Temperature effect on the temporal dynamic of terrestrial invertebrates in technosols formed after reclamation at a post-mining site in Ukrainian steppe drylands

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The research was carried out at the Research Centre of the Dnipro State Agrarian and Economic University in Pokrov city. Sampling was carried out in 2013–2015 on a variant of artificial soil (technosols) formed on loess-like loam, red-brown clay, green-grey clay, technological mixture of rocks, and also formed on loess-like loam with a humus-rich 70 cm top soil layer. To investigate the spatiotemporal variation in the abundance, species richness and species composition of invertebrate assemblages within the experimental polygon, the animals were sampled using pitfall traps. In total, 60 pitfall traps were operated simultaneously during each sampling period. Each year the pitfalls were emptied 26 times every 7–9 days. Invertebrates (Arthropoda and Mollusca) of 6 classes, 13 orders, 50 families and 202 species or parataxonomic units were recorded. Diplopoda was most abundant taxonomic group, though it was represented by only one species *Rossiulus kessleri* (Lohmander, 1927). Coleoptera and Araneae were the most numerous taxonomic groups. Readily available water for plants, precipitation, wind speed, atmospheric temperature (daily minimum, daily maximum, daily mean), atmospheric humidity and atmospheric pressure were used as environmental predictors. Two dimension geographic coordinates of the sampling locations were used to generate a set of orthogonal eigenvector-based spatial variables. Time series of sampling dates were used to generate a set of orthogonal eigenvector-based temporal variables. The moisture content in the technosols was revealed to be the most important factor determining the temporal dynamics of the terrestrial invertebrate community in conditions of semi-arid climate and the ecosystem which formed as a result of the reclamation process. Following soil moisture, the factor most strongly affecting invertebrates in the technosols was temperature. From the total set of the invertebrates, two relatively homogeneous species groups in terms of thermal preferences were extracted: the microtemperature and mesotemperature groups. The microtemperature species are more tolerant to the thermal factor, and the mesotemperature species are more sensitive. The Huisman-Olff-Fresco approach expanded by Jansen-Oksanen provides a wide set of ecologically relevant models which are able to explain species response. The species response to temperature is affected by a complex of other environmental, temporal and spatial factors. The effect of other factors on the species response must be previously extracted to find real estimations of the species temperature optima and tolerance. The approaches to solving this problem may be the object of future investigation.

Keywords: species response; temperature; niche; tolerance; reclamation; gradient; temporal dynamic.

Introduction

Niche theory is a powerful approach to understanding mechanisms underlying the temporal and spatial dynamic of populations or communities (Schoener, 1989; Tokeshi, 1999). Niche theory predicts that the distribution of species is forced by the differences between species optima and environmental factors (Hutchinson, 1957). The ecological niche may be considered in the context of the two dimensions: Grinnellian and Eltonian (Soberon, 2007). The Grinnellian niche takes into account the importance of a given set of resources for the survival of a species (Devictor et al., 2010; Sokolov & Zhukov 2017). The Grinnellian niche is considered in two ways: on the one hand as a complex of the habitat conditions and on the other hand as behavioural adaptations allowing organisms to persist and produce offspring (Grinnell, 1917). The Eltonian niche is concentrated not only on the consideration of species response to impact of environment but on the consideration of species impact within the environment. The niche reflects the place of a species in the biotic environment, its relations to food and enemies (Elton, 1927).

The terrestrial macroinvertebrate communities of arid and semi-arid ecosystems are represented by insects, spiders, mollusks, and myriapods (Pakhomov et al., 2008; Gerlach et al., 2013; Brygadyrenko, 2016). Among insects, the ground-dwelling beetles (especially Carabidae, Scarabaeidae, and Tenebrionidae) form the most considerable component of the community in arid ecosystems (Konstantinov et al., 2009). Spiders are the dominant predators and a species-rich group in most terrestrial ecosystems (Wise, 1993; Rushton & Eyre, 1992). Saprophagous macroarthropods provide a key role in organic matter turnover within most ecosystems (Paoletti et al., 2007). Millipedes, woodlice and other saprophagous macroarthropods are classified as litter transformers (Lavelle et al., 1997) and represent key regulators of plant litter decomposition within ecosystems (David & Handa, 2010). The sensitivity of saprophagous macroarthropods to environmental impacts makes them invaluable bioindicators (Paoletti & Hassall, 1999; Souty-Grosset et al., 2005). Humidity and moisture affect activity and distribution of terrestrial isopods (Warburg et al., 1984). Climatic factors, predation and parasitism are the frequent drivers of Isopoda population dynamic (Warburg et al., 1984). Shrub cover and herbaceous species richness were shown to be the best drivers of detritivore

