

Original Article

<https://doi.org/10.35885/1684-7318-2021-1-35-46>

Spatial structure of *Globularia bisnagarica* L. (Plantaginaceae, Magnoliopsida) coenopopulations

A. O. Kondratieva, A. S. Parkhomenko, A. V. Bogoslov,
I. V. Shilova, A. S. Kashin ✉

Saratov State University
83 Astrakhanskaya St., Saratov 410010, Russia

Received: 11 December 2020 / revised: 14 January 2021 / accepted: 27 January 2021

Abstract. The paper presents the results of the spatial distribution analysis of 18 *Globularia bisnagarica* L. coenopopulations in the Saratov, Samara, Ulyanovsk and Orenburg regions and the Republic of Tatarstan. The analysis was carried out with the Spatstat package of the R environment for statistical computing. The research reveals an aggregation tendency for the *G. bisnagarica* coenopopulations. It is suggested that this tendency may be attributed to the prevalence of seed reproduction and certain peculiarities of dissemination (barochory) in the studied coenopopulations as well as to the confinement of the species to eroded landforms (slopes of watersheds, gullies, runoff hollows, etc.) characterized by high heterogeneity of environmental conditions. It has been established that the majority of *G. bisnagarica* coenopopulations grow in heavily or moderately sodded habitats. Nevertheless, in the studied communities, *G. bisnagarica* occurs abundantly and dominates along with *Stipa pennata*, *Bromus inermis*, *Salvia nutans*, *Elytrigia repens*, *Poa compressa*, etc. Finally, the spatial structure of *G. bisnagarica* coenopopulations is impacted by the interspecific competition in calciphilous phytocenoses under the invasion of eurybiontic steppe grasses.

Keywords: *Globularia bisnagarica*, spatial structure, Ripley's *K*-function, R environment

For citation: Kondratieva A. O., Parkhomenko A. S., Bogoslov A. V., Shilova I. V., Kashin A. S. Spatial structure of *Globularia bisnagarica* L. (Plantaginaceae, Magnoliopsida) coenopopulations. *Povolzhskiy Journal of Ecology*, 2021, no. 1, pp. 35–46. <https://doi.org/10.35885/1684-7318-2021-1-35-46>

INTRODUCTION

Spatial structure is considered a key complex parameter for evaluating the inherited adaptive potential and competition capacity of a population under environmental conditions

✉ Corresponding author. Botanical Garden, Saratov State University, Russia.

ORCID and e-mail addresses: <https://orcid.org/0000-0001-5000-8914>, popova.ao@mail.ru (Anna O. Kondratieva); <https://orcid.org/0000-0002-9948-7298>, parkhomenko_as@mail.ru (Alena S. Parkhomenko); <https://orcid.org/0000-0002-2248-1285>, dandelioncave@mail.ru (Artem V. Bogoslov); <https://orcid.org/0000-0002-9828-4229>, schiva1952@yandex.ru (Irina V. Shilova); <https://orcid.org/0000-0002-2342-2172>, kashinas2@yandex.ru (Alexandr S. Kashin).

(Dumacheva, Cherniavskih, 2014). The examination of spatial structure in rare species populations promotes their stable and fairly sustainable existence in a particular biocoenosis and is therefore a critical part of environmental protection action.

Spatial structure is defined as an arrangement of specimens and their groups in space. Such arrangement depends on external environmental factors as well as biological species traits – plant life-form, reproduction type, seed dissemination, vegetative vagility, etc.

Conventionally, there are two approaches to estimating coenopopulation spatial structure – functional and geometrical. The functional approach is concerned with the use of resources by a coenopopulation and environmental factors it is subject to. The geometrical approach involves the evaluation of the vertical and horizontal arrangement of coenopopulation spatial structure elements (Zaugol'nova, 1994; Fardeeva, Rogova, 2012; Gu et al., 2017; Abellanas, Pérez-Moreno, 2018). According to V. S. Ipatov and L. A. Kirikova (1997), there are four types of coenopopulation horizontal structure: random, aggregated, regular, and clinal.

Random spatial distribution refers to an arrangement where all specimens may occur in any point within the studied area with equal probability. According to ecological literature, coenopopulations exhibit random structure when they grow under homogeneous and optimal conditions, whereas any deviations from this distribution type are found under unfavorable conditions (Zaugol'nova, 1994; Ipatov, Kirikova, 1997; Mirkin et al., 2001).

