
Intra-population spatial structure of the land snail *Vallonia pulchella* (Müller, 1774) (Gastropoda; Pulmonata; Valloniidae)

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ABSTRACT. This paper summarizes the mechanisms behind the patterning of the intra-population spatial arrangement of the land snail *Vallonia pulchella* in terms of edaphic and vegetation properties. The molluscs were collected from a regular grid in recultivated soil (the research station of Dnipro State Agrarian and Economic University, Pokrov, Ukraine). As predictors of the snail population abundance, spatial variables were used, as well as edaphic and vegetation indices. It is shown that *V. pulchella* prefers microsites characterized by higher soil electrical conductivity, which contain larger aggregate fractions with low mechanical impedance and the low temperature at the depth of 0-10 cm, with a more developed dead plant layer, low-light and low hygromorph and heliomorph index values of the vegetation.

Introduction

Majority of the studies dedicated to habitat selection by land snails is based on the comparison of mollusc communities from geographically different sampling points which differ in vegetation cover, soil type, moisture level [Millar, Waite, 1999; Martin, Sommer, 2004; Müller *et al.*, 2005; Weaver *et al.*, 2006; Książkiewicz-Parulska, Ablett, 2017]. Among the edaphic factors which affect the molluscs, the most significant are the calcium content in the soil, pH, the soil texture [Ondina *et al.*, 2004], and the content of exchangeable cations and aluminum [Ondina *et al.*, 1998]. An important role is played by soil moisture [Nekola, 2003]. However, Ondina *et al.* [2004] pointed out the limitations of the role of soil moisture data at any given time because of the significant variability of this parameter. To solve this problem the use of phytointication data is adequate for evaluation of molluscs' autecological features and community structure [Horsák *et al.*, 2007; Dvořáková, Horsák, 2012]. Ellenberg

phytointication scales have been successfully applied to describe the habitat preferences of the mollusc *Vertigo geyeri* Lindholm, 1925 in Poland and Slovakia [Schenkova *et al.*, 2012].

Research on a large-scale has established 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]. Of particular interest is the problem of the spatial scale and the hierarchy of factors acting on molluscs [Nekola, Smith, 1999; Bohan *et al.*, 2000; McClain, Nekola, 2008; Myšák *et al.*, 2013; Kramarenko *et al.*, 2014].

Habitat is characterized by the presence of a certain range of resources and ecological conditions for a given species, thereby making it possible to occupy, survive and reproduce in a given area [Hall *et al.*, 1997]. To study the selection of habitat types is to identify the characteristics of the environment, which makes a place suitable for the existence of a species [Calenge, Basille, 2008].

Thus, the main aim of this study is analysis of the mechanisms patterning the intra-population spatial structure of the land snail *Vallonia pulchella* (Müller, 1774) in terms of vegetation and edaphic properties.

Material and methods

Collection of materials. The studies were conducted at the research station of Dnipro State Agrarian and Economic University in Pokrov in June 2012 (geographic coordinates of the southwest corner of the polygon are 47°38'55"N, 34°08'33"E). 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. A perennial legume-grass agrophytocenosis was cultivated at this research station between 1995 and 2003, following which the process of recovery of vegetation began [Zhukov *et al.*, 2017].

Sampling area consisted of seven transects of 15 samples each. The sampling points formed a regular grid of a mesh size of 3 m. From the center of each sampling site a soil sample with size 5×5×5 cm was collected from which 100 g soil was weighted. Each sample was examined in the laboratory with a 10x binocular microscope MBS-9 and the number of live specimens of *V. pulchella* was noted.

Evaluation of edaphic parameters. Soil mechanical impedance was measured in the field using a hand penetrometer Eijkelkamp to a depth of 50 cm at intervals of 5 cm. The average error of the instrument measurement results was ±8%. For measuring we used a cone with a cross-sectional dimension of 1 cm². Within each cell soil mechanical impedance was measured once. Determination of the aggregate composition was produced by dry sieving [Vadyunina, Korchagina, 1986].

