Ekológia (Bratislava) Vol. 38, No. 4, p. 367–381, 2019
DOI:10.2478/eko-2019-0027

FITTING COMPETING MODELS OF THE POPULATION ABUNDANCE DISTRIBUTION: LAND SNAILS FROM NIKOPOL MANGANESE ORE BASIN TECHNOSOLS

OLGA KUNAKH, DARYA KOVALENKO

Oles Honchar Dnipro National University, pr. Gagarina, 72, 49010 Dnipro, Ukraine; e-mail: kunah_olga@ukr.net
Bogdan Khmelnitsky Melitopol State Pedagogical University, 20, Hetmanska Street, 72318, Melitopol Zaporizhzhya, Ukraine; e-mail: dashuliakovalenko30@gmail.com

Abstract

Kunakh O., Kovalenko D.: Fitting competing models of the population abundance distribution: land snails from Nikopol manganese ore basin technosols. Ekológia (Bratislava), Vol. 38, No. 4, p. 367–381, 2019.

This paper examines the temporal dynamics of terrestrial mollusks of the Nikopol manganese ore basin technosols. The research was carried out at the Research Centre of the Dnipro Agrarian and Economic University in Pokrov (Ukraine). Sampling was carried out in 2012–2014 on four variants of artificial soil: formed on red-brown clays, on loess-like loams, on gray-green clays, and on humus-rich layer. The distribution of the number of individuals in a mollusk population was described by broken stick, Motomura, log-normal, Zipf, and Zipf-Mandelbrot models. It was shown that the series of models that best describe mollusk abundance distribution is specific for a particular species and technosols type and generally is invariant over time.

Key words: land snails, technosols, distribution, population.

Introduction

Habitat is characterized by the availability of a certain range of resources and ecological conditions for a given species, which creates conditions to occupy, survive and reproduce in a given territory (Hall et al., 1997). Finding appropriate statistical distributions for the analysis of animal populations at different hierarchy levels is an important subject of investigation in ecology (Zipkin et al., 2014). The detection of ecological properties, which makes an area fitting for the existence of a species, is important to study the habitat selection (Calenge, Basille, 2008). The investigations of mollusk communities from different biotopes, which differ in vegetation cover, soil type, and moisture level, were devoted to study the habitat selection by land snails (Millar, Waite, 1999; Martin, Sommer, 2004; Müller et al., 2005; Weaver et al., 2006). The importance of soil factors in the spatial distribution, abundance and diversity of mollusk communities has been revealed (Nekola, Smith, 1999; Juřičková et al., 2008; Szybiak et al., 2009). The soil properties, such as the calcium content, pH, the soil texture (Ondina et al., 2004, Juřičková et al., 2008), soil moisture (Nekola, 2003) and the content of exchangeable cations and aluminum (Ondina et al., 1998), have a significant impact on the mollusks population. The best predictor of land snail species composition is the content of carbonate calcium in topsoil (Juřičková et al., 2008). The litter moisture was shown as being the leading factor affecting the microspatial distribution of the terrestrial mollusks (Książkiewicz-Parulska, Ablett, 2017). The phytoindication data application is useful for the evaluation of land snails' ecological properties (Horsák et al., 2007; Dvořáková, Horsák, 2012; Yorkina et al., 2018, 2019). The habitat preferences of the land snail *Vertigo geyeri* in Poland and Slovakia were effectively explained by Ellenberg phytoindication scales (Schenková et al., 2012). Human disturbance at the habitat and landscape scales benefited *Cepaea nemoralis* through the creation of suitable habitats (Rosin et al., 2017).

The open cast mining is one of the most intense disturbances on terrestrial ecosystems. Gastropods are sensitive to habitat disturbance (Kappes et al., 2009). A considerable diversity of the land snails community of a partially reclaimed abandoned coal mine site was revealed (Arruda, 2014). Snails were shown as being highly sensitive to microclimatic fluctuations and structural changes of the man-made structures (Kappes et al., 2012). The habitat transformation on reclaimed land is able to induce a rapid and considerable evolutionary differentiation of the *C. nemoralis* (Schilthuizen, 2013).

The abundance estimates are used to determine the population status for the assessment of the impact on environmental factors and to monitor population trends (Zipkin et al., 2014). Different statistical distributions were used for population abundance fitting such as the Poisson distribution (Caraco, 1980; Kunakh et al., 2018), the negative binomial distribution (Beauchamp, 2011; Wood, 1985), the geometric distribution (Okubo, 1986), and the power law distribution (Bonabeau et al., 1999). The mechanisms behind the patterning of the intra-population abundance distribution of the land snail *Vallonia pulchella* were summarized. For the analysis of the snail population abundance, the following models were proposed: broken sticks model, niche preemption model, log-normal model, Zipf model, and Zipf-Mandelbrot models (Kunakh et al., 2018).

The aim of our work is to examine the temporal dynamics of terrestrial mollusks of the Nikopol manganese ore basin technosols, as well as to find regularities in nature of statistical laws, which explain the distribution of the snail populations.

Material and methods

The research was carried out at the Research Centre of the Dnipro Agrarian and Economic University in Pokrov (Ukraine). The Research Centre (47°38'55.24"N.L., 34°08'33.30"E.L.) for the study of optimal regimes of agricultural reclamation was established in 1968–1970 (Fig. 1). Sampling was carried out in 2012–2014 on four variants of artificial soil (technozems): formed on red-brown clays (RedBrown), on loess-like loams (Loess), on gray-green clays (GrayGreen) and on humus-rich layer (Pedozem) (Fig. 2). According to WRB 2007 (IUSS Working group WRB, 2007), the examined soil belong to the RSG Technosols (Yorkina et al., 2018). From 1995 to 2003, a long-term legume-cereal agrophytocenosis grew on the site, after which the process of naturalization of the vegetation began. In each variant of the technosols, the test polygon was laid, within which sampling was done consisting 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. The test point size is 0.5 × 0.5 m. A quadrat was fixed on the soil surface prior to taking the snail individuals. The snail individuals were manually collected from the soil samples and plants. Each site within the polygons was examined three times a year: in the spring (early May), summer (end of June) and autumn (late September – early October).

