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Diversity and spatial structure of cryophytic steppes of the Minusinskaya intermountain basin in Southern Siberia (Russia)

Diversität und kleinräumliche Verbreitung von Kryophyten-Steppen im Minusinskaya-Gebirgsbecken in Südsibirien (Russland)

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Abstract

Cryophytic steppes in the Minusinskaya intermountain basin containing plant species that are predominantly distributed in the alpine zone such as *Androsace dasyphylla*, *Dryas oxyodonta*, *Festuca sphagnicola*, *Kobresia myosuroides*, *K. filifolia*, *Minuartia verna*, *Oxytropis bracteata*, *Sagina saginoides*, *Papaver nudicaule*, *Patrinia sibirica*, *Pedicularis lasiostachys*, *Pulsatilla ambigua*, *Saussurea schanginiana*, which are considered remnants of the Pleistocene vegetation. Based on 89 relevés, we classified cryophytic steppes using the Braun-Blanquet method within two phytosociological classes: Central Asian steppes of the *Cleistogenetea squarrosae* and West Palearctic steppes of the *Festuco-Brometea*. Three associations (*Androsaco dasyphyllae-Caricetum pediformis*, *Pulsatillo patentis-Caricetum pediformis* and *Bupleuro multinervi-Helictotrichetum desertori*) with three subassociations and three variants were described with respect to their phytosociological affinities and ecology. DCA ordination showed floristic differences between syntaxa, while correlations of DCA axes and floristic and environmental variables detected substrate type and temperature regime as presumably main drivers for vegetation differentiation. Another driver for vegetation differentiation seems to be continentality of the climate. Small scale distribution of cryophytic steppes were mapped using satellite images with resolution of 1.8 m. Cryophytic steppes always occupy only small areas in landscapes, on convex parts of undulated micro-relief of mountain slopes and summits characterised by drought in summer and deep soil freezing in winter. These special micro-ecological conditions play an essential role for the existence of alpine flora in the Minusinskaya intermountain basin.

Keywords: *Cleistogenetea*, dry grassland, *Festuco-Brometea*, glacial relicts, plant ecology, syntaxonomy, vegetation mapping

Erweiterte deutsche Zusammenfassung am Ende des Manuskripts

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1. Introduction

Cryophytic steppes occurring at local sites of the Minusinskaya intermountain basin (South Siberia) represent an ecologically outstanding vegetation type. They contain a remarkable combination of relic alpine plants and widespread moderately thermophilous and drought-resistant steppe species. At present there are few data available on this vegetation type. Occurrences of relic alpine species in steppes were first reported and interpreted as glacial relicts by REVERDATTO (1934, 1940) and SOBOLEVSKAYA (1941). KUMINOVA et al. (1976) provided a general characterisation of steppe formations with alpine species, and NAMZALOV (1994) named them "cryophytic steppes". However, the peculiarities of ecology and geographic distribution of cryophytic steppes as well as their position in the syntaxonomic system have been unclear so far. Until now there is only one paper (KOROLYUK & MAKUNINA 1998) that describes one association of cryophytic steppes from the Minusinskaya intermountain basin, although a number of papers on syntaxonomy of South Siberian steppes have been published during the last 15 years (KOROLYUK & MAKUNINA 2001, KOROLYUK 2002, MAKUNINA 2006, ERMAKOV et al. 2009, ERMAKOV 2012, ERMAKOV et al. 2012).

The main aim of the current study is to present new data on diversity, ecology and distribution of cryophytic steppes of the Minusinskaya intermountain basin in South Siberia.

2. Study area

The study area (Fig. 1) is located in the Minusinskaya basin (South Siberia, Russia) placed between large mountain systems of the Kuznetskij Alatau in the West, Western Sayan in the South and Eastern Sayan in the East (53° 03′ – 55° 19′ N; 90° 13′ – 92° 27′ E). The area represents flat or gently undulating landforms on Quaternary deposits at altitudes of 400–900 m. The dominant geological substrate of the area is metamorphic Devonian bedrock most often represented by limestones and base-rich chloride slates. The Minusinskaya intermountain basin is located in the rain shadow of the Kuznetskij Alatau mountain ridge. The climate of the area is ultracontinental with cold winters and hot summers (GAVLINA 1954, PROKOFIEV 2005). The average temperature in January varies from -19 °C to -25 °C between years. The mean July temperature is about 20 °C. The mean annual precipitation is only 250–360 mm, of which 80% falls during summer (GIDROMETEOIZDAT 1966–1970). In winter the snow cover is unevenly distributed, reaching a maximal depth of 10–20 cm. Due to wind, snow can be removed from open areas and hilltops leading to exposed soil surface and thus contributing to its deep freezing. During summer the wind causes rapid evaporation of moisture from the unsheltered surfaces leading to extreme desiccation. The altitudinal zonation of the vegetation is represented by a steppe belt in the lower central part of the intermountain basin and a forest-steppe belt related to the elevated foothills of surrounding mountain ridges. Zonal steppes dominated by *Stipa krylovii*, *Artemisia frigida* and *Caragana pygmaea* on well-developed black loamy soils occupy wide flat areas between low mountain ridges and hillocks, while mountain slopes with active erosion processes are covered by various types of petrophytic steppes. In the forest-steppe landscapes, steppe regularly occurs on south-facing slopes, and forest occurs on north-facing slopes. Mountain steppes in the forest-steppe zone are often dominated by *Stipa capillata*, *Carex pediformis* and *Spiraea media*. Some of the mountain steppes occurring on mesic soils form dense and species-rich tall-grass stands called meadow steppes.

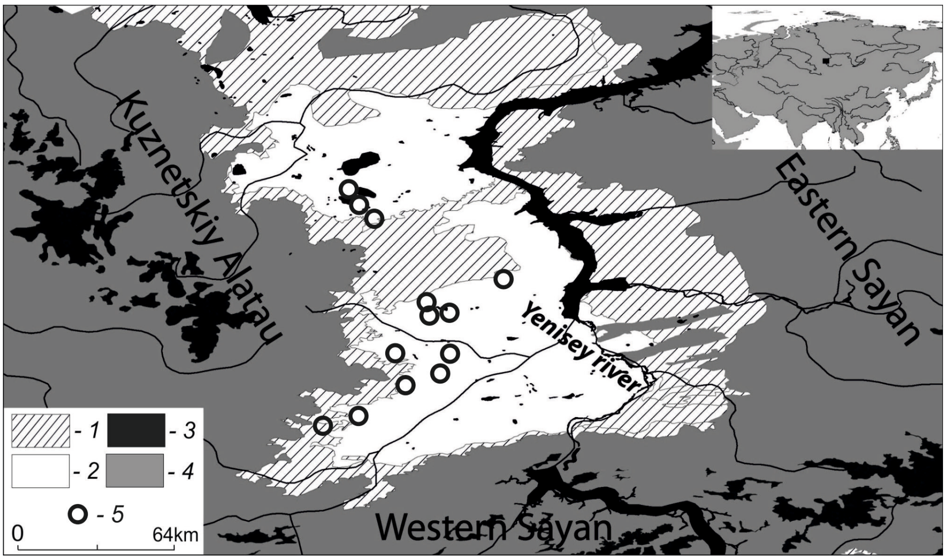

Fig. 1. Geographical position of the Minusinskaya intermountain basin (small figure) and distribution of altitudinal vegetation belts in this region (1 – forest-steppe, 2 – steppe, 3 – alpine, 4 – forest). Relevé locations (5) are indicated by circles.

