

Analysis of the spatial distribution of the ecological niche of the land snail *Brephulopsis cylindrica* (Stylommatophora, Enidae) in technosols

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The aim of our work is to describe the ecological niche of the land snail *Brephulopsis cylindrica* (Menke, 1828) 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 loess-like clays) using the ecological niche factor analysis (ENFA). The research was carried out at the Research Centre of the Dnipro Agrarian and Economic University in Pokrov. Sampling was carried out on a variant of artificial soil (technozems) formed on loess-like clays. The test site where the sampling was conducted consists of 7 transects of 15 samples each. Test points form a regular grid with a mesh size of 3 m. Soil mechanical impedance, aggregate-size distribution, soil electrical conductivity, vegetation physiognomic characteristics, and Didukh phytointication scales were used as ecogeographic predictors of the mollusc's ecological niche properties. Phytointication assessment indicates that the technosol ecological regimes are favourable for sub-mesophytes, hemi-hydrocontrastophiles, neutrophiles, semi-eutrophs. The test for statistical significance showed that an axis of marginality of the ecological niche of *B. cylindrica* and axes of specialization are significantly different from the random distribution. We found that the ecological niche of the mollusc is determined by both edaphic factors and ecological features of vegetation. The marginality of *B. cylindrica* ecological niche over the entire period of study is determined mainly by preferences for physiognomic vegetation types, higher values of the continentality and thermality regimes. Often greater content in the soil of aggregates 1–3 mm in size coincides with greater numbers of *B. cylindrica* individuals. Individuals of this species avoid physiognomic type III and areas with higher soil alkalinity and mineralization detected both by means of the phytointication approach and soil electrical conductivity data. Ecological niche optima may be presented by integral variables such as marginality and specialization axes and plotted in geographic space. The spatial distribution of the *B. cylindrica* habitat suitability index (HSI) within the technosols is shown, which makes it possible to predict the optimal conditions for the existence of the species.

Keywords: molluscs; marginality; biodiversity; ecological niche; spatial distribution; ecological niche factor analysis.

Introduction

The small scale spatial distribution of land-snail species and individuals has been extensively researched (Myšák et al., 2013; Faly et al., 2018). Much of the research on the habitat selection by land molluscs is based on comparison of mollusc 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). Mollusc populations may be relatively evenly distributed or highly aggregated (Kralka, 1986; Locasciulli & Boag, 1987). These patterns may be associated with the distribution of microhabitats (Walden, 1981; Kralka, 1986; Hylander et al., 2005). The effect of microhabitat conditions was detected (Hylander et al., 2005; Jurickova et al., 2008).

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 mollusc communities (Nekola & Smith, 1999; Juříčková et al., 2008; Szybiak et al., 2009). The response of species to mineral richness (Horsák, 2006), humidity gradient (Čejka & Hamerlík, 2009), or calcium content gradient (Juříčková et al., 2008) was studied. Particular attention is drawn to the problem of spatial scale and hierarchy of factors affecting molluscs (Nekola & Smith, 1999; Bohan et al., 2000; McClain & Nekola, 2008; Myšák et al., 2013). Habitat is characterized

by the presence of resources and conditions for a given species in a particular territory, as a result of which the colonization of this territory becomes possible, including the species' 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 ecological niche model for a species is measured in terms of marginality (the difference between the mean of the distribution of the cells representing species observations and the global cells) and specialization (the difference between the variance of the species and the global cells) (Skov et al., 2008). The performance of six presence-only models that have been selected to represent an increasing level of model complexity (BIOCLIM, HABITAT, Mahalanobis distance, DOMAIN, ENFA, and GARP) was compared using data on the distribution of 42 species of land snails, nesting birds, and insectivorous bats. These

models showed relatively small (though statistically significant) differences in predictive accuracy (Tsoar et al., 2007).