Next, aggregated structure is observed when specimens aggregate in some localities within the studied area and are absent (or very few) in others. This type of spatial distribution is attributed to uneven seed dispersal, heterogeneous ecotope, reproduction type of a species, etc.

Regular arrangement suggests that specimens are fairly equally spaced from one another. This type of structure rarely occurs in the wild; in planting, regular arrangement is nondurable because, with time, specimens are unevenly eliminated due to their varying vitality under given conditions.

Finally, clinal structure is marked by the gradual change of specimen density over the studied territory; this change results mainly from the spatial changes in habitat (e.g., along the slope). Clinal structure comes in the following forms: clinal-random (the probability of occurrence of a specimen in any spatial point gradually changes across the area) and clinal-aggregated (the number and size of aggregations evolve).

MATERIAL AND METHODS

The subject of the research is *Globularia bisnagarica* L. (= *G. punctata* Lapeyr., *G. willkommii* Nylan) – a relict flora element in the forest-steppe zone of South-Eastern Europe. The species grows mainly in Atlantic, Central and Southern Europe, the Mediterranean region (Hazler Pilepić et al., 2016; Affenzeller et al., 2018). Another fragment of the species range is found more than 1500 km away from its main range – in European Russia and Kazakhstan. The species is listed in the Red Books of several states and regions: the Russian Federation and Kazakhstan, the Republics of Bashkortostan and Tatarstan, the Stavropol Krai, and the Orenburg, Samara, Saratov and Ulyanovsk regions

(The Red Book, 2008, 2014). The species is strictly confined to elevated landforms and calcareous substrates. It is an obligate calciphile, erosiophyte and cenophobe; it becomes scarcer with an increase of sodding and the development of grass-forb communities on chalk outcrops and slopes (Kuznetsova, 2003).

The research was carried out in May and early June of 2019–2020 in 18 *G. bisnagarica* coenopopulations (CP) in: a) the Saratov region: Tep – Volsky district, near the Teplovka village; Pch – Khvalynsky district, near the Eremkino village, the Piche-Pandra mountain; Elh – Khvalynsky district, near the Khvalynsk town, the Eloha ridge; Zay – Khvalynsky district, near the Khvalynsk town, the Zayats mountain; Trm – Volsky district, near the Truyevaya Maza village; b) the Samara region: Bkm – Krasnoyarsky district, near the Bolshaya Kamenka village, Kms – Kamyshlinsky district, near the Kamyshla village; Nkv – Shentalinsky district, near the Novy Kuvak village; Srg – Sergievsky district, near the Staroye Yakushkino village, the Vysokaya mountain; c) the Ulyanovsk region: Cha – Radishchevsky district, near the Chaushi village; Grm – Radishchevsky district, near the Gremyachy helmet; Lhv – Mainsky district, near the Lyakhovka village; Skv – Pavlovsky district, near the Shikovka village; d) the Orenburg region: Alb – Ponomaryovsky district, near the Alyabyevo village; Slt – Aleksandrovsky district, near the Sultakay village; and e) the Republic of Tatarstan: Bkv – Severny district, near the Bakaevo village; Bvl – Bavlinsky district, near the Bavly town; Krb – Bugulminsky district, near the Karabash settlement (Fig. 1).

At the field stage, we used traditional phytocoenotic methods based on sample area mapping; the size and form of sample areas were selected in accordance with the specimen plant life-form. For each CP, two 1 m² sample areas were mapped. Considering that the species plant life-form is a caudex-forming perennial herbaceous plant with the tap-root system, a specimen of seed origin was selected as a measurement unit (Kuznetsova, 2003). Specimen ontogenetic state was also taken into account.

Next, we took images of the provisional coordinates of measurement units within the maps. The obtained coordinates were subject to the subsequent analysis of spatial structure. In order to conduct a spatial analysis and determine the significance value of the revealed spatial patterns, various mathematic methods were required (Fardeeva et al., 2009; Fardeeva, Rogova, 2012; Gu et al., 2017; Abellanas, Pérez-Moreno, 2018). In the present paper, the spatial analysis of point patterns was performed with the tools implemented in the Spatstat package (Baddeley et al., 2015) of the R environment for statistical computing (R Core Team R..., 2020).

In the description of our methods below, a “point” refers to a measurement unit – a *G. bisnagarica* specimen of seed origin.

First, we assessed the intensity of a process producing the observed point arrangement and visualized its spatial variations in the form of local density maps using the kernel method (Silverman, 1986; Scott, 1992).