and herbivore beetle community species composition. For predator species composition, shrub height and cover were found to be the best predictors (Liu et al., 2016). The herbivorous and predatory arthropods' range characteristics were shown to be correlated with both diet breadth (Brandle et al., 2002; Beck & Kitching, 2007) and habitat breadth (Brandle et al., 2003). The distribution and abundance of spiders depends on three niche axes: wind, moisture and temperature (Wise, 1993). Spider species occurrence is frequently related to factors such as vegetation structure, soil moisture, disturbance and management regime (Marc et al., 1999; Bonte et al., 2002). The importance of the effect of habitat landscape properties on spider assemblages was reported (Gallé et al., 2011). Four clearly separable spider species groups (salt meadows, dunes, meadows and floodplain forests) along a soil salinity and moisture gradient were extracted (Buchholz, 2009). It is also important to note that several studies failed to find convincing correlations between the environment and the occurrence of spiders (Mallis & Hurd, 2005). The spatial distribution of carabids around arable field-woodlot boundaries was explored using logistic curves with the Huismann-Olf-Fresco models (Knapp et al., 2019). The species‑specific effects of shrub cover on Arthropoda animal groups that act as indicators of degradation were revealed due to focusing on species niche breadths and optima (Hering et al., 2019). Coexistence mechanisms at multiple scales in insect assemblages were explored with Huisman-Olff-Fresco models (Laporta & Sallum, 2014). The vegetation and vegetation-soil interactions are important determinants of beetle community assemblies. The vegetation changes had stronger effects on the functional group composition than changes in the soil did (Liu et al., 2016).

Deep underground hard-rock mining has a considerable impact on the landscape, transforming original habitats and leaving landscapes in altered states (Szczepanska & Twardowska, 1999; Hodecek et al., 2015; Klimkina et al., 2018; Yorkina et al., 2019). The landscape transformation due to open-pit coal mining causes major changes in terrain structures, waterways, microclimates, land uses, and living organism communities (Sklenicka et al., 2004; Hendrychova et al., 2011; Yorkina et al., 2018; Zadorozhnaya et al., 2018). The technical and biological reclamation phase is essential for managing a disturbed landscape (Hildmann & Wunsche, 1996; Rehor et al., 2006; Hodecek et al., 2016). The technical phase of the reclamation processes is a significant disturbance that slows down the successional rate of beetle communities (Hodecek et al., 2015).

In this study, we applied different approaches to assess temperature optima and tolerance of the ecological niche temporal projection of the terrestrial invertebrates within an experimental polygon created to investigate the dynamic of reclamation processes after deep underground hard-rock mining in the Ukrainian steppe drylands. Our main objective here was to determine whether the temperature variability affects the temporal dynamic of the terrestrial invertebrates and to find properties of the species response curves to temperature.

Materials and methods

The research was carried out at the Research Centre of the Dnipro State Agrarian and Economic University in Pokrov city. Sampling was carried out on a variant of artificial soil (technosols) formed on loess-like loam, red-brown clay, green-grey clay, technological mixture of the rocks, and formed on loess-like loam with a humus-rich 70 cm top soil layer (the geographic coordinates of the experimental polygon are 47°38'55.24"N.L., 34°08'33.30"E.L.). The data set comprised 20 plots from five technosol types presented within the experimental polygon.

