

## Qualitative and quantitative spatial variation in soil wire-worm assemblages in relation to climatic and habitat factors

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Penev, L. D. 1992. Qualitative and quantitative spatial variation in soil wire-worm assemblages in relation to climatic and habitat factors. – *Oikos* 63: 180–192.

This paper considers large-scale variation in both species composition and alpha diversity of wire-worm assemblages (Coleoptera, Elateridae) of oak forests along a latitudinal gradient in Central Russia. The study is based on original data equal in both sample size and collecting technique. Changes in assemblage characteristics are analysed in terms of species and/or community responses to macroclimatic parameters as well as to local habitat conditions. Species composition based on presence/absence data is found to be the best indicator of macro-environmental changes caused by climate. The species abundances are affected by both climatic trends and local habitat characteristics. There is little evidence for a strong effect of the environmental factors upon the quantitative assemblage parameters such as species richness, total abundance, and various alpha diversity indices. Species diversity does not depend on the age of the habitat and the level of disturbance. The patterns observed suggest that species and community responses to the environment may play a significant role in explaining variation amongst isolated continental communities in addition to or instead of theories of island biogeography and interspecific competition.

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The aim of the study is to analyse patterns among communities of a similar type along a latitudinal gradient covering several biomes. Assemblages of click beetle larvae (Coleoptera, Elateridae) were chosen as a model group for study due to their high abundance and importance in forming soil macrofauna communities.

Large-scale variation in local assemblages of organisms (floras, faunas, communities) can be attributed to five principal groups of factors (after Brown and Gibson 1983, with some changes):

(1) Macroclimatic factors determining nature zonation in a certain geographic region.

(2) Between-region differences mostly due to historical reasons.

(3) Variation in local habitat conditions (for communities) or habitat diversity in a certain locality (for local floras or faunas).

(4) Temporal variation caused by seasonal periodicity or between-year dynamics.

(5) Inter-specific relationships.

The degree of harshness and productivity of communities (Brown and Gibson 1983) as well as habitat changes caused by human activity can also add to spatial variation. The joint effect of all these variables upon local biotas appears to be extremely difficult to analyse. Thus, the first step should be to discriminate the effect of the different factors by a proper choice of the scale of variation (Wiens et al. 1986, Hengeveld 1987, 1990). Secondly, one has to choose between various biotic parameters so as to find an adequate indicator of a certain factor of interest. Two groups of parameters can be distinguished:

(1) Characteristics dependent on species composition

Accepted 26 September 1991

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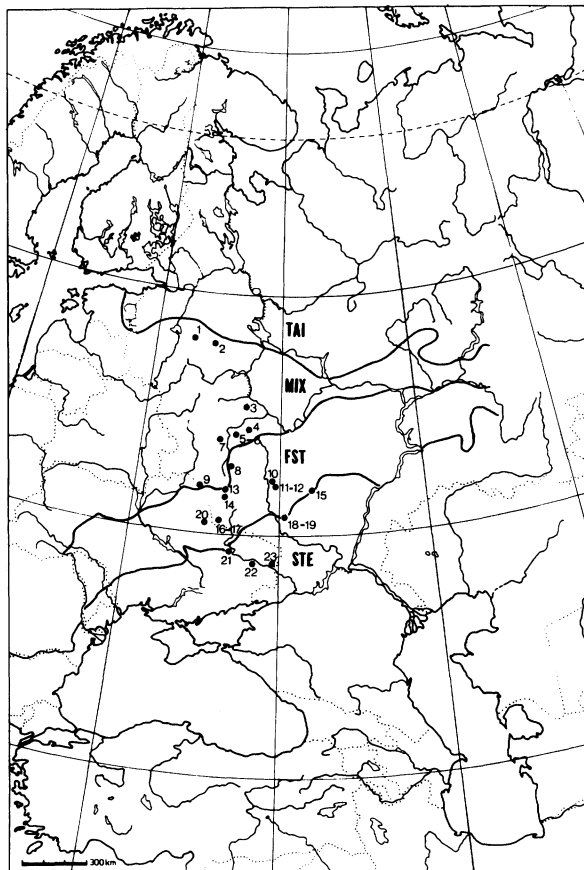


Fig. 1. Geographical location of the study sites. Numbers of sites refer to Appendix 1. Solid lines show borders between zones, as follows: TAI – taiga, MIX – mixed forest zone, FST – forest-steppe, STE – steppe zone.

expressed either qualitatively as a species listing, or quantitatively as species abundances or other importance measures.

(2) Quantitative characteristics independent of the species composition such as species richness, total abundance (biomass, energy fluxes, etc.), and a large number of diversity measures. The difference between these two groups of parameters is often underestimated, especially in animal ecology. The majority of papers dealing with variation in widely separated local assemblages focuses on purely quantitative characteristics such as species richness, total abundance or alpha diversity indices. The theory of island biogeography (MacArthur and Wilson 1967) is commonly used as a basic model for explaining observed patterns (cf. Gilbert 1980, Brown and Gibson 1983, Wiens 1989). When species composition is taken into account, the patterns are often analysed in terms of interspecific relationships such as competition, predation or mutualism. However, surprisingly little attention has been paid to large-scale variation in species composition in relation to the envi-

ronment, although several sophisticated classification and ordination techniques were developed in the last decade (cf. Jongman et al. 1987, Ter Braak 1988). The importance of studying geographic variation in species composition of local assemblages has been emphasized by Haila et al. (1987) and Brown and Kurzius (1987). Moreover, as Chernov (1975, 1984) pointed out, the clear distinction between the “faunal” and “demecological or geozoological” levels of organization of the animal assemblages seems important not only from a viewpoint of methodology or organization of science, but also because both phenomena are controlled by factors different in nature.

In the light of the ideas outlined above, I focused attention on the effect of two groups of environmental factors (local habitat conditions and macroclimatic gradients) upon both qualitative and quantitative assemblage characteristics.

## Material and methods

### Study area and sampling sites

The material was collected during five transect expeditions carried out in 1988–1990. The 19 localities situated in the central part of the Russian Plain extended over a distance of about 1100 km from north to south and about 560 km from west to east (Fig. 1 and Appendix 1). The sampling sites were selected so as to be similar regarding two general aspects: (1) predominance of *Quercus robur* L. and (2) moderate moisture conditions. The moisture conditions were estimated from the occurrence of some dominant mesophilous herb species such as *Aegopodium podagraria* L., *Carex pilosa* Scop., *Asarum europaeum* L., *Stellaria* spp., *Polygonatum multiflorum* (L.) All., *Pulmonaria obscura* Dumort., and *Galium odoratum* (L.) Scop. Another additional criterion was the state of the forest, i.e. we tried to stick to the most mature and well-preserved patches of oak forests in each locality. Despite this, Appendix 1 shows that the sites varied considerably in habitat conditions due to large geographic distances or other local factors. However, compromises are unavoidable when ‘local precision has to be sacrificed for geographic generalism’ (Haila et al. 1987). To minimize the possible influence of artifacts we used collecting methods identical in both design and sample size and restricted the field work to relatively short periods in May–June and September.

### Sampling procedure

Twenty soil samples of 25 × 25 cm each were taken at each site according to Ghilarov (1975). The soil macrofauna was sampled from 10 cm thick soil layers on oilskin in the field. This method is quite tedious but it has the advantage of independence of electricity or run-

Table 1. TWINSpan table of the wire-worm assemblages based on species abundances using the default cut-levels (0.25 10.20).

