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Article

Analysis of the spatial organization of *Vallonia pulchella* (Muller, 1774) ecological niche in Technosols (Nikopol manganese ore basin, Ukraine)

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Abstract
The ecological niche of *Vallonia pulchella* (Muller, 1774) was investigated by means of the general factor analysis of GNESFA. It was revealed that the ecological niche of a micromollusk is determined by both edaphic factors and ecological features of vegetation. Ecological niche optima may be presented by integral variables such as marginality and specialization axes and may be plotted in geographic space. The spatial distribution of the *Vallonia pulchella* habitat suitability index (HSI) within the Technosols (sod-lithogenic soils on red-brown clays) is shown, which allows predicting the optimal conditions for the existence of the species.

Key words: mollusks, marginality, biodiversity, ecological niche, spatial organization, Ukraine.

Introduction

Much of the research on the selection of habitat by land mollusks is based on the comparison of mollusk communities from geographically different sampling points that differ in plant cover, soil type, and moisture level (Millar, Waite, 1999, Martin, Sommer, 2004, Müller et al., 2005; Weaver et al., 2006). Of the edaphic factors that affect molluscs, the most significant one is the content of calcium in the soil, pH and soil texture (Ondina et al., 2004), as well as the content of exchangeable cations and aluminum (Ondina et al., 1998). The moisture content of soils plays an important role (Nekola, 2003), however, Ondina et al. (2004) note the limited data on the role of soil moisture at a given time in view of the significant variability of this parameter. To solve this problem, it is appropriate to use phytoindication data to assess the autecological features of mollusks and the structure of their communities (Horsák et al., 2007; Dvořáková, Horsák, 2012).

For describing habitat preferences of the mollusk *Vertigo geyeri Lindholm*, 1925, the Ellenberg phytoindication scales were successfully used in Poland and Slovakia (Schenková et al., 2012).

Studies at a large scale level have made it possible to determine the role of edaphic factors in the spatial distribution, abundance, and diversity of mollusks communities (Nekola, Smith, 1999; Juřičková et al., 2008; Szybiak et al., 2009). Particular attention is drawn to the problem of spatial scale and hierarchy of factors affecting mollusks (Nekola, Smith, 1999, Bohan et al., 2000, McClain, Nekola, 2008, Myšák et al., 2013).

The habitat is characterized by the presence of resources and conditions for given species in some territory, as a result of which the colonization of this territory becomes possible, including its survival and reproduction (Hall et al., 1997). The purpose of studying the choice of habitats for species is to identify the characteristics of the environment that make the place suitable for the existence of the species (Calenge, 2005).

Ecological niche models are useful for describing the choice of habitat by species. Hutchinson (1957) proposed a formal, quantitative concept of the ecological niche as a hyper volume in a multidimensional space, defined by ecological variables delimiting where stable populations can be maintained (Kearney et al., 2010). Methodologically, an ecological niche can be described by means of a General niche-environment system factor analysis (GNESFA) (Calenge, Basille, 2008).

The factor analysis of ecological niches is based on the assumption that species are not randomly distributed with respect to ecogeographic variables (Hirzel et al., 2002). The species can be characterized by marginality (which is expressed in the difference between the species mean and the global mean of the ecogeographic variable) and by specialization (which manifests itself in the fact that the species variance is smaller than the global variance).

GNESFA can be implemented in the form of three versions – FANTER, ENFA and MADIFA. Factor analysis of the ecological niche, taking the environment as the reference (FANTER) considers the deformation of the ecological niche relative to the ecological space, which is accepted as referential, i.e. the axes of this space lead to such a state that the ecological space has an ideal spherical shape. On the contrary, the spherical shape is attached to the ecological niche in the analysis of MADIFA (Mahalanobis distances factor analysis), and the curvature of the ecological space indicates the degree of difference in environmental properties from the ecological optimum of the species. Based on the results of MADIFA, the most correct habitat preference map for this species can be constructed (Calenge et al., 2008).

A special point of view is possible in which two distributions (an ecological niche and an ecological space) are considered as focal and referential. This symmetrical viewpoint has an advantage beyond the choice of the reference distribution. This special case is the basis of the ecological niche factor analysis (ENFA). In ENFA, the first axis completely corresponds to marginality, and the subsequent axes describe the specialization of the species. Integration of these axes also makes it possible to build a habitat preference map, but unlike MADIFA, this result within ENFA is not mathematically well-founded.

Caruso et al. (2015) note that, despite the benefits of GNESFA, this type of analysis is not well represented in scientific literature. Even after the publication of the paper (Calenge, Basille, 2008), a number of articles continue to use the ENFA approach not only as a research tool, but also for building habitat preferences maps (De Angelo et al., 2011; Galparsoro et al., 2009; Valle et al., 2011). A number of authors use only MADIFA to describe the distribution of species (Halstead et al., 2010; Hemery et al., 2011; Thiebot et al., 2011). Along with the original work (Calenge, Basille, 2008) in the article by Caruso et al. (Caruso et al., 2015) the environmental niche of a cougar in South America is described using all of the GNESFA techniques.

Mollusks *Vallonia pulchella* (Muller, 1774) is Holarctic species found around the world at high latitudes. In Europe it reported from wetter habitats such as wet meadows and marshes, as well as dry dunes and grasslands (Kerney, Cameron, 1979). In Ukraine it prefers moderately dry and wet meadow habitats. Calciphilic appearance (Gural-Sverlova, Gural, 2012). The population density of *V. pulchella* in alder and oak forests of Belarus was 4-8 individuals/m^2 (Zemoglyadchuk, 2005), in ash-elm forests in Poland it did not exceed the average of 0.13 individuals/m^2 (Koralewska-Batura, Błoszyk, 2007), and in floodplain forests of Slovakia it was 0.07 individuals/m^2 (Čejka, Hamerlik, 2009). On the other hand, J. Hermida et al. (1993) estimated the average density for three studied populations of *V. pulchella* in Spain (meadow and forest habitats, as well as near the river bank) to be 5.9-10.1 individuals/m^2, reaching on separate test plots values of the order of 200 individuals/m^2. In bush willow depressions in Kazakhstan K. Uvalieva (1990) a density of 224 individuals/m^2 was estimated. There are no evidence about ecological properties of the *V. pulchella* population in artificial soils.

The aim of our work is to describe the ecological niche of the micromollusk *Vallonia pulchella* (Muller, 1774) in terms of the edaphic properties and properties of the vegetation cover and to show the spatial features of the variation of the habitat preference index within the artificial soil body – Technosols (soddy-lithogenic soils on red-brown clays) using GNESFA.

Material and Methods

The research was carried out at the Research Centre of the Dnipro Agrarian and Economic University in Pokrov (Fig. 1). The experimental site for the study of optimal regimes of agricultural recultivation was established in 1968–1970. Sampling was carried out on a variant of artificial soil (technozems) formed on red-brown clays (the geographic coordinates of the southwestern corner of the test site are 47°38'55.24"N.L., 34°08'33.30"E.L.). According to WRB 2007 (IUSS Working group WRB, 2007), examined soil belong to the RSG Technosols. Examined profile, also, satisfies the criterion for Spolic prefix qualifier having 20 percent or more artefacts (consisting of 35 percent or more of mine spoil) in the upper 100 cm from the soil surface. From 1995 to 2003, a long-term legume-cereal agrophytocenosis grew on the site, after which the process of naturalization of the vegetation began.