Abb. 1. Geographische Lage des Minusinskaya-Beckens (kleine Abbildung) und Verbreitung der Vegetations-Höhenstufen in dieser Region: 1 – Waldsteppe, 2 – Steppe, 3 – alpine Vegetation, 4 – Wald). Die Kreise (5) zeigen die Aufnahmeorte.

3. Material and methods

For our analysis we used a subset of 89 relevés of cryophytic steppes from our large data set of steppe vegetation from the Minusinskaya intermountain basin assembled 2005–2012. Cryophytic steppes were defined as steppes containing at least one alpine species with a cover ≥ 1%. Plot size was 100 m^2. The distribution of sampling locations in the study area is shown in Figure 1. In each plot we measured the set of environmental variables: Altitude was measured with a GPS. Climatic variables (mean temperature of the warmest (July) and coldest month (January) and mean annual amplitude of temperatures (July–January) were estimated from a climatic model prepared with ArcGIS 10.0 (http://www.esri.com). This model was based on a combination of Russian climate station data and altitudes from a digitised 1 : 200,000 topographic map. Temperature values for different altitudes were computed based on the adiabatic lapse rate of 6.5 K/km. Mean precipitation of the vegetation period (April to October) and of winter (November to March) was computed from precipitation-altitude charts compiled for each of the aridity-humidity sectors of the Altai-Sayan region (POLIKARPOV et al. 1986). Slope inclination was measured with a clinometer and slope aspect with a compass. Cover of stones was estimated in the field as the percent proportion of superficially visible stones and rocks. The number of glacial relic species was counted for each plot.

The classification of plant communities was carried out using the Braun-Blanquet approach (WESTHOFF & VAN DER MAAREL 1973). The records were organised in TURBOVEG (HENNEKENS & SCHAMINÉE 2001). For characterisation of the syntaxa, the Braun-Blanquet cover-abundance scale (r, +, 1, 2, 3, 4, 5) was used. All relevés were standardised before quantitative analysis: Occurrences of species in shrub and herb layer were combined, and old Braun-Blanquet cover scale values were changed to the allowed values: r and + – for 1; 1 – for 2; 2 – for 3; 3 – for 4 and 4 for 5. Classification was performed by cluster analysis using Ward's method and Euclidean distances in SPSS 14 (SPSS Inc., Chicago, USA). To achieve floristically and ecologically homogeneous units, the cluster analysis results were manually modified by subsequent shifting of 5 relevés from one cluster to another. Syntaxonomic affiliation of each defined low-rank group of relevés was conducted using the steppe syntaxa diagnoses from the existing phytosociological literature (HILBIG 1990, 1996, 2000, KOROLYUK 2002, MAKUNINA 2006, ERMAKOV et al. 2009, ERMAKOV et al. 2012).

Detrended correspondence analysis (DCA) ordination was applied in order to check the position of the classified vegetation types along main floristic gradients. 89 relevés with log-transformed percent cover values were analysed by DCA in CANOCO 4.5 with down-weighting of rare species (TER BRAAK & ŠMILAUER 2002). For interpreting the ordination pattern, we correlated ordination axes with floristic and environmental variables in SPSS 14. Significant Pearson correlation coefficients ($P < 0.05$) were then projected onto the ordination plot and displayed by vectors.

In our field studies, we used World View – 2 multispectral satellite images (with 2.0 m resolution) acquired from SOVZOND Company (Moscow, Russia) as an aid to locate the cryophytic steppes within the steppe belt vegetation. Vegetation types and their combinations were identified in the corresponding satellite images by visual analysis of natural contours of plant communities and landscape features using a GPS to locate the position of control points. The analysis of the multispectral satellite images was carried out with computationally efficient segmentation algorithms described in PESTUNOV et al. (2011), PESTUNOV & RYLOV (2012).

Nomenclature of syntaxa follows the International Code of Phytosociological nomenclature (WEBER et al. 2000). Vascular plant nomenclature follows that of the former USSR (CHEREPANOV 1995), bryophyte nomenclature IGNATOV & AFONINA (1992) and lichen nomenclature ANDREEV et al. (1996).

4. Results

4.1 Classification

The cryophytic steppes of the Minusinskaya intermountain basin do not belong to just one syntaxonomic unit. They occupy a wide spectrum of habitats and show essential differences in ecology and floristic composition.

Cluster analysis resulted in six low-rank groups of relevés assigned to subassociations and variants, each of which shows a distinctive floristic composition and clear ecological characteristics (Fig. 2). The six communities were assigned three associations within three alliances and two orders within the Central Asian steppes of the *Cleistogenetea squarrosae* and the West Palearctic steppes of the *Festuco-Brometea* (Table 1 in the supplement).

The proposed syntaxonomical scheme of cryophytic steppes is summarised as follows:

Class: *Cleistogenetea squarrosae* Mirkin et al. 1992
- Order: *Festucetalia lenensis* Mirkin in Gogoleva et al. 1987
  - – Suborder: *Festuco valesiacae-Caricenalia pediformis* Ermakov, Larionov et Polyakova 2012
    - Alliance: *Eritrichio pectinati-Selaginellion sanguinolentae* Ermakov, Chytrý et Valachovič 2006
      - Association: *Androsaco dasyphyllae-Caricetum pediformis* Korolyuk et Makunina 1998
        - – Subassociation: *typicum*
        - – Subassociation: *typicum* var. *Pulsatilla turczaninovii*
        - – Subassociation: *helictotrichetosum desertori* Korolyuk et Makunina 1998
        - – Subassociation: *dryadetosum oxyodontae nova prov.*
    - Alliance: *Festuco valesiacae-Caricion pediformis* Ermakov, Larionov et Polyakova 2012

Association: *Pulsatillo patentis-Caricetum pediformis* Makunina, Maltseva et Parshutina 2007 Variant *Kobresia filifolia*

Class: *Festuco-Brometea* Br.-Bl. et Tx. ex Soó 1947

Order: *Stipetalia sibiricae* Arbuzova et Zhitlukhina ex Korolyuk et Makunina 2001