To investigate the temporal dynamic in the abundance, species richness and species composition of invertebrate communities within the experimental polygon, animals were sampled using pitfall traps. The term "activity-density" is employed in some studies as this value is affected not only by population density but also by animal movement activity (Knapp et al., 2019). We investigated seven invertebrate groups closely associated with the soil environment or aboveground vegetation strata: (1) mollusks (Mollusca: Gastropoda), (2) spiders (Chelicerata: Arachnida), (3) millipedes (Myriapoda: Diplopoda), (4) centipedes (Myriapoda: Chilopoda), (5) terrestrial isopods (Malacostraca: Isopoda:

Oniscidea); (6) insects (Tracheata: Insecta). In total, 60 pitfall traps were operated simultaneously during each sampling period. In each plot, three pitfalls were placed in a triangle of 3 m base (Desender et al., 1999; Pontegnie et al., 2005) and emptied each 7–9 days. In 2013 pitfalls were placed on April 9. The pitfalls were emptied 26 times each year. The exact sampling dates were as follows in 2013: April 15, April 22, April 30, May 7, May 14, May 21, May 28, June 4, June 11, June 18, June 25, July 2, July 9, July 17, July 24, July 31, August 7, August 15, August 23, August 30, September 7, September 15, September 23, September 30, October 7, October 14. In 2014 pitfalls were placed on April 5. The exact sampling dates were as follows in 2014: April 13, April 20, April 28, May 5, May 13, May 21, May 30, June 8, June 17, June 24, July 1, July 8, July 17, July 25, August 1, August 9, August 18, August 26, September 4, September 11, September 18, September 26, October 5, October 12, October 19, October 27. In 2015 pitfalls were placed on April 6. The exact sampling dates were as follows in 2015: April 14, April 21, April 28, May 5, May 13, May 20, May 27, June 3, June 10, June 17, June 24, July 1, July 9, July 17, July 24, August 2, August 11, August 18, August 26, September 4, September 11, September 20, September 28, October 6, October 15, October 22. The pitfall traps were made of 1-litre glass cups (10 cm in diameter) buried in the soil with the rim of the cup level with the soil surface. The cups were filled with 250 ml of preservative fluid made from concentrated NaCl solution, which seems to be efficient for collecting invertebrates and is relatively non-toxic to non-target organisms. Traps were covered by roofs made of a polyethylene sheet to prevent flooding during heavy rain. Roofs were placed 5 cm above the openings of the cups using four long rods that penetrated the corners of the roofs.

Vascular plant species lists were compiled in 2015 for each site along with visual estimates of species cover using the nine-degree Braun-Blanquet scale (Westhoff & van der Maarel, 1978). The projective cover of plant species was recorded at ground level. We were able to make species level identification for all sites. Based on geobotanical descriptions, phytoindicative assessment of soil thermal regime according to Didukh (2011) was made. Phytoindicational evaluation of environmental factors was performed by the ideal indicator method of Buzuk (2017). The readily available water for plants (RAW, mm in 1 m soil layer), precipitation (mm), wind speed (m/s), atmospheric temperature (daily minimum, daily maximum, daily mean, ºC), atmospheric humidity (%) and atmospheric pressure (gPa) were used as environmental predictors (Kunah et al., 2019).

Ecological structures and processes occur across multiple spatiotemporal scales (Nash et al., 2014). Ecological systems are hierarchically structured and may be decomposed into structural and process components (La Notte et al., 2017). These components can be defined over a range of spatial and temporal scales (Allen et al., 2014). The elucidation of the mechanisms underlying observed spatial and temporal patterns and different scale levels is a key to prediction and understanding to the development of principles of management (Levin, 1992). The importance of stochastic processes was found to be dependent on the size of the study area (Bonsall & Hastings, 2004). The complexity has to be accounted for in order to model temporal patterns in time series (Baho et al., 2015). The principal coordinates of neighbour matrix method (PCNM) is an effective procedure able to identify temporal structures of varying scale in time data (Borcard & Legendre, 2002; Borcard et al., 2004; Dray et al., 2006). The PCNM-based approach was developed in distance-based Moran's eigenvector maps (MEM) (Dray et al., 2006; Baho et al., 2015).

The two dimension geographic coordinates of sampling locations were used to generate a set of orthogonal eigenvector-based spatial variables (Spatial dbMEMs), each of them representing a pattern of particular scale within the extent of the sampling area. Likewise, but only, the one dimension time series of sampling dates were used to generate a set of orthogonal eigenvector-based temporal variables (Time dbMEMs), each of them representing a pattern of particular scale within the extent of the investigated time period (Borcard & Legendre, 2002; Dray et al., 2012). The spatial and time dbMEMs-variables were used as spatial and temporal predictors of the species responses (Zhukov et al., 2019).