To measure *in situ* soil conductivity we used a sensor HI 76305 (Hanna Instruments, Woodsocket, RI), working in conjunction with a portable device HI 993310. The tester estimated overall electrical conductivity of the soil, i.e. the combined conductance of the soil air, water and particles. The instrument measurement results are in units of saturation of the soil salts solution – g/l. Comparison of the measurement results of the HI 76305 device with laboratory data allowed us to estimate the transfer rate units as 1 dSm/m= 55 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].

Soil drying shrinkage was measured by the A.F.Vadyunina and Z.A.Korchagina's [1986] method. The sieved soil samples were brought to a moisture of 31.17±0.35%. After gradual drying, the samples were further dried in a laboratory oven at 105°C for 5 hours. Soil sample size after shrinkage was measured by caliper [Zhukov *et al.*, 2013].

Evaluation of the vegetation parameters. The description of the vegetation cover was made based on description of the digital images of the surface of the sampling area taken at a height of 1.5 m. Visually six types of vegetation soil cover were allocated: 1 – cereals (dominant *Bromus sguarrosus* L.); 2 – dominant eastern moon carrot (*Seseli campestre* Bess.); 3 – dominant blue lettuce (*Lactuca tatarica*

(L.)); 4 – legumes (dominant alfalfa *Medicago sativa* L.); 5 – dead vegetation; 6 – bare soil not covered by vegetation. For the pictures, the fragments most characteristic for the corresponding types were chosen for which their colour properties were installed in RGB-format. Subsequently they were used as a training set for the discriminant analysis. Later, decoding of all the pictures was carried out, which allowed us to assess the proportion occupied by each of the physiognomic types of cover in each sampling site.

Ecomorphic vegetation analysis was discussed in work Zhukov *et al.* [2017]. We found that in the plant community of the study area, hygromorphs are represented mainly by xeromesophytes (KsMs) and mesoxerophytes (MsKs). Therefore, as a quantitative measure of hygromorphic structures we selected the proportion of the xeromesophytes in plant community. Trophomorphs were represented mainly by mesotrophs and megatrophs. Therefore we characterized the trophomorphic structure using the proportion of megatrophs (MgTr). The coenomorph structure was represented mainly by stepants (St) and pratants (Pr). Helimorphs were represented by heliophytes and sciopheliophytes. Adaptation of plants to the light regime is characterized by the proportion of heliophytes (Hel).

Furthermore, the D.N.Tsyganov's [1983] phytointication scales were used, which characterized the following parameters: thermal climate (Tm), continentality of climate (Kn), humidity of climate (Om), cryo-climate (Cr), soil water regime (Hd), total salt regime (Tr), nitrogen content in soil (Nt), soil acidity (Rc) and lighting (Lc).

Methods of statistical analysis. Spatial heterogeneity using vegetation and edaphic parameters was evaluated both by classical statistical criteria (range, mean and testing the hypothesis of normality of the empirical distribution using the Shapiro-Wilk's test), and by means of geostatistical techniques (local Moran's *I* coefficient).

To assess the degree of influence of edaphic and vegetation indicators of the abundance of *V. pulchella* within the sample plots, two approaches were used. In the first case, we took into account only the presence/absence of snails and testing of the null hypothesis was carried out based on a logistic regression model. In the second case the null hypothesis evaluation was performed using the Spearman coefficient of rank correlation (excluding the spatial distribution of the sample plots), as well as Moran's *I* coefficient of spatial autocorrelation (taking into account the spatial distribution of the sample plots).