Alliance: *Aconito barbati-Poion transbaicalicae* Korolyuk et Makunina 2001

Association: *Bupleuro multinervi-Helictotrichetum desertori* Makunina in Korolyuk et Makunina 2001 Variant *Festuca sibirica*

Androsaco dasyphyllae-Caricetum pediformis (Table 1 in the supplement, rel. 1–64)

The association includes typical cryo-petrophytic steppes widespread in the Minusinskaya intermountain basin on shallow rubble soils forming on calcareous bedrocks at altitudes of 550–620 m. They occur only on convex parts of micro-relief (summits of low mountain ridges and hillocks). A peculiarity of these sites is strong local variations of leading ecological factors (temperature and humidity) both in summer and winter, which are typical for ultracontinental climate. The typical feature of the association is the predominance of drought-adapted species widespread in Central Asian steppes (*Artemisia frigida*, *Bupleurum bicaule*, *B. scorzonerifolium*, *Caragana pygmaea*, *Cleistogenes squarrosa*, *Ephedra monosperma*, *Goniolimon speciosum*, *Heteropappus altaicus*, *Poa botryoides*, *Polygala tenuifolia*, *Potentilla acaulis*, *P. bifurca*, *P. sericea*, *Stipa krylovii*) as well as of obligate petrophytic plants (*Adenophora rupestris*, *Alyssum obovatum*, *Arctogeron gramineum*, *Elytrigia geniculata*, *Eritrichium jenisseense*, *Orostachys spinosa*, *Silene graminifolia*, *Thymus serpyllum*), which form a layer with a cover of 25–50%, an average height of 8–14 cm, a maximal height of 18–20 cm and a species richness varying between 31 and 47 species per relevé. It includes eight alpine species. Five of them show high constancies (constancy classes III–V), and three species are dominant. The association includes three subassociations and one variant.

A.d.-C.p. typicum (Table 1 in the supplement, rel. 1–25) represents the most cryophytic communities of the association occurring at altitudes of 600–750 m. A cold thermal regime and stony soils are indicated by high constancy values (III–V) of alpine species (*Androsace dasyphylla*, *Festuca sphagnicola*, *Kobresia filifolia*, *Minuartia verna*, *Patrinia sibirica*) and petrophilous species (*Adenophora rupestris*, *Alyssum obovatum*, *Arctogeron gramineum*, *Elytrigia geniculata*, *Orostachys spinosa*, *Silene graminifolia*, *Thymus serpyllum*).

A.d.-C.p. typicum var. *Pulsatilla turczaninovii* (Table 1 in the supplement, rel. 26–59) includes communities occurring in less cold sites with more developed soil at altitudes of 500–650 m. Here the number and constancy values of alpine and petrophilous species decrease, while the role of typical thermophilous steppe species increases.

A.d.-C.p. helictotrichetosum desertori (Table 1 in the supplement, rel. 60–64)

The community occurs at the periphery of the intermountain basin where it occupies more humid upper parts of northern mountain slopes at altitudes of 550–700 m. The herb layer covers 50–60% and is subdivided into two sub-layers. In the first sub-layer (up to 30 cm high), the two alpine species *Festuca sibirica* and *F. sphagnicola* predominate, while in the second sub-layer (up to 8–9 cm high), petrophilous species like *Alyssum obovatum*, *Androsace dasyphylla*, *Arctogeron gramineum*, *Dendranthema zawadskii*, *Hedysarum setigerum* and *Thymus serpyllum* prevail. Most alpine species show high values of constancy and cover there. Moreover, one alpine species, *Papaver nudicaule*, occurred only in this subassociation.

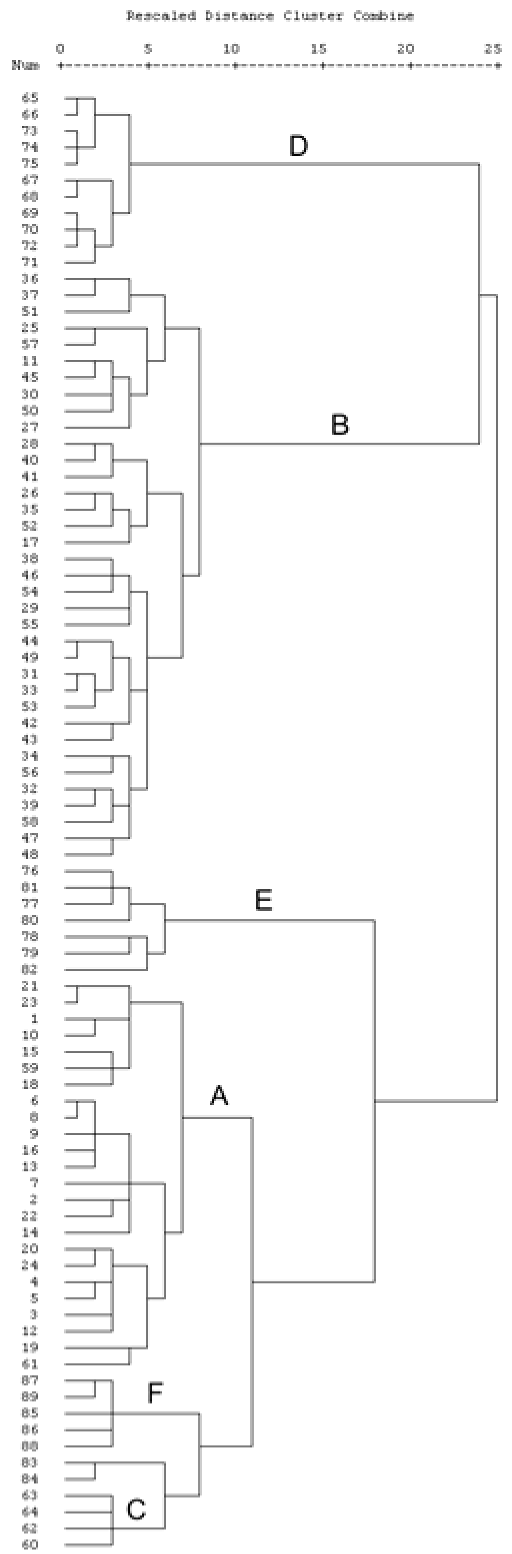

Fig. 2. Results of the cluster analysis of 89 relevés based on Ward's method and Euclidean distance. Relevé numbers in the dendrogram correspond to the relevé numbers in Table 1 in the supplement.

Abb. 2. Ergebnisse einer Clusteranalyse von 89 Aufnahmen auf Grundlage der Ward-Methode und euklidischer Distanzen. Die Aufnahmenummern entsprechen Tabelle 1 als Beilage.