The species abundances were used as the weights in calculating the ecological factor average (Šmilauer & Lepš, 2014):

$$WA = \frac{\sum_{i=1}^{n} Env_i \times Abund_i}{\sum_{i=1}^{n} Abund_i},$$

where Env_i is the value of environmental variable in the i-th sample, and $Abund_i$ is the abundance of the species in the i-th sample.

The species tolerance which is presented by the width of the bell-shaped curve can be calculated as the square root of the weighted mean of the squared differences between the species optimum and the actual value in the sample. The value is analogous to standard deviation (Šmilauer & Lepš, 2014):

$$SD = \sqrt{\frac{\sum_{i=1}^{n}(Env_i - WA)^2 \times Abund_i}{\sum_{i=1}^{n} Abund_i}}.$$

Generalized linear mixed models were used for modeling species-environment relationships. This approach is useful in the case of the unimodal symmetric species response (Jamil & ter Braak, 2013). In the environment R the model can be fitted by (Oksanen, 2004):

mod <- glm(y ~ x + I(x^2), family=poisson)
b <- coef(mod)
u <- -b[2]/2/b[3]
t <- sqrt(-1/2/b[3])

where y – species response, x – environmental factor, u – species optimal value, t – species tolerance.

The use of symmetric Gaussian response functions in gradient analysis is not a universal approach due to systematic deviation of the real data from symmetric response (Austin, 1976, 1999, 2013; Austin et al., 1999). Huisman, Olff and Fresco (1993) hierarchical models (HOF) along with a symmetric response also include a skewed response. Two bimodal (skewed and symmetric) response shapes were included to cope with species that are restricted to gradient extremes due to competition (Jansen, Oksanen, 2013; Michaelis & Diekmann, 2017). The Huisman-Olff-Fresco models expanded by Jansen-Oksanen (HOFJO) are ranked according to the increasing complexity of biological information contained (Huisman et al., 1993; Jansen & Oksanen, 2013). Model I: no significant trend in space or time:

$$y = M \frac{1}{1 + e^a}.$$

Model II: an increasing or decreasing trend where the maximum is equal to the upper bound M:

$$y = M \frac{1}{1 + e^{a+bx}}.$$

Model III: an increasing or decreasing trend where the maximum is below the upper bound M:

$$y = M \frac{1}{1 + e^{a+bx}} \frac{1}{1 + e^c}.$$

Model IV: increase and decrease by the same rate – symmetrical response curve:

$$y = M \frac{1}{1 + e^{a+bx}} \frac{1}{1 + e^{c-bx}}.$$

Model V: increase and decrease by different rates – skewed response curve:

$$y = M \frac{1}{1 + e^{a+bx}} \frac{1}{1 + e^{c+dx}}.$$

Model VI: bimodal symmetric responses:

$$y = M \frac{1}{1 + e^{a+bx}} \frac{1}{1 + e^{c+b(x-d)}} + \frac{1}{1 + e^{a+b(x-d)}} \frac{1}{1 + e^{c-b(x-d)}}.$$

Model VII: bimodal skewed responses:

$$y = M \frac{1}{1 + e^{a+bx}} \frac{1}{1 + e^{c+b(x-d)}} + L \frac{1}{1 + e^{a+b(x-d)}} \frac{1}{1 + e^{c-b(x-d)}},$$

where y and x are the response and the explanatory variable respectively, a, b, c and d the parameters to be estimated (b and d have opposite signs), and M – a constant which equals the maximal value which can be attained (for relative frequencies M = 1, for percentages M = 100), L – a constant which equals the maximal value for minor extreme value.

Huisman-Olff-Fresco models were fitted in the R statistical program (v. 3.3.1) (R Developmental Core Team, 2019) using the package "eHOF" (Jansen & Oksanen, 2013, version 3.2.2). The Akaike information criterion corrected for small data sets (AICc) was used (Burnham & Anderson, 2002). Optimum value and relative species tolerance limits, or the Central Borders, were calculated as implemented in the eHOF package (Jansen & Oksanen, 2013).