Brephulopsis cylindrica (Menke, 1828) (Stylommatophora, Enidae) is a land snail native to the Crimean Peninsula (Ukraine). Now it is widely distributed in the grasslands of the Black Sea Lowlands and some adjacent regions in Ukraine (Sverlova et al., 2006; Vychalkovskaya, 2008; Balashov & Gural-Sverlova, 2012; Balashov et al., 2013; Balashov et al., 2018). The intra-population variation of conchiometry traits in the land snail *B. cylindrica* were estimated (Kramarenko, 2009). In the Crimean Peninsula this terrestrial snail inhabits open dry habitats such as steppe and rocky grasslands (Sverlova et al., 2006). The dispersal of the different populations of this species was measured in different experimental conditions (Vitchalkovskaya & Kramarenko, 2006). Analysis of the genetic structure of continuous and ephemeral populations of the land snail *B. cylindrica* led to the conclusion that small, isolated animal populations (including, urban) tend to experience reduced levels of genetic diversity, which arises due to the manifestation of genetic and stochastic processes (Kramarenko & Snegin, 2015). The formation of spatial variability patterns with distinct fractal nature was explained as result of the self-similar elements in spatial distribution of *B. cylindrica*. The relative roles both of the random and the regular components were detected for separate characters according to the degrees of proximity (Kramarenko & Dovgal, 2014). Live and dead lichens and plants are the favourable *B. cylindrica* feeding habitat (Balashov & Baidashnikov, 2013). Outside the native area, *B. cylindrica* is often spread by people transporting plants, building materials etc., thus extending its range (Sverlova et al., 2006). It is most likely that its expansion outside the Crimea to mainland Eastern Europe took place in the Holocene (Balashov et al., 2018). The aim of our work is to describe the ecological niche of the land snail *B. cylindrica* 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 loess-like clays) using the ecological niche factor analysis (ENFA).

Material and methods

The research was carried out at the Research Centre of the Dnipro Agrarian and Economic University in Pokrov (Fig. 1). This experimental site for the study of optimal regimes of agricultural recultivation was established in 1968–1970. The territory has a temperate-continental climate with an annual mean maximum decade temperature of 26.4 °C, and a minimum of –8.2 °C, and with a mean annual precipitation of approximately 511 mm (20 year average according to data of the Nikolop meteorological station).

Sampling was carried out on a variant of artificial soil (technozems) formed on loess-like clays (the geographic coordinates of the south-western 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), the examined soil can be classified among the RSG Technosols. The examined profile, also, satisfies the criterion for the prefix qualifier Spolic having 20% or more artefacts (consisting of 35% 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. Sampling was carried out during May 2012, 2013, and 2014. Samples consisted of a single block of soil, 25 × 25 × 10 cm deep, dug out quickly. A quadrat was fixed on the soil surface prior to taking the soil samples. The molluscs were collected from the soil samples by hand.

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). 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 a given 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 enable one 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. 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. (2015) the environmental niche of the cougar in South America is described using all of the GNESFA techniques.

Soil mechanical impedance was measured in the field using an Eijkelkamp manual penetrometer at a depth of up to 50 cm with an interval of 5 cm (Zhukov et al., 2016). The average error in the instrument measurement results is ± 8%. For the measurement, a cone with a cross-sectional dimension of 1 cm² 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. To measure the electrical conductivity of soil in situ, an HI 76305 sensor (Hanna Instruments, Woodsocket, R. I.), working in conjunction with the portable instrument HI 993310, was 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 obtained with the instrument HI 76305 with laboratory data allowed us to estimate the conversion factor of units as 1 dS/m = 155 mg/l.

The vegetation cover was described within squares with a lateral side of 3 m. 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. The main physiognomic types of vegetative cover were singled out visually: type I – cereals (indicator *Bromus sguarrosus* L.); type II – *Seseli tortuosum* L.; type III – *Lactuca tatarica* (L.) C. A. Mey.; type IV – legumes (*Medicago sativa* L.); type V – dead plant residue; type VI – open soil cover. The most typical fragments for the corresponding species were chosen for the images, according to which their colour 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 (Yorkina et al., 2018).

Geobotanical prospecting became the basis for phytoindication of environmental regimes (Zhukov et al., 2016). Didukh (2011) distinguishes edaphic and climatic phytoindication scales. Soil water regime (Hd), variability of damping (fH), soil aeration (Ae), soil acidity (Rc), total salt regime (Sl), carbonate content in soil (Ca), nitrogen content in soil (Nt) comprise the edaphic scales. The scales for the next four factors comprise the climatic scales. These are radiation balance (Tm), aridity or humidity (Om), cryoclimate (Cr) and continentality (Kn). In addition, the scale of light regime (Lc) is allocated as the microclima-

te scale. We can assume that edaphic scales and the scale of light regime will be light-sensitive properties of soil variability at a single point, which can be the basis for the application of phytoindication scales for large-scale mapping. Thermal properties of soils are indicated by the radiation balance scale; hydrothermal properties of soils are indicated by aridity scale (Didukh, 2012). Phytoindication scales are presented by Didukh (2011). Phytoindication assessment of gradations in environmental factors is presented by Buzuk (2017).