A.d.-C.p. dryadetosum oxyodontae (Table 1 in the supplement, rel. 65–75)

This cryophytic steppe occurs locally in the steppe belt of the Abakanskij and Kuznetskij Alatau mountain ridges. It was found at summits of low mountains with exposed calcareous bedrocks at altitudes of 900–1100 m. The herb layer cover is 45–60%, average height 10 cm, maximal height up to 30 cm and species richness 20–37 species per plot. The characteristic feature of this subassociation is the fact that the largest number of alpine species was found here in comparison with all steppe associations of the Minusinskaya intermountain basin. Alpine species (*Dryas oxyodonta*, *Kobresia myosuroides*, *Pulsatilla ambigua*, *Saussurea schanginiana*) are dominant or subdominant in the herb layer on a par with typical steppe xerophilous species (*Carex humilis*, *Festuca valesiaca*) and obligate petrophytes (*Adenophora rupestris*, *Thymus serpyllum*). At the same time, one can observe an essential decrease in the number of drought-adapted characteristic steppe species of the classes *Cleistogenetea squarrosae* and *Festuco-Brometea*. These peculiarities bring together the subassociation *Androsaco-Caricetum pediformis dryadetosum oxyodontae* and high mountain dry grasslands of the *Carici rupestris-Kobresietea bellardii*.

Pulsatillo patentis-Caricetum pediformis **variant *Kobresia filifolia*** (Table 1 in the supplement, rel. 76–82)

This association represents a moderately xerophilous type of zonal Central Asian steppes (Central Tuvinian and Minusinskaya intermountain basins) occurring on well-developed tschernozem soils. It is widespread in the steppe belt where it occupies gentle northern mountain slopes at altitudes of 500–550 m. This is the only type of cryophytic steppes not related to petrophytic sites. It occupies slightly elevated (5–20 cm) sites in undulations of gentle mountain slopes with well-developed soils. The occurrence of a high number of alpine plants in these habitats is conditioned by regional ultracontinental climate peculiarities, namely low winter temperatures and extremely low winter precipitation resulting in the absence of a snow layer on the convex elements of the micro-relief and the increase in local cryogenic processes. The variant *Kobresia filifolia* is characterised by a well-developed herb layer with a 70% cover and an average species richness of 30–48 species per plot. The steppe grasses *Helictotrichon altaicum* and *Stipa capillata* predominate in the first sub-layer (35–40 cm high). The second (main) sub-layer (10–20 cm in height) is dominated by *Carex pediformis*, *C. humilis*, *Festuca pseudovina*, *Hedysarum gmelinii* and *Iris ruthenica*. The community contains few alpine species; however, *Kobresia filifolia* and *Festuca sibirica* are dominant or subdominant.

Bupleuro multinervi-Helictotrichetum desertori **variant *Festuca sibirica*** (Table 1 in the supplement, rel. 83–89)

This is the only association containing alpine species that is included into the West Palearctic class *Festuco-Brometea*. Unlike the Central Asian cryophytic steppes that have developed under the ultracontinental climate of the central part of the Munusinskaya intermountain basin, this association occurs in the forest-steppe belt of the Krasnoyarskaya forest-steppe and the Kuznetskij Alatau mountain ridge with distinct features of cyclonic climate. The community occupies convex parts of northern slopes with exposed outcrops in the upper parts of small mountains at altitudes of 650–800 m. Ecological peculiarities of these extrazonal sites similar to habitats of all other cryophytic steppes are large seasonal changes of temperature and precipitation as well as the absence of a snow cover during winter. The herb layer cover is 30–40%, average height 18–25 cm, maximal height 35–40 cm and species richness 35–50 species per plot. The characteristic feature of the floristic composition is the predominance of moderately xerophylous meadow-steppe species of the European-Siberian class *Festuco-Brometea* (*Artemisia sericea*, *Campanula sibirica*, *Galium boreale*, *Polygala comosa*, *Scabiosa ochroleuca*, *Stipa pennata*) indicating the reduced continentality and moderate deficit of soil humidity. An important ecological peculiarity of the community are the high constancy values of obligate petrophytes (*Adenophora rupestris*, *Elytrigia geniculata*, *Eritrichium jenisseense*, *Silene graminifolia*, *Thymus serpyllum*). Four alpine species (*Festuca sibirica*, *Kobresia filifolia*, *Minuartia verna*, *Patrinia sibirica*) were found in the community. All of them show high values of constancy. Two species (*Kobresia filifolia* and *Festuca sibirica*) are subdominant in the herb layer.

4.2 Detrended Correspondence Analysis

The low-rank units of cryophytic steppes (subassociations and variants) were clearly separated along the two main axes of a DCA ordination (Fig. 3). Correlations of the main axes with environmental and floristic variables are given in Table 2. The main complex environmental gradient associated with DCA axis 1 is that of increasing cover of stones and decreasing mean temperature of the warmest month (July). The number of alpine species in plant communities also strongly correlates to axis 1. All three variables correlate to altitude. The thermal factor appears on axis 1, due to the fact that the extreme right position is occupied by cryophyte steppes of the *Androsaco-Caricetum pediformis dryadetosum oxyodontae* (with the highest number of alpine species) occupying the highest altitudes (900–1100 m), and the extreme left position is occupied by cryophyte steppes of the *Pulsatillo patentis-Caricetum pediformis* var. *Kobresia filifolia* (with the lowest number of alpine species) common at lower altitudes (500–550 m). However, the clarity of the syntaxa sequence on axis 1 matching this factor is violated by the position of the *Bupleuro multinervi-Helictotrichetum desertori* var. *Festuca sibirica*, which is geographically distributed in a relatively warm forest-steppe but contains an increased number of alpine species. Obviously certain habitat micro-conditions (absence of a snow layer during the cold season) have a stronger environmental compensatory effect on the vegetation than the baseline climate conditions. A high correlation of rock cover values with axis 1 is explained by a successive substitution of communities related to different types of substrates along this axis: non-petrophytic steppes – values 0–1 (*Pulsatillo patentis-Caricetum pediformis* var. *Kobresia filifolia*), moderately petrophytic steppes – values 1–2.8 (*Androsaco dasyphyllae-Caricetum pediformis typicum*, *A.d.-C.p. helictotrichetosum desertori* and *Bupleuro multinervi-Helictotrichetum desertori* var. *Festuca sibirica*) and steppes that are common at rock outcrops – values 2.8–4 (*Androsaco-Caricetum pediformis dryadetosum oxyodontae*). The high correlation of stone cover and altitude is explained by more intensive denudation processes in the upper parts of mountain ridges. At the same time, a low correlation of slope inclination with altitude is explained by the occurrence of cryophytic steppes in eroded landforms of different steepness (flat summits, plateaus and slopes of various inclinations). Axis 1 also shows high positive correlations with mean precipitation of the cold period (November–March) and mean precipitation of the warm period (April–October). Generally this indicates the predominance of mesophilous steppe types at higher altitudes. However, the parameters of mean precipitation of the cold period (November–March) do not correspond to increasing snow layer thickness in cryophytic steppe habitats because of the disappearance of snow on elevated parts of the micro-relief after strong winds and snow sublimation.