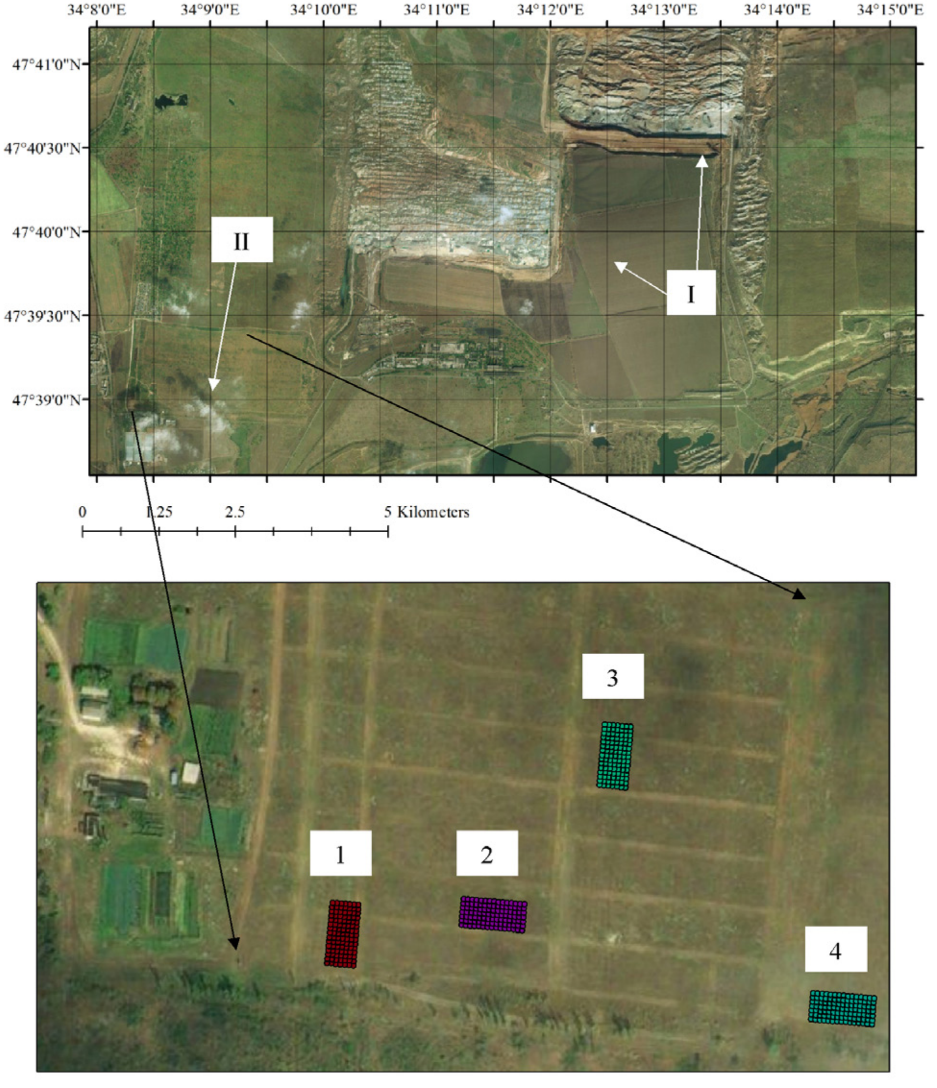

Fig. 1. Location of the test polygons within the Nikopol manganese ore basin.
Notes: I. – Zaporizhia pit mining of manganese ore; II. – an experimental field with different technosols variants: 1 – technosols on loess-like loams; 2 – technosols on red-brown clays; 3 – technosols on gray-green clays; 4 – technosols on humus-rich layer (pedozem).

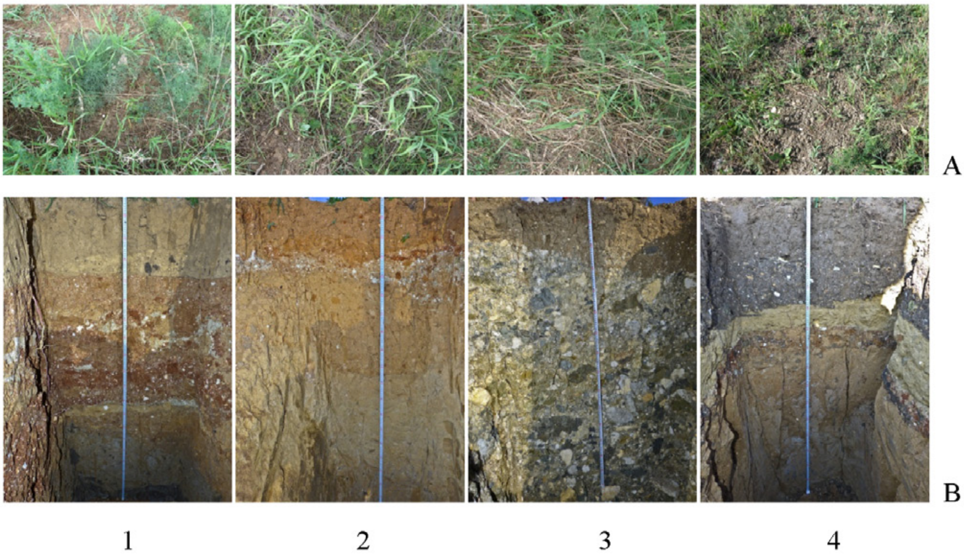

Fig. 2. Plant cover (A) and soil section of the test polygons.
Notes: 1 – technosols on loess-like loams; 2 – technosols on red-brown clays; 3 – technosols on gray-green clays; 4 – technosols on humus-rich layer (pedozem).

The distribution of the number of individuals in a mollusk population may also be described by the dependence "rank-abundance", which are often used in community ecology (Whittaker, 1965). In this case, the individual sample plot sites with mollusks may be regarded as equivalents of individual species in the community (Kunakh et al., 2018). For the analysis in this case, the following model can be used:

broken stick model (MacArthur, 1957):

$$\hat{a}_r = \frac{N}{S}\sum_{k=r}^{S}\frac{1}{k} \; ; \qquad (1)$$

Motomura model (the Whittaker niche preemption model) (Motomura, 1932):

$$\hat{a}_r = N\alpha(1-\alpha)^{r-1}; \qquad (2)$$

log-normal model (Preston, 1948, 1962):

$$\hat{a}_r = \exp[\log(\eta) + \log(\sigma)\Phi] \; ; \qquad (3)$$

Zipf model (Zipf, 1949):

$$\hat{a}_r = N\hat{p}_1 r^{\gamma} \; ; \qquad (4)$$

Zipf-Mandelbrot model (Mandelbrot, 1983):

$$\hat{a}_r = N\,(r+\beta)^{\gamma} \; ; \qquad (5)$$

where $\hat{a}_r$ is the expected abundance of species of rank r; S is the number of species; N is the number of individuals; Φ is a standard normal distribution function; $\hat{p}_1$ is the estimated proportion of the most abundant species; α, μ, σ, γ, β and c are the parameters in each model.