Statistical calculations were performed using the Statistica 12.0 (StatSoft Inc., 2014, version 12, www.statsoft.com) 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 program and ArcGis 10.0 (ESRI, 2011, ArcGIS Desktop: Release 10, Redlands, CA, Environmental Systems Research Institute).

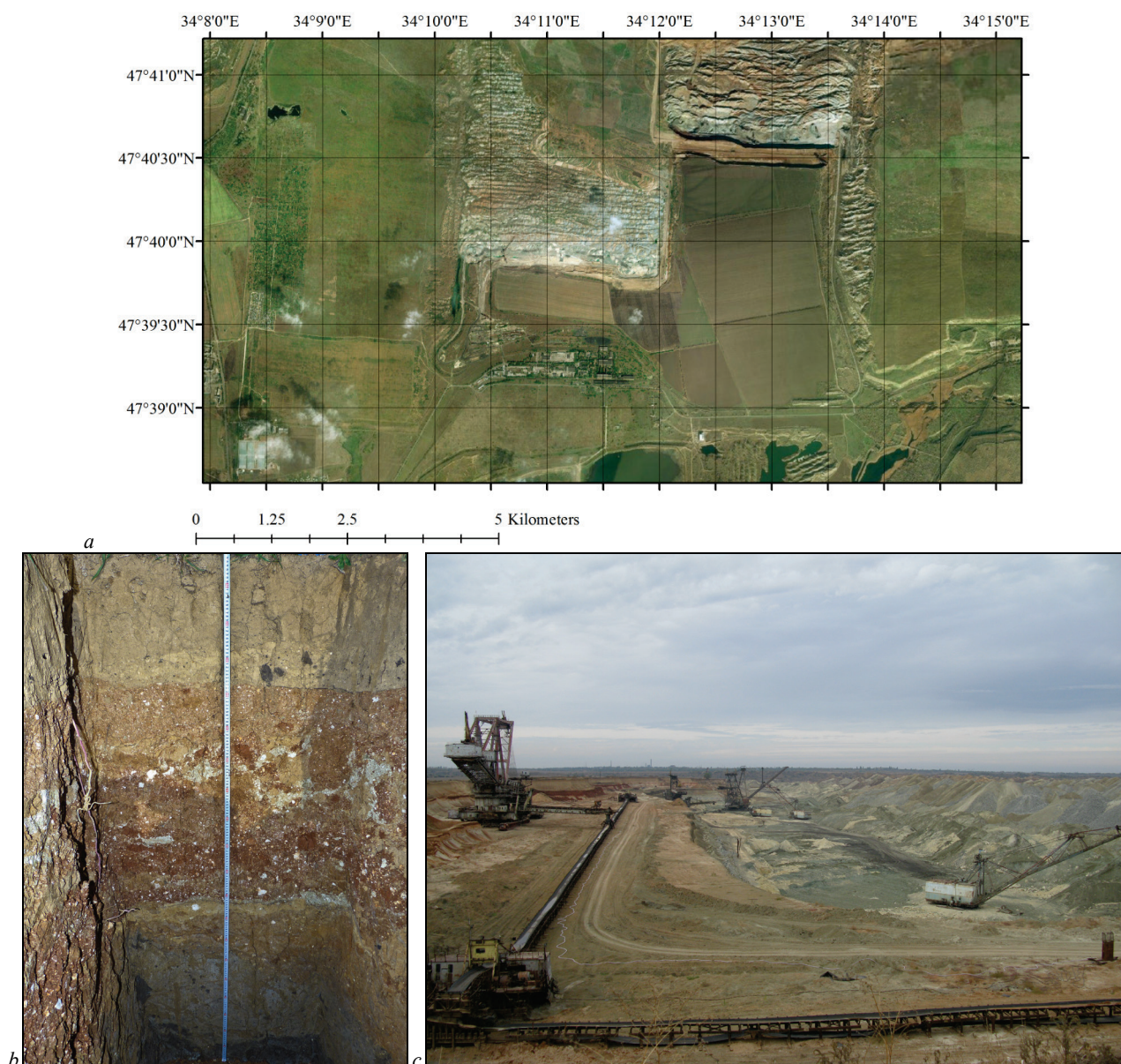


Fig. 1. Research Centre of the Dnipro Agrarian and Economic University near the town Pokrov (Ukraine):
a – satellite image of the study area (1 – reclaimed land; 2 – mining quarry), b – technosols profile, c – quarry panorama view