To analyze the spatiotemporal variation in the species composition of invertebrate assemblages, multivariate ordination techniques were applied. To decrease the dimension of community space, nonmetric multidimensional scaling (NMDS) was applied (Jansen & Oksanen, 2013). For ecological data with many zeros, the Hellinger transformation is useful (Rao, 1995). In this regard, prior to analyses, species data were Hellinger-transformed (Legendre & Gallagher, 2001). In our data there were no rare species represented by less than 7 sites; that is why all species were included in the analyses, resulting in a final dataset of 202 species or parataxonomic units. For the statistical analyses we used the appropriate procedures of Statistica (Version 5.5, StatSoft Inc., www.statsoft.com) or R (version 3.5.2; R Core Team, 2018).

Results

In total 35 species of herbaceous plants were found within the experimental polygon. At each site, the number of plant species varied from 11 to 31 (Table 1).

Table 1
Plant species number and phytoindicator estimation of the thermoregime

Site	Technosols	Species number	Thermal climate indicator value	Phytoindicator estimation of the radiation balance, MJ•m^{-2}•year^{-1}	The favourable eco-groups by the relation of plant species to thermoregime*
1		23	10.4	2175.1	sub-mesotherms
2		17	11.1	2327.5	mesotherms
3	Loess-like loam	21	11.1	2333.9	mesotherms
4		15	10.6	2217.1	sub-mesotherms
5		20	10.9	2281.9	sub-mesotherms
6		26	11.0	2309.5	mesotherms
7		11	9.8	2049.5	sub-mesotherms
8	Red-brown clay	31	9.6	2001.8	sub-mesotherms
9		30	10.1	2107.9	sub-mesotherms
10		13	10.9	2274.4	sub-mesotherms
11	Green-grey clay	23	10.6	2224.0	sub-mesotherms
12		23	10.5	2208.3	sub-mesotherms
13	Humus-rich	13	10.0	2083.0	sub-mesotherms
14	70 cm top soil	16	9.9	2070.5	sub-mesotherms
15	layer formed on	16	10.3	2154.0	sub-mesotherms
16	loess-like loam	16	10.6	2222.6	sub-mesotherms
17		15	9.5	1985.6	sub-mesotherms
18	Technological	16	8.3	1729.2	sub-microtherms
19	mixture of rocks	19	10.2	2128.9	sub-mesotherms
20		20	9.7	2024.3	sub-mesotherms

Note: * – according to Didukh (2011) phytoindicator scale.

The phytoindication estimation of thermal climate was in the range 8.3–11.1 according to 23-points of the Didukh (2011) thermal climate scale. The phytoindication values can be converted to the value of the radiation balance. This rate can be estimated to be in the range of 1729.2–2333.9 MJ•m^{-2}•year^{-1}. Qualitatively, the thermal climate range can be evaluated as favourable for plants in the range from sub-mesotherms to mesotherms.

In total, 257,437 invertebrate (Arthropoda and Mollusca) individuals of 6 classes, 13 orders, 50 families and 202 species or parataxonomic units were recorded. Diplopoda was most abundant taxonomic group, though it was represented only one species *Rossiulus kessleri* (Lohmander, 1927). This species took up 49.4% of the total community abundance. Coleoptera and Araneae were the considerably numerous taxonomic groups, which took up 22.4% and 18.2% of the total community abundance. These taxa were the most species-rich. Coleoptera was represented by 122 species and Araneae was represented by 67 species. 71 species among the investigated 202 species occurred 50 times or less.