The degree of adequacy of the model was evaluated using Akaike›s information criterion (AIC) and the Bayesian information criterion (BIC). The best model has the lowest AIC and BIC. 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 *vegan* (Oksanen et al., 2018).

Results and discussion

The four species of terrestrial mollusks were found within the investigated technosols: *Brephulopsis cylindrica* (Menke, 1828), *Monacha cartusiana* (O.F. Muller, 1774), *Chondrula tridens* (O.F. Muller, 1774), *Helix lucorum* Linnaeus, 1758. The abundance of the *Brephulopsis cylindrica* in the studied habitats varies from 3.68 ± 0.43 to 74.55 ± 4.46 ind./m^2 (Fig. 3). The population abundance is statistically significantly different between the studied types of technosols (Kruskal-Wallis test: $H = 1812.7$, $p < 0.001$). The most favorable conditions for this snail species are formed in the gray-green clays and loess-like loams (Fig. 1). The less favorable habitats are formed in the pedozems and most extreme is in the red-brown clays. During the study period, the statistically significant trend of the *B. cylindrica* abundance decline in years was reveled (Kruskal-Wallis test: $H = 52.3$, $p < 0.001$). A common feature is the tendency to reduce the abundance of *B. cylindrica* during the year (Kruskal-Wallis test: $H =$ 24.6, p = $p < 0.001$). But deviation from the specified pattern can be observed depending on the technosol type and from year to year. Thus, in 2012, for all technosol types, *B. cylindrica* population decreased during the year. The local minimum of population size was observed in the 2013 summer on loess-like loams and gray-green clay, and vice versa; at the same time, there was a local maximum of *B. cylindrica* population size on pedozems and red-brown clays. In 2013, in technosol types except loess-like loams, the local maximum of the *B. cylindrica* abundance was detected. In 2013, the local maximum of the population abundance was observed in the spring. Deviations from the general trend of decline for the year occurred in the conditions of total low abundance of snails in the spring.

Most often the log-normal and the Zipf-Mandelbrot models are the best for the analytical fitting of empirical data on *B. cylindrica* abundance patterns (Table 1). The Zipf-Mandelbrot model is the best in a slightly greater number of cases than the log-normal model. The Zipf-Mandelbrot model gives the best results in a considerable number of cases for *B. cylindrica* population in biotopes on loess-like loams, and almost parity between these models is observed for other technosol types. For the spring season, there is a slight advantage of the log-normal model for fitting the *B. cylindrica* abundance. For the summer season, there is parity in the descriptive abilities of the models, and Zipf-Mandelbrot model has priority in the autumn.

Thus, distributions of the *B. cylindrica* abundance in the technosol types, which are significantly different in terms of the environmental conditions that is indicated in the total level of the abundance and features of population dynamics can be described by the two models – log-normal and Zipf-Mandelbrot. The Zipf model is very close to the Zipf-Mandelbrot model and quite likely to reasonably choose one of them, the larger data set is needed. The Motomura (geometric series) model describes a system with a high level of competitive relations. The broken stick model on the contrary, describes the situation with a random distribution of system components, which is possible under the conditions of abundant resources and the

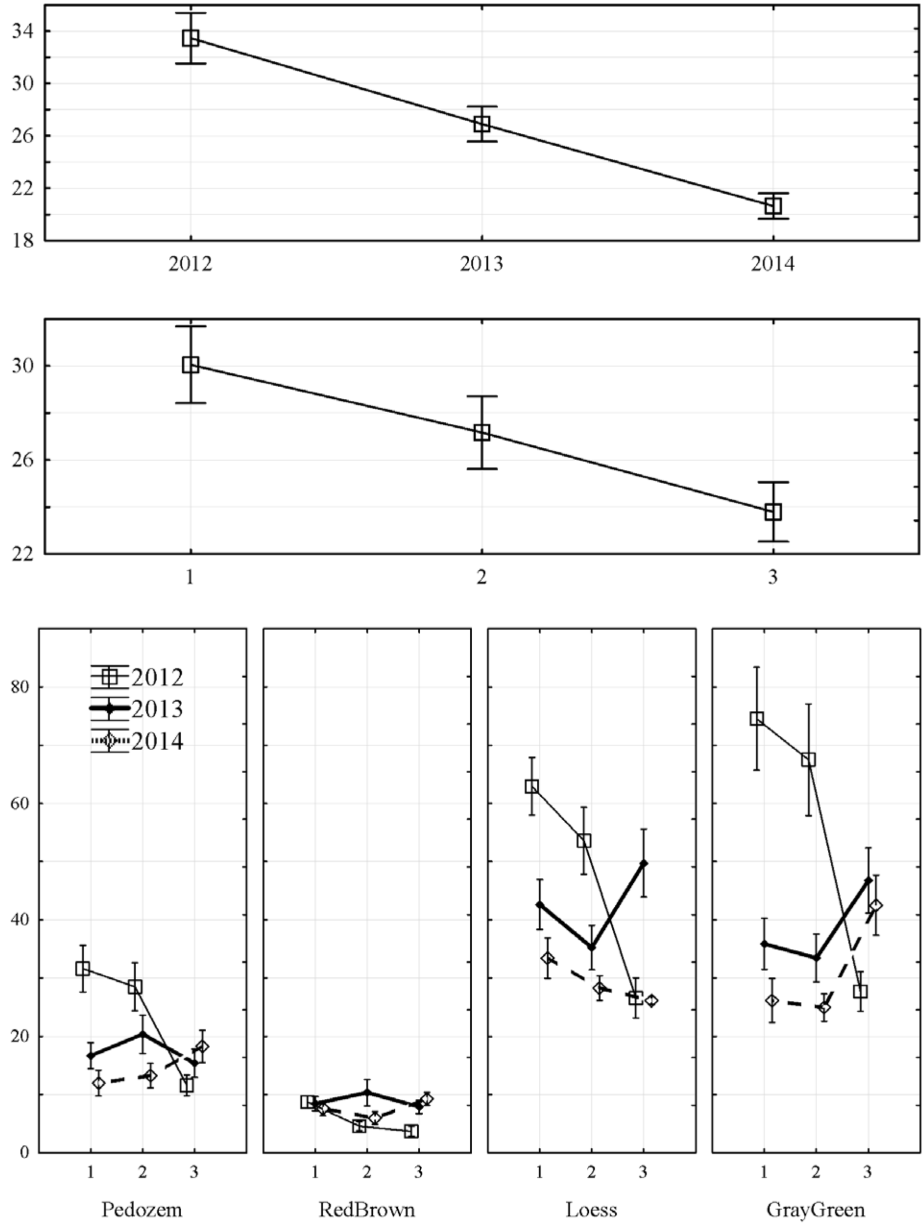

Fig. 3. Dynamics of the *Brephulopsis cylindrica* population abundance in different technosol types (ind./m², mean ± 95% confidence interval).
Notes: 1 – spring; 2 – summer; 3 – autumn.