Results

The mollusc *B. cylindrica* population decreased during the study period (Fig. 2). The greatest abundance was detected in 2012. This index was 56.4 ± 1.8 ind./m². The smallest abundance was found in 2014 – 32.1 ± 1.5 ind./m². The electrical conductivity of the technosol is in the range of 0.51 to 0.52 dSm/m (Table 1). In aggregate fraction, dominant sizes were 1–5 mm. The soil penetration resistance of the soil top layer was between 2.48–3.66 MPa and increased with depth. The sharpest increase in soil penetration resistance was observed at a depth of 10–15 cm, and then the growth of this index is rather moderate. Vegetation-free soil surface was between 38.2–41.4%. The physiognomic types II, III and V had the highest degree of projective cover.

Phytoindication assessment indicates that the technosol water regime is favourable for sub-mesophytes. According to Didukh (2011), sub-mesophytes are the plants adapted to rather dry forest-meadow habitats with moderate rain and melted water drenching of the soil layer where plant roots penetrate. The regime of the water damping variability was favourable for hemi-hydrocontrastophiles. Technosol acidity was favourable for neutrophiles, plants which grow on acidulous and neutral (pH = 6.5–7.1) soils. The total salt regime was favourable for semi-eutrophs. This ecological group indicates soils enriched with salt (150–200 mg/l) with a content of HCO³⁻ 4–16 mg/100 g of soil, and trace of SO₄²⁻ and Cl⁻. The content of carbonates creates conditions that were favourable for carbonatophiles. These plants grow best on carbonate soils where CaO, MgO = 5–10%. The regime of the nitrogen content was favourable for hemi-nitrophiles. Hemi-nitrophiles indicate soils

moderately rich in mineral nitrogen (0.2–0.3%). The sub-aerophiles formed the dominant ecological group that indicates highly aerated habitats with inclusions of broken stones. The lighting regime was indicated to be characteristic of open spaces.

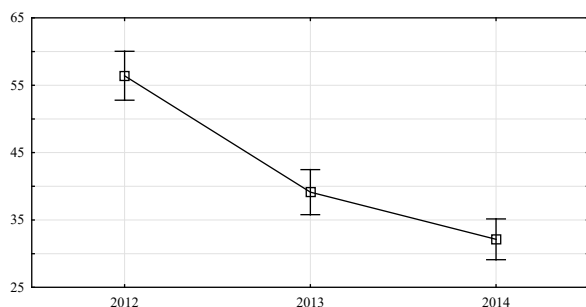


Fig. 2. Dynamic of the *Brephulopsis cylindrica* population density: on the abscissa axis – years, on the ordinate axis – population density (ind./m²), means and 95% confidence interval, n = 105

Table 1
Descriptive statistics of the ecological properties used as ecogeographic variables ($\bar{x} \pm SE$)