Patterns of specimen spatial distribution in the areas under study were revealed with Ripley's $K(r)$ – function (Ripley, 1976, 1977). The function value is proportional to the expected number of points N_x in a random sub-area B_r , which is shaped as a circle with a radius r : $K_{(r)} = E[N_x(B_r)]/\lambda$, where λ is the intensity of a process producing the observed pattern. In the case of complete spatial randomness (CSR), where points are arranged

randomly, the value of Ripley's function amounts to the area of a circle with a radius r : $K_{CSR}(r) = \pi r^2$. $K(r)$ deviations from $K_{CSR}(r)$ indicate aggregation or sparseness of points for a given r value. When $K(r)$ function curve is above $K_{CSR}(r)$, there are more points at a distance less than or equal to r than in the case of random distribution. When $K(r)$ is below $K_{CSR}(r)$, there is a regular (sparse) distribution of points at a distance less than or equal to r . For convenience, $K(r)$ is depicted as $L(r)$ - r function, where $L(r)$ is calculated as follows: $L(r) = \sqrt{K(r)/\pi}$ (Besag, 1977). Functions $K(r)$ and $L(r)$ are cumulative and may exhibit spatial interaction between objects as high as r ; the latter complicates interpretation of the results. In this regard, we also estimated the pair correlation function (PCF): $g(r) = K'(r)/2\pi r$, where $g(r)$ is a pair correlation function and $K'(r)$ is a derivative of $K(r)$ Ripley's function (Illian et al., 2008). PCF displays aggregation or regularity at a distance equal to r .

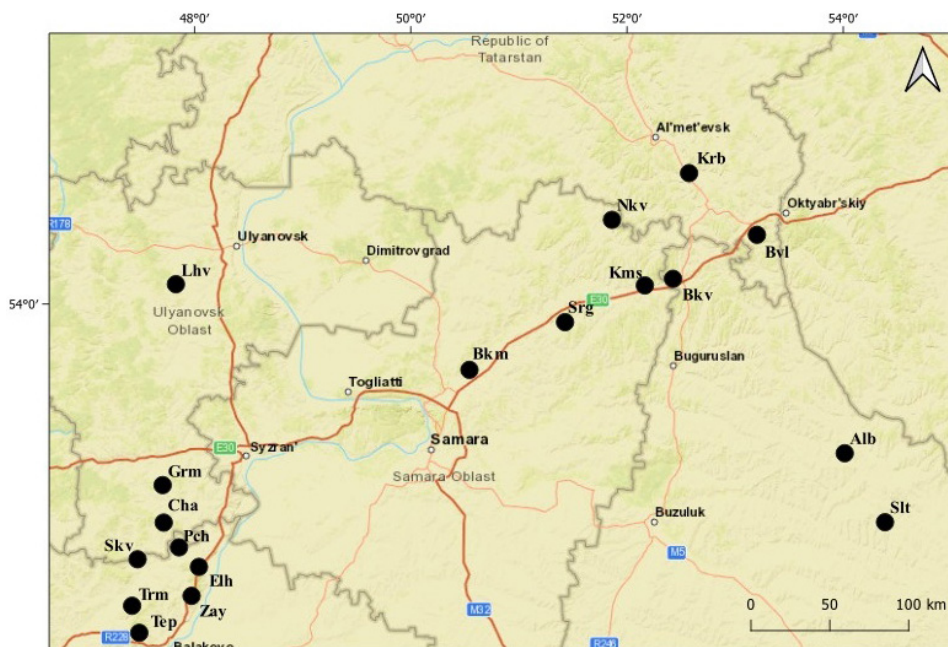


Fig. 1. The geographical distribution of the studied *Globularia bisnagarica* coenopopulations: *Saratov region*: Tep – Volsky district, near Teplovka; Pch – Khvalynsky district, near Eremkino, Piche-Pandra mountain; Elh – Khvalynsky district, near Khvalynsk, Eloha ridge; Zay – Khvalynsky district, near Khvalynsk, Zayats mountain; Trm – Volsky district, near Truyevaya Maza; *Samara region*: Bkm – Krasnoyarsky district, near Bolshaya Kamenka; Kms – Kamyshlinsky district, near Kamyshla; Nkv – Shentalinsky district, near Novy Kuvak; Srg – Sergievsky district, near Staroye Yakushkino, Vysokaya mountain; *Ulyanovsk region*: Cha – Radishchevsky district, near Chaushi; Grm – Radishchevsky district, near Gremyachy; Lhv – Mainsky district, near Lyakhovka; Skv – Pavlovsky district, near Shikovka; *Orenburg region*: Alb – Ponomaryovsky district, near Alyabyevo; Slt – Aleksandrovsky district, near Sultakay; *Republic of Tatarstan*: Bkv – Severny district, near Bakaevo; Bvl – Bavlinsky district, near Bavly; Krb – Bugulminsky district, near Karabash

