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Article

The ecological and coenotic features of plant communities containing *Colchicum bulbocodium* subsp. *versicolor* (Colchicaceae) in the Lower Volga region

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Abstract. The article presents a phytocoenotic description of 23 plant communities with *Colchicum bulbocodium* subsp. *versicolor* studied during the period of mass flowering in 2014–2018. It was found that, across the Lower Volga region, the studied communities with *C. bulbocodium* subsp. *versicolor* are mostly confined to the slopes of south- and east-facing arroyos and more seldom to the southern and northern hill slopes, plains, arroyo and liman bases, and floodmeadows. During the period of mass flowering, 207 vascular plants were detected in the studied communities. Every community description included 9 to 36 species. Biological diversity was assessed with the Shannon index and polydominance index; the degree of dominance was measured with the Simpson index. The species similarity of the communities was evaluated through pairwise comparison with the Jaccard coefficient. It was revealed that *C. bulbocodium* subsp. *versicolor* occurs in communities varying in diversity and species composition. The subspecies is not confined to specific phytocoenoses. It usually grows on rich and, more seldom, fairly rich and slightly saline soils. Their alluviality is more often weak rather than moderate. Watering usually corresponds to the dry steppe or semi-desert climate type, rarely to the middle steppe type, being moderately variable and in some cases highly variable. The impact of grazing is usually weak, but it is either moderate or strong in some communities. The communities with *C. bulbocodium* subsp. *versicolor* are dominated by hemicryptophytes: mostly tap-root, short-rhizome and long-rhizome herbaceous perennials. In phytocoenotic terms, most species belong to the zonal type of vegetation, namely steppe vegetation. The participation of meadow species is prominent. The share of weed species is rather high, which indicates a significant anthropogenic load on the studied communities.

Keywords: *Colchicum bulbocodium* subsp. *versicolor*, Lower Volga region, plant communities

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Научная статья
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Эколого-ценотическая характеристика растительных сообществ с участием *Colchicum bulbocodium* subsp. *versicolor* (Colchicaceae) в Нижнем Поволжье

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Аннотация. В период массового цветения *Colchicum bulbocodium* subsp. *versicolor* в 2014–2018 гг. сделаны фитоценотические описания 23 сообществ с его участием. Изученные сообщества с *C. bulbocodium* subsp. *versicolor* в Нижнем Поволжье произрастают чаще всего на склонах балок южной или восточной экспозиции, реже – на южных и северных склонах холмов, равнинных участках, днищах балок и лиманов, заливных пойменных лугах. Во всех сообществах с *C. bulbocodium* subsp. *versicolor* в период его массового цветения отмечено 207 видов сосудистых растений. На одно описание приходилось от 9 до 36 видов. Биологическое разнообразие оценивали с помощью индексов Шеннона и полидоминантности, а доминирование – с помощью индекса Симпсона. Разнообразие сообществ охарактеризовано с помощью индекса полидоминантности. Для выяснения видового сходства сообществ при попарном сравнении использовали коэффициент Жаккара. Выявлено, что *C. bulbocodium* subsp. *versicolor* входит в состав довольно разнообразных сообществ, отличающихся по богатству, разнообразию и видовому составу. Подвид не имеет строгой приуроченности к определенным фитоценозам. Произрастает чаще всего на богатых, реже – довольно богатых или слабосолонцеватых почвах. Аллювиальность их чаще слабая, чем умеренная. Чаще увлажнение соответствует сухостепному либо полупустынному типу, редко – среднестепному, являясь умеренно переменным, в некоторых случаях – сильно переменным. Влияние выпаса – слабое, в отдельных сообществах – умеренное и даже сильное. В сообществах с *C. bulbocodium* subsp. *versicolor* преобладают гемикриптофиты, преимущественно стержнекорневые, короткокорневищные и длиннокорневищные травянистые многолетники. В фитоценотическом отношении большинство видов принадлежит к зональному типу растительности – степному. Заметно участие луговых видов. Весьма велика доля сорных видов, что свидетельствует о большом антропогенном воздействии на сообщества.

Ключевые слова: *Colchicum bulbocodium* subsp. *versicolor*, Нижнее Поволжье, растительные сообщества

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Introduction

Colchicum bulbocodium subsp. *versicolor* (Ker Gawl.) K. Perss. is a subspecies listed under the name of *Bulbocodium versicolor* (Ker-Gawler) Spreng. in the Red Book of Russian Federation [1] and the Red Books of all regions where it occurs [2–8]. It is a relic of the post-glacial period of Mediterranean origin with a border of its range passing the territory under study [9, 10]. *C. bulbocodium* subsp. *versicolor* populations are currently disjunctive; some are declining. Plants usually grow in small groups, where generative specimens prevail [11]. In some localities, populations of *C. bulbocodium* subsp. v*ersicolor* are already completely lost. In the Lower Volga region and the adjacent territories, the decline of the studied subspecies is prominent as well [9, 12]. Considering that insufficient knowledge about ecological and phytocoenotic features of small-size species and subspecies is often an obstacle to their protection and restoration, we propose that the study of ecological and phytocoenotic conditions of the habitat of *C. bulbocodium* subsp. *versicolor* during its flowering is of particular importance.

Material and methods

The research was carried out in the period of mass flowering of *C. bulbocodium* subsp. *versicolor* (the middle of April) in 2014–2018. In some years, additional descriptions were made during the period of fruit maturation (the middle of May). The study involved 23 plant communities with *C. bulbocodium* subsp. *versicolor* located in the Volga Upland, the Oka-Don Lowlands, the Don Ridge, the Kalachyov Ridge and in the south of the Szyrt Plain (Fig. 1, Table 1). The studied territory comprised the eastern part of the subspecies range within the geographical Lower Volga region.