The test site within which sampling was made consists of 7 transects of 15 samples each. Test points form a regular grid with a mesh size of 3 m. Thus, the total test point number is 105. In each test point 10 samples of 10 g weight of dry soil were collected. In each sample molluscs were extracted by sorting with dissecting needle.

Soil mechanical impedance was measured in the field using the Eijkelkamp manual penetrometer at a depth of up to 50 cm with an interval of 5 cm. The average error in the instrument measurement results is ± 8%. For the measurement, a cone with a cross-sectional dimension of 1 cm^2 was used. Within each cell, soil mechanical impedance measurements were made in one-fold replication.

Determination of the aggregate-size distribution was carried out by means of dry sieving (Vadyunina, Korchagina, 1986).

To measure the electrical conductivity of soil in situ the HI 76305 sensor (Hanna Instruments, Woodsocket, R. I.), working in conjunction with the portable instrument HI 993310 were used. The tester estimates the total electrical conductivity of the soil, i.e. combined conductivity of soil air, water and particles. The results of measurements of the device are presented in units of saturation of the soil solution with salts - g/l. Comparison of the measurement results with the instrument HI 76305 with laboratory data allowed estimating the conversion factor of units as 1 dS/м = 155 mg/l.

The humus content was determined by «wet chemistry» method. The essence of the method lies in the determination of organic carbon by oxidation with a mixture of potassium dichromate and sulphuric acid. The organic carbon values obtained can be recalculated into humus or organic matter using the mean coefficient (1.724) (Nelson & Sommers, 1982; Slepetiene et al., 2008). The content of humus is determined by the method of Tyurin. Shrinkage of the soil upon drying was measured according to Vadyunina & Korchagina (1986). Sifted soil samples were brought to a humidity of 31.17 ± 0.35%. After gradual drying in the laboratory, the samples were further dried in an oven at 105°C for 5 hours. The size of the soil samples after shrinkage was measured with a caliper.

The vegetation cover was described within squares with a lateral side of 3 m. The material was collected in June 2012. The physiognomic characteristics of the vegetation cover were established by the results of decoding the digital photographs of the surface of the experimental plot made from a height of 1.5 m (Fig. 2). The main physiognomic types of vegetative cover were singled out visually: 1 – cereals (*Bromus squarrosus* L.); 2 – *Seseli tortuosum* L.; 3 – *Lactuca tatarica* (L.) C.A. Mey.; 4 – legumes (*Medicago sativa* L.); 5 – dead plant residue; 6 – open soil cover. The most typical fragments for the corresponding species were chosen for the images, according to which their color characteristics in RGB format were set. They were used as a testing sample for discriminant analysis. After that, all pictures were decoded, which allowed us to estimate the share that each of the physiognomic types in the cover occupies.

Ecomorphic analysis of vegetation was carried out according to Bel'gard (1950). Biological and ecological characteristics of plants were used according to the work by Tarasov (2012). In the plant community of the studied type of technosoils, the hygromorphs are mainly represented by xeromesophiles

(KsMs) and mesoxerophiles (MsKs) (98.89% of the number of samples). Therefore, as a quantitative measure of the hygromorphic structure of the vegetation, the proportion of xeromesophiles in the plant community was chosen. Plant trophomorphs are represented by mesotrophs and megatrophs. The trophomorphic structure is characterized by the proportion of megatrophs. In the ceonomorphic structure, mainly the stepants (steppe species) (82.37%) and the pratant (meadow species) (17.53%) are represented. Quantitatively, the cenomorphic structure is described with the help of stepants ratio. Heliomorphs are represented by heliophytes (59.88%) and scioheliophytes (40.12%). The adaptation of plants to the light regime is characterized by the proportion of heliophytes (Hel).

In the work the phytoindication scales of Tsiganov (1983) were used (Database of "Flora of vascular plants of Central Russia", http://www.jcbi.ru/eco1).

Statistical calculations were performed with the help of the Statistica 7.0 program and the project for statistical computations R (www.r-project.org) using adehabitat libraries (Calenge, 2006) and vegan (Oksanen, 2011), two-dimensional mapping, estimation of geostatistics and creation of asc-files with data of spatial variability of the environment indicators - using the programs Surfer 8.0 and ArcGis 10.0. The coefficient of spatial correlation of I-Moran was calculated using the Geoda 1.6.6 program (Anselin et al., 2006).

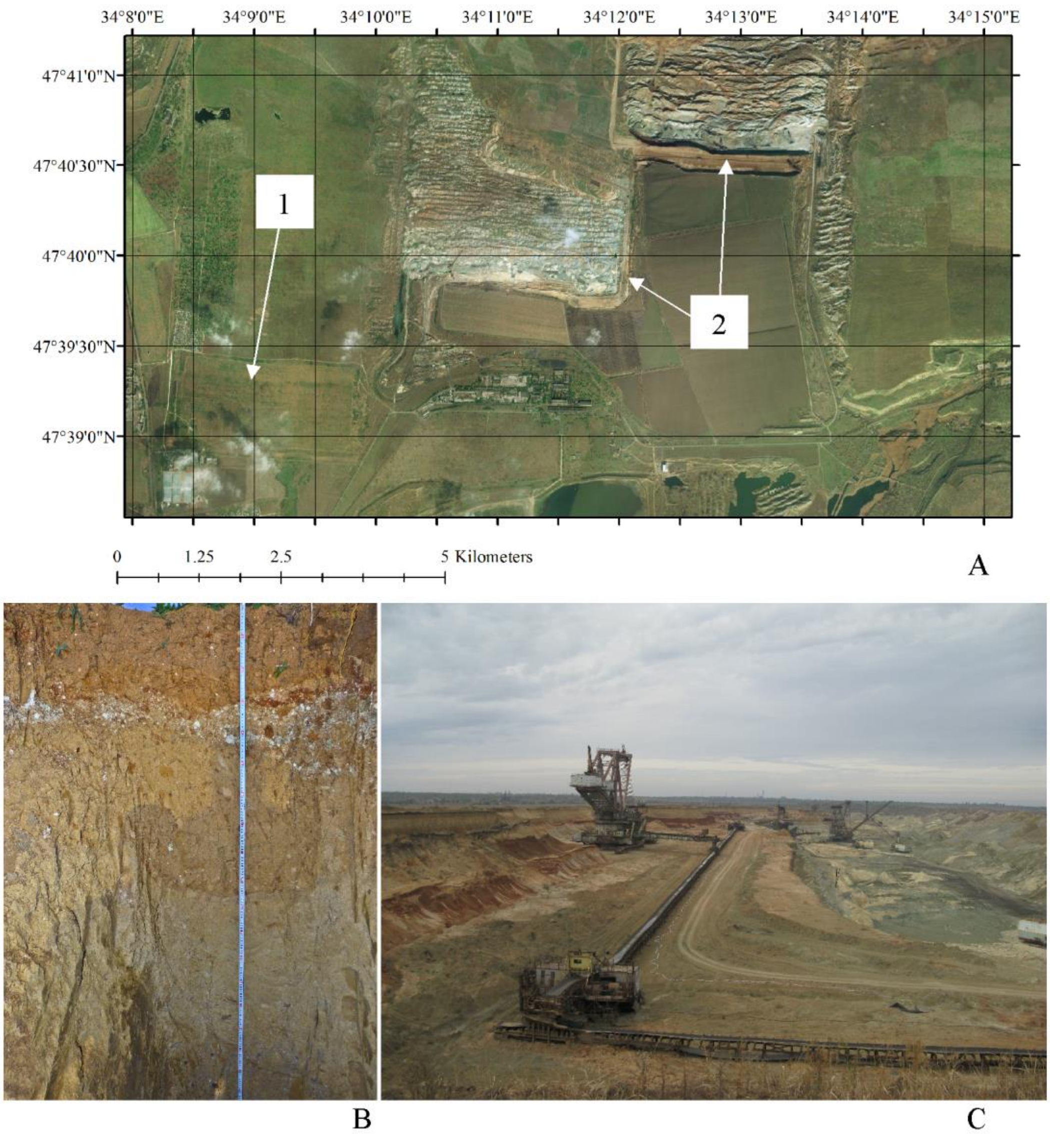

Figure 1. Research Centre of the Dnipro Agrarian and Economic University in Pokrov (Ukraine). A – satellite image of the study area (1 – reclaimed land; 2 – mining quarry); B – technosoils profile; C – quarry panorama view.