In order to determine the significance of deviation of the empirical functions $L(r)$ - r and $g(r)$ from their patterns under random spatial distribution, we employed the Monte Carlo simulation method (Besag, Diggle, 1977). The Monte Carlo test involves generating simulated realizations from the null hypothesis. If the empirical functions lie outside the interval bounded by the upper and lower envelopes of CSR, the null hypothesis is rejected.

When interpreting the results, we also took into account some traits of *G. bisnagarica* communities: total projective cover (TPC) and projective cover (PC) of dominant species – and habitat parameters: slope steepness (angle) and exposure, distribution of precipitation in relation to micro-elevation.

RESULTS AND DISCUSSION

The analysis of $L(r)$ - r and $g(r)$ function patterns (regardless of ontogenetic state) reveals three types of *G. bisnagarica* specimen distribution: random, aggregated, and clinal-aggregated.

In most communities, specimens are distributed in a clinal-aggregated pattern where the number and size of aggregations gradually evolve. The behavior of $L(r)$ - r and $g(r)$ functions indicates the presence of aggregations of varying size and density; aggregations are either randomly arranged or prone to cluster. In some coenopopulations (CPs Bkm and Srg), slight specimen sparseness for low r values is observed. Based on the size and mutual arrangement of aggregations, this spatial distribution type is subdivided into three subtypes (Fig. 2).

The first subtype is marked by the formation of articulated aggregations within a radius of 0.02–0.25 m and by gradual density reduction with an increase of interaction radius. The coenopopulations belonging to this subtype (Krb, Bkv, Skv) are located on relatively low-angle slopes (5–10°; 20° in one CP) of north-eastern, eastern and western exposure; slope steepness gradually decreases with a change of exposure from north-eastern through eastern to western. CP Krb growing on a 20° slope is the northernmost in the studied range area. CP Bkv growing on a medium-steepness slope is located in the north-east, while CP Skv growing nearly on plain (slope angle is approximately 5°) – in the south-west of the studied area (Fig. 1). Therefore, in the first subtype coenopopulations, slope steepness gradually declines from the north-east to the south-west, which might be due to the fact that, along this geographical gradient, precipitation decreases while insolation increases. In the communities of the mentioned ecotopes, TPC comprises 75–90%, whereas *G. bisnagarica* has high PC values of 50–75%. Sodding increases with the decline of slope angle as well as in the direction from the north-east to the south-west. It is more likely connected to a degree of slope steepness and, consequently, precipitation volume rather than to the geographical location of CPs or their exposure: otherwise, a rise of aridity (linked to geographical location) and insolation (related to exposure) would have led to the decrease of sodding from the north-east to the south-west. In the communities under thick sodding (Skv, TPC=90%), *G. bisnagarica* dominates along with *Stipa pennata*. Under moderate sodding (Krb, TPC=75%), the following species predominate: *G. bisnagarica*, *Elytrigia repens* and *Oxytropis spicata*. In one community (Bkv, TPC=75%), *G. bisnagarica* is the only dominant species with PC amounting to 75%.