Statistical calculations were performed using STATISTICA 7.0 software package (StatSoft). The two-dimensional mapping, evaluation of geostatistical parameters and creation of *asc*-data files of

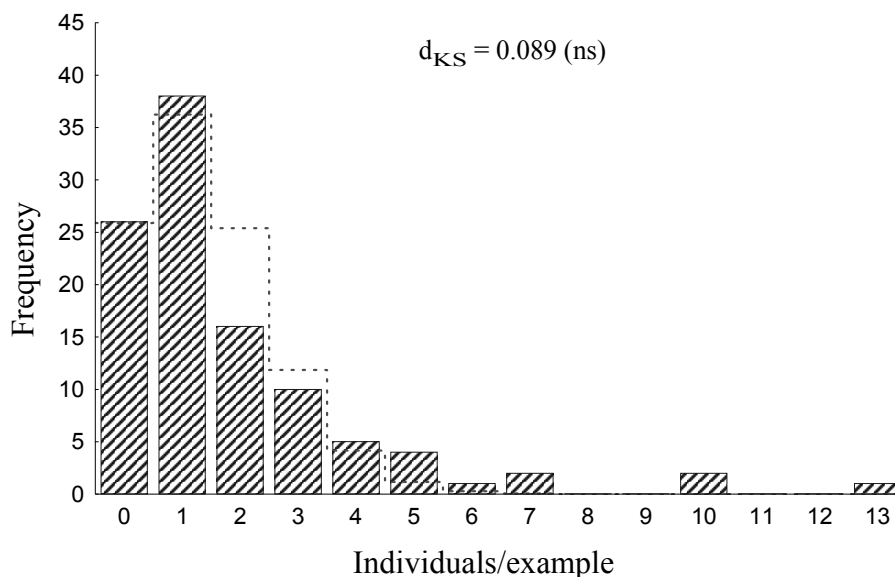


FIG. 1. The empirical distribution of *V. pulchella* per 100 g of soil sample. Dashed line marks the theoretical Poisson distribution for $\lambda = 1.40$.

РИС. 1. Гистограмма эмпирического распределения моллюска *V. pulchella* в 100 г пробах грунта. Пунктиром отмечена теоретическая линия распределения Пуассона для $\lambda = 1.40$.

spatial variability of environmental parameters was conducted using Surfer 8.0 (Golden Software Inc., 2002) and ArcGIS 10.0 (Environmental Systems Research Institute, 2011) software. The Mantel statistic as a matrix correlation between two dissimilarity matrices [Mantel, 1967] was found by vegan's *mantel* function [Oksanen *et al.*, 2017]. The partial Mantel statistic as the partial matrix correlation between three dissimilarity matrices was found by function *mantel.partial*. The Mantel statistic is tested through a permutational Mantel test performed by *mantel* function. Estimation of the Moran's *I* coefficient of spatial autocorrelation was calculated using GeoDa 1.6.6 software [Anselin *et al.*, 2006].

Results

In examining 105 samples 193 *V. pulchella* were detected. Thus, the arithmetic mean of the occurrence of this species during the study period was 1.84 individuals per 100 g of soil sample. The observed distribution of *V. pulchella* abundance is adequately described by the Poisson law (Kolmogorov-Smirnov test: $d_{KS}=0.089$, $p>0.05$) (Fig. 1).

The spatial distribution of individuals is evident in the formation of "hot spots", which are areas with a high accumulation of molluscs (Fig. 2).

Moreover, spatial autocorrelation analysis indicates that the pattern has a relatively high nonrandom component (Fig. 3). In this case, between test sites located 6-7 m apart a positive correlation is

revealed (i.e., these sites are more similar to each other in the number of molluscs registered in them), whereas between test sites located 30-35 m apart, in contrast, a negative correlation holds (areas less similar to each other). The average diameter of the "spot" (i.e., areas occupied by snails) can be estimated as the *X*-axis point of the intersection line connecting the highest positive value of the Moran's *I* statistic with the highest negative values [Legendre, Fortin, 1989]. Roughly, this value is about 15 m.

It can be assumed, that non-random distribution of *V. pulchella* individuals within the study area may be associated with the presence of factors that have an organizational impact on the snail population.

As we can see, even within the small area of the experimental site (21×45 meters), most of these indicators were characterized by substantial heterogeneity. In this case, most of them have a distribution which significantly deviates from normal (Shapiro-Wilk's test: $p<0.001-0.05$). The exception is mainly composed of indices which characterize the soil mechanical impedance within the sample plots at a depth of 15-50 cm, and phytoindicator values according Tsyganov (Table 1).