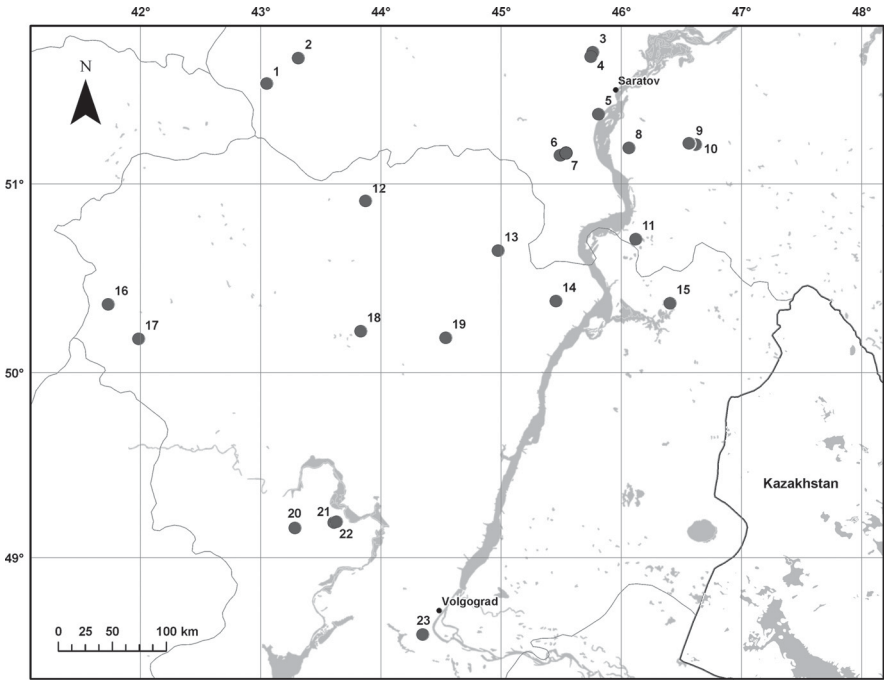

Fig. 1. The localities of the studied plant communities containing *Colchicum bulbocodium* subsp. *versicolor.* Here and elsewhere*: in Saratov Province:* 1 and 2 – Balashovsky District, 3 and 4 – Tatishchevsky District, 5 – Gagarinsky District, 6 and 7 – Krasnoarmeysky District, 8, 9 and 10 – Engelsky District, 11 – Rovensky District; *in Volgograd Province:* 12 – Elansky District, 13 – Zhirnovsky District, 14 – Kamyshinsky District, 15 – Staropoltavsky District, 16 and 17 – Nehayevsky District, 18 – Danilovsky District, 19 – Kotovsky District, 20 – Kletsky District, 21 and 22 – Ilovlinsky DIstrict, 23 – Svetloyarsky District

The plant communities were described based on 100 m^2 sample plots. The floristic composition of the communities was revealed. The abundance of species was evaluated with the Drude scale; the distance between specimens was taken into account. The total projective cover (TPC) and the projective cover (PC) of species in the studied communities were measured as well. The total number of descriptions amounted to 102. The descriptions comprised the data on the geographical location, confinement to a particular landscape element, exposition, and immediate neighbors of a community as well as on the negative factors affecting a community as a whole and a population of *C. bulbocodium* subsp. *versicolor* in particular. The assessment of habitat state and grazing load was performed based on the state of plant cover according to the ecological scales [13, 14] and the supplements to those scales made for specific regions [15] in the EcoScaleWin software [16, 17]. The descriptions also contained the results of ecomorph spectrum analysis. The subdivision of species into ecomorphs was carried out following the scientific resources [18] and the authors' observations.

The plant nomenclature was provided according to the "Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; http://www.plantsoftheworldonline.org/ Retrieved 07 February 2023" [19].

The species diversity of the studied communities was assessed with the diversity indices calculated in several ways [20–24]. The species similarity of the communities was evaluated through pairwise comparison with the Jaccard coefficient (K_j) [20] and displayed as Terentiev's correlation pleiades

[25]. The similarity of a pair of communities was considered significant when K_j was 50% and above, while the similarity line in the pleiad was thick. The similarity of a community pair was seen as moderate when K_j amounted to 30–49% and the line was thin. The similarity was low when K_j was below 30%, while there was no similarity line in the pleiad. For the calculation of the diversity indices, the projective cover (%) was used as an abundance measure. Biological diversity was assessed with the Shannon index [20] and the index of polydominance [26]. The dominance was evaluated with the Simpson index [27]. The calculations were performed in the GRAPHS software module [25, 28]. All described communities were evaluated with the Koch index of biological dispersion (IBD) [29, 30].

Results and discussion

Across the Lower Volga region, the studied communities with *C. bulbocodium* subsp. *versicolor* are mostly confined to the slopes of south- and east-facing arroyos and more seldom to the southern and northern hill slopes, plains, arroyo and liman bases, and floodmeadows. Detailed descriptions of the studied communities are provided in Table 1.

Our analysis of the subspecies habitats based on the plant cover showed that *C. bulbocodium* subsp. *versicolor* mostly grow on rich and, more seldom, fairly rich and slightly saline soils. Their alluviality is more often weak than moderate. Watering comes in the form of precipitation and sometimes floodwater. Watering usually corresponds to the dry steppe or middle steppe climate type and half as much to the meadow-steppe and dry meadow climate type, being moderately variable and in some cases highly variable. According to Ramensky's scales, in most plant communities, the impact of grazing is moderate and sometimes weak. Some communities were subject to steppe fires and mowing during the years of observation.