Results

In total air-dry soil weighing 10.5 kg were examined, in which 193 specimens of *Vallonia pulchella* (Muller, 1774) were found. Thus, the average density of this species in sod-lithogenic soils on red-brown clays during the study period was 1.84 ind./m^2. In the spatial distribution of individuals, it manifests itself in the formation of “hotspots” - localities with a high concentration of mollusks (Fig. 1, 3).

Figure 2. Soil surface and physiognomic characteristics of the vegetation cover. 1 – type_1 (Bromus sguarrosus L.); 2 – type_2 (Seseli tortuosum L.); 3 – type_3 (Lactuca tatarica (L.) C.A. Mey.); 4 – type_4 (Medicago sativa L.); 5 – type_5 (dead plant residue); 6 – type_6 (open soil cover).

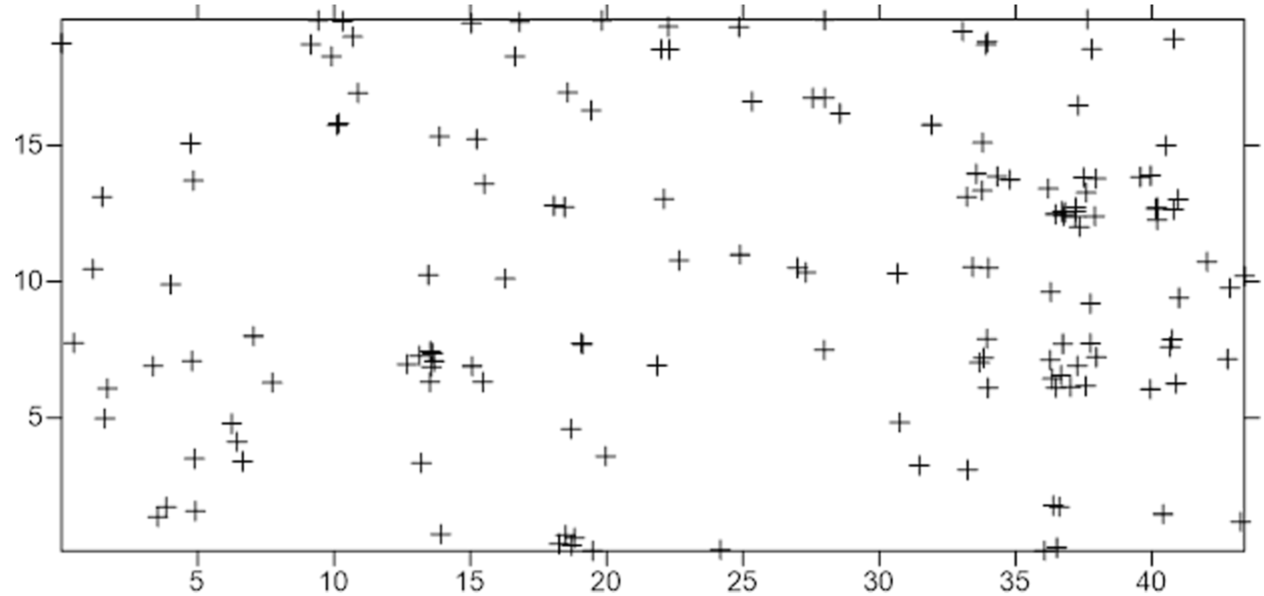

Figure 3. Spatial placement of *Vallonia pulchella* molluscs along the site on sod-lithogenic soils on red-brown clays. The coordinates are in meters.

In order to describe the dependence of the mollusk population of *Vallonia pulchella* on environmental factors, along with the Pearson correlation coefficients (not taking into account the spatial context), I-Moran statistics were calculated (Table 1).

The Pearson and I-Moran correlation coefficient reflects various aspects of the relationship between the mollusc population and environmental factors. Thus, the Pearson correlation coefficient does not indicate a correlation between the density of the mollusc population and the content of humus in the soil. Pearson correlation coefficient reflects the presence of a linear connection. The I-Moran coefficient takes into account the spatial context, since it indicates the correlation of spatially averaged indicators of the compared features. We established a positive and reliable correlation between the number of molluscs and the content of humus by the I-Moran coefficient.

According to soil mechanical impedance indicators, statistically significant Pearson correlation coefficients were established in the absence of statistically significant I-Moran coefficients (except for the 0-5 cm layer). It is obvious that the mechanical impedance indices at the investigated depth of up to 50 cm reflect the state of the soil structure as combination of the density and soil pore space composition. The measurement range extends beyond the area within which animals were selected. It is likely that the variability of the technosoil structure is of a local nature and is not characterized by spatial patterns at a selected scale level. Variations in the composition of clay soil are due to the processes of swelling and shrinkage, as a result of which the soil fissuration is appeared. These processes largely determine the variability of soil mechanical impedance. These processes, being by their nature physico-mechanical, do not form significant spatial patterns.

The aggregate structure of the artificial soil is also a consequence of the physical and mechanical processes of swelling and shrinkage, but in addition to these processes biological processes also affect the soil aggregation. The root systems of plants form the soil structure, as well as the trophic and pedoturbational activity of soil animals. The spatial variability of the vegetation cover, its continuity in time and space lead to the formation of spatially regular structures. As a consequence, we observe a correlation between the number of *Vallonia pulchella* mollusk populations and aggregate structure indices according to two correlation coefficients. Also the correlation with the characteristics of vegetation (physiognomic types and phytoindication indicators) should be noted.

Thus, we found that the mollusks *Vallonia pulchella* are sensitive to the soil aggregate structure. The number of *Vallonia pulchella* increases with an increase in the proportion of aggregates 3-5, 5-7 and 7-10 mm in size and decreases with the growth of the components of small aggregates - <0.25, 0.25-0.5, 0.5-1 mm. Obviously, interaggregate porosity, which is formed in the soil in the presence of aggregates of appropriate size, is an essential condition for the life of these mollusks for their breathing and migration. Small aggregates form a system of pores of small dimensions, which are unfavorable for the life of the micromollusks studied.