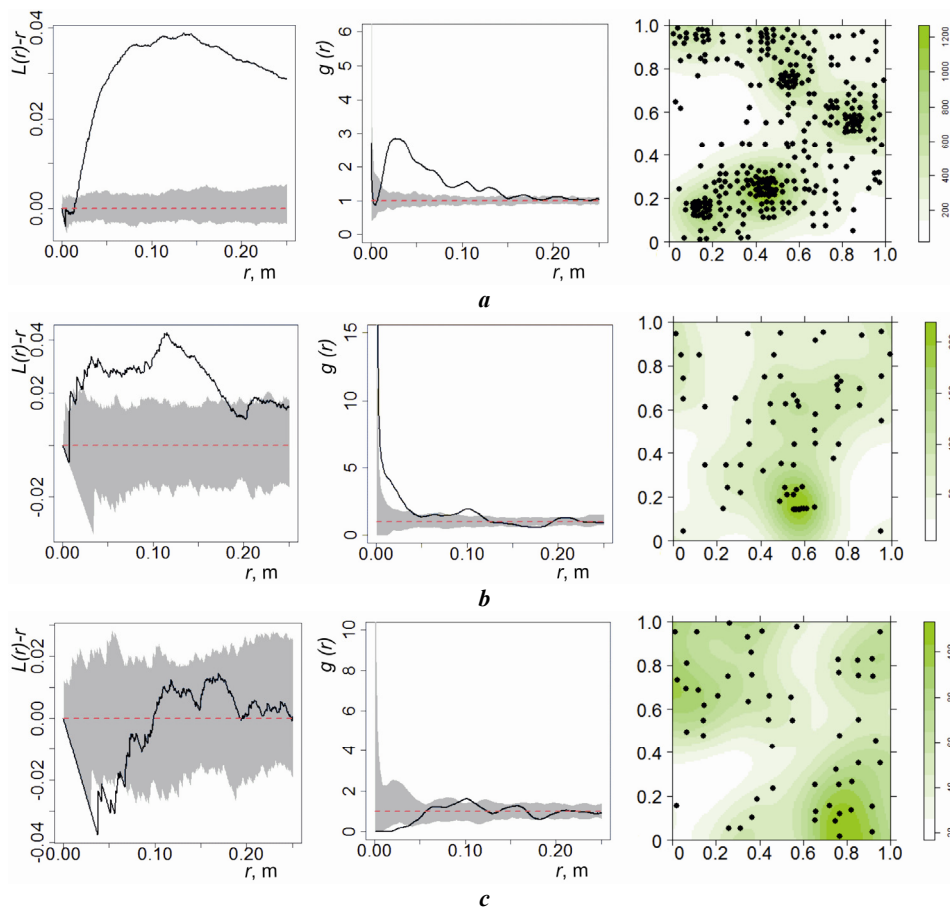


Fig. 2. $L(r)-r$, $g(r)$ functions and local density maps of the clinal-aggregated spatial distribution of specimens in *G. bisnagarica* coenopopulations: *a* – gradual density reduction with an increase of interaction radius; *b* – formation of small aggregations with their subsequent association in a larger scale; *c* – regularity in small interaction radius and complete spatial randomness at larger distances. On plots: solid black line – the empirical functions values; red dotted line – the theoretical functions under CSR; shaded areas – the simulation envelopes of CSR

The second subtype comprises four CPs: Tep, Cha, Grm and Lhv. This subtype is characterized by the formation of small aggregations within a radius of 0.04–0.13 m with their subsequent association in larger scale with an interaction radius of 0.22–0.90 m. The coenopopulations belonging to this subtype grow along the western border of the studied range area. Their habitats are confined to 5–40° watershed slopes, primarily, of the south-western and south-eastern exposure. CP Lhv is the only one that grows on a south-facing slope which is also rather steep (40°); in terms of geographical location, it is the northernmost of the second subtype CPs. Of the three remaining CPs growing in

the south-west of the studied range area, CP Cha is located on a minimum-angle slope (5°) of the south-eastern exposure. CP Grm grows on a medium-steepness slope (15°) of the west-north-western exposure; CP Ter grows on a larger-steepness (20–30°) slope of south-western exposure. Therefore, the CPs comprising this subtype are located on maximum-steepness, south-facing slopes in the far north-west of the studied area and prefer slopes of low and medium steepness and north-western and south-eastern exposure in the far south-west. This is easily explained by the fact that climate aridity and total insolation level increase from the north-west to the south-west; thus, towards the south, the CPs are drawn to lower-steepness slopes and to slopes of north-western and south-eastern rather than southern exposure. Also, TPC values of the communities rise from the north (25% – Lhv) to the south (80% – Tep, Cha, Grm). In general, in this subtype, *G. bisnagarica* PC values are below the PC values of the first subtype coenopopulations (25–80% versus 75–90%, respectively). In a community with minimum sodding, *G. bisnagarica* is abundant and the only dominant species. In the communities with the highest TPC values (80%), PC of *G. bisnagarica* varies considerably. In CP Cha, *G. bisnagarica* PC is 50%, while there are two equally dominant species: *G. bisnagarica* and *Stipa pennata*. In CP Grm, *G. bisnagarica* has a dominant status and a PC of 25%; *Bromus riparius* and *Salvia nutans* dominate along with *G. bisnagarica*.