The distribution of temperature weighted by species abundances is multimodal and can be presented as a mixture of two normal distributions (Kolmogorov-Smirnov d = 0.032, P = 0.98). The temperature optimum has a 0.64 chance of following a distribution with a mean 17.1 ℃ and variance 2.2. The chance is 0.36 that plant available moisture distribution has a mean 21.5 ℃ and a variance 1.5. Thus, the temperature optimum of in-

vertebrates dwelling in the technosols varies in the range from 11.5 to 25.4 ℃. The thermal range between the species optima is distributed unevenly. The distribution of species tolerance to temperature assessed on the basis of variance of the temperature weighted by species abundances has a normal distribution (Kolmogorov-Smirnov d = 0.053, P = 0.59). The analysis of distributions indicates the existence of two relatively homogeneous species groups in terms of thermal preferences : microtemperature and mesotemperature. This identification of groups is based on the phytoindicative estimates of thermoclimate which is in the range from microtemperature to mesotemperature conditions. There is a negative correlation (r = –0.48, P < 0.001) between estimated species thermal optima and

tolerance values. Thus, the microtemperature species are more tolerant to the thermal factor, and vice versa – the mesotemperature species are more sensitive. Probably, the high temperatures that occur within the studied area are close to the physiological limits of endurance of living organisms, as high temperatures act as a strong limiting factor.

The requirement of symmetry and bell-shaped response to the impact factor is necessary to use weighted average method for assessing the optimum and tolerance within a gradient of the temperature conditions. But it should be noted that this consideration does not always hold. It should be pointed out that the HOFJO-approach offers opportunities for species response modeling using more flexible models (Fig. 1).
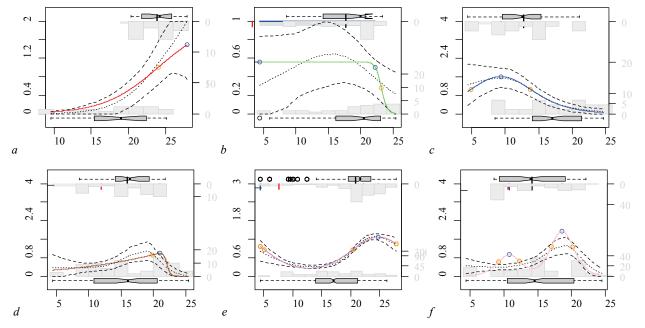

Fig. 1. The model diversity of species response to soil moisture gradient: X-axis – the soil moisture presented as plant available moisture in 1 m soil layer (mm); Y-axis – the number of individuals; HOFJO-model: A – model II (*Anoxia pilosa*), B – model III (*Asida lutosa*), C – model IV (*Galeruca tanaceti*), D – model V (*Haplodrassus bohemicus*), E – model VI (*Harpalus serripes*), F – model VII (*Onthophagus vitulus*)

The analysis showed that invertebrates' responses to the effect of temperature may be explained by all seven HOFJO models. The models V and VII have the most considerable ability to explain the species response patterns. The model VII is sensitive to the asymmetric bimodal response, and model V is sensitive to the asymmetric unimodal response. Thus, the vast majority of the invertebrates' responses to the temperature factor are asymmetric. Symmetrical models IV and VI apparently describe a fraction of invertebrate response patterns. Symmetrical responses provide an ideal situation, the impact of only the physical factor on the biological status of a species. In reality, there is a set of abiotic factors with simultaneously an important role of the biotic factors. Asymmetric unimodal response is most likely to be regarded as the result of the interaction of factors of an abiotic nature that violates perfect symmetry response to the impact of a single factor. Bimodality can be best explained by competitive exclusion of two or more species due to optimum overlap.

The procedures of the community ordination are usually sensitive to the pattern types of species response to the impact of environmental factors. One exception is the multidimensional scaling procedure (MDS) which is not sensitive to such restrictions. The stress is a goodness-of-fit measure of the multidimensional scaling procedure. This measure allows us to extract the appropriate number of the dimension. In the case where further increasing of the dimension number does not lead to a decrease in stress, one decides on the appropriate number of the dimension in the ordinate solution. In our case, with the value of stress 0.1 we have stopped on a solution of four dimensions. The nature of these dimensions can be interpreted by fitting environmental factors and MDS dimensions (Table 2).

The results of this procedure indicate that variation of the structure of the invertebrate community is due to meteorological factors, spatial and temporal variables, and also depends on the technosols' typological fea-

tures. Moisture content in the soil is the most important factor of the community variation, as it determined 87% of variability in the structure of the complex. A group of species whose variation is described in dimension 1 is the most sensitive to the water content in technosols. It should be noted that the correlation of this dimension with air temperature is extremely insignificant. The temperature is capable of explaining 41% to 44% of variability in the community structure, indicating a second role among environmental factors that affect invertebrate fauna. The dimensions 2, 3 and 4 are correlated with temperature.