	Site numbers					
	1 1290	11 1 372461	111 589	12 2 11 61504837	22 23	
<i>Agriotes lineatus</i>	1---	-----	---	-----	---	11111
<i>Actenicerus sjaelandicus</i>	1---	-----	---	-----	---	11111
<i>Mosotalesus</i> sp.	1---	-----	---	-----	---	11111
<i>Mosotalesus impressus</i>	2---	-----	---	-----	---	11111
<i>Mosotalesus nigricornis</i>	22---	-----	---	-----	---	11111
<i>Ctenicera pectinicornis</i>	-2---	-----	---	-----	---	11111
<i>Ectinus aterrimus</i>	---5	-11---	---	-----	---	11110
<i>Dalopius marginatus</i>	4555	444425	-34	-1-----	---	1110
<i>Denticollis linearis</i>	-11-	---2-	---	---1---	---	110
<i>Athous subfuscus</i>	4243	43-2-	-24	---1---	---	110
<i>Ampedus pomorum</i>	---	---1	-1	-----	---	10
<i>Agriotes pilosellus</i>	---	---1-	---	1-----	---	10
<i>Athous vittatus</i>	---	545533	455	55434344	31	01
<i>Athous haemorrhoidalis</i>	3312	43-33-	335	44443212	55	01
<i>Selatossomus aeneus</i>	1-12	-----2	435	-----	5-	0011
<i>Prosternon tessellatum</i>	---	-----	132	-----	53	001011
<i>Melanotus rufipes</i>	---	-----	---	-----	21	001010
<i>Ampedus pomonae</i>	---	-----	---	-----	1-	001010
<i>Ampedus sanguinolentus</i>	---	-----	---	-----	22	001010
<i>Agriotes obscurus</i>	---	-----	---	-----	-3	001010
<i>Agrypnus murinus</i>	---	-----	---	-----	3-	001010
<i>Selatossomus cruciatus</i>	---	-----	---	-----1-	-1	00100
<i>Pseudanostirus globicollis</i>	---	-----	-54	-2-----	---	000
<i>Cidnopus minutus</i>	---	-----	1-	-----	---	000
<i>Cidnopus parvulus</i>	---	-----	524	-2-----	---	000
<i>Athous niger</i>	---	-----	---	-----1-	---	000
	0000	000000	111	11111111	11	
	0000	111111	000	00000000	11	
		000001	000	11111111		
		00001		00111111		
				001111		
	1	2	4	3	5	

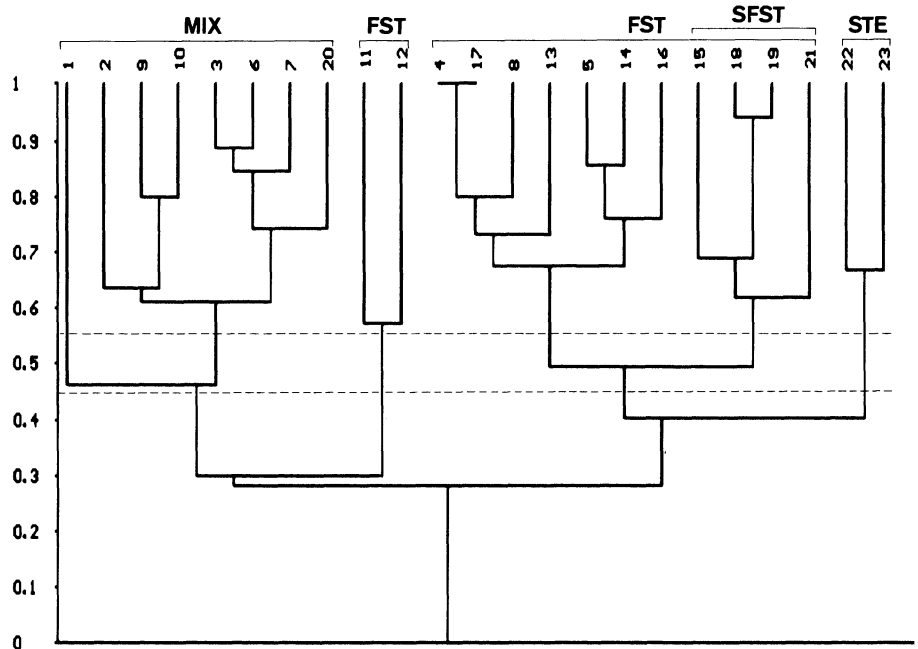
ning water necessary for most kinds of extracting devices. The depth of each sample was determined by the presence of soil macrofauna, i.e. a sample was not finished until no more individuals were found. The minimal depth of the samples was never less than 20 cm, in most cases 30–40 cm. The samples were taken along short transects (200–500 m as a rule) within homogeneous forest patches. In the case of ravines, ten samples were taken on plateau and the remaining ten on the adjacent slopes. To reveal possible microhabitat differences, the samples were taken randomly in consequent series of 3 samples each and systematically within series: the first sample just at a tree trunk, the second one between trees, and the third one in a small forest ‘window’ (but not in a clearing!).

**The environmental data set**

The environmental characteristics of the sites are described in Appendix 1. Preliminary analyses carried out with the environmental variables showed strong inter-correlations among some of them. Several climatic pa-

rameters, especially those derived from temperature, as well as mean annual relative humidity and mean annual precipitation were found to have a strong linear relationship with latitude (in all cases  $r > 0.65-0.70$ ,  $P < 0.01$ ). Another problem arises from multicollinearity between some habitat characteristics (‘humus depth’, ‘soil type’) and climate. This is hardly surprising, because zonal determinants of the prevailing soil type in a certain biome are well-known (Dokuchaev 1899). However, other habitat variables, such as ‘soil composition’ and ‘condition of the forest’ were independent of either geographical location or climate. All qualitative characteristics were transformed before the analyses into ‘dummy’ presence/absence variables (Jongman et al. 1987, Ter Braak 1988). Negative values of the mean temperature of the coldest month ( $T_{jan}$ ) were avoided with adding 15 to all values. The factor ‘condition of the forest’ was represented by a four-class variable, as follows: 1 = younger (40–100 yr) forests with some features of disturbance; 2 = relatively old (100–200 yr), slightly disturbed forests; 3 = relatively old (100–200 yr) undisturbed forests; 4 = very old (200–300 yr) undisturbed forests. The depth of humus ( $A_1 +$

Fig. 2. Group average clustering dendrogram of the wire-worm assemblages based on the Czekanowski-Sørensen similarity index for presence/absence data. MIX – mixed forest zone, FST – forest-steppe, SFST – southern forest-steppe subzone, STE – steppe zone. Numbers of sites as in Appendix 1.



A<sub>1</sub>A<sub>2</sub> horizons) was roughly divided into three classes: 1 = 5–20 cm; 2 = 20–30 cm; 3 = 30–40 cm and more.

### The species data set

Almost all the analyses were done on a pooled data set (Appendix 2), containing both the spring and the autumn observations. At some of the sites (5 & 6, 16 & 17) sampling was carried out both in autumn and spring to estimate whether seasonal periodicity causes variation in the data. The number of species was too small to allow statistical tests at alpha diversity level. In general, however, the autumn and spring samples seemed to differ in the presence of rare species but they were very similar or even identical in ranking of the two or three most abundant species.

### Statistical methods

The divisive classification procedure was performed with TWINSpan (Hill 1979) and all ordination techniques with CANOCO (Ter Braak 1988). The program BIODIV (Baev and Penev 1991) was used for group average clustering, calculation of diversity indices, and rarefaction. Among many existing diversity indices I chose those (Appendix 2) that are mathematically different and independent or considerably less dependent of each other (Peet 1974, Pesenko 1982, Magurran 1988). The formulas of similarity and diversity indices are not given here because they are well-known and easily available from recent reviews (Hill 1973, Peet 1974, Pielou 1975, Alatalo 1981, Pesenko 1982, Magur-

ran 1988, Molinari 1989). Expected number of species (E(S)) was calculated with the rarefaction method (James and Rathbun 1981, Magurran 1988) for a standard sample of 10 individuals. The significance of the correlations and the Mann-Whitney U-test was estimated in all cases using Fisher's z-statistics.