The third subtype is marked by specimen regularity in small interaction radius (up to 0.04 m) and complete spatial randomness or poorly articulated aggregation in a radius of 0.07–0.22 m. Two CPs belong to this subtype: Bkm and Srg. Their habitats are located on 5–10° south-facing slopes. The communities exhibit a fairly equal degree of sodding: TPC amounts to 60% in Bkm and 75% in Srg. In both cases, *G. bisnagarica* has 50% PC. Apart from *G. bisnagarica*, the following species dominate in the mentioned communities: *Caragana frutex*, *Festuca valesiaca*, *Potentilla incana*, *Stipa pennata*, *Viola ambigua*, *Pimpinella tragium* and *Psephellus marshallianus*.

Overall, in *G. bisnagarica* CPs with the clinal-aggregated type of spatial distribution, the degree and size of aggregation decline as slope exposure changes from north-eastern and western through south-eastern to southern. In the same direction, specimens are more prone to shift from aggregated to random distribution. The latter shift is also evident as sodding declines and erosion increases in the direction from the bottom to the top of a slope.

Thus, the clinal-aggregated type of spatial distribution prevails on relatively low-angle, weakly eroded slopes under sufficient precipitation and fairly low insolation. In this type of spatial distribution, *G. bisnagarica* grows abundantly and hence contributes significantly to the total projective cover. Apparently, the growing conditions of warm slopes, on which moisture is distributed more or less evenly, facilitate seed germination and seedling development. However, given the peculiarities of seed dispersal (barochory), young specimens are unevenly spread, especially in communities with high TPC values. Their distribution becomes more uneven and a degree of aggregation rises as slope exposure changes from southern to western, eastern and north-eastern.

Our observations show that small aggregations of high density observed in the first subtype CPs are mostly constituted of pre-generative plants. Mature and senescent plants exhibit a tendency towards random distribution. Therefore, along the defined exposure

shift, coenopopulations become more able to self-restore. This type of distribution is, apparently, a result of intra- and interspecific competition under thick sodding (TPC of 75–90%). In communities on steeper slopes (the second subtype), TPC values remain high and *G. bisnagarica* still dominates, but with lower values of PC. In these communities, aggregation density is lower; aggregation borders are faded; distribution is verging on random. This tendency is even more prominent on lower-angle, south-facing slopes (the third subtype). Since *G. bisnagarica* is an erosiophyte and an obligate calciphile, it spreads more actively over areas with disrupted slope surface and calcareous rock outcrops than over sodded areas. Nevertheless, in disrupted slope areas, specimen density and aggregation drastically decline with a rise of altitude; it is most likely due to soaring moisture deficit.

Random spatial distribution, where all specimens may occur in any spatial point within the studied area with equal probability, is found in six CPs: Alb, Nkv, Elh, Trm, Bvl and Zay. The analysis of $L(r)$ - r and $g(r)$ function behavior does not reveal any significant deviations from complete spatial randomness (Fig. 3). The CPs grow on steep slopes (10–45°) of eastern, western and north-western exposure. The only exception is CP Bvl which grows on a south-facing steep slope (40°) and is located, similar to CP Krb belonging to the first clinal-aggregated subtype, in the north-east of the studied area. TPC values amount to 40–90%. PC values of *G. bisnagarica* are 10–60%. Under maximum sodding (Elh, TPC=90%), PC of *G. bisnagarica* is 30%; the communities are dominated by *Bromus riparius*, *Polygala comosa*, *Stipa pennata* and *Viola ambigua*. Under moderate sodding (Elh, TPC=40%), *G. bisnagarica* is the only dominant species with 30% PC. In one community (Bvl), *G. bisnagarica* specimens are scattered (PC=10%), while *Stipa pennata* and *Aster alpinus* prevail. In literature, random distribution is treated as an indicator of growing conditions stability (Ipatov, Kirikova, 1997; Fardeeva, Rogova, 2012). This is confirmed by our research results. *G. bisnagarica* remains a dominant species even when calciphilous communities are inhibited by firm-bunch grasses such as *Stipa pennata* and *Stipa tirsia* as well as by other steppe species (*Bromus riparia*, *Poa compressa*, *Salvia verticillata*, *Viola ambigua*).