Discussion

The problems of range, spacing, and nonlinearity are highly important in resolving the issue of the measurement of niche properties (Colwell & Futuyma, 1971). The position and width are qualitative attributes of the niche (Gregory & Gaston, 2000). The species niche parameters considerably depend on the mathematical constraints like model shape (Jansen & Oksanen, 2013). The interaction with other environment factors is also important for the accurate estimation of the niche attributes. Thus, our results reveal that the nature of the effects of air temperature on the invertebrates' community structure is extremely complicated. The estimation of ecological complexity is increased, taking into account the influence of other meteorological factors, such as precipitation (mainly indicated by the dimensions 2 and 4), wind (indicated by the dimensions 2, 3 and 4), air humidity (indicated by the dimensions 2, 3 and 4), and atmospheric pressure (indicated by the dimensions 3 and 4). Our result is in agreement with concept that the intraspecific and interspecific interactions and environmental conditions affect niche position and niche width (Brown, 1999; Lawton, 1999).

Table 2
Fitting environmental factors onto ordination dimensions

Predictors	Dimensions				R^2	Pr(>r)	Significance codes
	NMDS 1	NMDS 2	NMDS 3	NMDS 4			
Climatic predictors							
Precipitation, mm	–0.73	–0.36	–0.04	–0.58	0.06	0.001	***
Wind speed, m/s	–0.15	0.34	0.56	–0.74	0.02	0.001	***
T_{min}	0.07	–0.82	–0.34	0.46	0.40	0.001	***
T_{max}	0.04	–0.69	–0.41	0.59	0.41	0.001	***
T	0.07	–0.76	–0.38	0.53	0.44	0.001	***
Atmospheric humidity, %	–0.23	0.47	0.42	–0.74	0.20	0.001	***
Atmospheric pressure, gPa	0.43	0.06	0.49	–0.76	0.11	0.001	***
RAW****	–0.87	0.39	–0.22	0.18	0.87	0.001	***
Time predictors (AEM-variables, statistically significant predictors are shown only)							
AEM_1	0.99	–0.10	0.03	0.11	0.68	0.001	***
AEM_2	0.04	0.78	0.39	–0.48	0.37	0.001	***
AEM_3	–0.08	–0.43	0.16	–0.88	0.06	0.001	***
AEM_4	–0.29	0.81	0.27	–0.43	0.03	0.001	***
Spatial predictors (dbMEM-variables, statistically significant predictors are shown only)							
Spat_1	0.01	0.00	–0.55	–0.84	0.46	0.001	***
Spat_2	–0.06	–0.37	0.93	0.00	0.51	0.001	***
Spat_3	0.01	–0.53	–0.12	–0.84	0.03	0.001	***
Spat_4	0.00	–0.37	0.19	–0.91	0.06	0.001	***
Spat_5	0.02	0.31	0.67	–0.67	0.07	0.001	***
Spat_6	–0.08	0.63	0.12	0.76	0.01	0.034	*
Spat_7	–0.07	0.02	0.89	–0.46	0.01	0.014	*
Technosols types, $R^2 = 0.12$, P < 0.001							
GG	0.07	0.08	–0.17	0.03	–	–	–
LL	0.01	0.01	–0.14	–0.09	–	–	–
PZ	–0.01	0.06	0.08	0.12	–	–	–
RB	0.02	0.00	–0.06	–0.06	–	–	–
TM	–0.05	–0.11	0.25	0.05	–	–	–

Note: significance codes: *** – < 0.001; ** – < 0.01; * – < 0.05; **** – readily available water content (mm); GG – green-grey clay, LL – loess-like loam, PZ – humus-rich 70 cm top soil layer formed on loess-like loam, RB – Red-brown clay, TM – technological mixture of rocks.

