
<i>Lotus krylovii</i>	40 ²¹	25 ¹¹
<i>Blasmus compressus</i>	30 ²⁰	...	15 ⁹
Ass. Knorringietum sibiricae														
<i>Knorringia pamirica</i>	69 ⁵⁰	30 ¹⁰
<i>Puccinellia humilis</i>	31 ³⁹
<i>Dilophia salsa</i>	38 ¹¹	38 ³²	5
<i>Atriplex pamirica</i>	23 ³²	5
<i>Ajania tibetica</i>	15 ²³
<i>Oxytropis boguschii</i>	15 ²¹	5
Ass. Puccinellietum pamiricae														
<i>Puccinellia pamirica</i>	38	100 ⁶⁶
<i>Oxytropis lehmannii</i>	22 ²⁹
<i>Saussurea faminzintana</i>	20 ²⁷
<i>Chenopodium iljinii</i>	22 ²⁶
All. Taraxacion murgabici														
<i>Taraxacum murgabicum</i>	62 ³¹	45 ¹⁸
<i>Glaux maritima</i>	50 ³⁶	...	38 ²⁰
<i>Carex pseudofoetida</i>	12	...	30 ²⁵	31 ²⁴	25 ⁶
O. Artemisietalia pauciflorae														
<i>Suaeda olufsenii</i>	8	8 ¹⁴
<i>Chenopodium pamiricum</i>	2
<i>Lepidium cordatum</i>	2
<i>Taraxacum atrans</i>	2
Comm. Limonium komarovii														
<i>Limonium komarovii</i>	100 ⁸⁰
<i>Salsola paulsenii</i>	100 ⁵⁹
<i>Salsola gemmascens</i>	100 ⁵⁸
<i>Artemisia tenuisecta</i>	100 ⁵⁴
<i>Artemisia rutifolia</i>	80 ³⁸
<i>Ephedra heterosperma</i>	80 ³⁶
<i>Camphorosma lessingii</i>	60 ³²
Ass. Carici physodis-Zygophylletum gontscharovii														
<i>Zygophyllum gontscharovii b</i>	86 ⁶¹	6	2
<i>Echinops knorringianus</i>	71 ⁴⁵
<i>Cymatocarpus popovii</i>	71 ⁴¹
<i>Carex physodes</i>	71 ⁴⁰
<i>Sisymbrium subspinescens</i>	57 ³⁸
<i>Tanacetopsis santoana</i>	86 ³⁸
<i>Erodium oxyrhynchum</i>	71 ³⁵	12
<i>Amberboa turanica</i>	57 ³⁰
<i>Salsola montana</i>	57 ³⁰
<i>Strigosella scorpioides</i>	57 ³⁰	...	7	...	10
<i>Meniocus lintifolius</i>	43 ²⁹
<i>Lappula mogoltavica</i>	57 ²⁸
<i>Arnebia obovata</i>	43 ²⁷
<i>Artemisia eremophila</i>	43 ²⁷
<i>Ziziphora tenuior</i>	43 ²⁴	17 ¹⁵	2	...
<i>Lachnoloma lehmannii</i>	71 ²⁴	83 ²²
<i>Climacoptera brachiata</i>	29 ²³
<i>Lolium subulatum</i>	29 ²⁰
Ass. Zygophylletum ferganensis														
<i>Zygophyllum ferganense b</i>	14	81 ⁵⁸
<i>Strigosella strigosa</i>	14	81 ³⁵
<i>Girgensohnia oppositiflora</i>	31 ³³
<i>Echinops nanus</i>	50 ²⁹
<i>Astragalus spinescens</i>	38 ²⁷
<i>Ephedra strobilacea</i>	31 ²⁵
<i>Silene glaucescens</i>	44 ²⁵
<i>Anabasis truncata</i>	14	38 ²⁴
<i>Reaumuria turkestanica</i>	31 ²²
<i>Salsola turkestanica</i>	50 ²¹	21 ⁷	17
Comm. Tamarix florida														
<i>Tamarix florida b</i>	80 ⁷⁸	17	15	...
<i>Halostachys belangeriana b</i>	14	73 ⁵³	2	...
<i>Climacoptera turkomanica</i>	20 ³⁵	8	6
<i>Orobanche mongolica</i>	47 ³⁵
<i>Limonium otolepis</i>	27 ³³
<i>Chaenorhinum spicatum</i>	40 ²⁵
<i>Rumex halascyi</i>	13 ²¹
Comm. Atriplex ornata-Heliotropium ellipticum														
<i>Heliotropium ellipticum</i>	14	44 ⁵	20	83 ⁵¹
<i>Gastrocotyle hispida</i>	100 ⁴⁰
<i>Tribulus terrestris</i>	20 ⁴	67 ³⁸
<i>Atriplex ornata</i>	7	83 ³⁵
<i>Salsola pestifera</i>	38 ⁸	20	...	100 ³²	17	...
<i>Alhagi canescens</i>	60 ¹⁷	...	100 ³¹	2	...
<i>Eremopyrum triticeum</i>	13	...	83 ³¹
<i>Chenopodium botrys</i>	33 ⁹	...	83 ³⁰
<i>Chrozophora hierosolymitana</i>	50 ²⁹	10 ²	...
<i>Hyoscyamus pusillus</i>	50 ²⁷
Cl. Haloxylon-Salsotea tomentosae														