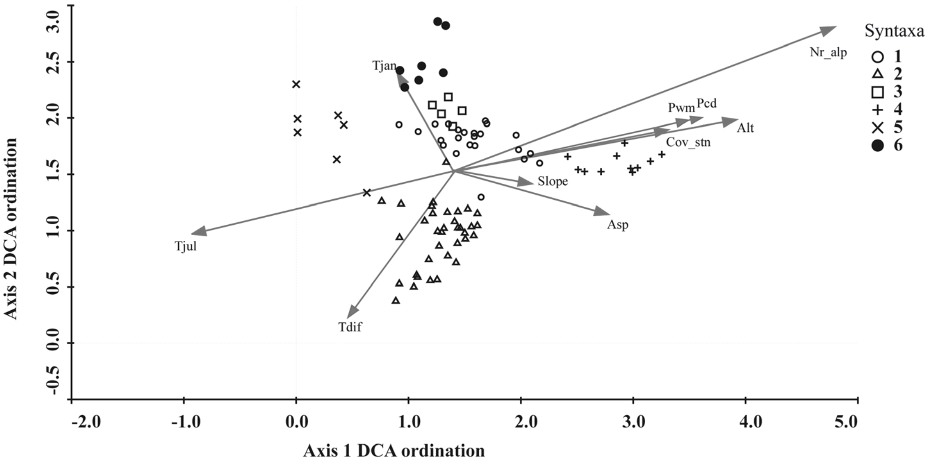

Fig. 3. DCA ordination diagram with axis 1 and 2 of relevés of cryophytic steppes in the Minusinskaya basin and passive projection of environmental and floristic variables. Values of individual variables increase in the directions of the arrows. Syntaxa: 1 – *Bupleuro multinervi-Helictotrichetum desertori* var. *Festuca sibirica*, 2 – *Pulsatillo patentis-Caricetum pediformis* var. *Kobresia filifolia*, 3 – *Androsaco dasyphyllae-Caricetum pediformis helictotrichetosum desertori*, 4 – *A.d.-C.p. dryadetosum oxyodontae*, 5 – *A.d.-C.p. typicum*, 6 – *A.d.-C.p. typicum* var. *Pulsatilla turczaninovii*. Ecological and floristic variables: Asp – Aspect, Slope – Slope inclination, Alt – Altitude, Tjul – Mean temperature of the warmest month (July), Tjan – Mean temperature of the coldest month (January), Tdif – Mean annual amplitude of temperatures (July–January), Pwm – Mean precipitation of the warm period (April–October), Pcd – Mean precipitation of the cold period (November–March), Cov_stn – Cover of stones, Nr_alp – Number of alpine species.

Abb. 3. DCA-Ordinationsdiagram der kryophytischen Steppenvegetation im Minusinskaya-Becken mit eingeblendeten Umwelt- und floristischen Variablen. Zur Bedeutung der Symbole der Syntaxa 1–5 siehe die englische Abbildungsunterschrift. Asp – Hanglage, Slope – Hangneigung, Alt – Meereshöhe, Tjul – Mitteltemperatur wärmster Monat (Juli), Tjan – Mitteltemperatur kältester Monat (Januar), Tdif – Amplitude der Monatsmitteltemperatur von Juli bis Januar, Pwm – Mittlere Niederschlagssumme der Vegetationsperiode (April–Oktober), Pcd – Mittlere Niederschlagssumme des Winters (November–März), Cov_stn – Anteil Skelett an der Oberfläche, Nr_alp – Anzahl alpine Pflanzenarten.

The main complex environmental gradient associated with DCA axis 2 is that of increasing Mean temperature of the coldest month (January) and decreasing mean annual amplitude of temperatures (July–January). Both factors negatively correlate to each other and determine the manifestation of an integral climatic factor – continentality – clearly observed in the transition from the periphery to the center of the intermountain basin. In accordance with this factor, the extreme high position on the axis 2 is occupied by the *Bupleuro multinervi-Helictotrichetum desertori* var. *Festuca sibirica* (class *Festuco-Brometea*), which is widely distributed in the Minusinskaya basin periphery with its moderate continental climate. Further along axis 2, one can observe replacements in the units of the class *Cleistogenetea squarrosae*, corresponding to an increase in continentality: from the *Androsaco dasyphyllae-Caricetum pediformis helictotrichetosum desertori* common in the continental climate sector to the *Androsaco dasyphyllae-Caricetum pediformis typicum* var. *Pulsatilla turczaninovii* formed in ultracontinental conditions. The number of alpine species in plant communities demonstrates a considerably weaker correlation with axis 2 than with axis 1.

Table 2. Correlations between DCA ordination axis and environmental variables. Significant correlations are shown in bold.

Tabelle 2. Korrelationen der DCA-Achsen mit Umweltvariablen. Signifikante Korrelationen sind fett dargestellt.

	Axis 1		Axis 2		Axis 3	
Eigenvalue	0.363		0.238		0.101	
	r	*p*	*r*	*p*	*r*	*p*
Aspect	**0.34**	**0.001**	-0.04	0.722	**-0.28**	**0.007**
Slope	0.17	0.105	0.08	0.443	-0.10	0.371
Altitude	**0.65**	**<0.001**	0.17	0.109	-0.11	0.301
Temp. warmest month	**-0.66**	**<0.001**	-0.18	0.097	0.10	0.349
Temp. coldest month	**-0.24**	**0.024**	**0.32**	**0.002**	-0.06	0.575
Temp. amplitude July–January	**-0.40**	**<0.001**	**-0.36**	**0.001**	0.12	0.251
Precipitation warm period	**0.62**	**<0.001**	0.18	0.089	-0.11	0.315
Precipitation cold period	**0.65**	**<0.001**	0.19	0.082	-0.11	0.301
Cover of stones	**0.47**	**<0.001**	0.11	0.323	-0.12	0.248
Number of alpine species	**0.85**	**<0.001**	**0.34**	**0.001**	0.05	0.638