Table 1. Correlation of the number of *Vallonia pulchella* with soil characteristics and vegetation properties (only correlation measures are shown that are significant for $p < 0.05$)

Characteristics	Mean. ± st. error	Optimal value ± st. error*	CV, %	Correlations coefficients	
				r-Pearson	*I*-Moran
Humus content and physical properties of soil					
Humus, % (Hum)	0.78±0.01	0.78±0.01	15.36	–	0.18
Conductivity, dSm/m (EC)	0.55±0.01	0.55±0.01	18.43	–	–
Maximum hygroscopic humidity,% (MGM)	8.51±0.16	8.91±0.09	18.78	0.21	0.18
Shrinkage,% (Comp)	20.73±0.35	18.95±0.45	17.51	0.44	0.16
The soil layer temperature in 0-5 cm 03.05.12, °C (Temp1)	22.61±0.10	22.27±0.06	4.65	–0.26	–0.16
The soil layer temperature is 0-5 cm 20.06.12, °C (Temp2)	33.07±0.25	32.69±0.14	7.63	–	–0.10
Aggregate structure, size of fractions, mm					
>10	23.15±0.99	23.98±0.67	43.98	–	–
7–10	7.81±0.24	8.89±0.17	31.05	0.37	0.23
5–7	8.33±0.32	9.78±0.26	39.04	0.37	0.25
3–5	14.39±0.46	16.18±0.33	32.53	0.32	0.22
2–3	13.33±0.46	13.58±0.30	35.68	–	–
1–2	18.54±0.60	17.58±0.43	33.43	–	–0.13
0,5–1	4.19±0.20	3.42±0.14	48.16	–0.31	–
0,25–0,5	6.07±0.30	4.84±0.19	50.89	–0.33	–0.16
<0,25	3.33±0.18	2.52±0.11	56.90	–0.35	–0.16
Soil penetration resistance in MPa at depth, cm					
0–5	3.26±0.08	3.00±0.07	25.01	–0.29	–0.14
5–10	4.49±0.16	3.82±0.12	35.37	–0.37	–
10–15	5.47±0.18	5.32±0.07	34.13	–0.39	–
15–20	6.18±0.21	6.24±0.05	35.35	–0.38	–
20–25	6.80±0.23	6.78±0.05	34.86	–0.33	–
25–30	7.17±0.25	7.12±0.07	36.10	–0.29	–
30–35	7.59±0.26	7.29±0.09	35.14	–0.32	–
35–40	7.80±0.28	7.45±0.11	36.47	–0.31	–
40–45	8.01±0.30	7.68±0.12	37.78	–0.31	–
45–50	8.16±0.31	7.76±0.13	39.31	–0.32	–
Physiognomic types of vegetation					
Type_1	0.07±0.003	0.08±0.003	51.17	0.26	–
Type_2	0.28±0.004	0.28±0.003	15.69	–	–
Type_3	0.19±0.007	0.20±0.005	35.77	–	0.16
Type_4	0.03±0.002	0.03±0.001	78.47	–	–0.09

..continued on the next page

TABLE 1.

Type_5	0.09±0.004	0.10±0.003	41.68	0.28	–
Type_6	0.35±0.009	0.33±0.006	26.89	–	–0.10
Tsyganov phytoindicator values					
Tm	9.73±0.007	9.73±0.005	0.72	–	–
Kn	10.54±0.008	10.52±0.006	0.80	–	–
Om	6.94±0.006	6.95±0.004	0.85	0.20	–
Cr	9.12±0.006	9.13±0.005	0.71	–	–
Hd	7.83±0.005	7.82±0.003	0.68	–	–0.18
Tr	6.38±0.006	6.37±0.003	0.93	–	–
Nt	5.31±0.016	5.30±0.008	3.07	–	–
Rc	9.92±0.009	9.92±0.006	0.97	–	–
Lc	2.21±0.015	2.16±0.008	0.98	–	–0.13
Bellagard ecomorphs					
Hygromorphs (KsMs ratio)	2.48±0.011	2.44±0.007	4.50	–0.32	–0.26
Trophomorphs (MgTr ratio)	2.46±0.016	2.50±0.010	6.47	0.21	0.18
Cenomorphs (St ratio)	0.70±0.004	0.70±0.002	6.08	–	–
Cenomorphs (Pr ratio)	0.12±0.005	0.11±0.003	43.99	–	–0.12
Heliomorphs (Hel ratio)	3.61±0.009	3.57±0.007	2.69	–0.41	–

Symbols: * – values weighted by V. pulchella density

It should be noted that mollusks prefer more xerophilic microstations within the test site with increased mineralization (trophicity) of the soil solution.

Information on the spatial distribution of animals allows comparing the distribution of resources within the site, as well as their particular distribution at the points where mollusks were found (Fig. 2, 4). Obviously, the fact that the general and partial distributions do not coincide indicates the structuring role of the corresponding variable in determining the shape of the ecological niche.

Estimation of the shape of the ecological niche, if the distribution of the availability of resources is set as reference, can be obtained by means of the FANTER analysis (Fig. 3, 5). The largest eigenvalues of the axes identified as a result of this analysis indicates that the marginality described by the axis is the largest and the specialization is the smallest. The smallest eigenvalue indicates a strong specialization and/or low marginality. Thus, both the first and the last axes by the eigenvalues value play an important role in the framework of the FANTER analysis.

The statistical significance of the axes allocated in the FANTER analysis was verified by a randomized test (999 random samples were generated for which the corresponding indices were calculated). The test showed that the first axis statistically significantly differs from the random alternative ($\gamma1 = 4.64$, $p <0.046$, the alternative hypothesis is less), and the second and last two axes of the ecological niche of *Vallonia pulchella* differ significantly from the random distribution ($\gamma2$ = 3,.36, $p <0.19$, the alternative hypothesis is less, $\gamma44 = 0.12$, $p = 0.93$, $\gamma45 = 0.09$, $p = 0.86$, alternative hypothesis is greater). This result suggests that within the studied area the distribution of molluscs is characterized by both marginality and specialization.

Marginality and specialization are determined both by edaphic factors and ecological features of vegetation (Table 2).

The ecological niche of *Vallonia pulchella* is characterized by marginality, which is characterized by shrinkage of soil, indicators of aggregate structure, and soil mechanical impedance. Of all the properties of vegetation in the definition of marginality, only the fraction of heliophytes and the ratio in the physiognomic structure of cereals (type 1) play a role. The specialization is determined by the humus content, the maximum hygroscopic humidity, the temperature of the upper soil layer, the aggregate structure, soil mechanical impedance at a depth of more than 25 cm, a wide range of physiognomic types, nitrogen content in soil according to phytoindication estimates.

Table 2. Results of analysis of the ecological niche of *Vallonia pulchella* by GNSFA methods (only correlation measures are shown that are significant for p <0.05)