absence of significant competition. Thus, the obtained results indicate that such alternatives as considerable competition in the population *B. cylindrica*, and complete lack of competition may be rejected.

The Zipf-Mandelbrot and log-normal models describe systems that are characterized by complex organization and nonlinear response to external effects. A competitive relationship between individuals of one species or different species in community can act as one of the mechanisms of such organization formation. We can assume that the role of a competitive relationship is variable and can change from the state of complete control of the population dynamics (as required by the Motomura model) to the absence of such control (as required by the broken stick model).

T a b l e 1. The number of the best models that describe the distribution of *Brephulopsis cylindrica* abundance in the different types of technosols or the seasons of the year.

The technosols types or seasons	**Model**	
	Lognormal	**Zipf-Mandelbrot**
Technosol type		
Loess-like loams	3	6
Gray-green clays	4	5
Red-brown clays	5	4
Humus-rich layer	4	5
Season		
Spring	7	5
Summer	6	6
Autumn	3	9
Total	16	20

T a b l e 2. The number of the best models that describe the distribution of *Monacha cartusiana* abundance in the different types of technosols or the seasons of the year.

The technosols types or seasons	**Model**			
	Lognormal	**Mandelbrot**	**Preemption**	**Null**
Technosol type				
Loess-like loams	4	3	1	1
Gray-green clays	4	5	–	–
Red-brown clays	7	–	2	
Humus-rich layer	6	2	1	–
Season				
Spring	5	5	2	–
Summer	8	2	1	1
Autumn	8	3	1	–
Total	21	10	4	1

The Zipf-Mandelbrot model can also describe a system characterized by fractal properties. The fractal properties were shown for populations of terrestrial molluscs. This allows you to hypothesize the existence of a hierarchical organization of spatial structure of populations of terrestrial molluscs, which are formed on technosols.

The abundance of the *Monacha cartusiana* in the studied habitats varies from 2.25 ± 0.27 to 18.64 ± 1.08 ind./m^2 (Fig. 4). The population abundance is statistically significantly different between the studied types of technosols (Kruskal-Wallis test: H = 324.14, $p < 0.001$).

The loess-like loams and red-brown clays form the most favorable conditions for this species. The gray-green clays are less favorable habitats. The pedozems are the most extreme. During the period of investigation, the greatest *Monacha cartusiana* abundance was observed in 2012, and the minimum – in 2013. The interannual differences of the abundances are

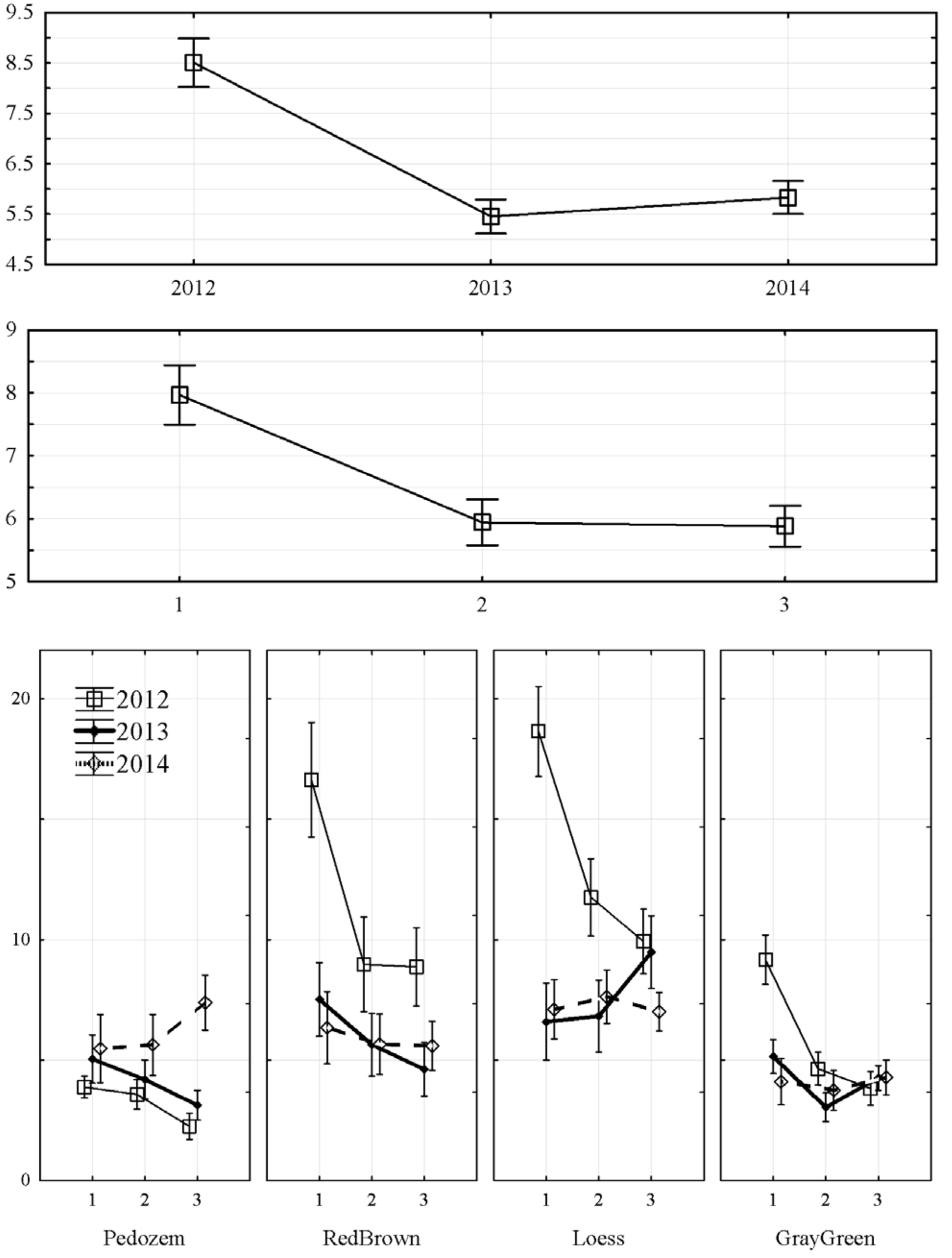

Fig. 4. Dynamics of the *Monacha cartusiana* population abundance in different technosol types (ind./m², mean ± 95% confidence interval).
Notes: 1 – spring; 2 – summer; 3 – autumn.