Moreover, a substantial part of the environmental factors used as predictors of the abundance of *V. pulchella* within the sample sites are spatially heterogeneous, as evidenced by the local Moran's *I* (Table 2).

The probability of finding at least one individual

Table 1. Descriptive statistics of edaphic and vegetation parameters in the experimental plot

Табл. 1. Статистические параметры эдафических и фитоценологических показателей на экспериментальном участке

Indices	Units	Statistical parameters		
		Limits	$\bar{X} \pm SE_{\bar{X}}$	Shapiro-Wilk's test
Humus content	%	0.60-1.04	0.78±0.01	***
Electrical conductivity	dSm/m	0.36-0.77	0.55 ± 0.01	*
Maximal hygroscopic wetness	%	5.59-12.71	8.51±0.16	ns
Shrinkage	%	12.00-26.50	20.73±0.35	**
Temperature of the top soil layer 0-5 cm (03.05.2012)	°C	20.6-25.4	22.6±0.1	*
Temperature of the top soil layer 0-5 cm (20.06.2012)	°C	29.2-40.0	33.1±0.3	***
The proportion of aggregate fractions, mm:				
> 10	%	8.42-53.38	23.15±0.99	***
7-10	%	3.30-14.03	7.81±0.24	*
5-7	%	1.07-15.69	8.33±0.32	*
3-5	%	6.22-25.82	14.39±0.46	**
2-3	%	5.65-28.03	13.33±0.46	**
1-2	%	2.34-32.30	18.54±0.60	ns
0.5-1	%	0.10-10.49	4.19±0.20	ns
0.25-0.5	%	1.10-18.74	6.07±0.30	***
< 0.25	%	0.73-9.61	3.33±0.18	***
Soil mechanical impedance at the depth, cm:				
0-5 cm	mPa	2.00-5.40	3.26±0.08	***
5-10 cm	mPa	2.20-9.00	4.49±0.16	***
10-15 cm	mPa	2.20-9.37	5.47±0.18	*
15-20 cm	mPa	2.00-11.36	6.18±0.21	ns
20-25 cm	mPa	2.00-12.54	6.80±0.23	ns
25-30 cm	mPa	1.69-13.24	7.17±0.25	ns
30-35 cm	mPa	1.64-14.87	7.59±0.26	ns
35-40 cm	mPa	2.01-15.42	7.80±0.28	ns
40-45 cm	mPa	1.86-16.60	8.01±0.30	ns
45-50 cm	mPa	1.89-17.71	8.16±0.31	ns
Physiognomic types of vegetation:				
Type 1	Proportion from 1	0.00-0.18	0.07±0.01	**
Type 2	Proportion from 1	0.15-0.40	0.28±0.01	*
Type 3	Proportion from 1	0.06-0.39	0.19±0.01	*
Type 4	Proportion from 1	0.00-0.09	0.03±0.01	***
Type 5	Proportion from 1	0.01-0.18	0.09±0.01	ns
Type 6	Proportion from 1	0.11-0.60	0.35±0.01	**
Phytoindication scales:				
Thermal climate	scores	9.52-9.88	9.73±0.01	ns
Continentality of climate	scores	10.42-10.77	10.54±0.01	***
Humidity of climate	scores	6.78-7.01	6.94±0.01	***
Cryo-climate	scores	8.98-9.28	9.12±0.01	ns
Soil water regime	scores	7.70-8.01	7.83±0.01	*
Total salt regime	scores	6.27-6.55	6.38±0.01	ns
Nitrogen content in soil	scores	4.88-5.68	5.31±0.02	*
Soil acidity	scores	9.70-10.15	9.92±0.01	***
Lighting	scores	2.01-2.89	2.21±0.01	***
Ecomorph indexes:				
Hygomorphs (KsMs proportion)	scores	2.27-2.71	2.48±0.01	*
Trophomorphs (MgTr proportion)	scores	2.13-2.85	2.46±0.02	ns
Coenomorphs (St proportion)	scores	0.59-0.79	0.70±0.01	ns
Coenomorphs (Pr proportion)	scores	0.03-0.25	0.12±0.01	***
Heliomorphs (Hel proportion)	scores	3.41-3.83	3.61±0.01	ns

* - $p < 0.05$; ** - $p < 0.01$; *** - $p < 0.001$; ns – there were no significant deviations in the Shapiro-Wilk's test from the normal distribution.

