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Article

Phytocenotic confinement and ecological features of habitats of *Eremogone saxatilis* (L.) Ikonn. in different parts of its range

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Abstract. Ecological features of *Eremogone saxatilis* (L.) Ikonn. habitats in the national parks of "Mariy Chodra" (Mariy El Republic), "Khvalynsky" (Saratov Region) and in the Voronezh Region were identified using D.N. Tsyganov's amplitude scales. Field studies were conducted from 2017 to 2024. The analysis of 12 geobotanical descriptions of plant communities with *E. saxatilis* (6 in the center and 6 at the boundary of the range), obtained through applying the route method, suggests that the core of the flora of plant communities in the center of the range in Voronezh and Saratov regions consists of meadow and true steppe (23% and 29%, respectively), as well as wet meadow (21.3% and 9%) species. In the "Mariy Chodra" National Park, pine forest-edge species of pine forests (51.3%) and fresh meadows (15.4%) predominate at the northeastern boundary of the range. The distribution of *E. saxatilis* is limited by the ombroclimatic, soil moistening and fertility, including moisture variability and illumination factors. In the Saratov Region, a reducing effect of the factor was noted on the cryoclimatic (up to 4.00 grades), ombroclimatic (up to 3.75), thermoclimatic (up to 4.00), and climate continentality scales (up to 4.25). The ecological position of the species on the soil nitrogen supply scale was within 1.00–4.92 (from nitrogen-free soils to soils sufficiently supplied with nitrogen) and on the soil acidity scale from 2.38 to 7.48. Plant communities with *E. saxatilis* most fully realized their ecological potential in the center of the range.

Keywords: ecological scales, Protected Areas, rare species, Mariy El Republic, Voronezh Region, Saratov Region

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Научная статья

Фитоценотическая приуроченность и экологические особенности местообитаний *Eremogone saxatilis* (L.) Ikonn. в разных частях ареала

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Аннотация. Экологические особенности местообитаний *Eremogone saxatilis* (L.) Ikonn. на территории национальных парков «Марий Чодра» (Республика Марий Эл), «Хвалынский» (Саратовская область) и в Воронежской области были выявлены с помощью амплитудных шкал Д.Н. Цыганова. Натурные исследования проводились в период 2017–2024 гг. В результате обработки 12 геоботанических описаний фитоценозов с *E. saxatilis* (6 в центре и 6 на границе ареала), полученных маршрутным методом, обнаружено, что ядро ценофлоры фитоценозов в центре ареала в Воронежской и Саратовской областях составляют виды луговых и настоящих степей (23% и 29% соответственно) и влажных лугов (21.3% и 9%). На северо-восточной границе ареала в национальном парке «Марий Чодра» преобладают боровые опушечные виды сосновых лесов (51.3%) и свежих лугов (15.4%). Распространение *E. saxatilis* ограничивают омброклиматический фактор, факторы увлажнения и плодородия почв, переменности увлажнения и освещенности. В Саратовской области отмечено расширение шкал в сторону снижения действия фактора по криоклиматической (до 4.00 баллов), омброклиматической (до 3.75), термоклиматической (до 4.00 баллов) шкалам, по шкале континентальности климата (до 4.25 баллов). Экологические позиции вида по шкале богатства почв азотом находятся в диапазоне от 1.00 до 4.92 баллов (от безазотных почв до достаточно обеспеченных азотом почв), по шкале кислотности почв варьируют в пределах 2.38–7.48 баллов. Наиболее полно ЦП *E. saxatilis* реализуют свои экологические возможности в центре ареала.

Ключевые слова: экологические шкалы, особо охраняемые природные территории, редкие виды, Республика Марий Эл, Воронежская область, Саратовская область

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Introduction

The need to monitor populations and search for new locations of rare species have been repeatedly emphasized at the state level in the course of implementation of environmental protection and integrated environmental monitoring programs, as well as exploratory scientific research (Butuzov et al., 2002). When determining the conservation status of a species, in addition to its relict nature and habitat vulnerability, it is vital to consider the species ecological confinement. Most protected species are stenotopic, and their habitats are particularly vulnerable that makes rare plants growing here valuable.

About one hundred taxa of the genus *Eremogone* are encountered in the temperate zone of the Northern Hemisphere, particularly in North America, the mountains of Eurasia, Asia, and Asia Minor. Nineteen species have been found in Turkey, twelve of which are endemic with distinctive morphological features (Armağan, 2023).

The aim of this study was to identify the ecological features of habitats and to analyze the ecological and coenotic structure of plant communities *E. saxatilis* (L.) Ikonn. in different parts of its geographical range: in the “Mariy Chodra” (Mariy El Republic) and “Khvalynsky” (Saratov Region) national parks. The information on Voronezh and Kirov regions was added from the literary sources.

Materials and methods

The study object

Eremogone saxatilis (L.) Ikonn. is the Eurasian or East Euro-Siberian boreal-temperate species (Alekseev et al., 1971; Byalt et al., 2004; Matveev, 2006; Mayevsky, 2006; Shishkin, 1936; Tsvelev, 2000). The range of the species is continuous (Meuzel et al., 1965) (Fig. 1).

In this study, the species *Eremogone saxatilis* (L.) taxonomically belongs to the genus *Eremogone* of the family Caryophyllaceae of the order Caryophyllales. In geobotanical works, such synonyms of this species as *Arenaria graminifolia* Schischk. & Knorring (sensu) p. p., *Arenaria graminifolia* Schrad., *Arenaria procera* Spreng., *Arenaria procera* ssp. *glabra* (F.N. Williams) Holub p. p., *Arenaria saxatilis* L., *Arenaria stenophylla* Ledeb., *Arenaria syreistschikowii* P.A. Smirn., *Eremogone graminifolia* (Schrad.) Fenzl., *Eremogone procera* (Spreng.) Rchb., *Eremogone stenophylla* (Ledeb.) Fisch. & C.A. Mey are often used (Maevsky, 2006)[1].