## Results

### Distribution of species among sites

The material collected comprised 1290 elaterid larvae belonging to 26 species (Appendix 2). The prevailing number of species (70%) was found only at one or two sites. According to their distribution over sites, the species can be divided into three groups (Table 1, Appendix 2). The first group consisted of only two species occurring in most of the sites (*Athous haemorrhoidalis* and *A. vittatus* found at 21 and 19 sites, respectively). *A. haemorrhoidalis* was more widely distributed but in 70% of the sites it was less abundant than *A. vittatus*. The abundance of *A. haemorrhoidalis* correlated positively with temperature parameters (Tann:  $r = 0.58$ ,  $P < 0.01$ ; Days w/F:  $r = 0.54$ ,  $P < 0.05$ ) and negatively with increasing precipitation and humidity (Prec:  $r = -0.63$ ,  $P < 0.01$ , Humi:  $r = -0.52$ ,  $P < 0.05$ ). In other words, the abundance of this species in local communities increased along a geographical gradient towards areas with a warmer and drier climate. This conclusion agrees with results obtained in other regions of the Russian Plain, as well as in the Balkan Peninsula; everywhere in the steppe zone of South Russia and in the Balkans *A. haemorrhoidalis* predominates in low-

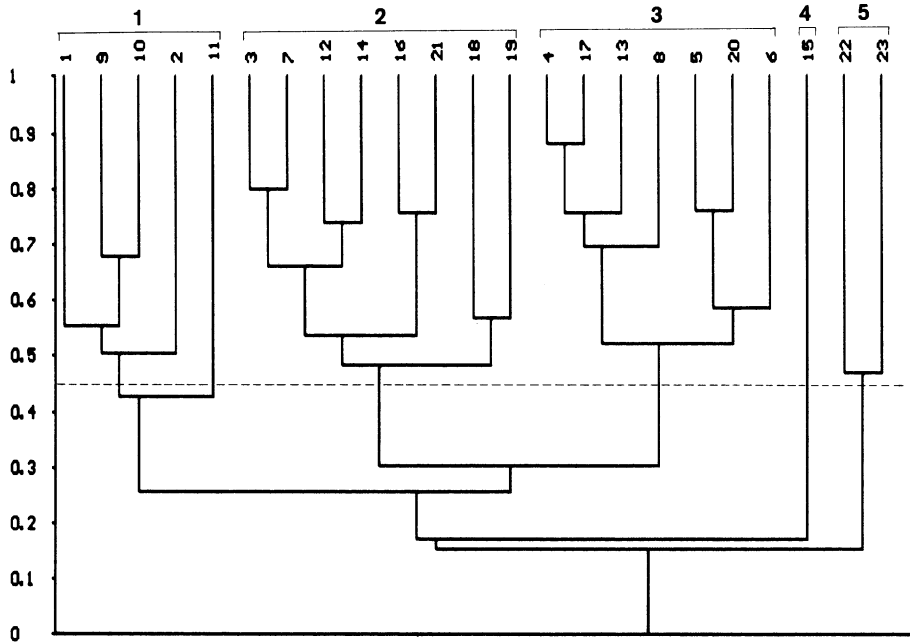


Fig. 3. Group average clustering dendrogram of the wire-worm assemblages based on the Czekanowski-Sørensen similarity index for abundance data. Number of sites as in Appendix 1.

land deciduous forests. It seems to be well adapted to summer drying of the soil in contrast to *A. vittatus* which is much rarer in the south and can be found only in either forest ravines or mesophilous deciduous forests of the middle mountain belt.

The second group comprised those species that tended to be more frequent in the northern part of the area studied (*Dalopius marginatus*, *Athous subfuscus*, *Ectinus aterrimus*, together with some rarer species such as *Mosotalesus nigricornis*, *M. impressus*, and *Ctenicera pectinicornis*). The relative abundance of *A. subfuscus* and *D. marginatus* correlated positively with latitude ( $r = 0.51$  and  $0.45$  respectively,  $P < 0.05$ ) and tended to correlate negatively with temperature parameters. A negative correlation was obtained with the depth of the humus layer ( $r = -0.67$  and  $-0.46$ ,  $P < 0.01$  and  $0.05$ , respectively) which confirmed the opinion of Ghilarov (1965) that these two species are indicators of soddy podzolic and related poor soils.

The third group contained species characteristic of the southern sites (*Cidnopus parvulus*, *Pseudanostirus globicollis*, and *Prosternon tessellatum*). It should be noted, however, that the presence of a certain species only in the southernmost sites does not necessarily mean a southern type of distribution. Many polyzonal or even boreal species penetrate the forest canopy only in the southern parts of their ranges due to the 'rule of habitat change' (Bey-Bienko 1966). Examples of this phenomenon are *Prosternon tessellatum*, *Agrypnus murinus*, and *Agriotes obscurus* (Ghilarov 1956, Arnoldi 1956). Almost all the species have vast and polyzonal geographical ranges, except *C. parvulus* and *P. glob-*

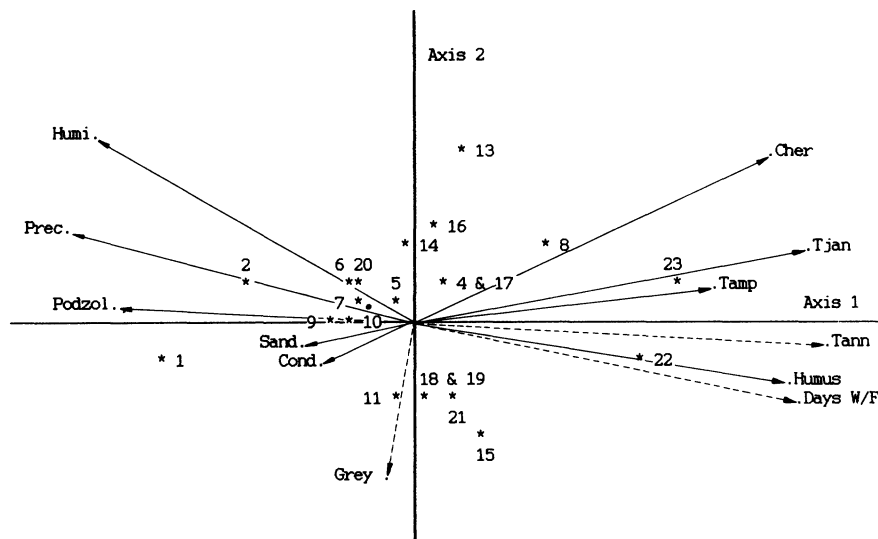
*icollis* which are confined in the Russian Plain to the forest-steppe and the northern steppe subzone.

### Classification of the species assemblages

There are two main approaches in cluster analysis, agglomerative and divisive (Jongman et al. 1987). I used both of them in order to find out and compare possible differences in classification patterns. A group average clustering of the presence/absence data produced 4 clusters at the 45% similarity level (Fig. 2), which corresponded closely to the borders between latitudinal zones. However, there are some exceptions from this general pattern. The forest-steppe sites 10 and 20 were related to the mixed forest zone and, in contrast, sites 4 and 5 were classified to the forest-steppe group. At the similarity level of 55% some within-zone differences appeared. For example, the sites situated at the southern forest-steppe boundary (15, 18, 19, and 21) were clearly distinguished from the northern and middle forest-steppe subzones. Thus, the classification of assemblages using presence/absence data followed the vegetation zones from north to south.

The dendrogram based on species abundances yielded 5 clusters at the 45% similarity level (Fig. 3): (1) assemblages of a boreal type on soddy podzolic or sandy-loam soils; (2) and (3) groups of sites situated in the mixed forest and forest-steppe zones which are difficult to interpret in terms of environmental conditions; (4) the species-rich assemblage of the Tellerman forest (site 15) characterized by the predominance of *Cid-*

Fig. 4. Detrended correspondence analysis (DCA) ordination diagram of the assemblages (\*) and environmental variables (arrows) based on presence/absence data. The point indicates the position of sites 3 and 12. Environmental variables designated with dotted lines were calculated separately as being multicollinear. Cond – condition of the forest, Cher – chernozem soil, Grey – grey forest soil, Podzol – soddy podzolic soil, Sand – sandy-loamy soil, the remaining symbols and numbers of sites as in Appendix 1.



nopus parvulus; (5) the floodland oak forests Kremennaya and Stanichno-Luganskoe (sites 22 and 23) situated in the steppe zone on meadow chernozem soils. In other words, the analysis based on species abundances revealed some new patterns which can be related to local peculiarities of the habitats. Yet, the between-zone and within-zone differences from Fig. 2 were masked considerably.