Animal community dynamic induced by reclamation is affected by plant cover and by abiotic regimes (Hendrychova, 2008; Buchori et al., 2018). The coherent dynamic of the invertebrate population was reflected by means of NMDS ordination approach. Community decomposition into NMDS-dimensions may be discussed in terms of structural and process context (La Notte et al., 2017). NMDS-dimensions can be processed over a range of spatial and temporal scales (Allen et al., 2014). Our results revealed that the dimensions obtained after NMDS-procedure were confirmed as being subject to certain time trends, which is indicated by the correlation with AEM-time variables. The AEM-1 variable simulates a monotonous sigmoidal trend, which correlates to the dimension 1. A gradual reduction of the soil water content during the year is quite good in compliance with this tendency, which cannot be said about the temperature. The dimensions 2–4 indicating the temperature dependent dynamics of the community correlate with AEM-variables 2–4. This result shows the fine-scale components in the variation of these dimensions. This also demonstrates that the temperature variability during the season is subject to certain regular patterns, which could affect the animals' adaptation and produce the appropriate phenological rhythms. The species following evolution demonstrated ability for adaptation only to the recurring environmental variation caused by geophysical cycles such as temperature and precipitation (Foster & Kreitzman, 2009). Therefore, in the case of structured temperature patterns in time, it is formally impossible to say whether the temperature really affects living organisms, or acts just the same as the rhythm of biological and temperature processes due to common synchronization with the third factor. As the results indicate, coincidence of the dynamics of temperature processes and dynamics of the community structure is very important. The time variables are able to explain 3–68% variation of the community structure. Obviously, the role of the temporal

component of the community variation should be previously extracted to assess the real role of temperature as the ecological factor. Phenology is discussed as the temporal aspect of natural history (Forrest & Miller-Rushing, 2010), that is why we interpret the temporal component of the variability as a natural course of phenological processes, the rhythm of which is guided by certain stimuli.

The spatial structuring of the community dynamics may be revealed by correlation of dimensions with dbMEM spatial variables. The understanding of the factors underlying observed spatial and temporal patterns and different scales is important for prediction of the community behaviour (Levin, 1992). In our investigation, spatial variables were found to explain 1–51% of variation of the community structure. The importance of the spatial variables was reduced as the spatial process frequency increases (indicated by the sequence number of variables). It should be noted that the dimension 1 reflects the site-non-specific processes, universal for the entire territory as a whole. Dimensions 3 and 4, which, as appropriate, are closely related to the temperature regime, are significantly spatially structured. Spatial structuring may be a result of processes of neutral nature (Zhukov et al., 2019) or a result of the influence of spatial structured properties of the environment (Karunaratne et al., 2015). The latter may be associated with the spatial heterogeneity of the technosols' distribution. In this result it can be assumed that the impact of temperature factors on invertebrate fauna depends on the characteristics of vegetation and soil. Thus, the influence of spatial factors on these processes should be extracted to assess the purely temperature component in the variation of the animal community and population.

The spatial allocation of the technosols can also be the cause of spatial structured variation of the animal community. In addition, technosols can have a specific significance in the variability of the environmental conditions and processes. The techonosol types generally define 12% of the variation in the invertebrate fauna. It is impossible to exclude the possibility that artificial soils that differ in their primary stratigraphy and the properties of rocks of which they are formed during half a century of the pedogenesis gain convergent similar properties, resulting in differences between them becoming less apparent. Thus, the role of the technosol types in the invertebrate community dynamics should also be extracted to determine the role of temperature for animals.

Conclusion

The most important environmental factor following soil moisture affecting invertebrates in the technosols is temperature. Temperature optimum for invertebrates dwelling in technosols varies in the range of 11.5 to 25.4 °C. From the total set of the invertebrates, the two relatively homogeneous groups in relation to thermal preferences of species were extracted: the microtemperature and mesotemperature groups. The microtemperature species are more tolerant to the thermal factor, and the mesotemperature species are more sensitive. The invertebrates' response to the effect of temperature can be approximated by the seven HOFJO models. The models V and VII most often have the higher explanatory ability to describe the species response to temperature gradient. The effect of temperature on the structure of invertebrate communities is complex and depends on other meteorological factors such as precipitation, wind, humidity and atmospheric pressure. The real values of the invertebrates' temperature optima and tolerance may be assessed only after extraction of the effect of the other environmental, spatial and temporal variables.

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