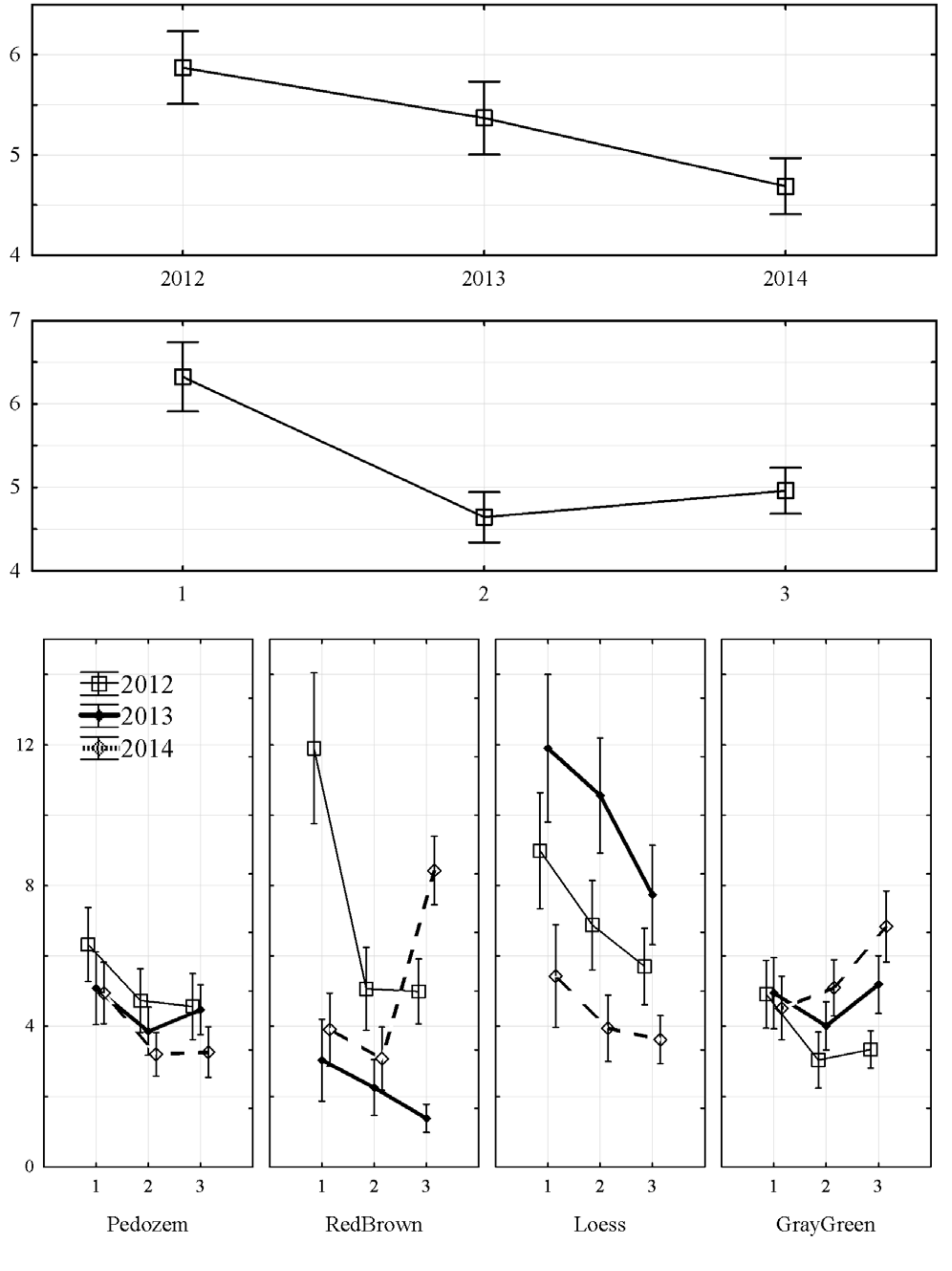

Fig. 5. Dynamics of the *Chondrula tridens* population abundance in different technosol types (ind./m[2], mean ± 95% confidence interval).
Notes: 1 – spring; 2 – summer; 3 – autumn.

T a b l e 3. The number of the best models that describe the distribution of *Chondrula tridens* abundance in the different types of technosols or the seasons of the year.

The technosol types or seasons	**Model**			
	Lognormal	**Mandelbrot**	**Zipf**	**Null**
Technosol type				
Loess-like loams	1	2	5	1
Gray-green clays	–	2	7	–
Red-brown clays	–	3	6	–
Humus-rich layer	–	1	8	–
Season				
Spring	–	4	7	1
Summer	1	1	10	–
Autumn	–	3	9	–
Total	1	8	26	1

T a b l e 4. *Helix lucorum* population abundance in different technosol types (ind./m^2, mean ± 95% confidence interval).