* - $p < 0.05$; ** - $p < 0.01$; *** - $p < 0.001$; ns – отсутствует достоверное отклонение от нормального распределения на основе теста Шапиро-Уилкса

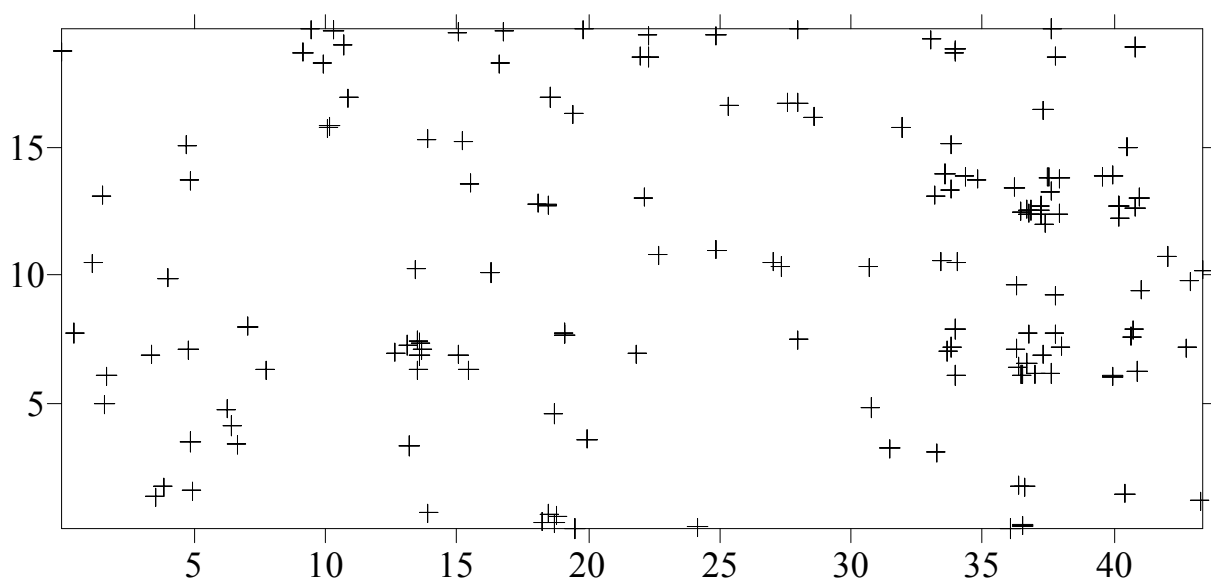


FIG. 2. Spatial distribution of *V. pulchella* within the study area (axes length are given in meters).

РИС. 2. Пространственное размещение моллюска *V. pulchella* в пределах исследованного участка. (Оси ОХ и ОУ приведены в метрах.)