The result from TWINSpan applied to presence/absence data was almost identical to that of group average clustering and is therefore not shown here. The two-way table produced from abundance data yielded a classification that is most easily interpretable (Table 1). At first division level the sites were divided into two main groups which can be characterized as 'northern' and 'southern'. The border between them corresponded closely with the line Kursk-Voronezh. Only two sites (4 and 8) situated north of this line were classified to the 'southern' group due to their small species number as

Table 2. Unweighted correlations between DCA axes and environmental variables. Lati – latitude, Long – longitude, Cond – 'condition of the forest', the remaining symbols as in Appendix 1.

	Presence/absence		Abundance	
	DCA1	DCA2	DCA1	DCA2
Lati	-0.74**	0.15	-0.44*	0.05
Long	0.47*	-0.47*	0.47*	-0.17
Tann	0.72**	-0.17	0.40	-0.28
Tjan	0.49*	0.08	0.15	-0.24
Tamp	0.43	-0.56**	0.55*	-0.16
Days W/F	0.74**	-0.05	0.56**	-0.06
Prec	-0.71**	0.14	-0.54*	0.35
Humi	-0.53*	0.48*	-0.36	0.43
Cond	-0.10	-0.05	0.14	0.08
Humus	0.71**	-0.04	0.57**	0.24

\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ .

well as to the lack of characteristic species. Thus, the first node can be interpreted as the boundary between the mixed forest and forest-steppe zones. The second and third nodes seemed to be affected, in addition, by local habitat conditions and produced five types of species assemblages:

(1) Assemblages on soddy podzolic and related sandy-loam soils dominated by *Dalopius marginatus* – *Athous subfuscus*.

(2) Assemblages on grey forest soils found in the southern part of the mixed forest zone and the northern forest-steppe, and marked by the predominance of *Athous vittatus* – *Dalopius marginatus*.

(3) Assemblages on grey forest or chernozem soils found mostly in the forest-steppe (with two exceptions), and characterized by a small number of species and predominance of *Athous vittatus* – *A. haemorrhoidalis*.

(4) Species-rich assemblages on grey forest soils found at the southern boundary of the forest-steppe zone. A remarkable feature is the considerably higher number of dominant species than in the first three groups (*Athous vittatus* – *A. haemorrhoidalis* – *Selatosomus aeneus* – *Cidnopus parvulus*), and the presence of other abundant species such as *Prosternon tessellatum* and *Pseudanostirus globicollis*.

(5) Species-rich assemblages found in floodland oak forests on meadow chernozems in the steppe zone; dominant species are *Athous haemorrhoidalis* – *Prosternon tessellatum*.

In general, both clustering approaches, agglomerative and divisive, produced comparable results. TWINSpan gave results that were easier to interpret in terms of underlying environmental gradients. However, the group average method elucidated some patterns in the data set not revealed by TWINSpan, such as the specifics of the wire-worm assemblage of the Tellerman forest (15). I performed analysis also with percentage

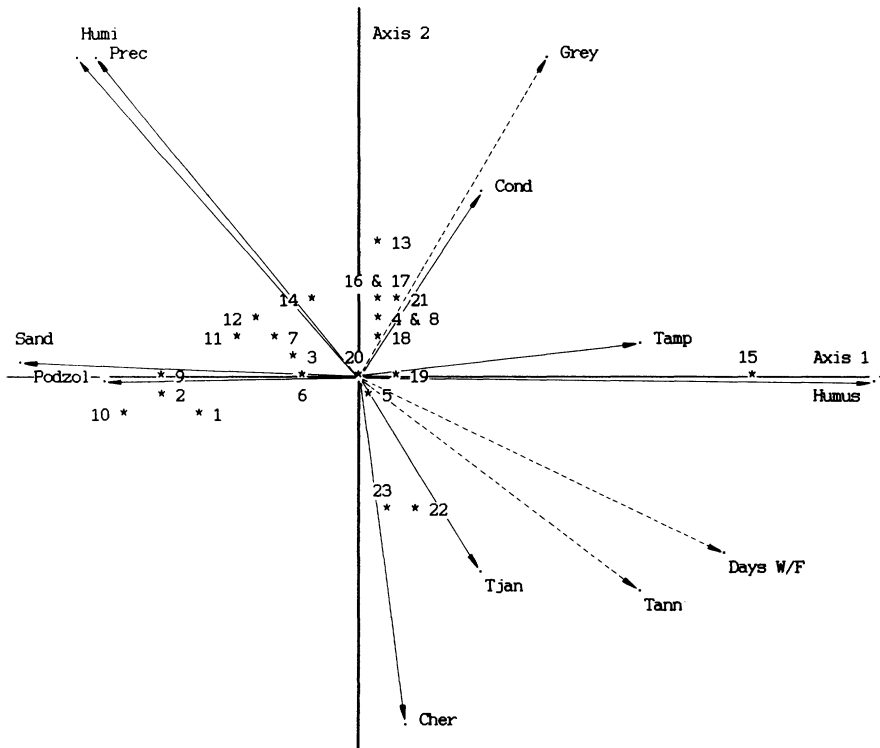


Fig. 5. DCA ordination diagram of the assemblages (\*) and environmental variables (arrows) based on abundance data. Environmental variables designated with dotted lines were calculated separately as being multicollinear. Abbreviation of the environmental variables as in Fig. 4, the remaining symbols and numbers of sites as in Appendix 1.

transformed data using both approaches of clustering, but this failed to contribute much to the understanding of the classification patterns.

### Gradient analysis

The classification procedures yielded some suggestions about background gradients and their possible explanation. To elaborate this I applied detrended correspondence analysis (DCA). The first two axes of the species-environment biplot based on presence/absence data (Fig. 4) accounted for 26.1 and 38.0% of the variation and have eigenvalues 0.60 and 0.40, respectively. The first axis clearly expressed a north-south gradient which can be identified as macroclimatic by the length and direction of vectors representing environmental variables, as well as by the unweighted correlations between the axis and environmental variables (Table 2). The influence of habitat variables independent of climate ('soil composition', 'condition of the forest') seemed to be much less. The second axis can be interpreted as a trend running from the sites at the southern forest-steppe boundary (18, 19, 15, and 21) with species-rich assemblages and more characteristic species to the sites situated northerly.

The same analysis based on species abundances added some new important information. The first axis (eigenvalue 0.66) of the species-environment biplot (Fig. 5) accounted for 32.0% of the variation. The

length and direction of the vectors expressing correlation of a particular environmental variable with the axis concerned suggested a possible common influence of both climatic parameters and local habitat conditions ('soil composition' and 'soil type' designated by the dummy variables 'Sand' and 'Podzol') upon the main trend in the variation of the species data. The gradient had a northwest-southeast orientation and correlated positively with the annual temperature amplitude (Tamp) and the number of frostless days (Days W/F), and negatively with mean annual precipitation (Prec) (Table 2). Similarity in the assemblage composition and the species abundances of the northernmost sites on soddy podzolic soil (1 and 2) with sites situated to the south on light sandy-loamy soils (9, 10, 11, and 12), already indicated by cluster analysis, becomes now clearer in terms of responses of the species assemblages to the environment (see the dummy variables 'Sand' and 'Podzol'). The depth of the humus layer also seemed to be an important explanatory factor, but it correlated with climate meaning that soils become richer from north to south.