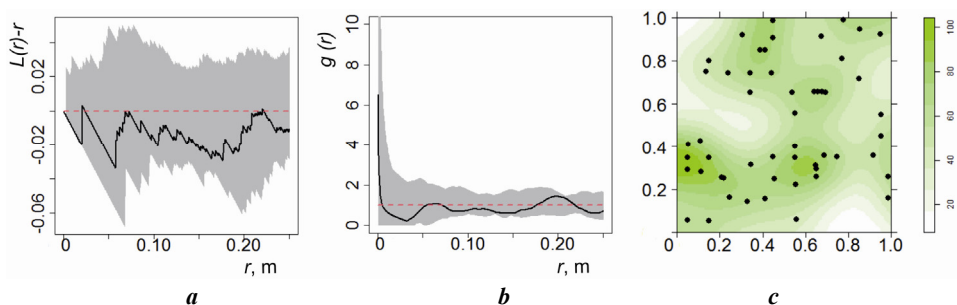


Fig. 3. $L(r)$ - r (a), $g(r)$ (b) functions and local density maps (c) of the random spatial distribution of specimens in *G. bisnagarica* coenopopulations. On plots: solid black line – the empirical functions values; red dotted line – the theoretical functions under CSR; shaded areas – the simulation envelopes of CSR

Thus, the confinement of random distribution CPs to west- and east-facing slopes and, in the north-west of the studied area, to south-facing slopes does not agree with the distribution pattern which was earlier revealed for clinal-aggregated CPs, where a degree of specimen aggregation declined as slope exposure changed from northern through western and eastern to southern. The research shows that, in the same direction, a tendency towards random specimen distribution increases as well. This may only be explained by high steepness of slopes in the habitat of random distribution CPs. Due to western or eastern exposure and higher latitude, the habitat of random distribution CPs is more favorable in terms of better precipitation and milder insolation; also, given that slopes are steeper and more eroded, competition with other species is weaker. Also, specimens grow here in a narrow strip on the border between the sodded and eroded parts of the slope and are subject to similar conditions – hence their random spatial distribution.

Aggregated spatial distribution is found in three CPs: Kms, Pch, and Slt. This type of specimen distribution is observed in communities where specimens aggregate in one locations and are absent (or scarce) in others (Ipatov, Kirikova, 1997). The analysis of $L(r)$ - r and $g(r)$ functions shows that the curves lie outside the interval bounded by the upper and lower envelopes of CSR (Fig. 4). The interaction radius is 0.03–0.18 m. In habitats of aggregated distribution CPs, slopes are not very steep (10 – 20°) and exclusively west-facing. TPC amounts to 50–90%. Under thick sodding (Slt), *G. bisnagarica* is scattered; its PC is 10%. In this community, *Stipa pennata*, *Salvia nutans* and *Onosma simplicissima* predominate. In one community (Kms), there is only one *G. bisnagarica* specimen with a PC of 1%; TPC is 75%; *Bromus inermis*, *Salvia verticillata* and *Medicago falcate* contribute to TPC the most. Therefore, in aggregated communities, the spatial distribution of *G. bisnagarica* is affected by the increased competition load resulting from the invasion of eurybiontic steppe species to calciphilous communities on relatively small-angle (10 – 20°) and, consequently, weakly eroded slopes of western exposure with good precipitation and moderate insolation. Also, as we mentioned above, another factor contributing to the aggregated specimen distribution is uneven dispersal of seeds which fall and germinate close to a maternal plant.

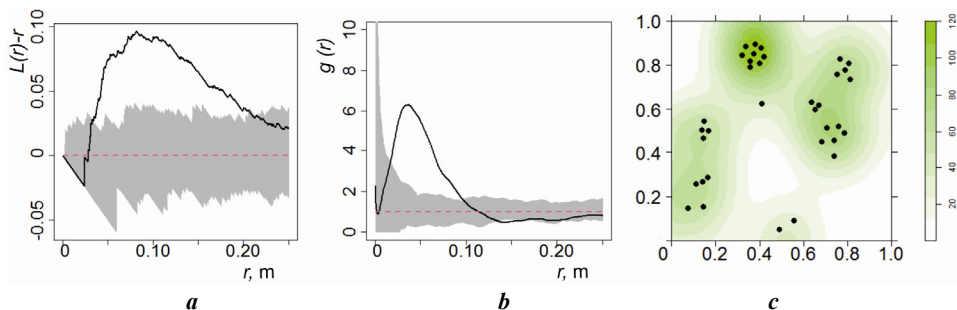


Fig. 4. $L(r)$ - r (a), $g(r)$ (b) functions and local density maps (c) of the aggregated spatial distribution of specimens in *G. bisnagarica* coenopopulations. On plots: solid black line – the empirical functions values; red dotted line – the theoretical functions under CSR; shaded areas – the simulation envelopes of CSR

CONCLUSION

Our analysis of the spatial structure of *G. bisnagarica* coenopopulations (regardless of ontogenetic state) reveals a strong tendency to aggregation. We suggest that this tendency is linked to the following factors: the species confinement to eroded landforms with a wide range of growing conditions (slopes of watersheds, gullies, runoff hollows, etc.); the prevalence of seed reproduction and certain peculiarities of dissemination (barochory) in specimens.