Properties	2012	2013	2014
Conductivity, dSm/m (EC)	0.51 ± 0.01	0.52 ± 0.01	0.52 ± 0.01
Aggregate structure, size of fractions, mm			
>10	7.49 ± 0.30	5.95 ± 0.21	5.90 ± 0.22
7–10	5.95 ± 0.17	4.21 ± 0.09	4.44 ± 0.08
5–7	7.83 ± 0.18	9.64 ± 0.15	9.61 ± 0.15
3–5	18.93 ± 0.47	20.58 ± 0.20	20.55 ± 0.21
2–3	16.97 ± 0.19	23.36 ± 0.24	23.48 ± 0.24
1–2	25.45 ± 0.29	15.57 ± 0.16	15.65 ± 0.16
0.5–1.0	5.17 ± 0.23	6.19 ± 0.13	6.18 ± 0.12
0.25–0.50	6.60 ± 0.30	7.73 ± 0.17	7.69 ± 0.15
<0.25	5.62 ± 0.21	6.77 ± 0.12	6.75 ± 0.12
Soil penetration resistance in MPa at depth, cm			
0–5	3.66 ± 0.13	2.69 ± 0.11	2.48 ± 0.09
5–10	6.10 ± 0.21	5.07 ± 0.19	4.80 ± 0.15
10–15	7.53 ± 0.10	6.85 ± 0.09	6.85 ± 0.15
15–20	8.00 ± 0.07	7.50 ± 0.07	7.82 ± 0.15
20–25	8.48 ± 0.08	7.50 ± 0.07	7.68 ± 0.13
25–30	8.71 ± 0.10	7.79 ± 0.09	8.61 ± 0.11
30–35	8.66 ± 0.16	7.82 ± 0.11	8.80 ± 0.12
35–40	8.85 ± 0.13	7.81 ± 0.13	8.79 ± 0.16
40–45	9.18 ± 0.16	7.95 ± 0.13	9.18 ± 0.12
45–50	9.28 ± 0.16	8.05 ± 0.14	9.14 ± 0.13
Physiognomic types of vegetation			
Type I	9.18 ± 0.33	9.99 ± 0.20	9.94 ± 0.20
Type II	17.40 ± 0.71	18.49 ± 0.28	18.76 ± 0.29
Type III	12.89 ± 0.60	18.31 ± 0.46	18.43 ± 0.48
Type IV	5.96 ± 0.41	6.75 ± 0.18	6.72 ± 0.18
Type V	11.72 ± 0.30	8.13 ± 0.19	8.05 ± 0.19
Type VI	41.36 ± 1.20	38.34 ± 0.60	38.24 ± 0.65
Didukh phytointicator values			
Hd	10.21 ± 0.13	12.99 ± 0.11	12.48 ± 0.14
fH	6.06 ± 0.12	5.66 ± 0.11	5.36 ± 0.14
Rc	8.91 ± 0.04	7.55 ± 0.10	8.07 ± 0.06
Sl	8.23 ± 0.06	8.44 ± 0.06	8.18 ± 0.07
Ca	11.29 ± 0.05	11.34 ± 0.04	11.32 ± 0.03
Nt	5.03 ± 0.13	5.99 ± 0.19	7.98 ± 0.10
Ae	6.38 ± 0.07	6.30 ± 0.06	6.64 ± 0.06
Tm	8.94 ± 0.06	10.00 ± 0.07	9.68 ± 0.06
Om	11.82 ± 0.06	10.99 ± 0.07	11.53 ± 0.06
Kn	8.92 ± 0.13	10.12 ± 0.13	10.45 ± 0.09
Cr	7.45 ± 0.13	8.62 ± 0.10	8.91 ± 0.08
Lc	8.81 ± 0.02	8.26 ± 0.08	7.36 ± 0.10

Note: Hd – soil humidity, fH – variability of damping, Rc – soil acidity, Sl – total salt regime, Ca – carbonate content in soil, Nt – nitrogen content in soil, Ae – soil aeration, Tm – thermal climate, Om – humidity, Kn – continental climate, Cr – cryoclimate, Lc – light regime; type I – *Bromus sguarrosus* L., type II – *Seseli tortuosum* L., type III – *Lactuca tatarica* (L.) C. A. Mey., type IV – *Medicago sativa* L., type V – dead plant residue, type VI – open soil cover.

Table 2

Results of analysis of the ecological niche of *Brephulopsis cylindrica* by ENFA methods (n = 105 only correlation measures are shown that are significant for $P < 0.05$)

Properties	2012		2013		2014	
	margi-nality	speciali-zation	margi-nality	speciali-zation	margi-nality	speciali-zation
Conductivity, dSm/m	–	0.13	0.20	–	–0.24	–0.16
Aggregate structure, size of fractions, mm						
>10	–0.08	–	–0.20	–	–0.12	–
7–10	0.12	0.12	0.29	–	0.27	0.11
5–7	0.14	–0.15	–	–	–	–
3–5	–	–	–	0.18	–	–0.11
2–3	–0.12	–	–	–	0.32	–
1–2	0.10	0.19	–	–	0.32	–
0.5–1.0	0.10	0.19	–	–	–	–0.13
0.25–0.50	0.08	–0.22	0.14	0.19	–	–
<0.25	–	0.15	0.21	–0.13	0.17	–
Soil penetration resistance in MPa at depth, cm						
0–5	–	–	0.27	0.25	0.22	–
5–10	0.14	–	0.23	–0.13	0.19	0.16
10–15	–	–	–	–	0.23	–
15–20	–	–0.38	–	–	0.15	–0.12
20–25	–0.09	0.36	–	–	–	–
25–30	0.08	–	0.15	–0.10	–	0.17
30–35	–	–	0.18	–	–	–
35–40	–0.09	–0.09	0.13	–	–	–
40–45	–	–0.12	–	–0.24	0.10	–0.34
45–50	–	0.27	–	0.21	0.10	0.19
Physiognomic types of vegetation						
Type I	–	–	0.10	0.11	–0.10	–
Type II	–0.27	0.44	–0.14	–	–	–
Type III	0.52	0.13	–0.11	0.33	–0.21	0.38
Type IV	–0.43	–0.18	–	–	0.15	0.33
Type V	–0.32	–0.31	0.21	–	0.11	0.18
Type VI	0.26	–	–	–	–	0.38
Didukh phytointicator values						
Hd	–0.20	–	–	–	0.11	0.09
fH	–	0.08	–0.20	–0.16	–	–0.17
Rc	–0.15	–	–0.19	–0.23	–	–
Sl	–0.09	–	–	0.32	–	0.08
Ca	0.07	–	0.43	0.22	0.17	–
Nt	–0.13	–	–0.36	0.50	0.25	–
Ae	–	–	–	–	0.29	–
Tm	–	–0.22	–	0.11	–	0.07
Om	–0.11	–	–	–	–	0.42
Kn	0.14	–	–	–0.14	–	–
Cr	–0.16	0.14	–0.26	0.10	–	–
Lc	–	–	–	0.11	0.27	–
p-level	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