The second axis of Fig. 5 (eigenvalue 0.39) contributed to 50.5% of the variation accounted for and can be interpreted as a finer-scale latitudinal gradient; it showed differences between the forest-steppe sites and neighbouring floodland oak forests of the steppe zone. No significant correlation between the second axis and environmental variables was found (Table 2). The local habitat characteristics ('condition of the forest', 'cher-

Table 3. Correlations between assemblage parameters and environmental variables. Symbols as in Table 2, Appendices 1 and 2.

	N	S	E(S)	1/C	Sh	F	G	HB	HEven
Lati	-0.47*	-0.46*	-0.01	0.06	-0.05	0.59*	0.60*	-0.04	0.50*
Long	0.64**	0.48*	0.29	0.29	0.34	-0.05	-0.01	0.37	0.14
Tann	0.47*	0.48*	0.01	-0.05	0.05	-0.55*	-0.55*	0.05	-0.48*
Tjan	0.11	0.19	-0.15	-0.10	-0.13	-0.47*	-0.48*	-0.15	-0.50*
Tamp	0.67**	0.51*	0.30	0.29	0.36	-0.10	-0.09	0.37	0.07
Days W/F	0.42	0.48*	0.19	0.11	0.20	-0.47*	-0.47*	0.15	-0.34
Prec	-0.37	-0.43	-0.02	0.04	-0.05	0.52*	0.52*	0.03	0.43
Humi	-0.50*	-0.34	0.10	0.12	0.04	0.38	0.34	-0.02	0.32
Cond	-0.05	-0.06	0.07	0.12	0.09	0.12	0.07	0.02	-0.04
Humus	0.26	0.17	-0.10	-0.18	-0.08	-0.57*	-0.61**	0.15	-0.40

\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ .

nozom soil', and 'grey forest soil') seemed important according to the biplot but their possible biological effect is difficult to assess. The second axis, however, can also be identified as a trend from the species-rich assemblages of the two southernmost sites 22 and 23, containing 8 and 7 species, respectively, to the less diverse assemblages in the middle and northern forest-steppe with 3–4 species.

### Changes in alpha diversity

All assemblage parameters analysed so far depend on species composition. Another group of parameters, irrespective of species identity, can be derived from quantitative characteristics such as total number of individuals, number of species and relative species abundance. Their values are given in Appendix 2.

The univariate correlation analysis did not reveal any significant linear relationship between the quantitative parameters and environmental variables, except for a weak ( $r = 0.56$ ,  $P < 0.05$ ) but significant correlation between the total number of individuals per site (N) and longitude. Species richness (S) appeared to be higher in both northernmost and southernmost sites ( $S = 6-9$ ) and lower in the central part of the study area ( $S = 2-5$ ). In general, species richness and total number of individuals tended to increase towards the south, although this pattern was not supported by significant linear rela-

tionship with neither latitude nor environmental variables. Neither the expected number of species per 10 individuals /E(S)/, nor all other measures of diversity and evenness indicated a meaningful pattern of variation or significant correlation with either climatic or habitat variables. The most diverse communities (18, 19, 22, 23, 1, 6, and 7) were found at the opposite extremes and in the centre of the latitudinal gradient. To avoid non-linearity caused by the high diversity values of the two sites in the north (1 and 2), I eliminated them and repeated the analysis. Although the results were similar (Table 3), they did reveal an important pattern. Contrary to diversity indices, evenness tended to increase with latitude according to all measures. This means that local abundances of the species in the centre of the study area were more evenly distributed than in the south. The opposite was seen in species richness and total number of individuals tending to increase to the south.

Most of the analyses of species composition and alpha diversity revealed the specifics of the southern forest-steppe sites as can be seen from a test of several averaged diversity parameters of three adjacent subzones (Tables 4 and 5). Average species richness, expected number of species, and total number of individuals of the southern forest-steppe sites was higher compared with the northern subzones. However, none of the other diversity and evenness measures revealed significant differences. The sites in the subzone of deciduous

Table 4. Averaged values (x), standard deviations (SD) and ranges (in brackets) of assemblage parameters for three subzones in the study area. n – number of sites in each subzone, sequential numbers of sites and symbols as in Appendix 2.

	n	N		S		E(S)		1/C		G	
		x	SD	x	SD	x	SD	x	SD	x	SD
Deciduous forest subzone (sites No 4–7, 9)	5	30.0	12.8 (17–44)	4.0	1.4 (2–5)	3.1	1.1 (2.0–4.5)	2.7	1.2 (1.7–4.2)	0.51	0.11 (0.24–0.63)
Northern and middle forest-steppe (sites No 8, 10–14, 16, 17, 20)	9	37.1	24.9 (10–80)	3.4	0.9 (2–5)	2.7	0.5 (1.9–3.3)	2.0	0.5 (1.4–2.8)	0.38	0.14 (0.16–0.66)
Southern forest-steppe subzone (sites No 15, 18, 19, 21)	4	104.5	49.8 (50–159)	6.7	2.2 (4–9)	4.0	1.3 (2.9–5.2)	3.6	1.3 (1.8–5.5)	0.36	0.17 (0.15–0.53)



Table 5. Between-subzone differences in some assemblage parameters evaluated with one-sided Mann-Whitney rank sum test (U-statistics). All symbols as in Table 4.

		Deciduous forest subzone (n = 5)					Northern and middle forest-steppe (n = 9)				
		N	S	E(S)	1/C	G	N	S	E(S)	1/C	G
Northern and middle forest- steppe (n = 9)	N	ns									
	S	-	ns								
	E(S)	-	-	ns							
	1/C	-	-	-	ns						
	G	-	-	-	-	ns					
Southern forest-steppe subzone (n = 4)	N	*	-	-	-	-	*				
	S	-	*	-	-	-	-	*			
	E(S)	-	-	ns	-	-	-	-	*		
	1/C	-	-	-	ns	-	-	-	-	ns	
	G	-	-	-	-	ns	-	-	-	-	ns

\* =  $P \leq 0.05$ , ns = not significant. - = not tested.

forest and the northern and middle forest-steppe did not differ between each other in any of the assemblage parameters.

Interestingly, no positive correlation existed between alpha diversity and either age of the forest or the degree of preservation. Doubtless, the most impressive in this respect site is Les-na-Vorskla Reserve being preserved since the XVII century and therefore representing an oak forest of about 300 years old with an almost undisturbed vegetation structure (Walter 1976, Goryshina 1986). Here, two samples taken in the spring of 1988 and the autumn of 1990 revealed a very low diversity of the wire-worm assemblages (Appendix 2). Two sites in the southern forest steppe (21 and 19) are another example. Being well preserved and very similar to each other in both environmental characteristics and plant cover, they differed considerably according to diversity parameters (Appendix 2). Why it is so is difficult to understand. However, it is clear that high diversity of a certain animal community does not necessarily mean better condition of the habitat.

## Discussion

### Laws of zonation and extrazonal exceptions

The general patterns in zonation of the nature are a traditional topic of interest in the Russian school of biogeography (Dokuchaev 1899, Alekhin 1936, Berg 1947, Grigoryev 1954, Chernov 1975). According to the classical concept, the zones are typological categories explained by latitudinal climatic gradients. Yet, local conditions such as relief, exposition, soil type, and composition can support species or communities untypical for a particular zone. My results fully agree with these insights. The wire-worm assemblages sampled in ancient floodland terraces on either sandy or sandy-loamy soils were 'moved' to the north in multivariate space,

that is they were closer to more northern sites than to those of the zone or even the subzone in which they were found. The extrazonal nature of the Usmansky Bor forest (sites 10, 11, 12), has been recognized for a long time (Keller 1921, Berg 1947). Evidence for this is the occurrence of several boreal plant species such as *Vaccinium myrtillus* L., *V. vitis-idaea* L., and *Pyrola rotundifolia* L. in pine as well as mixed pine-oak forests on sandy soils. This phenomenon was indicated by the variables 'Podzol' and 'Sand' on the species-environment biplot (Fig. 5) and can be explained by soil-forming processes on sandy soils which have some common features with podzolic soil types (Turin 1922, Rode and Sedletsky 1939). There is an opposite viewpoint, however, according to which the sandy soils cannot be considered as podzolized (Gael and Malanyin 1977, Khabarov 1977). My results demonstrated that the wire-worm assemblages on soddy podzolic and sandy soils are similar.