E. saxatilis is encountered in Eastern Europe, the Caucasus, Western, Eastern, and Southern Siberia (mainly in the steppe and forest-steppe zones), including Central Asia (Belova, 2021; Butuzov et al., 2002; Krupkina, 2020; Matveev, 2006). E.V. Baranova et al. (1971) refer *E. saxatilis* to a group of Euro-Siberian subtaiga species. According to the ecocoenotic groups’ classification by O.V. Smirnova (2004), *E. saxatilis* is a pine forest edge species of sparse pine forests. Cenopopulations (CPs) of this species are found in green moss pine forests and pine forests with Koeleria along the left bank of the Volga River and railways, in sandy areas, and on sandy forest clearings (Notov, 2000). Being a forest edge-steppe species of psammophytic habitats, a hemicryptophyte and a 15–35 cm short-rhizome herbaceous perennial with a tuft of rough-at-edges basal leaves up to 15 cm long, *E. saxatillis* sometimes

[1] Depository of Living Systems. Herbarium of Moscow State University. Web page. URL: https://plant.depo.msu.ru/open/public/scan.jpg?pcode=MW0067113&fp-type=florus (accessed: 11.12.2024).

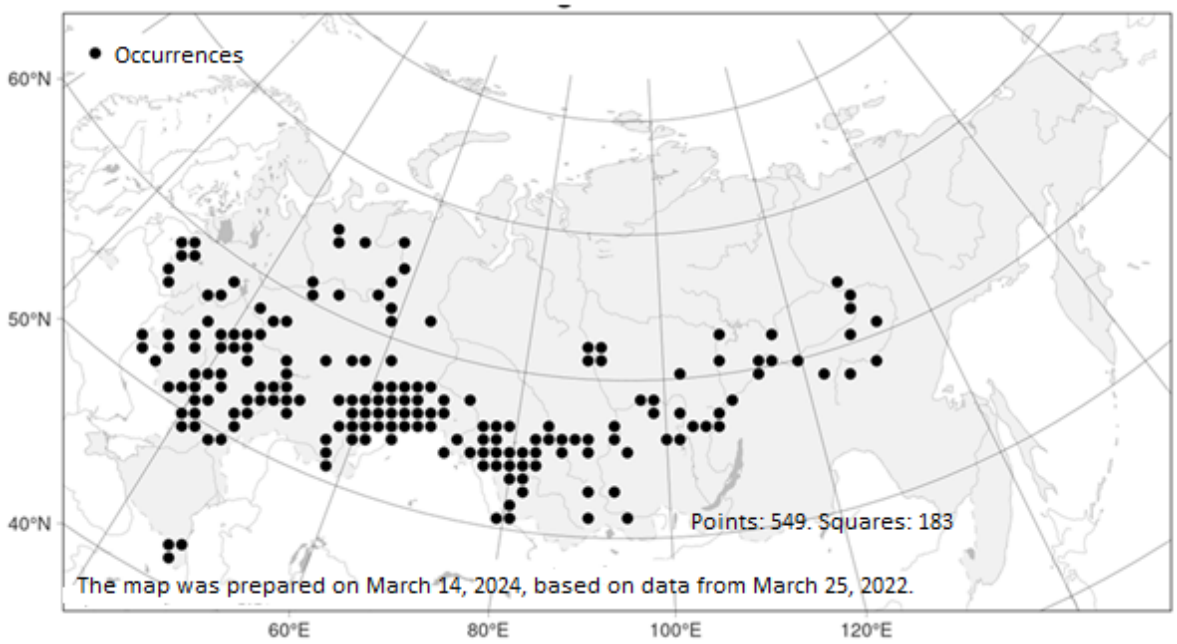

Fig. 1. Range of *Eremogone saxatilis* in Russia.

forms a turf (Koposova and Savinykh, 2019; Matveev, 2006; Notov, 2000). Flowers of *E. saxatilis* are pentamerous, corolla petals are not fused and have a greenish midrib, petals are white. In the spring of 2024, the authors found a polypetalous flower in chalk habitats near the city of Khvalynsk. A fruit of *E. saxatillis* represents a capsule.

The species belongs to the late-spring group of the spring flowering cycle: it retains green vegetative organs until mid-July and has a summer-green phenotype. Due to a delicate fragrance of numerous bright white flowers in a paniculate inflorescence, the flowers of *E. saxatilis* are successfully pollinated by insects (species of the latter are not identified). Seeds ripen in June–July, fall under their own weight and are dispersed by wind (Matveev, 2006). Seed production and reproductive efficiency have not been studied yet. This ornamental plant has been introduced into cultivation. Scientists from the Udmurt University successfully introduced it *in vitro* in culture and propagated through explants from renewal points for microcutting followed by rooting of newly formed shoots (Baranova et al., 2011; Dedyukhina et al., 2011). In nature, *E. saxatilis* grows as isolated complexes with an area of approximately 400 m^2; sometimes, single or widely separated individuals are found. The biomorphological features, ontogenesis, and cenopopulation structure of this species have been studied in Ukraine, the Kirov Region, Mariy El and Udmurt republics (Dedyukhina, 2008; Koposova and Savinykh, 2019; Polyanskaya, 2023; Usmanova, 2011).

Despite the extensive spread (mostly at the range boundary), *E. saxatilis* is listed in the Red Data Books of various regions of Russia and neighboring countries. At the northern and northeastern limit of its distribution, the species was recorded in Vologda (Krasnaya kniga..., 2004), Leningrad (Krasnaya.., 2018), Pskov (Sudnitsyna, 2014), Tver (Krasnaya.., 2002), Kirov (Krasnaya..., 2014) Regions, in Khanty-Mansi Federal Okrug (Krasnaya..., 2013), in Udmurt (Krasnaya..., 2012) and Mariy El (Krasnaya..., 2023) republics in category 3 (rare species) and in the Republic of Crimea at the southern border of its range (Krasnaya.., 2015). Previously, the species (found at the western boundary of its range) was registered in Red Data Books of Ukraine, Estonia and Latvia[2]. In 21 regions, *E. saxatilis* has been included in the lists of protected species. Plant communities with *E. saxatilis* are protected in the “Sebezhsky” and “Mariy Chodra” National Parks and the “Malaya Sos’va” Nature Reserve (Ryzhova et al., 2023; Sudnitsyna, 2014; Vasina, 2018). The species is cultivated in Botanical Gardens of Tver’ and Udmurt State Universities (Dedyukhina, 2008; Dedyukhina et al., 2011; Notov, 2000). *E. saxatilis* is a rare relict species of the Holocene xerothermic period (Vasina, 2018).