4.3 Vegetation steppe mapping

The analysis results on the position of cryophytic steppes within the steppe belt vegetation of the Minisinskaya intermountain basin provide important information about peculiarities of their ecology and geography. In the study region, cryophytic steppes do not represent a rare vegetation type; however, they occupy only small areas of the landscape, on convex parts of undulated micro-relief of mountain slopes and summits characterised by special temperature and moisture regimes. Low winter temperatures and very shallow or even absence of snow cover in these sites result in deep soil freezing and a long period of seasonally frozen soils melting in spring. The small sizes of cryophytic steppe communities make them invisible in satellite images of medium resolution (Lansat-7) and sometimes even in direct field observations. That is why cryophytic steppes as a specific vegetation type have never been depicted on small- and middle-scale vegetation maps. The application of high resolution satellite images (2.0 m) allowed the study of the vegetation mosaic (micro-combinations of cryophytic and moderately thermophilous steppes) of the steppe belt at the level of certain phytocoenoses. Large-scale vegetation maps of the key area located in the central part of the Minusinskaya intermountain basin show the position of cryophytic steppes in two typical steppe micro-combinations related to low mountain ridges and hillocks (Fig. 4 and 5). The first micro-combination is related to active erosion processes on steep mountain slopes resulting in the formation of a petrophytic vegetation set oriented from the top to the bottom of the mountain (Fig. 4). Cryophytic steppes of the *Androsaco dasyphyllae-Caricetum pediformis* typicum occupy convex eroded tops and summits of mountains with shallow soil and exposed calcareous bedrock. During the winter season, winds blow off the snow cover and intensify erosion. Long periods of severe frost (about 5 months) favour the formation of a (up to 2.5 m) deep layer of frozen earth with distinct cryogenic processes. The thinness or even absence of snow cover on these sites during the cold season plays a major role in the

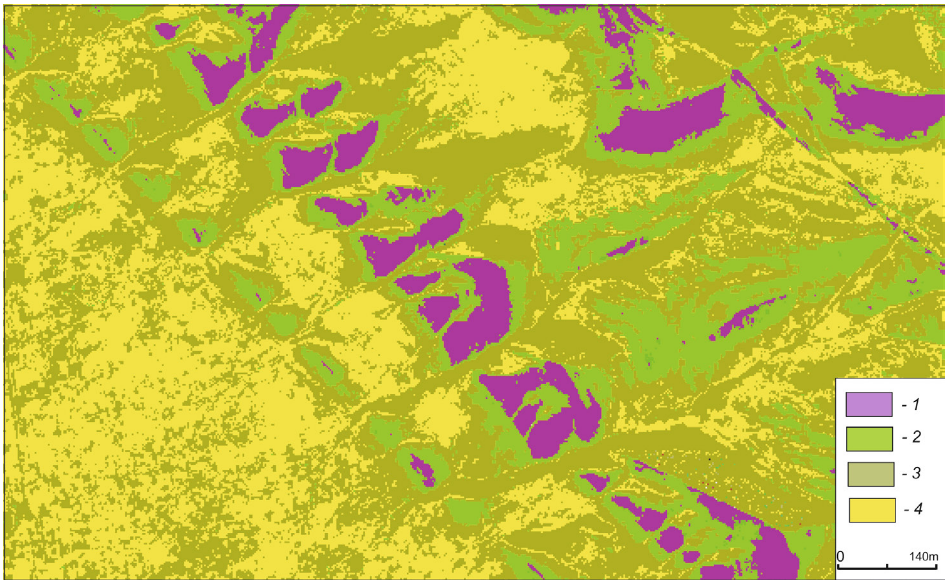

Fig. 4. Large-scale vegetation map demonstrating the position of cryophytic steppes in a vegetation micro-combination related to steep mountain slopes in low mountain ridges of the Minusinskaya inter-mountain basin. 1 – cryophytic steppes of the *Androsaco dasyphyllae-Caricetum pediformis typicum* occupying the convex eroded tops and summits of mountains, 2 – petrophilous steppes of the *Youngio tenuifoliae-Agropyretum cristati* occupying the eroded upper and middle parts of steep mountain slopes, 3 – moderately petrophilous steppes of the *Pulsatillo turczaninovii-Caricetum pediformis* occupying more gentle pediments, 4 – zonal steppes of the *Thalictro foetidi-Festucetum valesiacae* occupying the flat areas between mountains with well-developed soils.

Abb. 4. Vegetationskarte mit Lage der kryophytischen Steppen an Hängen und Graten im Minusinskaya-Gebirgsbecken. 1 – kryophytische Steppen des *Androsaco dasyphyllae-Caricetum pediformis typicum* an konvex geformten Berggipfeln, 2 – petrophile Steppes des *Youngio tenuifoliae-Agropyretum cristati* an den erodierten Ober- und Mittelhängen, 3 – moderat-petrophile Steppen des *Pulsatillo turczaninovii-Caricetum pediformis* an den sanft geneigten Bergfüßen, 4 – zonale Steppen des *Thalictro foetidi-Festucetum valesiacae* auf den ebenen Flächen mit gut entwickelten Böden zwischen den Bergen.

distribution of cryophytic steppes. Thermophilous steppes occupy southern, eastern and western mountain slopes as well as areas between mountains. They form a petrophytic set ranging from communities of eroded upper and middle parts of steep mountain slopes (*Youngio tenuifoliae-Agropyretum cristati* Makunina 2006) towards communities of more gentle pediments (*Pulsatillo turczaninovii-Caricetum pediformis* Makunina et al. 2007) and zonal steppes of flat areas between mountains with well-developed soils (*Thalictro foetidi-Festucetum valesiacae* Makunina 2006) (Fig. 5).

The second peculiar micro-combination of plant communities with the participation of cryophytic steppes occurs in upper parts of gentle (3–5°) terraced northern slopes of hillocks (Fig. 5). The terraced micro-relief of mountain slopes results in an uneven distribution of snow cover between shallow depressions (where it forms a layer of 5–7 cm) and knoll tops (where it is absent) and thus in the formation of a combination of two ecologically different associations occupying special positions in the uneven micro-relief of terraced slopes. Cryo-

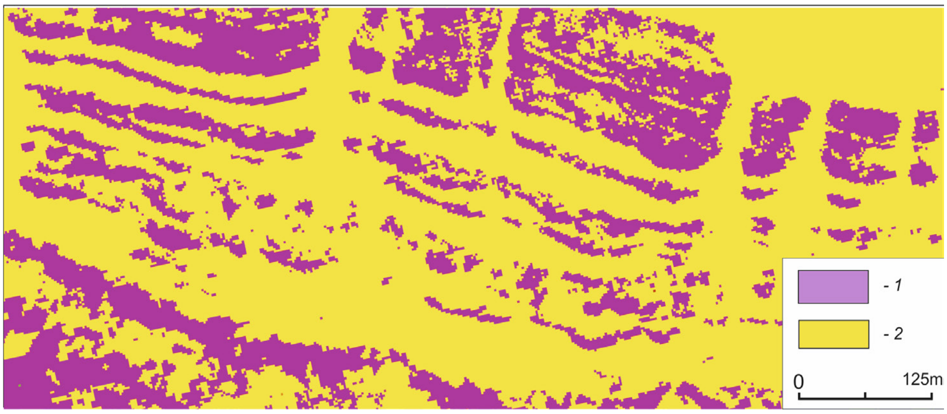

Fig. 5. Large-scale vegetation map demonstrating the position of cryophytic steppes in a vegetation micro-combination related to upper parts of gentle (3–5°) terraced northern slopes of hillocks in the Minusinskaya intermountain basin. 1 – cryophytic steppes of the *Androsaco dasyphyllae-Caricetum pediformis typicum* var. *Pulsatilla turczaninovii* occupying slightly convex knolls (size 2–30 m² and height 7–10 cm), 2 – thermophilous steppes of the *Youngio tenuifoliae-Agropyretum cristati* occupying narrow (40–280 cm) depressions.