Note: see Table 1.

The test for statistical significance showed that an axis of marginality of the ecological niche of *B. cylindrica* ($\gamma_{\text{marg}} = 0.11–0.17$, $P < 0.001$) and axes of specialization ($\gamma_{\text{spec}} = 1.53–1.68$, $P < 0.001$) are significantly different from the random distribution. Marginality of the ecological niche of the mollusc is determined mainly by the following ecological-geographical predictors; contents of some aggregate fraction in the soil, physiognomic types of plant cover and such soil regimes as humidity, carbonate and nitrogen content (Table 2). In 2012 the effect of soil electrical conductivity on the ecological niche was not found. According to the results of the ENFA-approach, it can be argued that the molluscs prefer sites with a high content of the aggregate fraction with size of < 0.25 to 0.5–1.0 mm and 5–10 mm and avoid areas with high contents of aggregate fraction with size 1–5 and > 10 mm. The role of soil penetration resistance as a marker of the ecological niche of *B. cylindrica* is not significant. In 2012, *B. cylindrica* preferred physiognomic types III and VI and avoided areas with a predominance of types II, IV, and V. In 2013, the mollusc preferred types I and V, and avoided types II and III. In 2014, they preferred types IV and V, and avoided types I and III. The main aspects of the *B. cylindrica* ecological niche specialization are content of the aggregate fraction with size 0.25–

0.50 and 0.5–1.0 mm, the soil penetration resistance at a depth of 20–25 cm, and cover of the physiognomic types II, IV and V.

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 (Yorkina et al., 2018) (Fig. 2). The results indicate the repeatability of the spatial patterns of molluscs in time. The repeatability of the spatial patterns may be explained by the time invariants of the ecological niche. The marginality of *B. cylindrica* ecological niche over the entire period

of study is determined mainly due to the preferences of physiognomic vegetation types II and IV, higher rates of the continentality and thermality regimes (Fig. 3). Often, higher content in soil of aggregates 1–3 mm in size and greater number of *B. cylindrica* individuals coincide. Individuals of this species avoid physiognomic type III and areas with higher soil alkalinity and mineralization detected both by means of the phytindication approach and soil electrical conductivity data. The small-sized aggregates (0.25–0.50 mm) indicate areas with relatively unfavourable conditions for *B. cylindrica*.