In 2014–2018, during the period of mass flowering, the communities with *C. bulbocodium* subsp. *versicolor* contained 207 vascular plants. Each description included 9 to 36 species (Table 2). In total, in all years of observation, six communities – communities *Colchicum bulbocodium subsp. versicolor* (no. 3), *Festuca valesiaca + Stipa capillata+ + Artemisia austriaca + C. bulbocodium subsp. versicolor* (no. 4), *Graminosa + C. bulbocodium subsp. versicolor + mh* (no. 5), *F. valesiaca + Poa bulbosa + + C. bulbocodium subsp. versicolor* (no. 6), *P. bulbosa + +F. valesiaca + C. bulbocodium subsp. versicolor* (no. 7), *C. bulbocodium subsp. versicolor + graminosa + +mh* (no. 11) – had 34 to 67 species per community. It was found out that trees and shrubs hardly ever occur in the communities with *C. bulbocodium* subsp. *versicolor.* Community *Graminosa + C. bulbocodium subsp. versicolor + mh* (no. 5) confined to the north-facing hill slope and located in close proximity to thick shrubs and oak forest was the only one which had individual young trees of *Quercus robur* and *Malus* sp. and shrubs of *Acer tataricum, Crataegus ambigua, Lonicera tatarica, Rosa canina,* and *Prunus spinosa.* Communities *F. valesiaca + P. bulbosa + +C. bulbocodium subsp. versicolor* (no. 6), *Poa angustifolia + C. bulbocodium subsp. versicolor* (no. 21) and *Graminosa + A. austriaca + Galatella villosa + mh* (no. 22) had individual specimens of *Spiraea hypericifolia;* community no. 21 also had *Rosa canina.* Dwarf semishrubs were represented by *Astragalus pallescens* in community *C. bulbocodium subsp. versicolor + P. bulbosa + A. austriaca* (no. 3), by *A. ucrainicus* in communities *Graminosa + C. bulbocodium subsp. versicolor + mh* (no. 5), *Graminosa + C. bulbocodium subsp. versicolor* (no. 13), *Stipa lessingiana + F. valesiaca + C. bulbocodium subsp. versicolor* (no. 20) by *A. varius* in community *F. valesiaca + S. capillata + + A. austriaca + C. bulbocodium subsp. versicolor* (no. 4), by *Bassia prostrata* in communities *C. bulbocodium subsp. versicolor + P. bulbosa + A. austriaca* (no. 3), *F. valesiaca + P. bulbosa + C. bulbocodium subsp. versicolor* (no. 6), *P. bulbosa + F. valesiaca + + C. bulbocodium subsp. versicolor* (no. 7), *F. valesiaca + C. bulbocodium subsp. versicolor* (no. 9 and 10), *Graminosa + C. bulbocodium subsp. versicolor* (no. 13 and 14), *S. lessingiana + C. bulbocodium subsp. versicolor* (no. 19), *S. lessingiana + F. valesiaca + + C. bulbocodium subsp. versicolor* (no. 20), *P. bulbosa + C. bulbocodium subsp. versicolor + Gagea pusilla* (no. 23), by *Ephedra distachya* in communities *P. bulbosa + F. valesiaca + C. bulbocodium subsp. versicolor* (no. 7), *Graminosa + C. bulbocodium subsp. versicolor* (no. 13 and 14), *Graminosa + A. austriaca + + G. villosa + mh* (no. 22), by *Krascheninnikovia ceratoides* in community *P. bulbosa + F. valesiaca + + C. bulbocodium subsp. versicolor* (no.7), and by *Thymus calcareus* in communities *S. capillata + + F. valesiaca + A. austriaca + C. bulbocodium subsp. versicolor* (no. 16) and *P. angustifolia + C. bulbocodium subsp. versicolor* (no. 21). The total projective cover of grass and dwarf semishrubs amounted to 45 to 90% in most communities, occasionally declining to 30–45% in some years of observation due to steppe fires, mowing and intensive grazing. In different years, 70–80% of the studied communities were dominated by *C. bulbocodium* subsp. *versicolor;* 50–60% by *Festuca valesiaca;* a slightly smaller portion of the communities were predominated by *Poa bulbosa, Stipa capillata, Elymus repens, Agropyron cristatum,*

Table 1

The geobotanical description of the plant communities containing *Colchicum bulbocodium* ssp. *versicolor* located in the Lower Volga region

№ CP	Coordinates		Phytocoenosis area, ha	Habitat	Exposition / Slope angle, °	Dominant species in the community	TPC, %
	N	E					
1	52°31′31″	43°05′30.9″	0.02	Floodmeadow	–	*Alopecurus pratensis, Festuca valesiaca, Galium verum, Plantago urvillei, Poa angustifolia, Rumex acetosa*	70–100
2	51°39′21.5″	43°18′25.4″	0.05	Floodmeadow	–	*Alopecurus pratensis, Ranunculus ficaria* subsp. *caltifolius, Colchicum bulbocodium* ssp. *versicolor, Fritillaria meleagroides, R. acris,(Poa angustifolia)*	100
3	51°41′11.2″	45°45′58.2″	0.25	Hill slope	S / 20–25°	*Artemisia austriaca, Colchicum bulbocodium* ssp. *versicolor, (P. bulbosa, Festuca valesiaca, Galatella villosa, Potentilla humifusa, Stipa capillata, Draba verna, Gagea pusilla, Artemisia santonica)*	45–75
4	51°40′5.3″	45°44′56.9″	1	Smooth hill slope	S–SE / 5°	*Festuca valesiaca, S. capillata, A. austriaca, C. bulbocodium* ssp. *versicolor, (Poa bulbosa, Valeriana tuberosa, Koeleria pyramidata, D. verna)*	75–90
5	51°21′37.9″	45°47′30.8″	1	Hill slope	N / 20–30°	*C. bulbocodium* ssp. *versicolor, (A. austriaca, Bromus riparius, Elymus repens, Euphorbia virgata, Festuca valesiaca, Fragaria viridis, Salvia nemorosa* ssp. *pseudosylvestris, Verbascum chaixii, Achillea setacea, Jacobaea vulgaris* ssp. *vulgaris, Plantago urvillei, Poa angustifolia, Seseli libanotis, Solidago virgaurea)*	90–100
6	51°09′44.8″	45°29′21.5″	0.021	Base of decrepit dyke	–	*Festuca valesiaca, C. bulbocodium* ssp. *versicolor, (P. bulbosa, Artemisia austriaca, Koeleria pyramidata, Stipa capillata)*	45–90
7	51°09′45.3″	45°29′27.8″	0.035	Arroyo slope	S / 3°	*C. bulbocodium ssp. versicolor, (P. bulbosa, S. capillata, Festuca valesiaca, Galatella villosa, A. austriaca, K. pyramidata)*	45–90
8	51°11′21.5″	46°03′48.7″	0.031	Base of wide arroyo	–	*P. bulbosa, C bulbocodium* ssp. *versicolor, (Agropyron cristatum, Artemisia austriaca, Gagea pusilla, A. marschalliana)*	30–90
9	51°12′33.9″	46°33′58.8″	0.042	Plain with micro-depressions	–	*F. valesiaca, (C. bulbocodium* ssp. *versicolor, P. bulbosa, Elymus repens, Valeriana tuberosa, A. austriaca, A. santonica, K. pyramidata)*	85–90
10	51°12′31.1″	46°37′19.2″	0.15	Plain with micro-elevations	–	*F. valesiaca, C. bulbocodium* ssp. *versicolor, (Agropyron cristatum, Artemisia austriaca, K. pyramidata, Tulipa sylvestris* ssp. *australis, P. bulbosa, Klasea erucifolia, Potentilla humifusa, V. tuberosa)*	90–95
11	50°42′59.7″	46°03′55.9″	10	Liman micro-depressions	–	*C. bulbocodium* ssp. *versicolor, (E. lolioides, Agropyron cristatum, Poa bulbosa, Allium angulosum, G. pusilla, K. cardunculus, Limonium bungei, V. tuberosa, A. santonica)*	60–85
12	50°54′26.1″	43°52′21″	0.25	Floodmeadow	–	*C. bulbocodium* ssp. *versicolor, F. valesiaca, Alopecurus pratensis, G. pusilla, (P. angustifolia, Achillea setacea, Pedicularis dasystachys)*	90–100