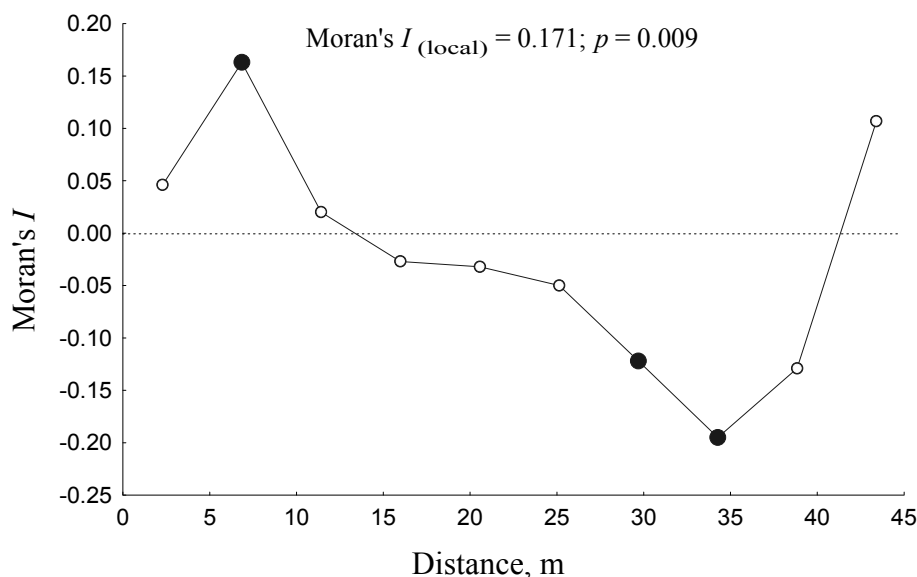


FIG. 3. Moran autocorrelation coefficients of *V. pulchella* spatial distribution within the study area. Significant values of Moran's index are in solid circles.

РИС. 3. Кореллограмма пространственного размещения моллюска *V. pulchella* в пределах исследованного участка. Достоверные оценки индекса Морана представлены черными кружками.

of the *V. pulchella* was shown to be higher on the sample plots characterized by a high electrical conductivity of the soil and containing larger aggregate fraction, low soil mechanical impedance and soil temperature of the layer at a depth of 0-10 cm, with a more developed litter layer, low light level and with a low proportion of hygromorphs and heliomorphs in the vegetation cover (Table 2).

V. pulchella individuals are sensitive to aggregate soil structure. *V. pulchella* abundance increased with increase in the share of soil aggregates of size

3-5, 5-7 and 7-10 mm and decreases with an increase in the share of fine soil aggregates (less than 0.25 mm, 0.25-0.5 and 0.5-1.0 mm).

V. pulchella preferred rather xerophilic microsites with increased mineralization (trophic) of the soil solution. Within steppe the *V. pulchella* snails avoided microsites with meadow vegetation patches (Table 2).

The Mantel's test for matrix measurement of distance constructed on the basis of the mollusc abundance (Euclidean distance) and of all the mea-

Table 2. The assessment of spatial heterogeneity of edaphic and vegetation parameters at the experimental station and their relationship with *V. pulchella* population abundanceТабл. 2. Оценки характера пространственной неоднородности эдафических и фитоценологических показателей на экспериментальном участке и их связи с численностью моллюска *V. pulchella*