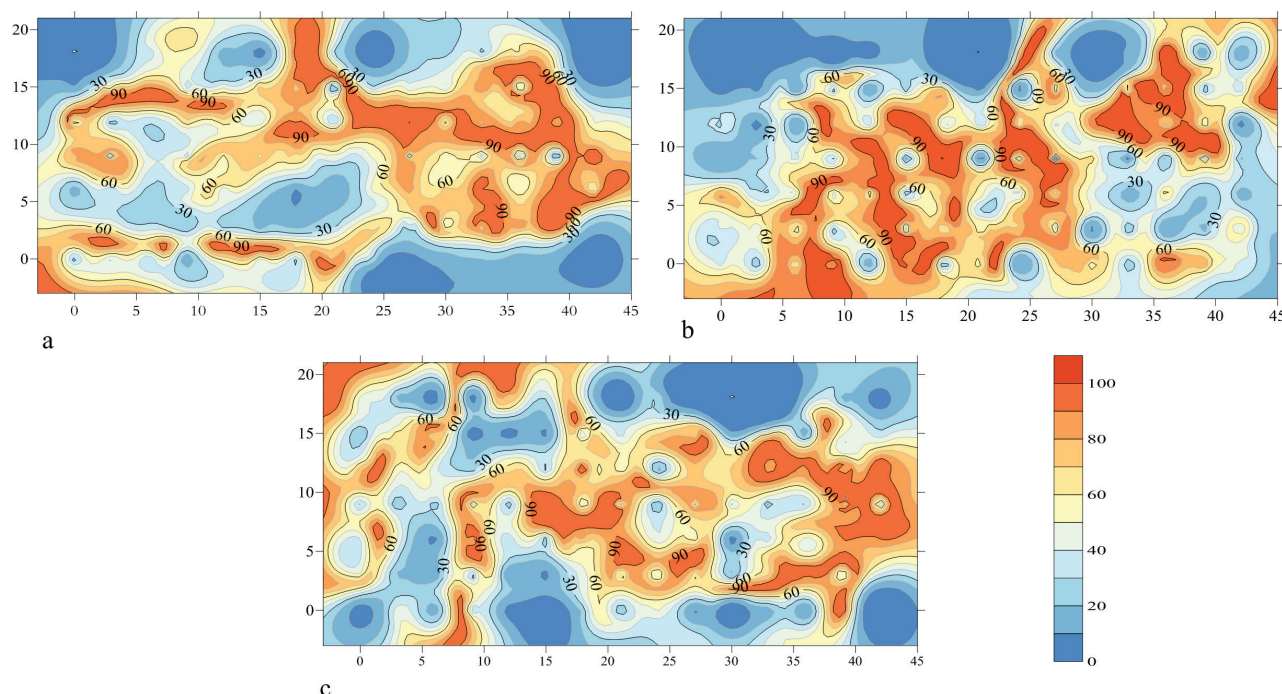


Fig. 2. Spatial distribution of the habitat suitability index (HSI) for *Brephulopsis cylindrica* within the experimental site on loess-like clays based on ENFA: *a* – 2012, *b* – 2013, *c* – 2014, on the abscissa ordinate axis – local polygon coordinates (m), scale – habitat suitability index (%)

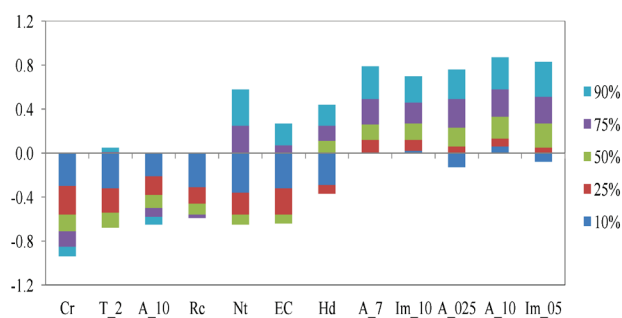


Fig. 3. Parameters of the *B. cylindrica* ecological niche marginality for the whole period of investigation (the largest and smallest marginality markers are presented): marginality percentiles of the relevant characteristics; Cr – cryoclimate, Rc – soil acidity, Nt – nitrogen content in soil, Hd – soil humidity, EC – electrical conductivity, T_I – cereals (indicator *Bromus sguarrosus* L.), A_025 – aggregate fraction with size < 0.25 mm, A_7 – aggregate fraction with size 5–7 mm, Agr_7 – aggregate fraction with size 7–10 mm, A_10 – aggregate fraction with size > 10 mm, Im_05 – soil penetration resistance at depth 0–5 cm, Im_10 – soil penetration resistance at depth 5–10 cm

Discussion

The remediation of disturbed territories simulates the initial stages of ecosystems' succession (Wali, 1999). The young artificial technosol is still very far from the quasi-steady state which is characteristic of the soil which had been in this place before the surface mining (Klimkina et al., 2018). The moisture content of soils plays an important role (Nekola, 2003). However, the limited data on the role of soil moisture at a given