[2] Plantarium. Web page. URL: https://www.plantarium.ru/page/view/item/14767.html (accessed: 29.05.2024).

The species' strategy has been poorly studied. When exploring *E. saxatilis* in green-moss pine forests of the “Medvedsky Bor” Natural Monument (Kirov Region), K.D. Koposova and N.P. Savinykh (2019) have revealed that under shaded conditions the species adopts a specific patient life strategy and is capable of surviving light deprivation for extended periods in a vegetative state. With changes in the light regime at forest edges and clearings, the plant community is restored and gets ready for reproduction and dispersal. There is evidence of strategy instability for this species in forest-steppe relicts. On the one hand, the plant communities are characterized by low abundance (Notov, 2000). However, after periodically recurring fires occurring in habitats, a noticeable increase in *E. saxatilis* number and improving its strategy are observed (Vasina, 2018). Some authors report about the factors limiting the species' vital functions: significant recreational pressure, grazing and herding of livestock (Butuzov et al., 2002).

Studying the ecological features of steppe plants outside their primary ranges is important for identifying their adaptation to other habitats. The ecological capabilities of *Arenaria graminifolia* Schrab. (synonym for *E. saxatilis*) were first estimated by L.G. Ramensky et al. (1956) (Table 1).

According to the soil moistening scale, *E. saxatilis* has a fairly broad spectrum of values that reflects the species confinement from arid and mid steppe to meadow-steppe conditions throughout its geographical range from a forest zone to semi-desert. The soil salinization range is also quite wide: from poor mesotrophic soils with a slightly acidic reaction (pH 6.0–6.5) to rich soils with a neutral reaction (pH 7.0–7.5). Analyzing the flora and vegetation of steppe and forest-steppe zones, N.M. Matveev (2006) provides the following point-based ecological characteristics for *E. saxatilis*: mesotroph (2), mesoxerophyte (1), heliophyte (4), mesotherm (3). K.D. Belova (2021) studied the ecological and cenotic properties of *E. saxatilis* habitats at the northeastern boundary of its range and identified the species ecological features based on seven scales proposed by D.N. Tsyganov. According to her research, *E. saxatilis* is a mesovalent in relation to climatic factors and a hemisthenovalent in terms of soil factors. When introduced into cultivation, despite the plant’s stenovalent nature, its high establishment is noted in soil substrates containing humus (33.3%) and vermiculite (20% of the total volume). In 60 days after planting into open ground, seedlings has well-developed tufts with 2–7 lateral shoots and a strong root system, regardless of the substrate type (Dedyukhina et al., 2011).In plant communities, *E. saxatilis* functions throughout its range as an assectator with TPC of 0.2–2%.

Table 1. Ecological scales for *E. saxatilis* according to L.G. Ramensky (1956); * – not established limits for ecological factors.

Scale	Abundance				
	En Mass: more than 8%	Abundantly: 2.5–8%	Moderately: 0.3–2.5%	Few: 0.1–0.2%	Single
Soil Moistening (SM)		38–44	29–53	26–56	23–65
Soil Salinization (SS)			10–13	8–17	7–*
Moisture Variability (MV)			7–9		
Alluvial intensity (A)			–4*	–6*	

The study area

The study was carried out in the Mariy El Republic (six geobotanical descriptions, 2017) and the Saratov Region (five geobotanical descriptions, 2011–2024). Data for the Voronezh Region (one description) were taken from the literary sources (Keller, 1936).

The “Mariy Chodra” National Park (36875 hectares with a buffer zone of 93400 hectares; established in 1985) is located in the eastern part of the Russian Plain and in the southwest of the Mariy El Republic (56°16' – 56°07' N and 48°51' – 48°22' E). The park is distinguished by alternating flat (Mariy Lowland) and elevated terrain of the Mariy-Vyatka Ridge with karst landforms and occurrence of cut-by-ravines uplands, hollows, and varying elevations. The climate is characterized by hot summers and frosty winters with stable snow cover. The average annual precipitation is 520–550 mm. (Letopys’ prirody..., 1996). During the warm period (April–October), precipitation amounts to 360–380 mm with a maximum of 60–70 mm in June–July, whereas in the cold period (November–March) it makes up 150–180 mm with a minimum of 22–30 mm in February. The average annual air temperature in the republic is +3.4...+5.0 °C (1981–2010). In general, a tendency towards its increase is noted.

The coldest month is January: the average monthly temperature is within −9.6...−11.4 °C with the absolute minimum of −44... −52 °C recorded in 1978. The warmest month is July, the average monthly temperature is +18.9...+20.1 °C with the absolute maximum of +37...+39 °C reached in 2010[3]. The park is located in the zone of coniferous-broadleaf forests with taiga and forest-steppe elements (Abramov and Papchenkov, 2006). Parent rocks were formed on the Permian bedrocks from different-thickness layers of ancient alluvial sands and sandy loams. In terms of botanical and geographical zoning of the European part of Russia, the republic is a part of the West Siberian Province, the Trans-Volga-Ural District, and the Volga-Kama Region (Fedorov, 1979). The boundaries of boreal and central European provinces of the Euro-Siberian floristic region run through the territory of the Mariy El Republic (Abramov, 2000).

In “Mariy Chodra” National Park (NP), *E. saxatilis* grows in the southern part of the park in steppe pine forests, forest edges, sandy outcrops, road embankments, and clearings (Abramov and Papchenkov, 2006).