Abb. 5. Vegetationskarte mit Lage der kryophytischen Steppen an oberen, sanft geneigten, terrassierten Nordhängen im Minusinskaya-Gebirgsbecken. 1 – kryophytische Steppen des *Androsaco dasyphyllae-Caricetum pediformis typicum* in der Variante von *Pulsatilla turczaninovii* an schwach konvexen, 2–30 m² großen und 7–10 cm hohen Kuppen, 2 – thermophile Steppen des *Youngio tenuifoliae-Agropyretum cristati* in 40–280 cm tiefen Senken.

phytic steppes of the *Androsaco dasyphyllae-Caricetum pediformis* var. *Pulsatilla turczaninovii* occur in slightly convex knolls (size 2–30 m^2 and height 7–10 cm). In satellite images they have strip-like or polygonal shapes where flat summits of knolls are separated by very shallow and narrow (40–280 cm) depressions occupied by moderately thermophilous steppes of the *Youngio tenuifoliae-Agropyretum cristati* Makunina 2006. Communities of the *Androsaco dasyphyllae-Caricetum pediformis* var. *Pulsatilla turczaninovii* and *Youngio tenuifoliae-Agropyretum cristati* are fundamentally different in species composition despite their very close locations and similar positions in relief (the difference in elevation between knoll tops and bottoms of micro-depressions is only a few centimetres). Nevertheless, the presence of even a very shallow snow layer in small depressions plays a crucial role in the formation of moderately thermophilous steppes, while snowless higher elements of the micro-relief are occupied by cryophytic steppes with alpine plants. The morphology of this micro-combination is defined by variations of bedrocks, talus transit and seasonal cryogenic processes. Vegetation slows the rate of the slope erosion. That is why the landforms with these micro-sites are very gentle and relatively stable. New opportunities for identification and monitoring of these unique Red Data Book vegetation types are possible using high resolution satellite images.

5. Discussion

The above-described units of cryophytic steppes are considered as relic communities preserved in the Minusinskaya intermountain basin after the last glacial period in Pleistocene (REVERDATTO 1934, 1940, KUMINOVA et al. 1976). Actually, cryophytic steppes are widespread in mountains of Southern Siberia and Mongolia; there, however, they occur in the high mountain area at altitudes of 2000–2500 m where alpine dry grasslands of the *Carici rupestris-Kobsietea bellardi* are in contact with Central Asian steppes of the *Cleistogenetea squarrosae* (KOROLYUK & NAMZALOV 1994, NAMZALOV 1994). Communities of the Minusinskaya intermountain basin occur within the steppe belt at altitudes of 450–600 m, and they are isolated from the alpine belt of the Altai and Western Sayan. Described associations and variants of cryophytic steppes are diverse in floristic composition and belong to different higher syntaxonomic units; nevertheless, they show some important ecological similarities. The main ecological reason for the existence of cryophytic steppes in lower altitudes is the particular combination of local meso-climate and topography. Semiarid and ultracontinental climate in the Minusinskaya intermountain basin is expected to have been stable since the last glacial period because of the "rain shadow" effect of the Kuznetskij Alatau mountain ridge in the west (GAVLINA 1954). A high seasonal variation with very low winter temperatures and little precipitation results in deep soil freezing and a long period of seasonally frozen soils melting in the beginning of the growth period (PROKOFIEV 2005). Very shallow snow cover or its absence plays an important role among other ecological factors of all cryophytic steppe micro-sites for the preservation of alpine flora. The presence of even a very shallow snow layer (5–7 cm) is favorable for the formation of moderately thermophilous steppes (NAMZALOV 1994). The majority of described units of cryophytic steppes of the Minusinskaya intermountain basin belong to the Central Asian geographical type (class *Cleistogenetea squarrosae*), which has developed under the colder ultracontinental climate of Mongolia and Eastern Siberia. However, one community belongs to the West Palearctic geographical steppes (class *Festuco-Brometea*). This is an important plant-geographical example demonstrating evolutionary relations of Eurasian steppes and alpine vegetation during the Pleistocene.

Erweiterte deutsche Zusammenfassung

Einleitung – Die kleinräumig verbreiteten Kryophyten-Steppen (= Steppen mit Pflanzenarten, die auf Frostböden wachsen) des Minusinskaya-Gebirgsbeckens in Südsibirien (Russland) enthalten eine bemerkenswerte Kombination alpiner Pflanzenarten, zu denen *Androsace dasyphylla*, *Dryas oxyodonta*, *Festuca sphagnicola*, *Kobresia filifolia*, *K. myosuroides*, *Minuartia verna*, *Oxytropis bracteata*, *Papaver nudicaule*, *Patrinia sibirica*, *Pedicularis lasiostachys*, *Pulsatilla ambigua*, *Sagina saginoides* und *Saussurea schanginiana* zählen. Als Eiszeitrelikte haben diese Arten in den im Gebiet großflächig entwickelten moderat-xerothermophilen Steppen mutmaßlich seit dem Pleistozän überdauert (REVERDATTO 1934, 1940, SOBOLEVSKAYA 1941, KUMINOVA et al. 1976). Das Hauptziel dieser Untersuchung ist die Präsentation aktueller Daten zur Diversität, Ökologie und Verbreitung der Kryophyten-Steppen des Minusinskaya-Beckens in Südsibirien.

Untersuchungsgebiet – Das Untersuchungsgebiet ist das südsibirische Minusinskaya-Gebirgsbecken in Russland (53°03'–55°19' N, 90°13'–92°27' E). Dieses bildet eine flache bis leicht hügelige Landschaft in Höhenlagen von 400–900 m (Abb. 1). Mit kalten Wintern und heißen Sommern ist das Großklima des Gebiets als arid-ultrakontinental zu bezeichnen. Die Januarmittel liegen zwischen -19 °C und -25 °C und die Julimittel um +20 °C. Der mittlere Jahresniederschlag beträgt 250–360 mm. 80 % der Niederschläge fallen im Sommer.