### Latitudinal trends in assemblage parameters

Latitudinal diversity gradients are commonly studied on two major scales: globally, from the equator to the poles, and zonally, within continents (Brown and Gibson 1983, Wiens 1989). A common result of such studies is 'the general failure to document smooth monotonic changes in diversity along linear transects' (Wiens 1989). This conclusion based on bird assemblages has also been drawn from studies on soil invertebrates such as earthworms (Perel 1979) and collembolans (Chernova and Kuznetzova 1988, 1990, Kuznetzova 1988, Chernov 1989). Obviously, the joint effect of processes at both global and local scales results in general trends but not in regular gradients. However, when average or maximum values of species richness are considered for a certain biome, the patterns are clearer. The upper threshold of species richness is principally determined

by global thermal conditions, while all other patterns of variation can be considered as secondary (Chernov 1989). The existence of upper threshold in variation of species richness in parts of the gradient has been shown by Tramer (1974) for bird communities, and Chernov (1989) for collembolan assemblages. This study demonstrated a similar pattern.

Recently, Haila et al. (1987) examined both qualitative and quantitative aspects of geographic variation in local bird assemblages of the western Palearctic taiga. Their conclusion that 'qualitative data tended to show more regular geographic patterns than census data did' has much in common with my findings, despite that the ecological relevance and dispersal capacity of birds and soil beetles differ markedly. However, these authors discussed the observed patterns mostly in terms of theories of (pen)insular biogeography and interspecific competition. Indeed, the explanatory power of these theories can not and should not be ignored completely in studies on geographic variation of continental communities but this does not mean that no other, presumably more powerful approaches exist (Wiens 1977, Connor and Simberloff 1979, Gilbert 1980, Higgs 1981, Abbott 1982, Lawton 1984, Brown and Bowers 1984, Brown and Kurzius 1987). In an extensive study on large-scale spatial variation of 202 local rodent assemblages in the North American deserts, Brown and Kurzius (1987) found 'highly individualistic' patterns of species distributions. Application of the individualistic concept of Ramensky and Gleason (see Whittaker 1975) at zonal scales has also been proposed by Chernov (1989). Hence, the logical conclusion is that further development of comparative studies on responses of species and communities to macro-environmental factors as well as local habitat conditions can contribute much to the understanding of patterns and processes in both community organization and broad-scale spatial variation.

## Conclusions

The objective of this study was to reveal patterns in large-scale variation of communities of a similar type lying in different biomes. The approach is exploratory (Tukey 1977, cited after James and McCulloch 1985), meaning that any patterns with a meaningful biological interpretation concerning species or community responses to environmental factors were searched for. Two important questions were considered: (1) which community parameters demonstrate a trend in variation along the latitudinal gradient and which do not, and (2) which environmental variables could explain these trends. Five conclusions can be drawn on these questions from a separate analysis of changes in both species composition and diversity:

(1) The main trend in species composition concerning presence/absence data correlated with climatic gradients.

(2) Adding species abundance in the same analysis demonstrated the effect of a habitat characteristic independent of climate such as soil composition.

(3) The number of species and total number of individuals tended to increase towards the south although this was confirmed statistically only for a subset of the data.

(4) Various diversity and evenness indices, as well as the expected number of species calculated with the rarefaction method, appeared to be less informative for the response of communities to environmental variables than is the species composition.

(5) Alpha diversity of the wire-worm assemblages did not depend on the age of the forest and the degree of habitat preservation.

*Acknowledgements* – Material used in the present study has been taken during field work together with Dr S. Golovatch and A. Vasilev. At certain sites, we were kindly assisted by A. Klimov, V. Karpova, A. Nazarov, and Dr V. Ostafitchuk. I am also grateful to Dr P. Baev for the help in computer work, to Dr L. Rybalov who supplied valuable comments on soil processes in sandy loam, as well as to Dr S. Golovatch again for the English corrections. Special thanks are due to Dr R. Hengeveld who was exceptionally patient in improving the text stylistically and made essential comments on the structure of the paper. I am also deeply indebted to Professor Yu. I. Chernov for the general support and supervision of this project.

Contribution No. 1 to the project 'Spatial variation in soil macrofauna communities of the East European oak forests in relation to environmental factors' carried out by L. Penev and S. Golovatch and sponsored by the USSR Academy of Sciences.

## References

- Abbott, I. 1983. The meaning of  $z$  in species/area regressions and the study of species turnover in island biogeography. – *Oikos* 41: 385–390.
- Alatalo, R. V. 1981. Problems in the measurement of evenness in ecology. – *Oikos* 37: 199–204.
- Alekhin, V. V. 1936. [Main regularities of the vegetation cover of the USSR] [In Russ.]. – In: Walter, H. and Alekhin, V. V. [Principles of botanic geography], Moscow, Leningrad, pp. 352–374.
- Arnoldi, K. V. 1956. [A review of the insect fauna and characteristics of soil and litter insect complexes in the Derkul flow] [In Russ.]. – *Tr. Inst. Iesa Akad. nauk SSSR* 30: 279–342.
- Baev, P. V. and Penev, L. D. 1991. BIODIV – a program for calculating biological diversity parameters, similarity, niche overlap and cluster analysis. – *Inst. Anim. Evolut. Morphol. & Ecol., Moscow*.
- Berg, L. S. 1947. [The geographic zones of the USSR. 1.] [In Russ.]. – *Geografiz, Moscow*.
- Bey-Bienko, G. Ya. 1966. [Change of habitats by terrestrial organisms as a biological principle] [In Russ. with English summary]. – *Zhurn. obshch. biol.* 37: 5–21.
- Brown, J. H. and Bowers, M. A. 1984. Patterns and processes in three guilds of terrestrial vertebrates. – In: Strong, D. R., Simberloff, D. Abele, L. G. and Thistle, A. B. (eds), *Ecological communities: conceptual issues and the evidence*, Princeton Univ. Press, Princeton, NJ, pp. 282–296.