The “Khvalynsky” National Park established in 1994 (26037 hectares, protected area – 114924 hectares) is located in the northeastern outskirts of the right bank of the Saratov River at the boundary of the Middle and Lower Volga regions (52°32' – 52°16' N and 47°30' – 48°20' E), on the residual conglomerate (the Khvalynsk Hills) of the Volga Upland and partially in the Tereshka River basin valley. Chalk ledges of the Khvalynsk Hills stretch meridionally along the Volga River and alternate with a strip of wide rolling plains occupying the entire interfluve of the Volga and Tereshka rivers. The length of hills of the main dividing ridge with elevations up to 380 m is approximately 27 km long and 3–10 km wide (Makarov et al., 2006). According to the map of landscape zoning, the territory covers the Volga-Tereshkinsky landscape area of the southern forest-steppe of the Volga upland-plain forest-steppe province, as well as the Central-Tereshkinsky landscape area of the northern steppe of the Volga upland-plain steppe province (Anikin et al., 2013; Makarov et al., 2006). The climate of the study area is temperate continental and arid, characterized by warm and dry summers (the average July temperature is +20.5 °C) and moderately cold winters with little snow (the average January temperature is −13 °C). The average annual air temperature fluctuates between +5.2 °C and +7.9 °C. The average relative humidity makes up 70% (minimum – 25%, maximum – 99%), the average annual precipitation amounts to 425–450 mm (Anikin et al., 2013). The territory belongs to the steppe zone with predominantly chernozem soils, the northeastern (Volsko-Khvalynsky) soil region of the forest-steppe zone with Upper Cretaceous rock outcrops. According to botanical-geographical zoning, the study area belongs to the Central Russian (Upper Don) subprovince of the East European forest-steppe province of the Eurasian steppe region (Isachenko and Lavrenko, 1980; Lavrenko, 1940; Tarasov, 1977). Here, zonal vegetation is represented by broadleaf forests dominated by *Quercus robur*, Norway maple *Acer platanoides*, and tillet, while in meadow steppes *Stipa capillata* and *Stipa pennata* dominate. Forests, framed by ecotone communities of meadow steppes, cover dividing ridges and hilltops. The lower parts of the slopes and plains are home to steppe communities (Boldyrev, 2005).

[3] Geography of Mariy El. Climate. Web page. URL: https://reo12.рф/atlas/2-4-климат (accessed: 10.12.2024).

Collection and processing of materials

The materials for the study were collected in the Klenovogorsky forestry of the “Mariy Chodra” National Park, the Khvalynsky and Sosnovo-Mazinsky forestries, as well as the protected area of the “Khvalynsky” National Park. The authors took a list of species of the plant community growing around the horse farm “Kultura” (Voronezh Region) from B.A. Keller's book "Vegetation of the Caspian Lowland between the Volga and Ural Rivers" (1936). The Voronezh Region was included in our study because Voronezh city and Khvalynsky habitats share the same parallel (52° N). The described Voronezh cenopopulation corresponds to the extreme southwestern distribution of the species in the center its range, further south, in Volgograd and Astrakhan Regions, *E. saxatilis* is no longer found.

Geobotanical descriptions were made in the habitats of *E. saxatilis* based on the generally accepted methods (Ipatov and Mirkin, 2008). The diversity of ecocoenotic groups (ECG) was assessed in accordance with the classification of ecocoenotic groups present in a vegetation cover of the forest belt of Eastern Europe (Smirnova, 2004). The ecological features of habitats were identified by the method of L.A. Zhukova (2004). The resulting species lists of plants in the studied plant communities were processed via using the EcoScaleWin computer program (Grokhlina and Khanina, 2006). The ecological regimes of plant communities were evaluated with the aid of the Weighted Average Method for ten amplitude scales proposed by D.N. Tsyganov (1983). The ecological diversity of plant communities with *E. saxatilis* was assessed from ecological valence fractions proposed by L.A. Zhukova et al. (2010).

Results and discussion

In the “Mariy Chodra” National Park, all plant communities with *E. saxatilis* were found in open spaces, mostly in the absence of woody species.

Sample Plot (SP) No. 1. Grass-forb, phytocoenosis I. Plot size: 8×1.5 m. Total projective cover (TPC) of the herb-dwarf shrub layer is 40%. Herbaceous plants are represented by 14 species, predominantly grasses: wood small reed (*Calamagrostis epigeios* (L.) Roth), June grass (*Koeleria glauca* (Spreng.) DC), meadow fescue (*Festuca pratensis* Huds.), sheep’ fescue grass (*Festuca ovina* L.), and meadow grass (*Poa pratensis* L.).

SP 2. **Fescue-mixed herb phytocoenosis**. Plot size: 4×1.5 m. TPC of the herb-dwarf shrub layer is 40%. Unlike the previous site, herbaceous plants are represented by 10 species with sheep’ fescue grass as a dominant.

SP 3. Cornflower-mixed herb phytocoenosis. Plot size: 6×6 m. TPC of the herb-dwarf shrub layer is 40%. Single specimens of Scots pine *Pinus sylvestris* L., Russian broom *Chamaecytisus ruthenicus* (Fisch. ex Vorosch.) Klask., and manzanita *Arctostaphyllos uva-ursi* (L.) Srpeng. are encountered in this site. Herbaceous plants are represented by 15 species with predominance of Swiss centaury *Centaurea Phrygia* L. and *E. saxatilis*.

SP 4. Grass-forb, phytocenosis 2. Plot size: 6×6 m. TPC of the grass-dwarf shrub layer is 25%. Herbaceous plants are represented by 7 species, among which wood small reed, June grass and sheep’ fescue grass dominate.

SP 5. Solomon's seal-pasture phytocenosis. Plot size: 3×3 m. TPC of the grass-dwarf shrub layer is 35%. Dyer's broom *Genista tinctoria* L. is present in the undergrowth. Herbaceous plants are represented by 12 species, among which the most prevalent are *Polygonatum odoratum* (Mill.) Druceand and *Trommsdorfia maculata* (L.) Bernh.