Ecological factors	FANTER					ENFA		MADIFA	
	Marginality		Specialization		M	Sp1	Sp2	C1	C2
	C1	C2	C44	C45					
Physiognomic type of vegetation cover									
Hum	–	–	0.26	–	0.22	–	0.24	0.25	–
EC	–	–	–	–	–	–	–	–	–
MGM	–	–	–	–0.21	0.47	0.22	–	–	–
Comp	–0.24	–	–	–	0.57	–	–	–	–
Temp1	–	–	–0.25	–	–0.47	–	–	–	–0.33
Temp2	–	–	–	–	–0.22	–	–	–	–0.24
Aggregate structure, aggregate dimensions, mm									
>10	–	–	0.23	–	–	–	0.20	0.27	–
7–10	–	–	–	–	0.59	–	–	0.20	0.23
5–7	–	–	–	–	0.60	–	–	–	–
3–5	–0.21	–	–	–	0.46	–	–	–	–
2–3	–	–	–0.21	–	0.08	–	–0.24	–	–
1–2	–	–	–0.26	–	–0.37	–	–	–0.23	–0.27
0,5–1	0.27	–0.29	–	–	–0.39	–	–	–	–
0,25–0,5	0.23	–	–	–	–0.54	–	–	–	–
<0,25	–	–	–	–	–0.51	–	–	–	–
Soil mechanical impedance at depth, cm									
0–5	–	–	–	–	–0.58	–	0.21	–	–
5–10	–	–	–	–	–0.71	–	–	–	–
10–15	0.28	–0.23	–	–	–0.76	–	–	–	–
15–20	0.24	–0.20	–	–	–0.72	–	–	–	–
20–25	–	–	–	–	–0.71	–	–	–	–
25–30	–	–	0.20	–	–0.66	–	–	–	–
30–35	–	–	–	–	–0.65	–	–	–	–
35–40	–	–	0.20	–	–0.64	–	–	–	–
40–45	0.20	–	0.20	–	–0.62	–	–	–	–
45–50	0.24	–	0.20	–	–0.61	–	–	–	–
Physiognomic type of vegetation cover									
Type_1	–0.28	–	–	–	–	–	–	–	–
Type_2	–	–	–	0.25	–	–0.26	–	–	–0.27
Type_3	–	–	–	–	0.32	–	–	–	–
Type_4	–	–	–0.33	0.27	–	–0.28	–0.41	–	–0.33
Type_5	–	–	–	0.24	0.35	–0.23	–	0.27	–
Type_6	–	–	–	–0.28	–0.35	0.28	–	–0.25	–
Phytoindication values of environmental factors									
Tm	–	–	–	–	–	–	–	–	–
Kn	–	–	0.21	–	–0.22	–	–	–	0.23
Om	–	–	–	–	0.40	–0.40	–	0.32	–0.27
Kr	–	–	–	–	–	–	–	–	–
Hd	–	–	–	–	–0.22	–	–	–	–
Tr	–	–	–	–	–0.23	–	–	–	–
Nt	–	–	0.44	0.19	–	–	0.52	–	0.30

..continued on the next page

TABLE 2.

Rc	–	–	0.34	–	–	–	0.41	–	0.25
Lc	–	–	–	–	–	–	–	–	–0.52
				Bellgard ecomorphs					
KsMs	–	–	–		–0.53	–	–	–0.21	–0.19
MgTr	–	–	0.25		0.54	–	–	0.32	–
St	–	–	–		–	–0.31	–	0.20	–0.27
Pr	–	–	–	–	–0.22	0.24	–	–0.25	–
Hel	0.24	–	–	–	–0.48	–0.20	–	–	–0.27

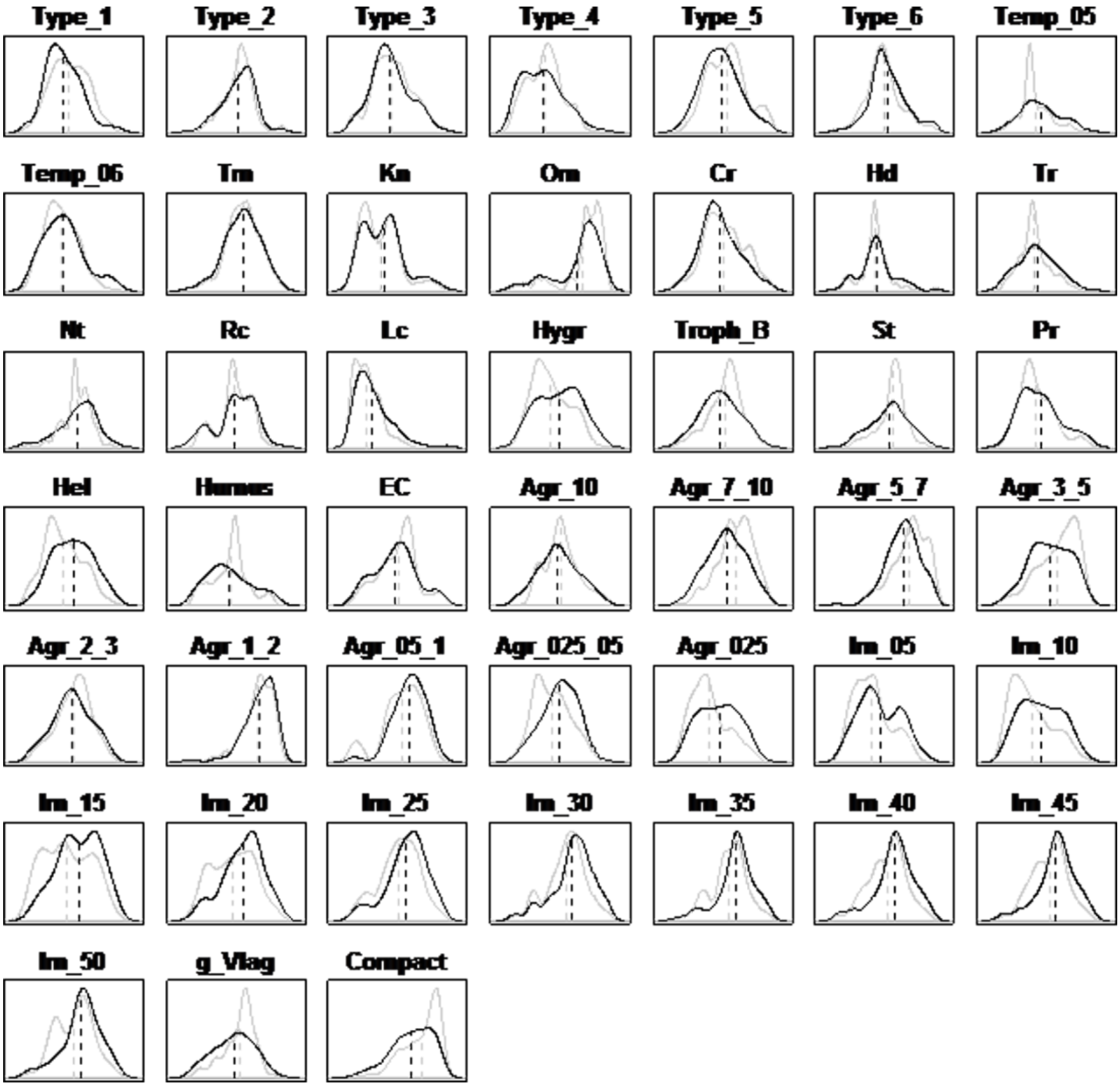

Figure 4. An histogram of the available resource units. Resource allocation (black bars) and an histogram of the used resource units distribution of resource use (gray bars) of *Vallonia pulchella*. Type_1 - type_6 - the proportion of physiognomic types of vegetation cover; temp_05 - top soil temperature (3-5 cm) May 3, 2012; temp_06 - temperature of the top layer of soil (3-5 cm) June 20, 2012; Tm - thermoclimate; Kn - continentality; Om - ombroclimate; Kr - cryoclimate; Hd - humidity; Tr - salt regime; Nt - nitrogen nutrition; Rc - acidity; Lc - lighting; St - stepants; Pr - pratants; Humus – humus comtant; EC – soil electrical conductivity, imp_05 - imp_50 - soil mechanical impedance at a depth of 5, ..., 50 cm, Agr_10 - Agr_025 - aggregate fractions of size> 10, ..., <0.25 mm, g_Vlag - hygroscopic humidity,%; Compact – soil shrinkage, in %.