Technosol type	**Рік**	**Season**		
		Spring	**Summer**	**Autumn**
Red-brown clays	2012	–	–	–
	2013	–	–	–
	2014	0.04 ± 0.04	–	–
Loess-like loams	2012	1.60 ± 0.25	0.46 ± 0.15	0.69 ± 0.16
	2013	0.53 ± 0.17	1.07 ± 0.22	0.72 ± 0.17
	2014	0.53 ± 0.14	0.30 ± 0.13	0.30 ± 0.13
Humus-rich layer	2012	0.04 ± 0.04	–	–
	2013	–	0.34 ± 0.11	–
	2014	–	–	–
Gray-green clays	2012	0.38 ± 0.13	0.19 ± 0.08	0.19 ± 0.08
	2013	0.11 ± 0.07	0.27 ± 0.10	0.50 ± 0.13
	2014	–	0.04 ± 0.04	–

statistically significant (Kruskal-Wallis test: H = 125.9, $p < 0.001$). For the total sample size of the role of seasonal changes during the year is statistically significant (Kruskal-Wallis test: H = 38.60, $p < 0.001$). The general trend is to reduce the population abundance from spring to summer and population stabilization from summer to autumn. The population abundance between summer and autumn is not statistically significantly different (Kruskal-Wallis test: = 1.53, $p = 0.37$). The clearest trend of downsizing for the year was observed in 2012 in all technosol types. In 2013, the decline during the year took place only in pedozems and red-brown clays. This year, the growth of the population abundance took place in the autumn on loess-like loams and red-brown clays. In 2014, to the overall low *M. cartusiana* abundance, there were fluctuation oscillations of the population that occurred during the year in all technosol types studied. Thus, the smaller the overall *M. cartusiana* population abundance, the less precise is the trend of the population dynamic during the season. For red-brown clays and loess-like loams, there were trends towards a decreasing of total abundance for the season with a sharp drop in the population between spring and summer. The stable abundance level of molluscs during the year is characterized for pedozems. The summer minimum of the *M. cartusiana* abundance and the subsequent compensatory increase in the autumn were revealed for the gray-green clays.

The lognormal model has the most explanatory capabilities to fit the distribution of the *M. cartusiana* abundance from the considered statistical models (Table 2). According Akaike criterion, Zipf-Mandelbrot model demonstrates a higher explanatory capacity in fewer cases, but fairly regularly. In some cases, the distribution of the *M. cartusiana* abundance is best described by Motomura or broken stick models.

Only the most general trends of explanatory capacity of the statistical distribution models of the abundance allow to distinguish the population within technosol types. Thus, significant dominance of the lognormal model explanatory capacity is characteristic for the population on the red-brown clays and pedozems. Almost complete parity of the lognormal and Zipf-Mandelbrot models was revealed for population on loess-like loams and gray-green clays. The *M. cartusiana* population distribution in the spring can be best described by the Zipf-Mandelbrot and lognormal models. The summer and autumn distributions can be best described by the Zipf-Mandelbrot model. In the seasonal aspect, there is a shift from such a distribution, which can mainly be explained by the Zipf's law in the spring and summer to such that is mainly be explained by the Motomura law in autumn. Thus, the *M. cartusiana* population dynamics over time was accompanied by changes in population characteristics of the statistical distribution of this species abundance. The population distribution during the abundance sharp increase can be described by the Zipf's model. The possibility of outbreaks is more typical for the habitat in loess-like loams, which can be considered as the most favorable environment for the existence of this species.

The abundance of the *Chondrula tridens* in the studied habitats varies from 1.38 ± 0.20 to 11.90 ± 1.06 ind./m^2 (Fig. 5). The population abundance is statistically significantly different between the studied types of the technosols (Kruskal-Wallis test: H = 81.04, $p < 0.001$). The loess-like loams form the most favorable conditions for this species. The *Ch. tridens* population density is much smaller in the red-brown clays, and the lowest in the pedozems and gray-green clays (the population density in the last two technosols are not statistically significantly different from each other, Kruskal-Wallis test: H = 0.58, $p = 1.00$).

The decline of the *Ch. tridens* population abundance was observed during the period of studies over the years (Kruskal-Wallis test: H = 21.66, $p < 0.001$). In the seasonal aspect, the population dynamics was characterized by a spring maximum and a summer minimum. The autumn raising was negligible in comparison with the summer population level. The abundance seasonal differences were statistically significant (Kruskal-Wallis test: H = 34.78, $p < 0.001$). The differences between abundances in summer and in autumn were not statistically significant (Kruskal-Wallis test: H = 1.86, $p = 0.18$). It should be noted that there are significant deviations from the established seasonal pattern of *Ch. tridens* population variability depending on the technosol type and every year. Throughout the year, the downward trend of the *Ch. tridens* population dynamic was revealed for loess-like loams. The similar pattern with less amplitude variation was also confirmed for pedozems. The considerable variability of seasonal dynamics was reveled for red-brown clays. In 2012, after the spring outbreak, in the summer a dramatic decline was detected with the further stabilization in the autumn. In 2013, monotonic decline was observed throughout the year with a very low starting abun-

T a b l e 5. The number of the best models that describe the distribution of *Helix lucorum* abundance in the different types of technosols or the seasons of the year.

The technosol types or seasons	**Model**			
	Preemption	**Zipf**	**Lognormal/Zipf**	**Null**
Technosol type				
Loess-like loams	3	4	–	2
Gray-green clays	4	–	1	2
Red-brown clays	–	–		1
Humus-rich layer	–	–	1	1
Season				
Spring	2	2	–	3
Summer	4	–	1	2
Autumn	1	2	1	1
Total	7	4	2	6

T a b l e 6. The number of the best models that describe the distribution of mollusks abundance in the different types of technosols or the seasons of the year.

Species	**Model**				
	Lognormal	**Mandelbrot**	**Null**	**Preemption**	**Zipf**
Brephulopsis cylindrica	16	20	–	–	–
Chondrula tridens	1	8	1	–	26
Helix lucorum	2	–	6	7	4
Monacha cartusiana	21	10	1	4	–
Total	40	38	8	11	30

dance in the spring. In 2013, the abundance outbreak occurred in the autumn after a summer minimum.

The Zipf model is the best to describe the *Ch. tridens* abundance distribution (Table 3). *Helix lucorum* is a large synanthropic land snail (Korábek et al., 2018), which has been recently reported from a studied territory (Balashov et al., 2013). Mollusk *H. lucorum* was regularly found in the loess-like loams and was often found in 2012 and 2013 in the gray-green clays. In this, the species was found twice in the pedozems, and only once in the red-brown clays (Table 4).

Distribution of the *H. lucorum* abundance can be best described by the Motomura or the broken stick models (Table. 5). The Zipf model best explains the mollusk population distribution in loess-like loams. The Motomura model is the best for population from the biotopes on gray-green clays. In the seasonal aspect, there is a certain predominance of one or another model to describe the abundance distribution of the *H. lucorum*. The broken stick model has an advantage in the spring, Motomura model has an advantage in the summer. The broken stick, Zipf, lognormal and Motomura models demonstrate the almost equal opportunity for abundance distribution fitting. Thus, a significant predominance of descriptive abilities of the two models – Motomury and a broken stick – indicates a certain level of statistical invariance of the *H. lucorum* distribution in a range of environmental conditions, which are formed in technosols. The loess-like loams and gray-green clays form consistently favorable conditions for the existence of mollusks *H. lucorum*. In two other types (pedozems and red-brown clays), the representatives of this species occur sporadically.