SP 6. Forb phytocoenosis. Plot size: 2×3 m. The plant community with *E. saxatilis* is encountered along the gas pipeline Yamburg-Yelets 2, which passes through the “Mariy Chodra” National Park. The community includes CPs of eight herbaceous plant species, a blackberry shrub (*Rubus caesius* L.), a bearberry shrub, and a juniper tree (*Juniperus communis* L.).

In the “Khvalynsky” National Park, clusters of *E. saxatilis* (sometimes with dwarf subshrubs and shrubs) were found in open spaces on the southern slopes of chalk rocks at elevations ranging from 180 to 320 m above sea level. Plot size: 10×10 m.

SP 1. Couch grass-halophytic-salsola-wermooth-tick trefoil-flax association on Mt. Kalancha**.** TPC is 20%. The composition consists of 10 species of dwarf subshrubs: *Artemisia austriaca* Jacq. (2%), *Artemisia salsoloides* Willd. (20%), *Onosma simplicissima* L. (20%), *Hedysarum grandiflorum* Pall. (20%), and *Scabiosa isetensis* L. (3%). There are 23 species of herbaceous perennials and biennials: *Elytrigia lolioides* (Kar. & Kir.) Nevski (5%), *Centaurea marschalliana* Spreng. (3%), *Scorzonera austriaca* Willd. (1%), *Securigera varia* (L.) Lassen (3%), *Alyssum tortuosum* Waldst. & Kitex Willd. (3%), *E. saxatilis*

(1%) and one shrub – *Crataegus volgensis Pojark*. (1%). The number of species in the community is 34. Soils are formed of carbonate lithosol and chalk.

SP 2. Forb (adonis-peony)-feather and reed grass community with microgroups of Volga cinquefoil *Potentilla volgarica* Juz. occupies the middle and lower parts of the southern slope of Mt. Pichepanda in the north of Khvalynsky district. TPP of the community is 70%. The community is polydominant, its co-dominants are feather grass *Stipa pennata* L. (5%), thin-leaved peony *Paeonia tenuifolia* L. (40%), spring adonis *Adonis vernalis* L. (8%), low almond *Amygdalus nana* L. (5%), eastern mullein *Verbascum orientale* (L.) All. (5%), *Centaurea marschalliana* (5%), *Onosma simplicissima* L. (3%), *Potentilla volgarica* (1%), *E. saxatilis* (1%). The community comprises 67 species. Distribution by life forms: 1 shrub (*Amygdalus nana*), 2 subshrubs (*Alyssum tortuosum* and rough woodruff *Asperula exasperata* V. Krecz.ex Klok.), 58 herbaceous plant species (52 perennials, 3 biennials, and 3 annuals). Soil is of sod-carbonate type.

SP 3. Tick trefoil-forb phytocenosis is dominated by the species *Tanacetum sclerophyllum* (Krasch.) Tzvel. (2%), *Hedysarum razoumovianum* Fisch. & Helmex DC. (7%), and *Salvia nutans* L. (2%). Co-dominant species include *Iris pumila* L. (2%), *Ephedra distachya* L. (1%), *Stipa pennata* (1%). TPP of the community is 8%. Projective cover of *E. saxatilis* during the period of mass flowering is 1%. Distribution by life forms: 3 subshrubs, 18 herbaceous plants. Total number of species is 21. Soils are formed of carbonate lithosol and chalk.

SP 4. The plant community with Stipa capillata inhabits the foot of Mt. Kalancha from the northwestern side.

TPC is 80–90%. The dominant species are weedle grass *Stipa capillata* L. (30%), randall *Festuca valesiaca* Gaud. (2%), and June crested grass *Keleria Koeleria cristata* (L.) Pers. (1%). The predominant herbs are common yarrow *Achillea mellifolium* L. (1%), nosebleed *Achillea nobilis* L. (5%), Jacob's ragwort *Senecio jacobaea* L. (1%), Dnieper catchfly *Silene borysthenica* (Grun.) Walters (1%), Kherson catchfly *Silene chersonensis* (Zapał.) Kleop. (1%), and rosettes of shoots and leaves of *Centaurea marschalliana* (5%). The community is floristically rich: 67 species of perennial herbs, 1 shrub, 2 subshrubs, 6 biennials, and 4 annuals. The projective cover of *E. saxatilis* during the period of mass flowering does not reach 1%. Soil is of sod-carbonate type.

SP 5. Forb (cinquefoil)-fescue-feather grass community on sand. TPC is 60%. The plant community is polydominant, its co-dominants are the species *Stipa pennata* (40%), *Festuca valesiaca* (2%), *Poa bulbosa* L. (5%), *Silene borysthenica* (1%), *Artemisia marschalliana* Spreng. (5%), *Potentilla arenaria* Borkh (10%), including *Linaria genistifolia* (L.) Mill. (1%), *Astragalus varius* S.G. Gmel. (3%), *Koeleria cristata* (2%), *Carex supina* Walld. ex Wahlend. (1%), *Hylotelephium stepposum* (Boriss.) Tzvel. (3%), and *Helichrysum arenarium* (L.) Moench (3%). The flora comprises 37 species: 28 perennials, 3 biennials, 3 dwarf subshrubs, and 3 annuals. Soils are of sandy chernozem-like type.

Below we present the description of CPs in Voronezh Region (Keller, 1936, pp. 26–29).

SP 1. Fescue-forb phytocenosis. Plot size: 10×10 m. TPC is 42%. The material was collected in the vicinity of the horse farm “Kultura” near the village of Tulnevaya (Voronezh Region). The description was made in spring (May) and in autumn (September). The phytocenosis contains 61 species of seed plants, among which *Festuca valesiaca*, *Koeleria cristata*, *Bromus scoparius* L., *Poa angustifolia* (L.) Arcang., *E. saxatilis* (*Arenaria graminifolia* according to B.A. Keller), *Draba repens* M. Bieb., *Filipendula vulgaris* Moench, *Potentilla humifusa* Willd. ex D.F.K. Schltdl., *Thymus marschallianus* Willd. dominate. Distribution by life forms: one species of shrub – *Chamaecytisus ruthenicus*, 60 species of perennial and annual herbaceous plants.