Continuation of the Table 1

№ CP	Coordinates		Phytocoenosis area, ha	Habitat	Exposition / Slope angle, °	Dominant species in the community	TPC, %
	N	E					
13	50°39′5.4″	44°57′12.5″	0.73	Arroyo slope	S / 5°	*C. bulbocodium* ssp. *versicolor*, (*Poa bulbosa, Stipa capillata, F. valesiaca, Artemisia austriaca, Galatella villosa)*	50–90
14	50°23′1.2″	45°27′20.5″	0.04	Arroyo slope	S / 5°	*E. repens, C. bulbocodium* ssp. *versicolor, P. bulbosa, (F. valesiaca, Gagea pusilla, A. austriaca, Koeleria pyramidata, Poa angustifolia)*	50–90
15	50°21′27.6″	46°23′32.7″	0.36	Floodmeadow	–	*F. valesiaca, C. bulbocodium* ssp. *versicolor, Eryngium planum, (G. pusilla, Valeriana tuberosa, Artemisia austriaca, A. santonica, Tanacetum achilleifolium)*	65–90
16	50°11′0.5″	41°59′0.2″	0.25	Depression in chalk hill	S / 5°	*Stipa capillata, F. valesiaca, A. austriaca, C. bulbocodium* ssp. *versicolor*	30
17	50°22′2.6″	41°43′47.8″	0.76	Inland plateau	–	*S. capillata, C. bulbocodium* ssp. *versicolor, Centaurea jacea, Poa angustifolia, Potentilla argentea*	75
18	50°13′18.7″	43°48′40.8″	1.47	Floodmeadow	–	*Colchicum bulbocodium* ssp. *versicolor, F. valesiaca, Gagea pusilla, P. angustifolia, Alopecurus pratensis*	95
19	50°11′14.5″	44°32′17.9″	0.02	Arroyo slope	E / 5°	*S. lessingiana, C. bulbocodium* ssp. *versicolor, (P. bulbosa, F. valesiaca, G. pusilla, Galatella villosa)*	75–90
20	49°10′05″	43°16′41.6″	0.72	Arroyo slope	SW / 5–10°	*S. lessingiana, C. bulbocodium* ssp. *versicolor, (F. valesiaca, G. villosa)*	95
21	49°11′35.6″	43°38′15.2″	0.09	Depression in chalk hill	E–NE / 15–20°	*P. angustifolia, C. bulbocodium* ssp. *versicolor*	70
22	49°11′18.6″	43°39′19.3″	0.04	Hill slope	NE / 20°	*Artemisia austriaca, Stipa capillata, C. bulbocodium* ssp. *versicolor, F. valesiaca, Galatella villosa, Gagea pusilla*	70
23	48°34′51.4″	44°20′56.2″	0.5	Arroyo slope	N–NE / 5°	*C. bulbocodium* ssp. *versicolor, Poa bulbosa, G. pusilla, T. achilleifolium*	90

Note. Species which were not dominant annually are in brackets.

Table 2

The biodiversity indices of the plant communities containing *Colchicum bulbocodium* subsp. *versicolor*

№ CP	Year	Number of species, pcs.	Index		
			Simpson's, *D*	Polydominance, 1/*D*	Shannon's, *H*
1	2015	26	*0.13*	**7.69**	**2.21**
2	2016	24	*0.14*	**7.21**	**2.10**
	2017	21	0.18	5.64	1.91
3	2014	17	0.28	3.53	1.50
	2015	23	0.20	4.97	1.73
	2016	9	0.15	**6.47**	1.93
	2017	11	0.20	4.88	1.75
	2018	20	0.15	**6.83**	**2.08**
4	2014	12	0.23	4.38	1.63
	2015	23	0.25	3.94	1.59
	2016	15	*0.13*	**7.96**	**2.17**
	2017	14	0.20	5.04	1.77
	2018	15	0.19	5.34	1.93
5	2014	25	**0.37**	*2.67*	1.23
	2015	15	0.21	4.68	1.73
	2016	36	*0.10*	**9.80**	**2.65**
	2017	6	0.24	4.11	1.48
	2018	14	0.19	5.16	1.73
6	2014	17	**0.49**	*2.02*	*1.11*
	2015	17	0.28	3.53	1.40
	2016	19	**0.35**	*2.84*	1.23
	2017	20	0.18	5.66	1.90
	2018	14	0.25	4.02	1.55
7	2014	18	**0.38**	*2.63*	1.36
	2015	19	**0.33**	3.05	1.38
	2016	25	0.22	4.55	1.71
	2017	27	*0.14*	**7.15**	**2.25**
	2018	23	0.19	5.28	1.96
8	2015	20	0.21	4.74	1.80
	2016	27	0.20	5.12	1.77
	2017	24	0.24	4.12	1.73
	2018	20	0.29	3.43	1.62
9	2014	11	**0.49**	*2.04*	*1.07*
	2015	11	**0.37**	*2.73*	1.36
	2016	30	0.23	4.44	1.83
	2017	20	0.24	4.20	1.75
10	2015	18	**0.33**	3.06	1.27
	2016	28	*0.14*	**6.91**	**2.12**
	2018	21	0.20	4.99	1.89