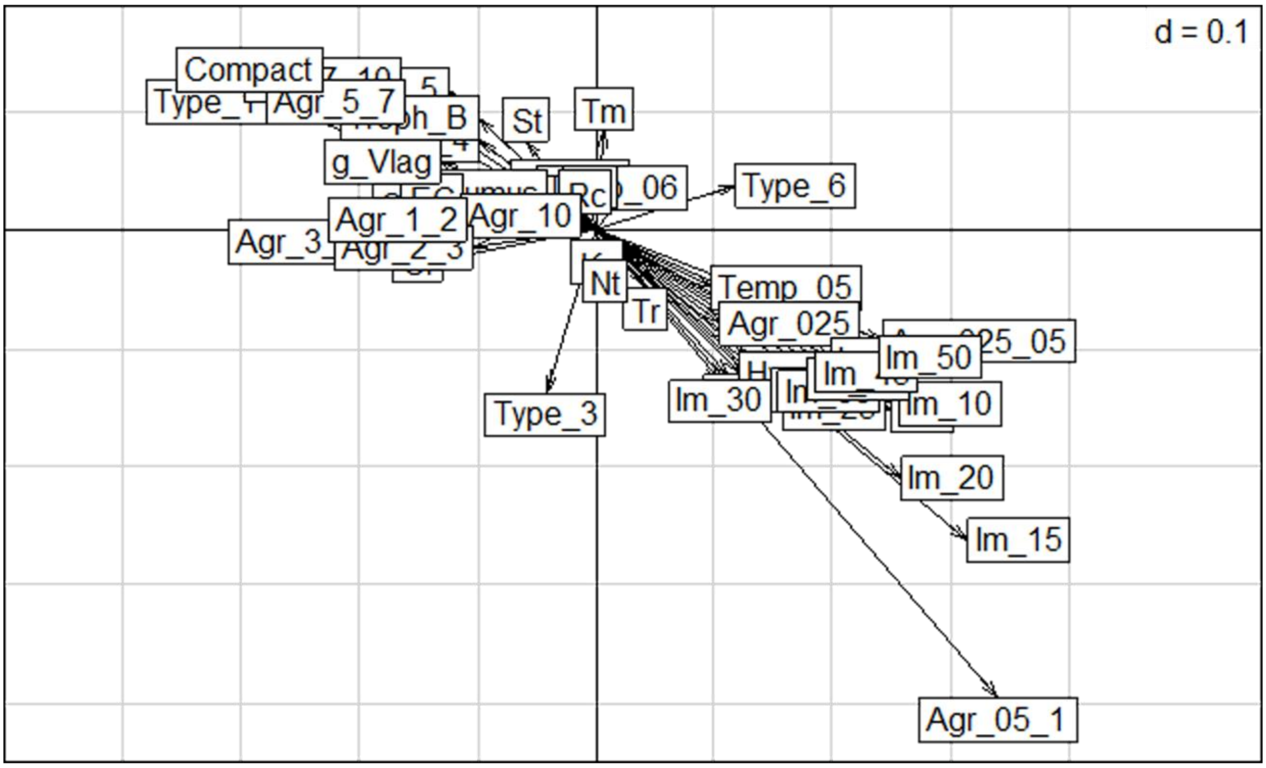

Figure 5. Correlation between the environment variables and the axes selected as a result of FANTER analysis. A – marginality axes 1 and 2; B - specialization axes 44 and 45**.** Type_1 - type_6 - the proportion of physiognomic types of vegetation cover; temp_05 - top soil temperature (3-5 cm) May 3, 2012; temp_06 - temperature of the top layer of soil (3-5 cm) June 20, 2012; Tm - thermoclimate; Kn - continentality; Om - ombroclimate; Kr - cryoclimate; Hd - humidity; Tr - salt regime; Nt - nitrogen nutrition; Rc - acidity; Lc - lighting; St - stepants; Pr - pratants; Humus – humus comtant; EC – soil electrical conductivity, imp_05 - imp_50 - soil mechanical impedance at a depth of 5, ..., 50 cm, Agr_10 - Agr_025 - aggregate fractions of size> 10, ..., <0.25 mm, g_Vlag - hygroscopic humidity,%; Compact – soil shrinkage, in %.

Thus, the FANTER-approach allowed establishing the marginality and specialization of the ecological niche of *Vallonia pulchella* molluscs within the studied territory.

The ENFA-approach allows distinguishing the axis of marginality and the axis of specialization (Fig. 4, 6).

The test for statistical significance showed that an axis of marginality of the ecological niche of *Vallonia pulchella* (γmarg = 4.30, p = 0.001) and two axes of specialization (γspec1 = 10.85, p <0.003; γspec2 = 6.71, p <0.006) are significantly different from the random distribution. According to the results of the ENFA-approach, it can be argued that molluscs prefer sites with a high content of humus in the soil, with higher maximum hygroscopic humidity and shrinkage, but a lower temperature of the upper soil layer. The marginality of the ecological niche of *Vallonia pulchella* is closely related to the variability of the aggregate structure: molluscs prefer sites with a larger proportion in the aggregate structure with sizes ranging from 2–3 to 10 mm and avoid areas where the share of smaller aggregates increases. Marginality indicators also point to the fact that molluscs avoid areas with increased soil mechanical impedance throughout the profile. An important role in the characteristic of marginality is played by indicators of the properties of the vegetation cover.

The analysis of MADIFA reflects the degree of difference in the observed ecological conditions from the ecological optimum of the species. The statistical significance test showed that the axes 1 and 2 isolated in the MADIFA analysis differed significantly from the random distribution (γ1 = 11.60, p = 0.16, γ2 = 6.71, p <0.006), but usually established the significance level which is not considered to be statistically significant. The main aspects of the difference of the ecological situation in the studied test site from the ecological optimum *Vallonia pulchella* are the humus content and soil temperature, the content of some aggregate fractions, the features of the vegetation cover, expressed with the help of indicators of the physiognomic structure and phytoindication scales (Fig. 5, 7).