- and Gibson, A. C. 1983. Biogeography. – C. V. Mosby Company, St. Louis.
- and Kurzius, M. A. 1987. Composition of desert rodent faunas: combinations of coexisting species. – *Ann. Zool. Fennici* 24: 227–237.
- Chernov, Yu. I. 1975. [Nature zonation and terrestrial animals] [In Russ.]. – Mysl, Moscow.
- 1984. Flora and fauna, plant and animal population [In Russ. with English summary]. – *Zhurn. obshch. biol.* 45: 732–748.
- 1989. [Thermal conditions and the arctic biota] (In Russ.). – *Ekologiya (Moskva)* 2: 49–57.
- Chernova, N. M. and Kuznetzova, N. A. 1988. General characters of the structure of collembolan population in forest soils [In Russ.]. – In: Chernova, N. M. (ed.), *Microarthropod ecology in forest soils*. Nauka, Moscow, pp. 5–24.
- and Kuznetzova, N. A. 1990. Principles of organization of a multispecies group of Collembola-saprophages [In Russ.]. – In: Shilov, I. A. (ed.), *General problems in biocoenology*, Nauka, Moscow, pp. 220–230.
- Connor, E. F. and Simberloff, D. 1979. The assembly of species communities: chance or competition? – *Ecology* 60: 1132–1140.
- Dokuchaev, V. V. 1899. [To a study of nature zones. Latitudinal and altitudinal soil zones] [In Russ.]. – Sankt Peterburg.
- Gael, A. G. and Malanyin, A. N. 1977. A note on soil formation on sands and soddy nonpodzolized soils [In Russ. with English summary]. – *Pochvovedenie* 4: 23–34.
- Ghilarov, M. S. 1956. [The soil fauna in woods and open steppe areas in the Derkul flow] [In Russ.]. – *Tr. Inst. lesa Akad. nauk SSSR* 30: 235–277.
- 1965. [Zoological method of soil diagnostics] [In Russ.]. – Nauka, Moscow.
- 1975. Taking censuses of larger soil invertebrates (“mesofauna”) [In Russ. with English summary]. – In: Ghilarov, M. S. (ed.), *Methods of soil zoological studies*. Nauka, Moscow, pp. 12–29.
- Gilbert, F. S. 1980. The equilibrium theory of island biogeography: fact or fiction? – *J. Biogeogr.* 7: 209–235.
- Goryshina, T. K. 1986. [On the history of the Les-na-Vorskla Reserve] [In Russ.]. – In: [Complex studies on the biocoenoses of the forest-steppe oak forests], Leningrad Univ. Publishing House, Leningrad, pp. 3–32.
- Grigoryev, A. A. 1954. [The geographic zonation and its regularities] [In Russ.]. – *Izv. AN SSSR, Ser. geograf. nauk* 5: 17–39, 6: 41–50.
- Haila, Y., Järvinen, O. and Raivio, S. 1987. Quantitative versus qualitative distribution patterns of birds in the western Palearctic taiga. – *Ann. Zool. Fennici* 24: 179–194.
- Hengeveld, R. 1987. Scales of variation: their distinction and ecological importance. – *Ann. Zool. Fennici* 24: 195–202.
- 1990. *Dynamic biogeography*. – Cambridge Univ. Press, Cambridge.
- Higgs, A. J. 1981. Island biogeography and nature reserve design. – *J. Biogeogr.* 8: 117–124.
- Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. – *Ecology* 54: 427–432.
- 1979. TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. – Cornell Univ., Ithaca, N.Y.
- James, F. C. and Rathbun, S. 1981. Rarefaction, relative abundance, and diversity of avian communities. – *Auk* 98: 785–800.
- and McCulloch, C. E. 1985. Data analysis and the design of experiments in ornithology. – In: Johnston, R. F. (ed.). *Current ornithology*, Vol. 2, Plenum Publishing Co., pp. 1–63.
- Jongman, R. H., Ter Braak C. J. F. and van Tongeren, O. F. R. 1987. *Data analysis in community and landscape ecology*. – Pudoc, Wageningen.
- Keller, B. A. 1921. [The vegetation of the Voronezh Province] [In Russ.]. – Voronezh.
- Khabarov, A. V. 1977. [Soil formation on sands in the south-eastern part of the Russian Plain] [In Russ.]. – Nauka, Moscow.
- Kuznetzova, N. A. 1988. Types of collembolan populations in coniferous forests of the European part of the USSR [In Russ.]. – In: Chernova, N. M. (ed.), *Microarthropod ecology in forest soils*. Nauka, Moscow, pp. 24–52.
- Lawton, J. H. 1984. Non-competitive populations, non-convergent communities, and vacant niches: the herbivores of bracken. – In: Strong, D. R., Simberloff, D., Abele, L. G. and Thistle, A. B. (eds), *Ecological communities: conceptual issues and the evidence*. Princeton Univ. Press, Princeton, NJ, pp. 67–99.
- MacArthur, R. H. and Wilson, E. O. 1967. *The theory of island biogeography*. – Princeton Univ. Press, Princeton, NJ.
- Magurran, A. E. 1988. *Ecological diversity and its measurements*. – Princeton Univ. Press, Princeton, NJ.
- Molinari, J. 1989. A calibrated index for the measurement of evenness. – *Oikos* 56: 319–326.
- Peet, R. K. 1974. The measurement of species diversity. – *Ann. Rev. Ecol. Syst.* 5: 285–307.
- Perel, T. S. 1979. Range and regularities in the distribution of earthworms of the USSR fauna [In Russ.]. – Nauka, Moscow.
- Pesenko, Yu. A. 1982. [Principles and methods of quantitative analysis in faunistic investigations] [In Russ.]. – Nauka, Moscow.
- Pielou, E. C. 1975. *Ecological diversity*. – Wiley, N.Y.
- Rode, A. A. and Sedletsky, I. D. 1939. Sandy soils of the Kama river terraces [In Russ. with English summary]. – *Tr. pochv. inst. im. Dokuchaeva* 19: 81–141.
- Ter Braak, C. J. F. 1988. CANOCO – a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical correspondence analysis, principal components analysis and redundancy analysis (version 2.1)]. – ITI-TNO, Wageningen.
- Tramer, E. J. 1974. On latitudinal gradients in avian diversity. – *Condor* 76: 123–130.
- Turin, I. V. 1922. [The sandy soil under pine forests in the vicinity of Kazan] [In Russ.]. – *Vestnik Kazanskoi oblastnoi khoz-opytnoi stantsii* 1: 10–22, 2: 1–40.
- Walter, H. 1976. *Die ökologische Systeme der Kontinente (Biogeosphäre): Prinzipien ihrer Gliederung mit Beispielen. II: Die kleinen Einheiten des ökologischen Systems. 3. Wald an der Worskla – Beispiel eines Biogeozonoses. 5. Phytomasse und Stoffproduktion des Eichenmischwaldes in der Waldsteppe*. – Fischer-Verlag, Stuttgart.
- Whittaker, R. H. 1975. *Communities and ecosystems*. – Macmillan, N.Y.
- Wiens, J. A. 1977. On competition and variable environment. – *Am. Sci.* 65: 590–597.
- 1989. *The ecology of bird communities*. – Cambridge Univ. Press, Cambridge, Vol. 1, 2.
- , Addicott, J. F., Case, T. J. and Diamond, J. 1986. Overview: the importance of spatial and temporal scale in ecological investigations. – In: Diamond, J. and Case, T. J. (eds), *Community ecology*. Harper & Row, New York, pp. 145–153.

**Appendix 1.** Geographical location and characteristics of 23 study sites. Tann – mean annual temperature, Tjan – mean temperature of the coldest month (January), Tamp – annual temperature amplitude, Days w/F – number of frostless days, Humi – annual relative humidity, Prec – mean annual precipitation. Biome: MIX – mixed forest subzone, DEC – deciduous forest subzone, FSN – northern and middle forest-steppe subzones, FSS – southern forest-steppe subzone, STE – northern steppe subzone.