Continuation of the Table 2

№ CP	Year	Number of species, pcs.	Index		
			Simpson's, *D*	Polydominance, 1/*D*	Shannon's, *H*
11	2014	17	**0.32**	3.16	1.56
	2015	20	0.21	4.75	1.68
	2016	17	0.17	5.83	1.89
	2017	10	0.23	4.35	1.73
	2018	12	0.17	**6.02**	1.89
12	2016	17	0.18	5.56	1.81
	2017	21	0.18	5.43	1.85
13	2015	15	0.30	3.32	1.43
	2016	21	0.15	**6.81**	**2.02**
	2018	23	0.24	4.12	1.80
14	2016	30	*0.14*	**6.95**	**2.06**
	2017	29	0.25	4.05	1.69
	2018	12	0.24	4.11	1.54
15	2016	14	0.18	5.62	1.92
	2017	8	0.22	4.63	1.69
	2018	11	**0.49**	*2.03*	*0.97*
16	2018	24	0.24	4.21	1.78
17	2018	15	0.29	3.47	1.59
18	2018	18	0.22	4.49	1.64
19	2016	11	0.21	4.72	1.63
	2017	22	0.22	4.60	1.70
	2018	17	0.30	3.37	1.33
20	2016	26	0.19	5.35	1.89
	2018	17	**0.34**	*2.94*	1.30
21	2017	36	0.25	4.03	1.75
	2018	31	**0.38**	*2.63*	1.41
22	2016	31	0.17	**6.03**	1.95
23	2018	18	**0.31**	3.27	1.53

Note. Minimum index values are in italic: *D* – below 0.15, 1/*D* – below 3.00, *H* – below 1.3. Maximum index values are in bold: *D* – above 0.30, 1/*D* – above 6.00, *H* – above 2.00. Designations are the same as in Fig. 1 and Table 1.

Galatella villosa, Artemisia austriaca; an even smaller share of the communities by *Koeleria pyramidata, Gagea pusilla;* and individual communities had up to 30 more grain and herb species as dominant and co-dominant species (Table 1).

It was revealed that the following rare protected species occur alongside *C. bulbocodium* subsp. *versicolor: Iris pumila, Adonis wolgensis, Anemone sylvestris, Leuzea altaica, Stipa pennata, Pedicularis dasystachys, Tulipa sylvestris* subsp. *australis, Fritillaria meleagroides*, and *Ephedra distachya.*

The values of the Jaccard coefficient (K_j) fluctuated from 2.44% to 51.52% (Fig. 2). In most cases, the communities had a moderate similarity in the species composition (K_j = 30−49%). Communities *Graminosa + mh* (no. 1), *Alopecurus pratensis + mh* (no. 2) and *Graminosa + C. bulbocodium subsp. versicolor + G. pusilla* (no. 18) had a moderate similarity with one and the same community *C. bulbocodium subsp. versicolor + graminosa + mh* (no. 12). Notably, all the four communities grow in floodmeadows.

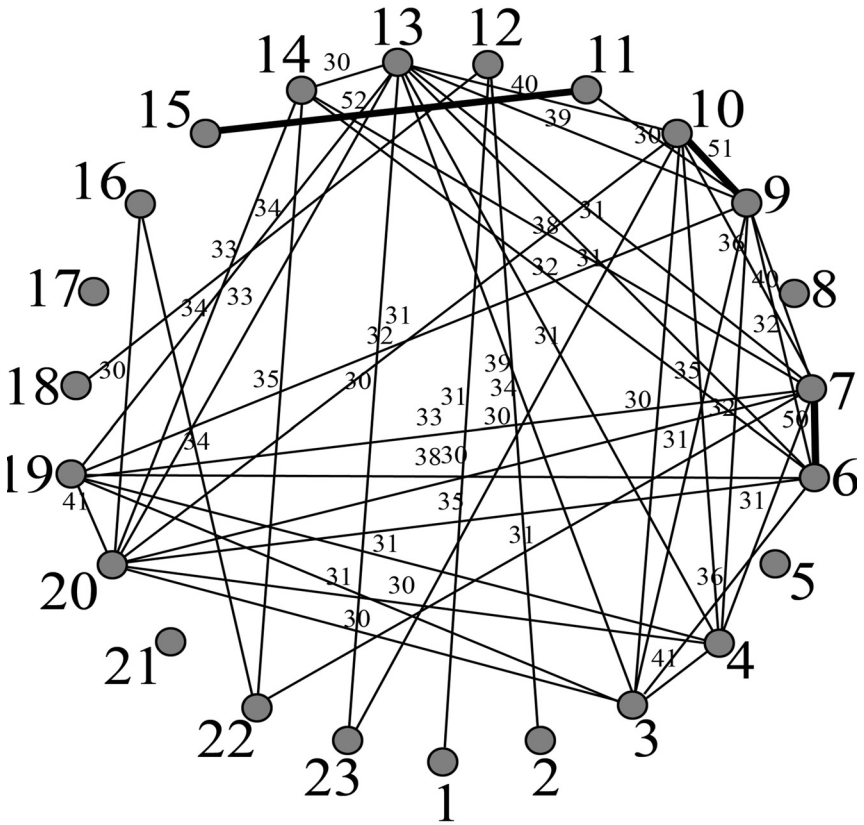

Fig. 2. The similarity of the plant communities containing *Colchicum bulbocodium* subsp. *versicolor* based on the Jaccard coefficient. The lines with a coefficient above 50 % are thick. Designations are the same as in Fig. 1 and Table 1

The following communities had no similarity with any other community – *Graminosa + C. bulbocodium subsp. versicolor + mh* (no. 5), *P. bulbosa + + C. bulbocodium subsp. versicolor + Agropyron cristatum* (no. 8), *S. capillata + C. bulbocodium subsp. versicolor* (no. 17) and *Poa angustifolia + + C. bulbocodium subsp. versicolor* (no. 21). Community no. 5 is located on the north-facing hill slope and comprises 67 species (from 6 to 36 in different years of observation). Community no. 8 grows on arenosols at the arroyo base and contains 45 species (20–27 species annually). Community no. 17 is confined to the inland plateau and has 15 species. Community no. 21 grows on the chalky north-eastern arroyo slope and is comprised of 47 species (31–36 species in different years of observation).