Indexes	local Moran's <i>I</i> criterion*	Logistic regression**	Correlation coefficients*	
			Spearman's	global Moran's <i>I</i>
Humus content	0.415	ns	ns	0.18
Electrical conductivity	0.248	4.62	ns	ns
Maximal hygroscopic wetness	0.385	ns	0.246	0.18
Shrinkage	0.358	ns	0.353	0.16
Temperature of the top soil layer 0-5 cm (03.05.2012)	0.535	12.09	-0.334	-0.16
Temperature of the top soil layer 0-5 cm (20.06.2012)	ns	4.29	ns	-0.10
The proportion of aggregate fractions, mm:				
> 10	0.132	8.24	0.206	ns
7-10	0.455	17.26	0.416	0.23
5-7	0.448	6.35	0.335	0.25
3-5	0.359	ns	0.281	0.22
2-3	0.331	ns	ns	ns
1-2	0.206	7.52	-0.223	-0.13
0,5-1	ns	ns	-0.225	ns
0.25-0.5	0.235	6.53	-0.370	-0.16
< 0.25	0.383	10.54	-0.479	-0.16
Soil mechanical impedance at the depth, cm:				
0-5	0.255	4.03	-0.265	-0.14
5-10	0.202	4.21	-0.383	ns
10-15	ns	ns	-0.334	ns
15-20	ns	ns	-0.347	ns
20-25	ns	ns	-0.325	ns
25-30	ns	ns	-0.304	ns
30-35	ns	ns	-0.323	ns
35-40	ns	ns	-0.304	ns
40-45	ns	ns	-0.307	ns
45-50	ns	ns	-0.295	ns
Physiognomic types of vegetation:				
Type 1	0.280	ns	ns	ns
Type 2	0.402	ns	ns	ns
Type 3	0.435	ns	ns	0.16
Type 4	0.516	ns	ns	-0.09
Type 5	0.200	4.06	0.254	ns
Type 6	0.383	ns	-0.193	-0.10
Phytoindication scales:				
Thermal climate	0.319	ns	ns	ns
Continentality of climate	ns	ns	ns	ns
Humidity of climate	0.417	ns	ns	ns
Cryo-climate	0.402	ns	ns	ns
Soil water regime	0.361	ns	ns	-0.18
Total salt regime	0.196	ns	ns	ns
Nitrogen content in soil	0.300	ns	ns	ns
Soil acidity	0.247	ns	ns	ns
Lighting	0.434	7.61	-0.292	-0.13
Ecomorph indexes:				
Hygomorphs (KsMs proportion)	0.684	12.79	-0.346	-0.26
Trophomorphs (MgTr proportion)	0.645	ns	0.268	0.18
Coenomorphs (St proportion)	0.703	ns	ns	ns
Coenomorphs (Pr proportion)	0.673	5.11	ns	-0.12
Heliomorphs (Hel proportion)	0.744	8.29	-0.371	ns

*Only significant estimates are presented. **Estimates of the Pearson Chi-square test (for $df = 1$).*Приведены только достоверные оценки. **Оценки критерия Хи-квадрат К.Пирсона (для $df = 1$).

sured environmental parameters (Euclidean distance) indicates a significant correlation between them ($r_m=0.15$, $p=0.014$). In this case, we found that in the complex of environmental indicators that affect the abundance of *V. pulchella*, a key role is played by edaphic factors ($r_m=0.15$, $p=0.016$) and vegetation parameters ($r = -0.11$, $p < 0.05$). The spatial distance (geographical distance matrix) between the test sites has no significant role in the variability of mollusc number ($r_m=0.04$, $p=0.120$).

Discussion

Land snail *V. pulchella* is a widespread Palearctic species which is also found in some regions of Canada and the US, where inhabit different types of habitats [Gerber, 1996]. At the same time it is characterized by a very high geographical variation in relation to population density. For example, the population density of *V. pulchella* in alder and oak forests of Belarus was 4-8 individuals/m² [Zemoglyadchuk, 2005], on artificial *Robinia* stands in a recultivated area near the town of Zhovti Vodi it was 5.6 individuals/m² [Kul'bachko, Unkovs'ka 2008], whereas in ash-elm forests in Poland it did not exceed the average of 0.13 individuals/m² [Koralewska-Batura, Błoszyk, 2007], and in floodplain forests of Slovakia it was 0.07 individuals/m² [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/m², reaching on separate test plots values of the order of 200 individuals/m². In bush willow depressions in Kazakhstan K.Uvalieva [1990] a density of 224 individuals/m² was estimated.

On the other hand, for typical soil species (such as, *V. pulchella*) it has been proposed to conduct sampling of soil (specific weight), followed by its analysis under a microscope in the laboratory. This method originated in paleozoology [Evans, 1972]. Using this approach, P. Davies *et al.* [1996] found the abundance of *V. pulchella* to be 0.4-40.4 individuals per 100 g sample of soil on chalky soils in UK, and for the Jurassic limestone in the center of Krakow, its abundance was 1-22 individuals per 100 g of soil sample [Gołas-Siarzewska, 2013]. The results are entirely consistent with the data obtained in this study – 1-13 individuals per 100 g of soil sample (Fig. 1).