The Zipf, lognormal or Zipf-Mandelbrot models have the best ability to explain the abundance distribution of the mollusks populations (Table 6). Mollusks species have some specific composition of models that best describe the abundance distribution of their population in technosols. Thus, the lognormal and Zipf-Mandelbrot models are the best for the most abundant mollusks *Brephulopsis cylindrica* and *Monacha cartusiana*. The Zipf model is the best, and to a lesser extent – the Zipf-Mandelbrot model for less abundant species *Chondrula tridens*. The broken sticks or Motomura models are the best for the rare species *Helix lucorum*.

T a b l e 7. The number of the best models that describe the distribution of mollusks abundance in the different time periods.

Time period	Model				
	Lognormal	**Mandelbrot**	**Null**	**Preemption**	**Zipf**
Year					
2012	12	16	2	4	9
2013	17	10	2	4	10
2014	11	12	4	3	11
Season					
Spring	12	14	4	4	9
Summer	16	9	3	5	10
Autumn	12	15	1	2	11
Total	40	38	8	11	30

T a b l e 8. The number of the best models that describe the distribution of mollusks abundance in the different technosols.

Technosol	Model				
	Lognormal	**Mandelbrot**	**Null**	**Preemption**	**Zipf**
Loess-like loams	8	11	4	4	9
Gray-green clays	11	8	1	1	8
Red-brown clays	9	12	2	4	7
Humus-rich layer	12	7	1	2	6
Total	40	38	8	11	30

The list and the proportion of the models that can best describe the distribution of the mollusk abundance, are almost invariable in time for years (Table 7). In the seasonal aspect the Zipf-Mandelbrot model relatively more often takes precedence in spring or in autumn and lognormal model – in summer. The Zipf, Motomura and broken stick models are not dependent on the time aspect.

A particular range of models that best describes the distribution of mollusks abundance is specific for each technosol type (Table 8). Lognormal model is often effective to describe the mollusk population in the red-brown clays and in the pedozems. The Zipf-Mandelbrot model is best to explain the distribution in loess-like loams and gray-green clays. The broken stick model is often suitable to describe populations in loess-like loams. The Motomura model is also effective in loess-like loams and in gray-green clays, and Zipf model is suitable for population in loess-like loams and pedozems.

Conclusion

The series of models that best describe mollusk abundance distribution is specific for a particular species and technosol type, and generally is invariant over time. Species with high overall level of population abundance that are characterized by distributions are well explained by lognormal model or Zipf-Mandelbrot model. It is believed that these models mark the steady state populations of mollusks, which allows to build complex relationships that combine both competition between individuals of the population, interspecific competition and the possibility of implementing reproductive potential under favorable ecological environment conditions. The abundance of the facultative populations, formed mainly by migration in terms of periodic extinctions micropopulations, is often described by the Motomura model or the broken stick model.

References

Arruda, J.A. (2014). The land snails of a partially reclaimed abandoned coal mine site. *Trans. Kans. Acad. Sci.*, 117(1–2), 15–20. DOI: 10.1660/062.117.0103.

Balashov, I.A., Kramarenko, S.S., Zhukov, A.V., Shklyaruk, A.N., Baidashnikov, A.A. & Vasyliuk A.V. (2013). Contribution to the knowledge of terrestrial molluscs in southeastern Ukraine. *Malacologica Bohemoslovaca*, 12, 62–69.

Beauchamp, G. (2011). Fit of aggregation models to the distribution of group sizes in Northwest Atlantic seabirds. *Mar. Ecol. Prog. Ser.*, 425, 261–268. https://www.jstor.org/stable/24874645

Bonabeau, E., Dagorn, L. & Freon P. (1999). Scaling in animal group-size distributions, *PANAS*, 96, 4472–4477. DOI: 10.1073/pnas.96.8.4472.

Calenge, C. & Basille M. (2008). A general framework for the statistical exploration of the ecological niche. *J. Theor. Biol.*, 252(4), 674–685. DOI: 10.1016/j.jtbi.2008.02.036.

Caraco, T. (1980). Stochastic dynamics of avian foraging flocks. *Am. Nat.*, 115(2), 262–275. www.jstor.org/stable/2460597.

Dvořáková, J. & Horsák M. (2012). Variation of snail assemblages in hay meadows: Disentangling the predictive power of abiotic environment and vegetation. *Malacologia*, 55(1), 151–162. DOI: 10.4002/040.055.0110.

Hall, L.S., Krausman, P.R. & Morrison M.L. (1997). The habitat concept and a plea for standard terminology. *Wildl. Soc. Bull.*, 25(1), 173–182. https://www.jstor.org/stable/3783301

Horsák, M., Hájek, M., Tichý, L. & Juřičková L. (2007). Plant indicator values as a tool for land mollusc autecology assessment. *Acta Oecol.*, 32(2), 161–171. DOI: 10.1016/j.actao.2007.03.011.

IUSS Working Group WRB (2007). *World reference base for soil resources 2006, first update 2007*. World Soil Resources Reports No. 103. Rome: FAO.

Juřičková, L., Horsák, M., Cameron, R., Hylander, K., Mikovcová, A., Hlaváč, J.C. & Rohovec J. (2008). Land snail distribution patterns within a site: The role of different calcium sources. *Eur. J. Soil Biol.*, 44, 172–179. DOI: 10.1016/j.ejsobi.2007.07.001.

Kappes, H., Jordaens, K., Hendrickx, F., Maelfait, J.P., Lens, L. & Backeljau T. (2009). Response of snails and slugs to fragmentation of lowland forests in NW Germany. *Landsc. Ecol.*, 24(5), 685–697. DOI: 10.1007/s10980-009-9342-z.

Kappes, H., Clausius, A. & Topp W. (2012). Historical small scale surface structures as a model for post-mining land reclamation. *Restor. Ecol.,* 20, 322–330. DOI: 10.1111/j.1526-100X.2011.00800.x.