Only three community pairs had a considerable similarity: communities *F. valesiaca + C. bulbocodium subsp. versicolor + Eryngium planum* (no. 15) and *C. bulbocodium subsp. versicolor + graminosa + + mh* (no. 11) growing on saline soils at the liman bases, occasionally submerged by melt water; communities *F. valesiaca + C. bulbocodium subsp. versicolor* (no. 9 and 10) located in the steppe along the bank of the Nahoy river; and communities *F. valesiaca + + P. bulbosa + C. bulbocodium subsp. versicolor* (no. 6) and *P. bulbosa + F. valesiaca + C. bulbocodium subsp. versicolor* (no. 7) confined to the steppe slope of the same arroyo and growing in close proximity to each other.

The analysis of all communities based on the biological dispersal index *IBD* confirmed that the degree of similarity between the communities is low (*IBD* amounts to 12.41%).

According to the values of the Simpson index, all communities have a high level of dominance (Table 2). The dominance is especially articulated, although in individual years of observation, in communities *F. valesiaca + P. bulbosa + C. bulbocodium subsp. versicolor* (no. 6), *F. valesiaca + C. bulbocodium subsp. versicolor* (no. 9) and *F. valesiaca + + C. bulbocodium subsp. versicolor + E. planum* (no. 15); slightly lower degrees of dominance is characteristic of communities *Graminosa + C. bulbocodium subsp. versicolor + mh* (no. 5), *P. bulbosa + F. valesiaca + + C. bulbocodium subsp. versicolor* (no. 7), *C. bulbocodium subsp. versicolor + graminosa + mh* (no. 11), *Graminosa + C. bulbocodium subsp. versicolor*

(no. 13), *S. lessingiana + C. bulbocodium subsp. versicolor* (no. 19), *S. lessingiana + F. valesiaca + + C. bulbocodium subsp. versicolor* (no. 20), *P. angustifolia + C. bulbocodium subsp. versicolor* (no. 21) and *P. bulbosa + C. bulbocodium subsp. versicolor + G. pusilla* (no. 23). The degree of dominance greatly varied in one and the same communities over the years of observation. The fluctuations of this parameter were particularly obvious in most communities in 2014. The highest variance of dominance was detected in communities no. 5, 6, 9 and 15. Communities *Alopecurus pratensis + mh* (no. 2), *Poa bulbosa + C. bulbocodium subsp. versicolor +Agropyron cristatum* (no. 8) and *C. bulbocodium subsp. versicolor + graminosa + mh* (no. 12) were the most stable in terms of the level of dominance which was also rather low; these communities are confined either to the arroyo base and poorly developed soil (community no. 8) or to floodmeadows (no. 2, 12). The lowest level of dominance was identified in communities *Graminosa + mh* (no. 1), *Alopecurus pratensis + mh* (no. 2), *F. valesiaca + S. capillata + A. austriaca + + C. bulbocodium subsp. versicolor* (no. 4), *Graminosa + + C. bulbocodium subsp. versicolor + mh* (no. 5), *P. bulbosa + F. valesiaca + C. bulbocodium subsp. versicolor* (no. 7), *F. valesiaca + C. bulbocodium subsp. versicolor* (no. 10) and *Graminosa + C. bulbocodium subsp. versicolor* (no. 14), especially in 2016 (Table 2).

Thus, the years 2014 and 2016 were remarkable in terms of the level of dominance: the maximum level of dominance was registered in the former year and the minimum level of dominance in the latter year. The communities growing on poorly developed soils or in floodmeadows were the most stable in terms of the level of dominance.

The polydominance index (1/D) ranged from 2.02 (community *F. valesiaca + P. bulbosa + C. bulbocodium subsp. versicolor* - no. 6, in 2014) to 9.80 (community *Graminosa + C. bulbocodium subsp. versicolor + mh* - no. 5, in 2016) (Table 2). According to the values of 1/D, the highest species diversity was observed in communities *Graminosa + mh* (no. 1), *Alopecurus pratensis + mh* (no. 2), *Bulbocodium versicolor +Poa bulbosa +Artemisia austriaca* (no. 3), *F. valesiaca + S. capillata + A. austriaca + + C. bulbocodium subsp. versicolor* (no. 4), *Graminosa + C. bulbocodium subsp. versicolor + mh* (no. 5), *P. bulbosa + F. valesiaca + C. bulbocodium subsp. versicolor* (no. 7), *F. valesiaca + C. bulbocodium subsp. versicolor* (no. 10), *C. bulbocodium subsp. versicolor + graminosa + mh* (no. 11), *Graminosa + C. bulbocodium subsp. versicolor* (no. 13 and 14) and *Graminosa + A. austriaca + G. villosa + mh* (no. 22). In most communities, species diversity was the highest in 2016. It was likely due to the warm spring of 2016 (warmest of all years of observation) which facilitated the quick regrowth of many species in the studied communities. Species diversity was the lowest in communities (no. 5), (no. 6), (no. 7), (no. 9), (no. 11), (no. 13), (no. 15), (no. 17), (no. 19), (no. 20), (no. 21) and (no. 23). In five communities (no. 5, 6, 7, 9, 11) the low values of this parameter were detected in 2014, while in other six communities (no. 15, 17, 19–21 and 23) – in 2018. In some of the latter communities, species diversity was low in 2015 and 2016 as well. In 2018, the delay of regrowth of many species was likely due to the cold spring. In other years of observation, the decline in species diversity was apparently linked to other factors. For instance, in 2014, community no. 5 exhibited a strong grassing by root grains which decreased biodiversity despite the abundance of species in the community. In communities no. 9 and 11, in 2014, flood water did not go down for a long time. In 2013, community no. 7 was subject to intensive grazing which damaged species composition both in 2014 and 2015.