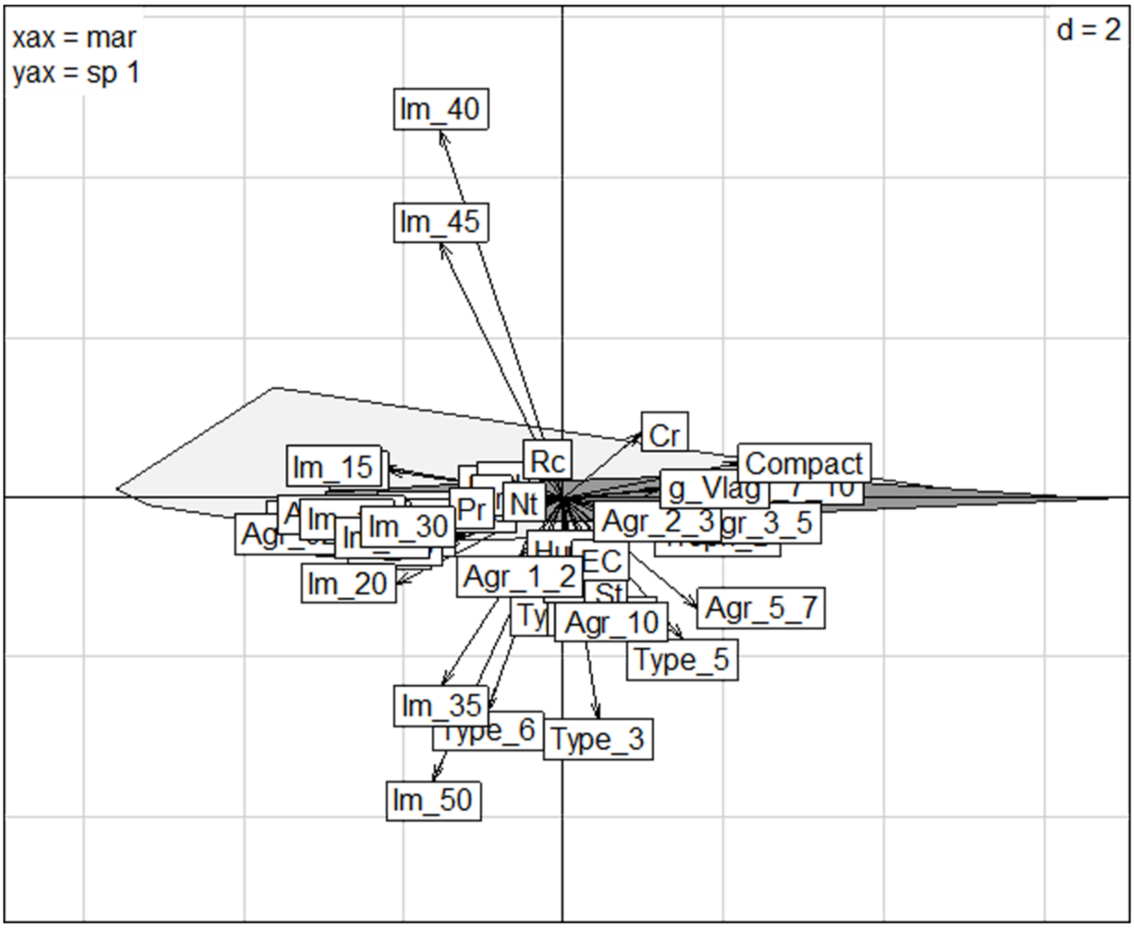

Figure 6. Results of ENFA-mapping of *Vallonia pulchella* ecological niche.

The GNESFA variants reveal the various aspects of linking the ecological niche of an animal with the ecological situation. The analysis of the correlation coefficients between the ENFA and FANTER axes shows that the marginality presented in the ENFA approach by one axis is divided into two axes within the framework of the FANTER approach (Table 3).

Table 3. Comparison of the results of ENFA, FANTER and MADIFA spatial analyzes of placement of *Vallonia pulchella* molluscs within the test site on sod-lithogenic soils on red-brown clays (only significant correlation coefficients p <0.05 are shown).

Analysis		**ENFA**		
		Marginality	Specialization 1	Specialization 2
FANTER	Component 1	–0.35	–	–
	Component 2	0.23	–	–
	Component 44	–	–	0.86
	Component 45	–	–1.00	–
MADIFA	Component 1	0.15	–0.78	0.35
	Component 2	–	0.65	0.48

It should be noted that the ENFA marginality is statistically significant, whereas the FANTER marginality only differs significantly from the random alternative, taking into account some arbitrariness of the boundary criterion p = 0.05. Thus, the partition of marginality within the framework of the FANTER approach leads to a decrease in the statistical validity of the allocation of the corresponding axes. Axes of specialization, identified in both approaches, are highly correlated.

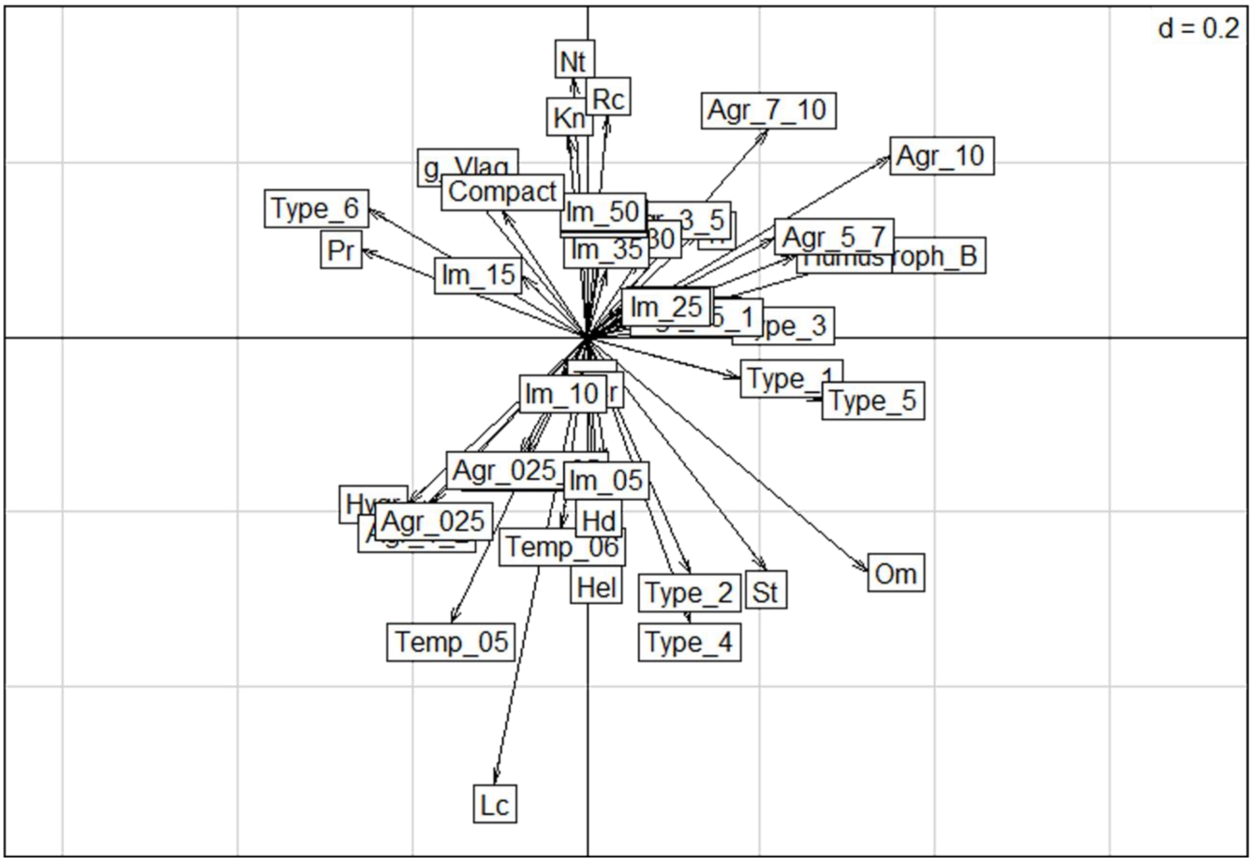

Figure 7. Results of MADIFA-mapping of *Vallonia pulchella* ecological niche.

Correlation of the ENFA and MADIFA axes indicates that the differences in the ecological situation within the studied range from the ecological optimum *Vallonia pulchella* (MADIFA axis) reflect the aspect of specialization of the ecological niche of this species to the greatest degree.

The weighted mean of a give environmental variable with respect to species abundance provides a computationally simple and reliable estimate of the taxon's optimum (Biggs, 1990). Ecological niche optima of the snail studied may be characterized by the ecological parameters values which most important for marginality and specialization axes identification. Ecological parameters correlated with axes show that species optimal conditions are possible if optimal value for all corresponding parameters occur simultaneously. Thus, ecological niche optima may be presented by integral variables such as marginality and specialization axes and may be plotted in geographic space by means of Habitat Preference Index (HSI) reproduction.