Diversity of ecocoenotic groups (ECGs) in 12 studied plant communities varied latitudinally. At the range boundary, the ECG spectrum comprised nine groups. Plant communities with *E. saxatilis* demonstrated ecological plasticity in survival through occupying the habitats even at the edges of dark coniferous and closed broadleaf forests, including black alder woods. In the area center, a decline in the ecocoenotic spectrum to six-seven groups was observed. Throughout the *E. saxatilis* range, the species of dry meadows were abundant in plant communities (Meadow Steppe/Dry Meadow according to the classification of ECGs in a vegetation cover of the Eastern European forest belt) (Smirnova, 2004) (Table 2).

According to the ECG classification, species groups clearly differ in the center and at the boundary of the range. The core of the flora of plant communities with *E. saxatilis* in the range's center (Voronezh Region) consists of meadow/true steppes (23 species, 38%) and wet meadow species (13 species, 21.3%) thus reflecting the geographical nature of the territory and corresponding to the forest-steppe natural zone. In plant communities of the "Khvalynsky" National Park, the core of the flora of plant communities with *E. saxatilis* involves species from meadow and true steppe (31 species, 29%), fresh meadows, and sparse pine forests (10 species each, or 9.35%). In the Mariy El Republic, the dominant group of plants in such plant communities at the northeastern boundary is represented by pine forest edge species of sparse pine forests (20 species, or 51.3%) and fresh meadows (6 species, or 15.4%). Thus, the flora composition in Voronezh and Saratov Regions is close to the optimal one and corresponds to the type of the southern forest-steppe natural subzone.

In the Saratov Region and the Mariy El Republic, we identified the ecological features of *E. saxatilis* habitats based on 10 Tsyganov's scales.

In terms of the thermoclimatic factor (Tm), which reflects heat distribution, *E. saxatilis*, with a potential ecological valence (PEV) of 0.41, takes a hemisthenovalent position. Actual species amplitudes in its mid area (Saratov Region) vary from 4.00 (subarctic/boreal) to 9.33 grades (nemoral/sub-Mediterranean regime type) thus being larger in contrast to those reported by D.N. Tsyganov. At the northern boundary, the species amplitude of 7.00 (subboreal) – 9.00 (nemoral regime) corresponds to the type of the natural zone of coniferous-broadleaf forests. Data on CPs occupy the central part of ecological scales. The resulting range is evidence of high temperature tolerance. The coefficient of environmental efficiency reaches 81.46% (Table 3).

On the climate continentality scale (Kn), *E. saxatilis* is the euryvalent species (PEV = 0.60) with potential amplitudes from 5 to 13 that contributes to its wide spread in the areas with different indices of climate continentality. Unlike other regions, the Saratov Region and its plant communities with *E. saxatilis* are distinguished by broader environmental conditions, having greater amplitudes, i.e. from 4.25 (suboceanic suite) to 9.00 grades (continental regime) (Table 3). Similar indices of the Voronezh cenopopulation correspond to the continental regime. The narrowest range of exclusively continental regime is characteristic of the species' habitats in the "Mariy Chodra" National Park. Spectrum values for the Kirov Region provided by K.D. Belova (2021) correspond to sub- to semicontinental conditions (7–10). At the northeastern and northern boundaries of the species range in the Kirov Region and the Mariy El Republic, most CPs demonstrate poor use of the potential ecological amplitude and low REV (0.053–0.20). For the "Khvalynsky" National Park (the Volga right bank), we obtained the data indicating increasing factor's amplitude up to 4.25 (intermediate between the oceanic and marine regimes).

On the ombroclimatic scale (Om), reflecting the ratio of precipitation and evaporation, plant communities with *E. saxatilis* fall within a narrow range of environmental conditions with PEV of 0.33 thus indicating stenovalence. Two neighboring territories (Kirov Region, Mariy El Republic) have similar REV; the conditions correspond to the subarid-subhumid-humid type (7.00–8.20). In the Saratov Region, the amplitude of CPs is wider – from 3.75 (mesoarid formation) to 7.00 (subarid formation) that is beyond the potential limits. The indicators of the Voronezh population correspond to a sub-arid regime (7.12). The range of 3.75–8.20 on Tsyganov's ombroclimatic scales (Om) reflects wide ecological amplitudes of the species: from conditions typical of dry rocky slopes (the lower limit of the range) to fresh and moist habitats (the upper limit).

On the cryoclimatic scale (Cr), which indicates the presence and duration of frosty days with low temperatures, plant communities with *E. saxatilis* are considered to be hemieuryvalent (PEV = 0.60). We have identified broad ranges of winter conditions: from 3.63 (moderate winters) to 9.00 (mild and warm winters). Such an amplitude of winter regime characterizes the habitats on the chalk dividing ridge subject to constant weathering and spring water erosion near the town of Khvalynsk. For the Kirov Region, warm winters with frequent thaws are typical (9 grades by the scale). The ecological optimum of the studied habitats of *E. saxatilis* corresponds to moderate winter conditions. The coefficient of environmental efficiency makes up 64.0%.

On the soil moistening scale (Hd), CPs of the model species takes a hemisthenovalent position (PEV = 0.43). This indicates a low species diversity of probable habitats in terms of soil moistening. Potential amplitudes of *E. saxatilis* on this scale vary from 3.00 (dry forest-meadow/wet forest-meadow type) to 12 grades (wet forest-meadow/swamp forest-meadow type). Forested areas (Kirov Region,

Table 2. Ecological and coenotic spectrum of species in plant communities with *E. saxatilis* in different parts of its range. The number of species is indicated above the line, and the share of the total number is given below the line.