It is established that, in *G. bisnagarica* coenopopulations, aggregated and clinal-aggregated structures are due to the increased competition load resulting from the invasion of eurybiontic steppe species to calciphilous communities. Both patterns are predominant on poorly-eroded, low-angle slopes with sufficient precipitation and fairly low insolation.

Furthermore, most *G. bisnagarica* coenopopulations are heavily or moderately sodded. Nevertheless, in the studied communities, *G. bisnagarica* is abundant and dominant along with *Stipa pennata*, *Bromus inermis*, *Salvia nutans*, *Elytrigia repens*, *Poa compressa*, etc. Finally, *G. bisnagarica* spatial distribution is impacted on by the interspecific competition in calciphilous phytocenoses under the invasion of eurybiontic steppe grasses.

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ПРОСТРАНСТВЕННАЯ СТРУКТУРА ЦЕНОПОПУЛЯЦИЙ *GLOBULARIA BISNAGARICA* L. (PLANTAGINACEAE, MAGNOLIOPSIDA)

А. О. Кондратьева, А. С. Пархоменко, А. В. Богослов,
И. В. Шилова, А. С. Кашин ✉

Саратовский национальный исследовательский государственный университет
имени Н. Г. Чернышевского
Россия, 410012, г. Саратов, ул. Астраханская, д. 83

Поступила в редакцию 11.12.2020 г., после доработки 14.01.2021 г., принята 27.01.2021 г.

Аннотация. Представлены результаты изучения пространственной структуры 18-ти ценопопуляций *Globularia bisnagarica* L. на территории Саратовской, Самарской, Ульяновской, Оренбургской областей и Республики Татарстан с использованием пакета Spatstat среды статистического программирования R. Выявлена тенденция к образованию агрегаций, что может быть обусловлено преобладанием семенного типа размножения и особенностями диссеминации изучаемого вида (барохория), а также приуроченностью местообитаний к эрозионным формам рельефа, отличающимся высокой неоднородностью условий (склоны водоразделов, балок, ложбины стока и др.). Установлено, что большинство ценопопуляций *G. bisnagarica* произрастает в условиях сильного и умеренного задернения. Однако, несмотря на это, в подобных местообитаниях *G. bisnagarica* в сообществах встречается обильно, и является доминантом наряду с такими видами как: *Stipa pennata*, *Bromus inermis*, *Salvia nutans*, *Elytrigia repens*, *Poa compressa* и др. Влияние межвидовой конкуренции в условиях заселения кальцефильных фитоценозов эврибионтными степными злаками так же вносит определенный вклад в формирование пространственного рисунка ЦП.

Ключевые слова: *Globularia bisnagarica*, пространственная структура, K-функция Рипли, среда R

Для цитирования. Kondratieva A. O., Parkhomenko A. S., Bogoslov A. V., Shilova I. V., Kashin A. S. Spatial structure of *Globularia bisnagarica* L. (Plantaginaceae, Magnoliopsida) ceno-populations [Кондратьева А. О., Пархоменко А. С., Богослов А. В., Шилова И. В., Кашин А. С. Пространственная структура ценопопуляций *Globularia bisnagarica* L. (Plantaginaceae, Magnoliopsida)] // Поволжский экологический журнал. 2021. № 1. С. 35 – 46. <https://doi.org/10.35885/1684-7318-2021-1-35-46>

✉ Для корреспонденции. Ботанический сад Саратовского национального исследовательского государственного университета имени Н. Г. Чернышевского.

ORCID и e-mail адреса: <https://orcid.org/0000-0001-5000-8914>, popova.ao@mail.ru (Кондратьева Анна Олеговна); <https://orcid.org/0000-0002-9948-7298>, parkhomenko_as@mail.ru (Пархоменко Алена Сергеевна); <https://orcid.org/0000-0002-2248-1285>, dandelioncave@mail.ru (Богослов Артём Валерьевич); <https://orcid.org/0000-0002-9828-4229>, schiva1952@yandex.ru (Шилова Ирина Васильевна); <https://orcid.org/0000-0002-2342-2172>, kashinas2@yandex.ru (Кашин Александр Степанович).