As noted by the creators of FANTER, the most correct habitat preference map for this species can be constructed according to the results of MADIFA (Calenge et al., 2008). The correlation coefficient of the HSI obtained with the help of two approaches is r = 0.60, p = 0.00. This indicates a high degree of consistency of the results that can be obtained with the help of MADIFA and ENFA procedures. This is also evidenced by consideration of the spatial variability of the HSI index (Fig. 6, 8). The features of the maps are due to the different accents that make approaches for assessing habitat preferences. In the framework of the ENFA-approach, marginality and specialization are taken into account, and within the framework of the MADIFA approach, the specialization of the ecological niche is taken into account.

Discussion

To describe the ecological niche as a hypervolume within the framework of GNESFA, there are several points of view: the niche side (FANTER allocates several axes of marginality and specialization, the separation of the latter is not clear), the environment (MADIFA allows making a mathematically correct estimate of the preference index habitats), and also their combination (ENFA allocates one axis of marginality and several axes of specialization). Another important problem is the choice of measured environmental parameters, in terms of which the ecological niche is described. Here, along with the ecological relativity of the parameters, the scale proportionality and instrumental feasibility of collecting the necessary amount of information is also of great importance. As a rule, the mapping of ecological space is associated with its mapping in the geographic space (Kunakh, Kolyada, 2010).

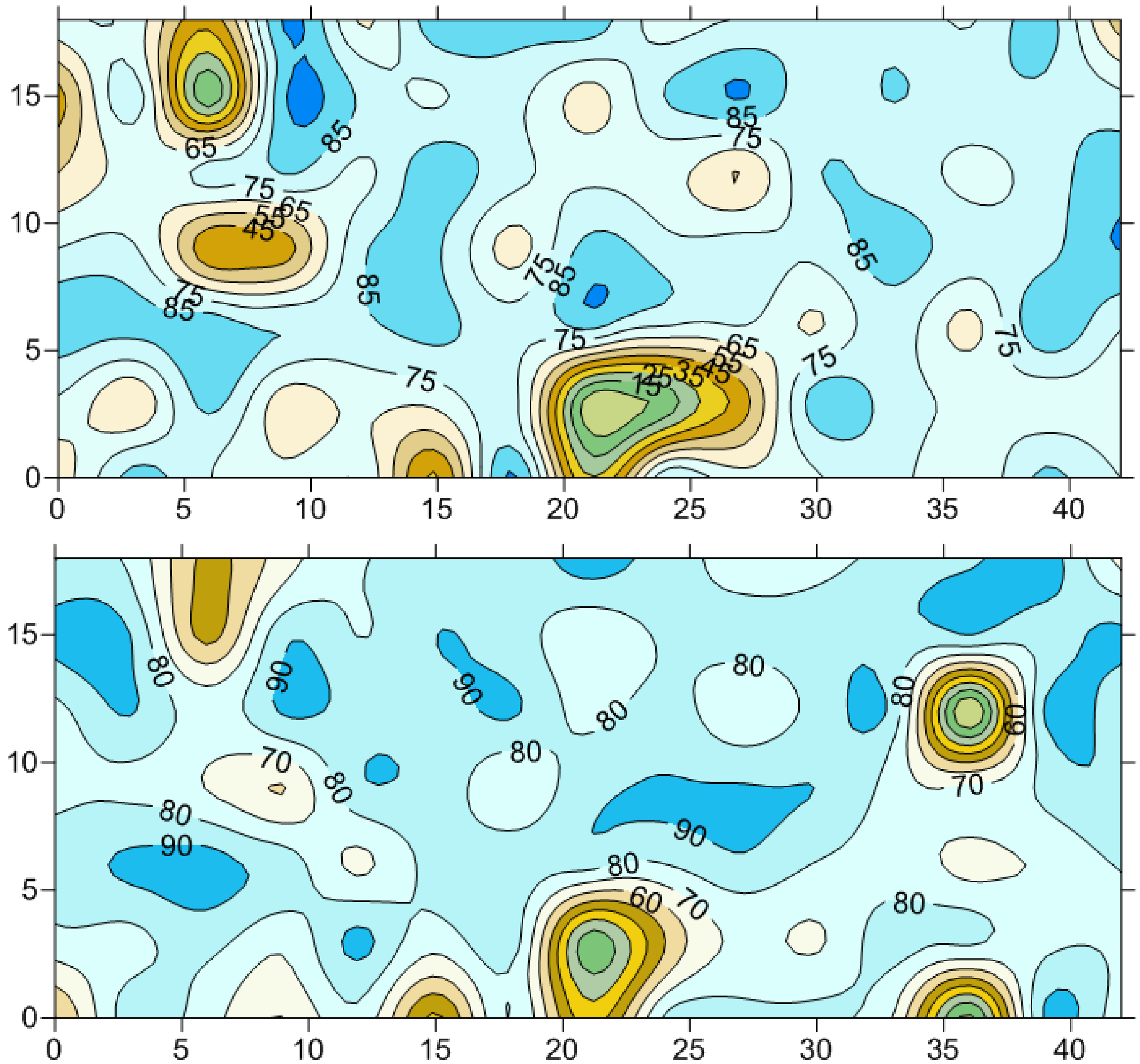

Figure 8. Spatial distribution of the habitat preference index (HSI) for *Vallonia pulchella* within the experimental site on red-brown clays based on ENFA (top) and MADIFA (bottom) procedures. The arrow indicates the zones of greatest difference.

Scale proportionality acts as a hierarchy of factors that determine and regulate the dynamics of the population (Begon et al, 1989). In relation to the mollusks *Vallonia pulchella*, the characteristics of the habitat can be divided into two categories: commensurate with the habitat of molluscs and superior to it. The first group includes characteristics that are measured directly in the same soil samples, of which the molluscs themselves are selected. These are the content of humus, electrical conductivity, temperature and shrinkage of the soil, its aggregate structure and soil mechanical impedance in the 0-5 cm layer. The second group can be referred to the soil mechanical impedance at a depth of more than 5 cm, as well as the characteristics of the plant. Soil mechanical impedance measurements go beyond the soil layer from which the molluscs are taken in the vertical direction, and the characteristics of the vegetation cover are 3 × 3 m in the horizontal direction, which also significantly exceeds the dimensions of the space within which one individual *Vallonia pulchella* presumably lives.

With a significant geographical extension of the study area, the indicators that determine the level of the mollusc population acquire importance - the moisture gradients, the calcium content and the acidity of the soil, as well as their phytoindication estimates (Millar, Waite, 1999; Martin, Sommer, 2004; Müller et al., 2005; Weaver et al., 2006; Schenková et al., 2012). On a large scale, chemical indicators, such as the availability of food elements or the characteristics of leaf litter, also usually attract attention. As our research shows, the indexes of the physical state of the soil - aggregate structure, shrinkage, temperature, play an important role for the *Vallonia pulchella* geobiont micro-mollusks. An important role of humus in soil is its value for the formation of soil structure (Medvedev, 2009). These indicators mainly determine the marginality of the ecological niche.

Conclusion

Local trends, as well as the mosaic nature of the organization of the soil body determine the structure of the vegetation cover. This explains the role of indicators in the organization of ecological niche of mollusk *Vallonia pulchella*, the dimension of which exceeds the size of the ecological space of an individual of this species. Soil mechanical impedance, as well as phytoindication indicators of vegetation, determine the peculiarities of marginality and specialization of the ecological niche of *Vallonia pulchella*. It is the measurement of these indicators that makes it possible to draw a map of habitat preferences for *Vallonia pulchella*.

Thus, ecological niche optima may be presented by integral variables such as marginality and specialization axes and may be plotted in geographic space by means of habitat suitability index reproduction.

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