Ecocenotic groups	Mariy El Republic (at the northeastern boundary of the range)	Saratov Region (in the center of the range)	Voronezh Region (in the center of the range, southwest)
Meadow Stepp Dry Meadow	3 / 7.7	4 / 3.74	2 / 3.28
Meadow Stepp Fresh Meadow	6 / 15.4	10 / 9.35	13 / 21.3
Advent	0 / 0	0 / 0	1 / 1.62
Boreal	2 / 5.13	0 / 0	0 / 0
Nemoral In Forest Nemoral	1 / 2.56	0 / 0	0 / 0
Nemoral	2 / 5.13	2 / 1.84	3 / 4.92
Nitrophilious	1 / 2.56	0 / 0	1 / 1.62
Pine Forest in Pine Forest	0 / 0	0 / 0	1 / 1.62
Pine Forest	20 / 51.28	10 / 9.35	4 / 6.56
Oak-Xerophilous	1 / 2.56	5 / 4.67	2 / 3.28
Meadow Stepp Steppe	2 / 5.13	31 / 28.97	23 / 37.7
Not defined	1 / 2.56	45 / 42.1	11 / 18.03
Total	39 / 100	107 / 100	61 / 100

Table 3. Ecological features of plant communities with *E. saxatilis* by Tsyganov's scales (1983). The actual spectrum of scale values is indicated above the line, and REV (realized ecological valence) is shown below the line. Values in bold demonstrate increasing amplitudes as compared to the previously identified indicators.

Scale range	Ecological position of the species on factor scale	PEV	Indicators					$K_{ec.ef.}$, %
			Kirov Oblast (Belova, 2021)	Mariy El Republic	Saratov Oblast	Voronezh Oblast	Generalized indicators	
Tm (1–17)	5–11	0.41	8.00–9.00 0.06	7.74–8.22 0.03	**4.00**–9.33 0.334	8.17	**4.00**–9.33 0.034	81.46
Kn (1–15)	5–13	0.60	7.00–10.00 0.20	8.42–9.15 0.053	**4.25**–9.00 0.34	8.56	**4.25**–10.00 0.411	68.50
Om (1–15)	5–9	0.33	7.00–8.00 0.07	7.68–8.20 0.038	**3.75**–7.00 0.233	7.12	**3.75**–8.20 0.319	96.67
Cr (1–15)	1–9	0.60	8.00–9.00 0.07	6.79–7.41 0.045	3.63–8.17 0.109	7.08	3.63–9.00 0.164	64.00
Hd (1–23)	3–12	0.43	11.00 0.0004	9.05–10.61 0.071	3.50–8.17 0.213	8.87	3.50–11.0 0.341	79.30
Tr (1–19)	5–11	0.37	5.00–6.00 0.05	6.46–7.46 0.057	**4.00**–6.60 0.145	7.49	**4.00**–7.46 0.183	49.50
Nt (1–11)		–	–	4.26–4.92 0.067	1.00–2.63 0.164	3.38	1.00–4.92 0.393	–
Rc (1–13)		–	–	6.90–7.32 0.086	2.38–4.07 0.143	6.67	2.38–7.32 0.426	–
Fh (1–11)	5–11	0.27	–	**4.82**–6.21 0.175	**1.75**–5.00 0.326	4.95	**1.75**–6.21 0.414	153.30
Lc (1–9)	1–3	0.33	3.00 0.001	2.68–**3.46** 0.097	1.00–2.50 0.189	2.63	1.00–**3.46** 0.284	86.10

Mariy El Republic) demonstrate small values of PEV in the right part of the scale (9.05–11.00). At the northern boundary of the range, *E. saxatilis* habitats correspond to conditions from meadow-steppe to dry forest-meadow on forest clearings and under the canopy of light pine forest. Habitats in the Saratov Region are distinguished by greater ecological amplitudes: 3.50–8.00 (Table 3), corresponding to regimes from semi-desert (developed on lithosols of chalk outcrops of the Khvalynsky dividing ridge) to the intermediate and meadow-steppe (on sodded slopes of chalk rocks).

On the soil salinity scale (Tr), *E. saxatilis* is the stenovalent species (PEV = 0.37). Interestingly, the ecological amplitude index of all studied CPs in all regions fluctuates from 4.00 (poor/not rich soils) for chalk rocks of the “Khvalynsky” National Park to 7.50 grades (fairly rich/rich soils) at the northern boundary of the range and in the steppe of the Central Chernozem region (Voronezh Region). The coefficient of environmental efficiency makes up 49.5%.

On the 11-level nitrogen supply scale (Nt), the species' ecological positions were not previously determined. Practical results suggest that the studied CPs occupy the left side of scales, ranging from 1 to 4. Ecological amplitude in *E. saxatilis* varies from 1.00 (nitrogen-free soils to very nitrogen-poor/ nitrogen-poor soils in the “Khvalynsky” National Park) to 4.92 (sufficient nitrogen supply of soils in the “Mariy Chodra” National Park) that is evidence of the species flexibility.