time in view of the significant variability of this parameter was noted (Ondina et al., 2004). To solve this problem, it is appropriate to use phytindication data to assess the autecological features of molluscs and the structure of their communities (Horsák et al., 2007; Dvořáková & Horsák, 2012). For describing habitat preferences of the mollusc *Vertigo geyeri* Lindholm, 1925, the Ellenberg phytindication scales were successfully used in Poland and Slovakia (Schenkova et al., 2012). The dynamism of the soil conditions creates the prerequisites for a high degree of heterogeneity in the soil conditions and the diversity of vegetation. The site age was the most important factor influencing plant species richness and abundance (Wali, 1999). A total of 96 plant species were detected in the study polygon (Maslikova et al., 2016; Zhukov & Maslikova, 2018). Such species diversity is enough to evaluate the spatial variation of environmental conditions by means of phytindication methods. Local trends, as well as the mosaic nature of the organization of the soil body determine the structure of the vegetation cover, which explains the role of indicators in the structure of ecological niches of molluscs (Yorkina et al., 2018).

Outside the native area, *B. cylindrica* mostly lives in anthropogenic habitats such as roadsides and tracks, lawns and wastelands (Gural-Sverlova & Gural, 2012). The abundance of *B. cylindrica* and the distribution of age groups in the adventitious populations vary during the season. Near Belgorod, the highest population densities are observed in late spring – early summer (149–205 ind./m²) (Adamova et al., 2018). Our data revealed that technosols create favourable conditions for this species. The population density of *B. cylindrica* reached a considerable value within the study period. Snails can reach high levels of species abundance even within single quadrats (1 m² areas or less) (Coles & Nekola, 2007; Cemohorsky et al., 2010; Kunakh et al., 2018). But ecological conditions for *B. cylindrica* within the study polygon are not uniform. This result is in agreement with data obtained for another invasive population near the Belgorod (Adamova et al., 2018).

Within the natural range the climatic conditions in the hot season are the most important factor determining the demographic population structure in the late season (Kramarenko & Popov, 1993). The *B. cylindrica* population abundance in the Crimea was found to decrease in value in September to 40 ind./m² (Kramarenko, 1997). 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; Marti & Sommer, 2004; Müller et al., 2005; Weaver et al., 2006; Schenkova et al., 2012). On a large scale, chemical indicators, such as availability of food elements or the characteristics of leaf litter, also usually attract attention. The indexes of the physical state of the soil – aggregate structure, shrinkage, temperature, play an important role for the *Vallonia pulchella* geobiont micro-molluscs (Yorkina et al., 2018). The selection of favourable microhabitats is the one of the key mechanisms for avoiding excess loss or gain of water (Luchtel & Deyrup-Olsen, 2001), which are related to specific plant cover (Horsák & Hájek, 2003; Stoll et al. 2012) and litter texture (Szybiak et al., 2009; Książkiewicz et al., 2013). Our data indicate that the vegetation structure is the key factor that determines the characteristics of the spatial distribution of *B. cylindrica*. Thus the nature of the impact varies greatly over time. Dead plant remains have the most invariant impact on mollusc abundance. *B. cylindrica* individuals avoid sites with a high projective cover of dead plant remains.

The most significant edaphic factors that affect molluscs are 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). For *B. cylindrica*, one feature of adaptive behaviour is known: these snails burrow in the soil (Kramarenko, 1993). Mostly *B. cylindrica* juveniles burrow in the soil in the hottest summer months (Kramarenko, 1997). This ecological property of *B. cylindrica* explains the effect of the soil condition on the spatial distribution of the mollusc population. Electrical conductivity may be used as a proxy measure of mineral richness. A unimodal response of local mollusc species diversity to mineral richness (expressed as conductivity) was found (Horsák, 2005). In our study, *B. cylindrica* individuals avoided areas with higher soil alkalinity and mineralization detected both by means of the phytoindication approach and soil electrical conductivity data.

Conclusion

Our data revealed that technosols create favourable conditions for this species. The population density of *B. cylindrica* reaches a considerable value within study period. The results indicate the repeatability of the spatial patterns of molluscs in time. The repeatability of the spatial patterns may be explained by the time invariants of the ecological niche. The marginality of *B. cylindrica* 's ecological niche over the entire period of study is determined mainly due to its preferences for physiognomic vegetation types II and IV, higher values of the continentality and thermality regimes. Often greater content in the soil of 1–3 mm aggregates coincides with greater number of *B. cylindrica* individuals. Individuals of this species avoid physiognomic type III and areas with higher soil alkalinity and mineralization detected both by means of the phytoindication approach and soil electrical conductivity data. The small-sized aggregates (0.25–0.50 mm) indicate areas with relatively unfavourable conditions for *B. cylindrica*.

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