Based on the Shannon index, biodiversity in the communities with *B. versicolor* fluctuated from 0.97 (in community no. 15 in 2018) to 2.65 (in community no. 5 in 2016). Communities no. 1–5, 7, 10, 13 and 14 had the highest biodiversity values, especially in 2016. The lowest biodiversity was detected in communities no. 5, 6, 9 and 15, mostly in 2014 (Table 2).

The above presented results indicate that *C. bulbocodium* subsp. *versicolor* occurs in rather diverse communities which differ in diversity and species composition. Most communities have a merely moderate similarity with others based on the Jaccard index. The similarity of all studied communities is extremely low, which is confirmed by the low value of the biological dispersal index (12.41%). This suggests that the species is not restricted to particular phytocoenoses. Its dispersal is most likely due to accidental drift of seeds or long isolated existence of populations. However, the values of the biodiversity and dominance coefficients greatly vary over the years of observation, and they are clearly affected by the environmental factors, such as temperature in the period of regrowth, watering by melt water, the level of soil development and grassing by root grains, as well as by anthropogenic factors, primarily intensive grazing.

The analysis of flora showed that, based on the biomorphological composition, the communities with *C. bulbocodium* subsp. *versicolor* in the Lower Volga region are dominated by hemicryptophytes,

which is typical for moderately cold floras of the Holarctic realm (Fig. 3, *a*). These hemicryptophytes include polycarpic herbs, mostly tap-root (*Artemisia santonica*, order of astragalus, *Centaurea scabiosa, Cephalaria uralensis, Cichorium intybus, Echinops ritro, Eryngium planum, Jurinea arachnoidea, Klasea erucifolia, Limonium bungei, Medicago falcata, Psephellus marschallianus, Salvia dumetorum, Seseli tortuosum, Trifolium pratense* etc.) and long-rhizome plants (*Anthoxanthum repens, Artemisia dracunculus, Elymus lolioides, Galatella sedifolia, Galium verum, Leymus racemosus, Ranunculus illyricus, Salvia verticillata, Securigera varia* etc.).

The number of cryptophytes is 6.5 smaller than that of hemicryptophytes. Cryptophytes are represented by the following groups: long-rhizome (*Bromus inermis, Calamagrostis epigeios, Elymus repens, Carex praecox, C. stenophylla, C. supina* etc.), brush-rhizome (*Pedicularis dasystachys, Ranunculus pedatus, Ranunculus polyrhizos*), tuberous (*Ranunculus ficaria* subsp. *caltifolius, Valeriana tuberosa*) and bulbous polycarpic plants (*Allium angulosum, A. globosum, Allium strictum, Bulbocodium versicolor, Fritillaria meleagroides, Gagea bulbifera, Gagea pusilla, Ornithogalum fischerianum, Tulipa sylvestris subsp. australis* etc.). There are also chamephytes:

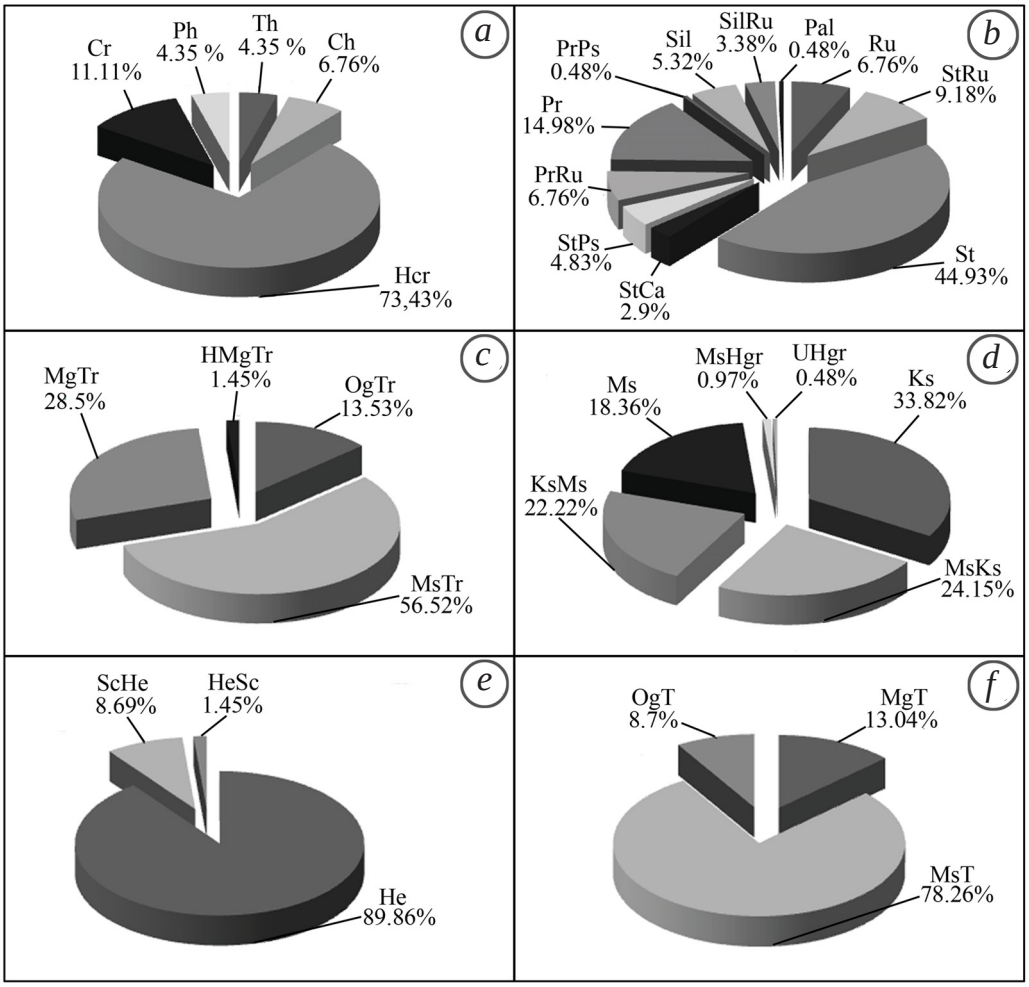

Fig. 3. The ecomorph spectrum in the plant communities containing *Colchicum bulbocodium* subsp. *versicolor*. Designations: *a – biomorphs*: Ph – phanerophytes, Ch – chamephytes, Hcr – hemicryptophytes, Cr – cryptophytes, Th – therophytes; *b – cenomorhs*: Sil – sylvants, SilRu – sylvant ruderants, Pr – pratents, PrRu – pratent ruderants, St – steppants, StCa – steppant calcephytes, StPs – steppant psammophytes, StRu – steppant ruderants, Ru – ruderants, Pal – paludants, PrPs – pratant psammophytes; *c – trophomorphs*: OgTr – oligotrophs, MsTr – mesotrophs, MgTr – megatrophs, HMgTr – halomegatrophs; *d – hygromorphs*: Ks – kserophytes, MsKs – mesoxerophytes, KsMs – xeromesophytes, Ms – mesophytes, MsHgr – mesohygrophytes, UHgr – ultrahygrophytes; *e – heliomorphs*: He – heliophytes, ScHe – scioheliophytes, HeSc – heliosciophytes; *f – thermomorphs*: MgT – megatherms, MsT – mesotherms, OgT – oligotherms

semishrubs (*Krascheninnikovia ceratoides*), dwarf subshrubs (*Astragalus pallescens, A. ucrainicus, Astragalus varius, Bassia prostrata, Thymus calcareus, T. pulegioides* subsp. *pannonicus*), tap-root sucker plants (*Artemisia absinthium*), short-rhizome (*A. marschalliana*), long-rhizome (*Veronica chamaedrys*) and other perennial plants. There is a small number of phanerophytes: trees and shrubs (*Acer tataricum, Crataegus ambigua, Lonicera tatarica, Prunus spinosa, Quercus robur, Rosa canina, Spiraea hypericifolia*), subshrubs (*Ephedra distachya*) – as well as therophytes (*Alyssum desertorum, Eragrostis minor, Erysimum marschallianum, Lepidium ruderale, Myosotis micrantha, Pulicaria vulgaris, Ranunculus falcatus, Stellaria media, Veronica verna*) (Fig. 3, *a*).

In the cenomorph spectrum, approximately half of the species belong to steppe vegetation; together with steppe weeds, calciphytes (*Cephalaria uralensis, Krascheninnikovia ceratoides, Linum perenne, Teucrium polium, Thymus calcareus* etc.) and psammophytes (*Dianthus polymorphus, Helichrysum arenarium, Jurinea cyanoides, Potentilla incana*) this group constitutes over 60% (Fig. 3, *b*), which is typical of the steppe zone where the studied communities are located. The presence of meadow species is also articulated and amounts, together with meadow weeds, to 20%. Apparently, it is due to the confinement of some coenoses to liman and flood meadows. The group of forest species is small and represented by individual specimens of wood and forest grass species (*Agrimonia eupatoria, Anemone sylvestris, Fragaria viridis, Peucedanum alsaticum* etc.).

We detected one species of the meadow psammophyte group (*Artemisia dracunculus*) and one species of the swamp psammophyte group (*Carex acuta*). The groups of proper weed plants (*Artemisia absinthium, Berteroa incana, Bromus squarrosus, Carduus uncinatus, Cirsium arvense* etc.) and steppe (*Alyssum desertorum, Artemisia austriaca, Carlina biebersteinii, Centaurea scabiosa* etc.), meadow (*Cichorium intybus, Elymus repens, Eryngium planum, Hieracium robustum, Pulicaria vulgaris* etc.) and forest weed plants *Anthriscus sylvestris, Galium boreale, Geum urbanum, Hieracium umbellatum* etc.) comprise 26% of the floristic composition. This fact strongly supports the large anthropogenic load on the communities with *C. bulbocodium* subsp. *versicolor.*

The trophomorphic ratio analysis indicates that the communities with *C. bulbocodium* subsp. *versicolor* grow on soils ranging from poor (low-fertility) soils with a predominance of oligotrophic species to saline soils preferable for halomegatrophites (Fig. 3, *c*). However, an obvious predominance of mesophytes suggests that the communities with *C. bulbocodium* subsp. *versicolor* are widely spread on fairly rich (medium-fertility) soils. A rather articulate presence of megatrophic species indicates that the communities under study are also widespread on rich (fertile) soils. Poor soils comprise a small share; saline soils make up an insignificant share as well.

The hygromorphic spectrum analysis shows that in the communities with *C. bulbocodium* subsp. *versicolor,* the soil watering regime ranges from dry to humid. The dry regime predominates, with a largest proportion of xerophytes; it is followed by the fairly dry regime, with an optimum for mesoxerophytes; fairly humid regime comes next, with an optimum for xeromesophytes; and the humid regime comes last, with an optimum for mesophytes (Fig. 3, *d*).

The ratio of heliomorphs indicates that heliophytic species, for which the light type of illumination is suitable, prevail (Fig. 3, *e*). The semi-light and semi-shadow type of illumination are preferable for small-size groups of scioheliophytes and heliophytes which are comprised of wood-shrubs and forest grass plants present in some communities with *C. bulbocodium* subsp. *versicolor.*

The confinement of the communities with *B. versicolor* to open spaces in the temperate zone explains an overwhelming prevalence of mesothermic plants (Fig. 3, *f*). Mere 13% of megathermic species prefer a warmer environment, whereas 9% develop better in a cooler environment.

To conclude, the communities with *C. bulbocodium* subsp. *versicolor* are dominated by hemicryptophytes, primarily tap-root, short-rhizome and long-rhizome grass perennials. In phytocoenotic terms, most species belong to the zonal vegetation, namely steppe vegetation. The presence of meadow species is also prominent. The proportion of weed plants is large, which indicates a strong anthropogenic load on the communities. The dry regime predominates, with a largest proportion of xerophytes; it is followed by the fairly dry regime, with an optimum for mesoxerophytes; fairly humid regime comes next, with an optimum for xeromesophytes; and the humid regime comes last, with an optimum for mesophytes. The communities are spread over medium-fertility and fertile soils. The light regime of illumination prevails. The predominance of mesothermic plants corresponds to the temperate zone.

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