J. Hermida *et al.* [1993; 2000] showed that within populations studied the abundance of *V. pulchella* is affected by a number of physico-chemical properties of the soil, especially calcium and magnesium concentration and pH of aqueous extract. Furthermore, an association has been found between the abundance of *V. pulchella* and pH and

conductivity of the water in marshy lowland central Scandinavia [Schenková *et al.*, 2015].

As we have shown above, the probability of finding at least one *V. pulchella* individual at a given site was higher on the microsites characterized by a high electrical conductivity of the soil and those containing larger aggregate fractions, low mechanical impedance and low soil temperature at layer a depth of 0-10 cm, with a more developed dead plants layer, low light and low vegetation indices of the hygromorphs and heliomorphs.

The results obtained using different approaches (considering only the presence/absence of *V. pulchella* specimens the various sample plots or with the number of registered individuals) may be different in some cases. Thus, it can be assumed that the models used reflect different aspects of the relationship between snail populations and environmental factors.

In terms of soil mechanical impedance, the statistically significant Spearman's correlation coefficients were revealed in the substantial absence of significant Moran's *I* coefficients (except for the layer 0-5 cm). Obviously, the soil mechanical impedance values at the researched depths of up to 50 cm reflect the state of the soil consistency. Variations of the clay soil consistency may be due to swelling and shrinking processes, which result in fracturing of the soil. These processes largely determine the variability of soil mechanical impedance. These processes, being physical-mechanical in nature, do not form spatial patterns of significant length. In addition, the range of soil mechanical impedance measurement extends beyond the area in which the *V. pulchella* molluscs were collected. Thus, variability of the soil consistency has a local character and is not characterized by spatial patterns on the selected scale level, which is confirmed by the nonsignificant estimates of the local Moran's *I* (Table 2).

The aggregate structure of soil is by its nature the consequence of the physical-mechanical process of swelling and shrinkage, but in addition to these processes the aggregate formation is also influenced by biological processes. Obviously, the inter-aggregate porosity, which is formed in the soil in the presence of aggregates of appropriate sizes, is an essential condition for the vital functions of molluscs, for their breathing and movement. Small aggregates form a system of small pore sizes that are unfavourable to micromollusc survival. The root system of plants forms the aggregate structure of the soil, as well as the trophic and pedoturbation activity of soil animals [Angers, Caron, 1998].

The spatial variability of vegetation, its continuity in time and space leads to the formation of spatially regular structures. As a consequence, the correlation of the abundance of *V. pulchella* with

aggregate structure indicators was observed (Table 2).

It should also be noted that there was a marked correlation between the abundance of *V. pulchella* in sample plots and the characteristics of the vegetation (physiognomic types and phytoindication parameters). In this case, the information value to describe the variation of the *V. pulchella* abundance of the phytoindicator values complex (both collectively and individually) was very low (Mantel test: in all cases $p > 0.05$).

Thus, analysis of the Mantel test results points to the specific nature of the influence of edaphic factors and vegetation on the population of *V. pulchella*. It is likely that the set of indicators selected for consideration is able to fully describe the spatial variation of the abundance of *V. pulchella* within the studied area.

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Внутрипопуляционная пространственная структура наземного моллюска *Vallonia pulchella* (Müller, 1774) (Gastropoda; Pulmonata; Valloniidae)

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РЕЗЮМЕ. В статье рассмотрены механизмы формирования паттерна внутрипопуляционной пространственной организации наземного моллюска *Vallonia pulchella* с точки зрения эдафических и фитоценологических характеристик мест обитания. Сбор моллюсков проводился с использованием регулярной сетки на рекультивированной почве (исследовательская станция Днепропетровского государственного аграрно-экономического университета, г. Покров, Украина). В качестве предикторов численности популяции улиток использовались пространственные переменные, а также физико-химические характеристики почвы и фитоценологические показатели. Показано, что *V. pulchella* предпочитает локальные участки, характеризующиеся более высокой электропроводностью почвы, содержащей более крупные агрегатные фракции, с низкой твердостью и температурой слоя на глубине 0–10 см, с более развитым сухостоем, низкой освещенностью и с низкой долей гигроморф и гелиоморф в растительном покрове.