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Supplement E1. Distribution maps of all halophytic types within the study area. 1 – *Paracolpodium leucolepis* community; 2 – *Hordeum turkestanicum* community; 3 – *Halerpestes sarmentosa* community; 4 – *Knorringietum sibiricae*; 5 – *Puccinellietum pamiricae*; 6 – *Limonium komarovii* community; 7 – *Carici physodis-Zygophylletum gontscharovii*; 8 – *Zygophylletum ferganensis*; 9 – *Tamarix florida* community; 10 – *Atriplex ornata-Heliotropium ellipticum* community; 11 – *Sphenopodo-Climacopteretum glaberrimae*; 12 – *Cephalorhizum popovii* community; 14 – *Cynodon dactylon-Tamarix ramosissima* community; 15 – *Aeluropus littoralis-Salsola leptoclada* community.

Anhang E1. Verbreitung der Halophytengesellschaften im Untersuchungsgebiet. 1 – *Paracolpodium leucolepis*-Gesellschaft; 2 – *Hordeum turkestanicum*-Gesellschaft; 3 – *Halerpestes sarmentosa*-Gesellschaft; 4 – *Knorringietum sibiricae*; 5 – *Puccinellietum pamiricae*; 6 – *Limonium komarovii*-Gesellschaft; 7 – *Carici physodis-Zygophylletum gontscharovii*; 8 – *Zygophylletum ferganensis*; 9 – *Tamarix florida*-Gesellschaft; 10 – *Atriplex ornata-Heliotropium ellipticum*-Gesellschaft; 11 – *Sphenopodo-Climacopteretum glaberrimae*; 12 – *Cephalorhizum popovii*-Gesellschaft; 14 – *Cynodon dactylon-Tamarix ramosissima*-Gesellschaft; 15 – *Aeluropus littoralis-Salsola leptoclada*-Gesellschaft.



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Supplement E2. Boxplots showing median (line), quartiles, outliers and the range of environmental and vegetation parameters of clusters within different halophytic vegetation classes: *Festuco-Puccinellietea* (1–5), *Haloxylon-Salsoletea tomentosae* (6–10), *Climacopteretea crassae* (11, 12, 15) and *Tamaricetea arceuthoidis* (14).

Anhang E2. Boxplots mit Median (Linie), Quartilen, Ausreißern und den Bereichen von Umwelt- und Vegetationsparametern in den Gruppen zu verschiedenen Vegetationsklassen: *Festuco-Puccinellietea* (1–5), *Haloxylon-Salsoletea tomentosae* (6–10), *Climacopteretea crassae* (11, 12, 15) und *Tamaricetea arceuthoidis* (14). Rote Linien geben Mittelwerte für jede Vegetationsklasse an. Verschiedene Buchstaben geben signifikante Unterschiede zwischen Klassen an. Die Nummern entlang der y-Achse beziehen sich auf die Pflanzengesellschaften.