Material und Methoden – In den Kryophyten-Steppen des Minusinskaya-Gebirgsbeckens wurden insgesamt 89 Vegetationsaufnahmen auf 100 m²-Flächen erstellt. Für jede Fläche wurden die Meereshöhe, Hangneigung, Hanglage, und der oberflächliche Anteil an Steinen gemessen oder geschätzt. Als Klimavariablen wurden die Mitteltemperaturen des wärmsten (Juli) und kältesten Monats (Januar), die mittlere Juli-Januar-Temperaturamplitude, das Niederschlagsmittel des Sommers (April–Oktober) und Winters (November–März) nach einem Klimamodell generiert. Die Klassifikation der Pflanzengesellschaften folgt grundsätzlich dem Ansatz von Braun-Blanquet (WESTHOFF & VAN DER MAAREL 1973). Die syntaxonomische Zuordnung der Bestände erfolgte durch Zuordnung zu Syntaxa nach Sichtung der pflanzensoziologischen Literatur (HILBIG 1990, 1996, 2000, KOROLYUK 2002, ERMAKOV et al. 2009, 2012). Gradienten in der Vegetation wurden mit einer *Detrended correspondence analysis* (DCA) untersucht. Zur Interpretation der DCA-Gradienten wurden diese mit floristischen und Umweltvariablen korreliert. Die kleinräumige Verbreitung der Kryophyten-Steppen innerhalb der vorherrschenden zonalen Steppen wurde mit Hilfe von Satellitenbildern und Geländebegehungen untersucht.

Ergebnisse – Sechs Aufnahmegruppen wurden mit Hilfe einer Clusteranalyse unterschieden (Abb. 2). Die Kryophyten-Steppen wurden zwei pflanzensoziologischen Klassen, den zentralasiatischen Steppen der *Cleistogenetea squarrosae* und den westpaläarktischen Steppen der *Festuco-Brometea*, zugeordnet. Der Hauptteil der Bestände wurde den petrophytischen Verbänden *Eritrichio pectinati-Selaginellion sanguinolentae* (*Cleistogenetea*) und *Aconito barbati-Poion transbaicalicae* (*Festuco-Brometea*) angeschlossen. Nur ein Verband, das *Festuco valesiacae-Caricion pediformis*, repräsentiert zonale *Cleistogenetea*-Steppen. Auf unterer syntaxonomischer Ebene wurden die Kryophyten-Steppen als vier Subassoziationen des *Androsaco dasyphyllae-Caricetum pediformis* und zwei Varianten des *Pulsatillo patentis-Caricetum pediformis* und *Bupleuro multinervi-Helictotrichetum desertori* klassifiziert. Alle untersuchten Syntaxa werden in einer geordneten Aufnahmetabelle präsentiert (Tab. 1 als Beilage).

In der DCA-Ordination wurden die sechs syntaxonomischen Einheiten klar voneinander getrennt (Abb. 5). Der floristische Hauptgradient in der Vegetation war eng positiv korreliert mit der Meereshöhe, Anzahl alpiner Arten und Deckung an Steinen und negativ mit der Mitteltemperatur des wärmsten Monats (Juli) (Tabelle 2). DCA-Achse 1 war außerdem mit dem Niederschlag positiv korreliert. Der Niederschlag im Winter war wohl wegen Verblasens des Schnees auf den Kuppen nicht mit der Dicke der Schneedecke korreliert. Als wichtigster zugrundeliegender Faktor des zweiten DCA-Gradienten wurde die Temperatur des kältesten Monats (Januar) und die Temperaturdifferenz zwischen Juli und Januar festgestellt. An dieser Stelle sei die Bedeutung der Kontinentalität hervorgehoben, die ein graduelles Ablösen der Steppen der *Festuco-Brometea*, die im Gebiet nur an den Rändern des Minusinskaya-Beckens unter moderat-kontinentalem Klima wachsen, durch die Steppen der *Cleistogenetea* im Zentrum des Minusinskaya-Beckens unter einem ultrakontinentalen Klima bewirkt.

Kryophyten-Steppen siedeln kleinflächig an konvexen Hängen sowie an Kuppen und Gipfeln und weisen ein spezielles Temperatur- und Feuchtigkeitsregime auf. Auf Satellitenaufnahmen mit mittlerer Auflösung sind sie praktisch nicht zu erkennen was ihr Fehlen in mittel-skalierten Vegetationskarten erklärt. Hochauflösende Satellitenaufnahmen zeigen jedoch die kleinräumigen Vegetationsmosaike aus kryophytischen und moderat-thermophilen Steppen deutlich. Vegetationskarten aus dem Kerngebiet des zentralen Minusinskaya-Gebirgsbeckens zeigen zwei typische Fälle der Verteilung der Kryophyten-Steppen an Bergrücken und -graten (Abb. 6 und 7).

Diskussion – Der wichtigste Grund für das Auftreten von Kryophyten-Steppen in tieferen Lagen von 450–600 m im Minusinskaya-Gebirgsbecken dürfte die spezielle Kombination aus Mesoklima und Topographie an ihren Wuchsorten darstellen. Das seit Ende des Pleistozäns im Gebiet herrschende semiarid-ultrakontinentale Klima ist durch hohe jahreszeitliche Klimaschwankungen mit kalten Wintern und geringen Niederschlägen charakterisiert. Dies führt zu tief und lang anhaltend gefroren Böden, die erst zu Beginn der Vegetationsperiode auftauen. Die dünne oder gar fehlende Schneedecke bildet in den Kryophyten-Steppen den wichtigsten ökologischen Faktor für das Vorkommen alpiner Pflanzenarten (NAMZALOV 1994). Die Mehrzahl der hier beschriebenen syntaxonomischen Einheiten der Kryophyten-Steppen des Minusinskaya-Gebirgsbecken gehört zu den zentralasiatisch verbreiteten Klasse der

Cleistogenetea squarrosae, die mutmaßlich unter dem kalten und ultrakontinentalen Klima der Mongolei und Ostsibiriens entstanden ist. Eine unserer Gesellschaften gehört zu den westpaläarktischen Steppen der *Festuco-Brometea*. Unsere Studie ist ein pflanzengeographisches Beispiel für die genetischen Beziehungen zwischen eurasischen Steppen und Alpinvegetation im Pleistozän.

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Supplements and Appendices

Supplement 1. Table 1. Syntaxonomic interpretation of cryophytic steppes containing alpine relic species in South Siberia.

Beilage 1. Tabelle 1. Syntaxonomische Gliederung kryophytischer Steppen mit alpinen Reliktarten in Süd-Sibirien.

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