Korábek, O., Juřičková, L., Balashov, I. & Petrusek A. (2018). The contribution of ancient and modern anthropogenic introductions to the colonization of Europe by the land snail *Helix lucorum* Linnaeus, 1758 (Helicidae). *Contrib. Zool.*, 87(2), 61–74. DOI: 10.1163/18759866-08702001.

Książkiewicz-Parulska, Z. & Ablett J.D. (2017). Microspatial distribution of molluscs and response of species to litter moisture, water levels and eutrophication in moist, alkaline ecosystems. *Belg. J. Zool.*, 147(1), 37–53. DOI: 10.26496/bjz.2017.3.

Kunakh, O.N., Kramarenko, S.S., Zhukov, A.V., Kramarenko, A.S. & Yorkina N.V. (2018). Fitting competing models and evaluation model parameters of the abundance distribution of the land snail *Vallonia pulchella* (Pulmonata, Valloniidae). *Regulatory Mechanisms in Biosystems*, 9(2), 198–202. DOI: 10.15421/021829

MacArthur, R.H. (1957). On the relative abundance of bird species. *Proc. Natl. Acad. Sci. USA,* 43(3), 293–295. DOI: 10.1073/pnas.43.3.293.

Mandelbrot, B.B. (1983). *The fractal geometry of nature*. New York: W.H. Freeman and Company.

Martin, K. & Sommer M. (2004). Relationships between land snail assemblage patterns and soil properties in temperate-humid forest ecosystems. *J. Biogeogr.*, 31(4), 531–545. DOI: 10.1046/j.1365-2699.2003.01005.x.

Millar, A.J. & Waite S. (1999). Mollusks in coppice woodland. *J. Conchol.*, 36, 25–48.

Motomura, I. (1932). On the statistical treatment of communities. *Zoological Magazine*, 44, 379–383.

Müller, J., Strätz, C. & Hothorn T. (2005). Habitat factors for land snails in European beech forests with a special focus on coarse woody debris. *European Journal of Forest Research*, 124(3), 233–242. DOI: 10.1007/s10342-005-0071-9.

Nekola, J.C. & Smith T.M. (1999). Terrestrial gastropod richness patterns in Wisconsin carbonate cliff communities. *Malacologia*, 41(1), 253–270.

Nekola, J.C. (2003). Large-scale terrestrial gastropod community composition patterns in the Great Lakes region of North America. *Divers. Distrib.*, 9(1), 55–71. DOI: 10.1046/j.1472-4642.2003.00165.x.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner H. (2018). *Community ecology package*. R package version 2.5-2. https://CRAN.R-project.org/package=vegan

Okubo, A. (1986). Dynamical aspects of animal grouping: Swarms, schools, flocks and herds. *Advances in Biophysics*, 22 (1986), 1–94. DOI: 10.1016/0065-227X(86)90003-1.

Ondina, P., Mato, S., Hermida, J. & Outeiro A. (1998). Importance of soil exchangeable cations and aluminium content on land snail distribution. *Appl. Soil Ecol.*, 9(1–3), 229–232. DOI: 10.1016/S0929-1393(98)00080-8.

Ondina, P., Hermida, J., Outeiro, A. & Mato S. (2004). Relationships between terrestrial gastropod distribution and soil properties in Galicia (NW Spain). *Appl. Soil Ecol.*, 26(1), 1–9. DOI: 10.1016/j.apsoil.2003.10.008.

Preston, F.W. (1948). The commonness, and rarity, of species. *Ecology*, 29 (3), 254–283. DOI: 10.2307/1930989.

Preston, F. (1962). The canonical distribution of commonness and rarity: Part I. *Ecology*, 43, 185–215. DOI: 10.2307/1931976.

Rosin, Z. M., Lesicki, A., Kwiecinski, Z., Skorka, P. & Tryjanowski P. (2017). Land snails benefit from humanalterations in rural landscapes and habitats. *Ecosphere*, 8(7), e01874. DOI: 10.1002/ecs2.1874.

Schenková, V., Horsák, M., Plesková, Z. & Pawlikowski P. (2012). Habitat preferences and conservation of *Vertigo geyeri* (Gastropoda: Pulmonata) in Slovakia and Poland. *J. Molluscan Stud.*, 78, 105–111. DOI: 10.1093/mollus/eyr046.

Schilthuizen, M. (2013). Rapid, habitat-related evolution of land snail colour morphs on reclaimed land. *Heredity*, 110, 247–252. DOI: 10.1038/hdy.2012.74.

Szybiak, K., Błoszyk, J., Koralewska-Batura, E. & Gołdyn B. (2009). Small-scale distribution of wintering terrestrial snails in forest site: relation to habitat conditions. *Pol. J. Ecol.*, 57(3), 525–535.

Weaver, K.F., Anderson, T. & Guralnick R. (2006). Combining phylogenetic and ecological niche modeling approaches to determine distribution and historical biogeography of Black Hills mountain snails (Oreohelicidae). *Divers. Distrib.*, 12(6), 756–766. DOI: 10.1111/j.1472-4642.2006.00289.x.

Whittaker, R.H. (1965). Dominance and diversity in land plant communities. *Science*, 147, 250–260. DOI: 10.1126/science.147.3655.250.

Wood, C.C. (1985). Aggregative response of common mergansers (Mergus merganser): predicting flock size and abundance on Vancouver Island salmon streams. *Can. J. Fish. Aquat. Sci.*, 42(7), 1259–1271. DOI: 10.1139/f85-157.

Yorkina, N., Maslikova, K., Kunah, O. & Zhukov, O. (2018). Analysis of the spatial organization of *Vallonia pulchella* (Muller, 1774) ecological niche in Technosols (Nikopol manganese ore basin, Ukraine). *Ecologica Montenegrina*, 17, 29–45. www.biotaxa.org/em

Yorkina, N., Zhukov, O. & Chromysheva, O. (2019). Potential possibilities of soil mesofauna usage for biodiagnostics of soil contamination by heavy metals. *Ekológia (Bratislava)*, 38(1), 1–10. DOI: 10.2478/eko-2019-0001.

Zipf, G. K. (1949). *Human behavior and the principle of least effort*. Cambridge: AddisonWesley.

Zipkin, E. F., Leirness, J. B., Kinlan, B. P., O'Connell, A. F. & Silverman, E. D. (2014). Fitting statistical distributions to sea duck count data: implications for survey design and abundance estimation. *Statistical Methodology*, 17, 67–81. DOI: 10.1016/j.stamet.2012.10.002.