On the 13-level acidity scale (Rc), the species' ecological positions were not previously determined. For the model species, they are estimated from 2.38 (intermediate between strongly acidic and acidic soils) to 7.48 (slightly acidic soils) in the “Mariy Chodra” National Park. Moreover, values for Saratov populations are on the left side and for the Mariy El Republic in the middle of the scale. Three interrelated factors are noted in plant communities of the “Khvalynsky” National Park: chalk outcrops (carbonate lithosol), the presence of steppe dwarf semi-shrubs, and the acidic reaction of the substrate beneath them. Calcium and magnesium carbonates predominate in carbonate soils (Kask and Niine, 1971). These soils contain little iron and potassium, including highly variable phosphorus contents (USSR Nature Reserves, 1989). Previously, the authors defined soil acidity for dwarf semi-shrubs of the “Khvalynsky” National Park: *Artemisia salsoloides* (3.17–9.55), *Dianthus rigidus* M. Bieb. (3.32–7.94), *Hedysarum razoumowianum* (3.10–9.67), and *Hyssopus cretaceus* Dubian. (4.10–9.55) (Suleimanova and Boldyrev, 2023). Dwarf subshrubs form unique "cushions" – microcenoses with a specific microclimate, humidity and temperature, which are essential for plant survival under extreme weathering and high insolation, e.g. when temperature at the soil surface rises to +60 °C in summer. Microcenoses are located in the so-called "flowerpots" – micro depressions formed in the relief. Plant residues accumulate at the bottom of the "flowerpots," decompose and release carbon dioxide into soil (Klechkovsky and Peterburgsky, 1967) followed by its conversion into carbonic acid able to dissolve calcium and magnesium compounds. Rain or meltwater transfer the resulting solutions to deeper soil layers and increase substrate acidity. The situation is aggravated by the presence of groundwater (springs) at the foot of chalk rocks. The results of *E. saxatilis* analysis on the soil acidity scale (Rc: 2.38–7.48) are fully consistent with this thesis. The indicated amplitudes shows that the species prefers non-saline soils with an acidic or neutral reaction and avoids alkaline ones. This confirms that *E. saxatilis* from the Volga Upland does not grow directly on fresh chalk, but settles on the poorly developed soils formed above it, where carbonates have already been partially leached and the pH is close to neutral. The habitats of *E. saxatilis* in the Voronezh Region are characterized by a slightly acidic reaction.

On the 11-level moisture variability scales (Fh), we identified ecological amplitudes in *E. saxatilis* from 1.00 points (relatively stable moistening) to 6.21 (slightly variable/moderately variable moistening). Unlike the Saratov cenopopulations, habitats in the forest zone (Mariy El Republic) differ by more humid conditions.

On the illumination-shading scales (Lc), the studied CPs occupy stenovalent positions (PEV = 0.33), i.e., they can exist in a rather narrow range of environmental conditions. From practical results it follows that actual ecological amplitudes for the majority of CPs correspond to Tsyganov’s potential values (1983), i.e. being within1.00 (open space regime) and 3.46 grades (semi-open space and light forest regime).

Conclusion

The species *E. saxatilis* is distinguished by its richness and diversity throughout the studied range. In the Voronezh Region, meadow and true steppe, as well as wet meadow species dominate. In the Saratov Region, these species are also predominant, but less represented. Furthermore, the number of Pine Forest species (sparse pine forest) in the forests of the Mariy El Republic has dropped from 10 (9.4%) to 20 (51%).

The meadow-steppe group (a subgroup of wet forests) is present in all studied sites. However, it is more abundant in the Mariy El Republic and Voronezh Region. Such a distribution of ECGs depends on soil conditions. In the Mariy El Republic, soil is more fertile (Tr 6–8) and rich in nitrogen (Nt 4–5). It is characterized by a neutral reaction, more favorable for root nutrition (Rc 6–8) and has moderate moisture variability (Fh 4–6). In contrast, the chalky soils of the “Khvalynsky” National Park exhibit extreme conditions: poor nitrogen content, up to its complete absence in soil solution (Nt 1–3), acidic reaction (Rc 2–4), unstable moisture variability (Fh 1–2.5), and low fertility (Tr 4–6). Spectrum of values for the mentioned indicators in CPs of the Voronezh Region and the Mariy El Republic is similar.

The conditions in the “Khvalynsky” National Park are optimal for the studied *E. saxatilis*. The Khvalynsk habitats demonstrate the greatest amplitudes in environmental factors. However, the specificity of chalk rocks (rich in certain minerals, but poor in organic matter needed for providing soil fertility) prevents from creating a good habitat for this species. Soil factors are limiting for *E. saxatilis* even in the center of its range. Apparently, good edaphic conditions for the species develop further south, i.e. in theVoronezh Region.

Overall, our studies confirm the ecological features of *E. saxatilis* on the cryoclimatic (the period of frost duration) scale (Cr). In the Saratov Region, we recorded an amplitude expansion towards a decreased influence of the factor on ombroclimatic (Om) – up to 3.75 (mesoarid formation), on thermoclimatic (Tm) up to 4.00 (subarctic/boreal type of regime), on climate continentality (Kn) up to 4.25 (suboceanic formation) scales. On the moisture variability scale (Fh), the increase in values of the relatively stable moisture regime up to 1.00 in the Saratov Region and up to 4.82 grades (relatively stable moisture/slightly variable moisture) in the Mariy El Republic was noted. The position of *E. saxatilis* on the nitrogen supply scale (Nt) from 1.00 (nitrogen-free or very nitrogen-poor soils) in the “Khvalynsky” National Park to 4.92 (sufficient nitrogen supply) in plant communities of the “Mariy Chodra” National Park and on the soil acidity scale (Rc) as 2.38 (intermediate between strongly acidic and acidic soils) in the Saratov Region to 7.48 (slightly acidic) in the Mariy El Republic was estimated for the first time. The phenomenon of elevated soil acidity can be explained by a combination of factors: the formation of particular microecotones in depressions on the chalk rocks and microcenoses with a specific microclimate, humidity and temperature under extreme conditions of weathering and increased insolation. These microcenoses create a green oasis amidst chalk outcrops and simultaneously concentrate organic matter thereby promoting further soil acidification. Groundwater (springs) at the foot of the chalk rocks contributes to this process.

Thus, plant communities with *E. saxatilis* most fully realize their ecological potential in the center of the range. This pioneer species grows in open well-drained warm and extremely nitrogen-poor soils (rocky slopes, scree, sandy terraces). It avoids rich-in-nitrogen soils, probably, because of competition. Wide climatic flexibility of *E. saxatilis* allows it to colonize habitats in different regions. Significant amplitudes on climatic scales indicate that *E. saxatilis* exploits a variety of ecological niches (from dry and warm slopes to wetter and cooler areas) and at the same time adheres to strict preferences in light, drainage, and soil nutrient deficiency.

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