Site No	Site	Province	Latitude	Longitude	Biome	Month	Year	Tann (°C)	Tjan (°C)	Tamp (°C)	Days w/F	Humi (%)	Prec (mm)
1	Sokolovo near Dubniki	Novgorod	58°00'	33°15'	MIX	IX	89	3.6	- 9.5	26.9	120–130	78	555
2	Udomlya	Tver	57°50'	35°10'	MIX	IX	90	3.7	- 9.6	27.0	130–140	79	628
3	Sharapovo near Malinki	Moscow	55°10'	37°15'	MIX	IX	90	4.1	-10.3	28.0	140–150	78	656
4	Vasilyovskoye near Venev	Tula	54°28'	38°12'	DEC	V	88	4.2	-10.1	28.5	140–150	77	547
5	Krapivna Forestry – 1	Tula	53°55'	37°10'	DEC	V	89	4.2	-10.1	28.5	140–150	77	565
6	Krapivna Forestry – 2	Tula	53°55'	37°10'	DEC	IX	90	4.2	-10.1	28.5	140–150	77	565
7	Chernysheno near Duminichi	Kaluga	53°48'	35°15'	DEC	V	89	4.6	- 9.1	27.4	140–150	80	580
8	Setukha east of Oryel	Oryel	52°55'	36°47'	FSN	IX	90	4.6	- 9.2	28.0	140–150	78	515
9	Sevsk	Bryansk	52°00'	34°10'	DEC	IX	90	5.5	- 8.1	27.2	130–140	78	594
10	Venevitinovo near Voronezh	Voronezh	51°52'	39°38'	FSN	V	89	5.1	- 9.9	29.2	130–140	74	589
11	Voronezh Reserve – 1	Voronezh	51°52'	39°40'	FSN	VI	89	5.1	- 9.9	29.2	130–140	74	589
12	Voronezh Reserve – 2	Voronezh	51°52'	39°40'	FSN	VI	89	5.1	- 9.9	29.2	160–170	74	589
13	Streletsky Les near Kursk	Kursk	51°35'	36°12'	FSN	V	88	5.3	- 9.0	27.7	160–170	79	570
14	Kazatsky Les near Kursk	Kursk	51°32'	36°18'	FSN	V	90	5.3	- 9.0	27.7	160–170	79	570
15	Tellerman Forestry	Voronezh	51°20'	42°05'	FSS	V	89	5.6	- 9.9	30.9	150–160	73	531
16	Les-na-Vorskla Reserve – 1	Belgorod	50°50'	36°00'	FSN	V	88	6.0	- 7.9	28.0	150–160	76	537
17	Les-na-Vorskla Reserve – 2	Belgorod	50°50'	36°00'	FSN	IX	90	6.0	- 7.9	28.0	150–160	76	537
18	Shipov Les Forestry – 1	Voronezh	50°32'	40°20'	FSS	VI	89	5.8	- 9.4	29.9	160–170	76	518
19	Shipov Les Forestry – 2	Voronezh	50°32'	40°20'	FSS	VI	89	5.8	- 9.4	29.9	160–170	76	518
20	Trostanets Forestry	Sumy	50°30'	34°50'	FSN	IX	90	6.5	- 7.2	27.3	150–160	76	525
21	Gaidary near Gottwald	Kharkov	49°35'	36°20'	FSS	V	90	6.6	- 7.6	28.2	170–180	74	538
22	Kremennaya	Lugansk	49°00'	38°15'	STE	V	90	7.6	- 6.7	28.5	160–170	74	496
23	Stanichno-Lugansky Reserve	Lugansk	48°30'	39°25'	STE	VI	89	7.6	- 7.2	29.2	170–180	71	433

Site No	Soil type	Soil composition	Humus* depth	Accompanying tree species	Forest age (years)
1	Soddy podzolic gleyed	Clayish	5–15	Picea, Populus tremula	150–220
2	Soddy podzolic gleyed	Heavy loam	10–15	Picea, Salix	150–250
3	Soddy podzolic	Moderate loam	8–10	Tilia, Betula, Picea, Acer	120–150
4	Grey forest	Moderate to heavy loam	20–30	Tilia, Betula, P. tremula	50–70
5	Grey forest	Moderate to heavy loam	10–25	Tilia, Acer	200–300
6	Grey forest	Moderate to heavy loam	10–25	Tilia, Acer	200–300
7	Grey forest	Moderate to heavy loam	10–20	Acer, Fraxinus, Betula, Ulmus	100–150
8	Chernozem	Moderate loam	40–50*	Acer, Betula, Picea	100–120
9	Grey forest	Sandy loam	15–20	Acer, Pinus	100–170
10	Grey forest	Sandy loam	3–20	Betula, Pinus	70–80
11	Grey forest	Moderate to sandy loam	8–40*	Tilia	60–70
12	Grey forest	Silty to sandy loam	5–40*	Fraxinus, Tilia, Betula	70–100
13	Chernozem	Moderate loam	30–40*	Acer, P. tremula, Pyrus	40–60
14	Chernozem	Moderate loam	20–40*	Acer, P. tremula, Pyrus	50–100
15	Grey forest	Moderate to heavy loam	25–40*	Fraxinus, Acer, Tilia	100–150
16	Grey forest	Loess-like to heavy loam	10–40*	Tilia, Acer, Fraxinus	200–300
17	Grey forest	Loess-like to moderate loam	10–40*	Tilia, Acer, Fraxinus	100–300
18	Grey forest	Moderate to heavy loam	20–40*	–	80–130
19	Grey forest	Moderate to heavy loam	7–40*	Acer, Tilia	80–150
20	Grey forest	Moderate loam	15–30*	Fraxinus, Acer, Tilia	100–150
21	Grey forest	Moderate loam	8–30*	Fraxinus, Acer, Tilia	120–150
22	Meadow chernozem-like	Moderate to heavy loam	20–40*	Fraxinus, Tilia, Acer	80–150
23	Meadow chernozem-like	Loess-like to moderate loam	10–40*	Acer, Fraxinus, Tilia	70–90

\* The humus depth exceeds 40 cm, in some samples

**Appendix 2.** Species composition and abundance (individuals per 0.0625 m<sup>2</sup>), and diversity statistics of the wire-worm assemblages. Site numbers as in Appendix 1.

	Site numbers																							Sites total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
<i>Agrypnus murinus</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-	1
<i>Athous haemorrhoidalis</i> (F.)	8	8	12	5	18	6	7	2	1	2	-	-	1	5	8	12	3	6	32	10	11	40	86	21
<i>A. vittatus</i> (F.)	-	-	22	12	10	5	16	7	-	-	9	20	10	33	16	53	14	24	36	9	33	9	1	19
<i>A. subfuscus</i> (Muell.)	10	2	14	-	-	3	7	-	10	9	-	-	-	-	-	-	-	3	10	1	-	-	-	10
<i>A. niger</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
<i>Cidnopus parvulus</i> (Panz.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	95	-	-	2	10	-	2	-	-	4
<i>C. minutus</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1
<i>Denticollis linearis</i> (L.)	-	1	-	-	-	2	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	4
<i>Ctenicera pectinicornis</i> (L.)	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Selatosomus aeneus</i> (L.)	1	-	-	-	-	-	-	-	1	4	4	-	-	-	11	-	-	9	40	-	-	24	-	7
<i>S. cruciatus</i> (L.)	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2
<i>Mosotalesus nigricornis</i> (Panz.)	2	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>M. impressus</i> (F.)	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Mosotalesus</i> sp.	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Prosternon tessellatum</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	5	2	-	-	24	5	5	
<i>Pseudanostirus globicollis</i> (Germ.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	13	-	4	-	-	3
<i>Actenicerus sjaelandicus</i> (Muell.)	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Ectinus aterrimus</i> (L.)	-	-	-	-	-	-	1	-	-	27	-	1	-	-	-	-	-	-	-	-	-	-	-	3
<i>Dalopius marginatus</i> (L.)	16	61	10	-	1	2	11	-	31	38	22	18	-	14	-	-	-	8	15	-	-	-	-	13
<i>Agriotes lineatus</i> (L.)	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>A. obscurus</i> (L.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	1
<i>A. pilosellus</i> (Schoenh.)	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	2
<i>Ampedus sanguinolentus</i> (Schrk.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	2
<i>A. pomonae</i> (Steph.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
<i>A. pomorum</i> (Hbst.)	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	2
<i>Melanotus rufipes</i> (Hbst.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	2
Individuals total (N)	42	79	58	17	29	18	42	10	44	80	36	39	12	53	132	66	17	77	159	21	50	107	102	
Number of species (S)	9	6	4	2	3	5	5	3	5	5	4	3	3	4	6	3	2	8	9	4	4	8	7	
Expected number of species (E(S))	4.66	2.81	3.74	2.00	2.34	4.56	3.95	2.89	2.63	3.36	2.99	2.26	2.67	2.82	2.96	2.04	1.95	5.05	5.17	2.95	2.90	4.30	2.36	
Inverse of Simpson's index (1/C)	4.08	1.64	3.64	1.71	1.98	4.15	3.71	1.85	1.82	2.81	2.23	2.10	1.41	2.14	1.84	1.47	1.41	4.96	5.59	2.41	2.03	3.99	1.39	
Exponent of Shannon's index (expH')	5.32	2.35	3.82	1.83	2.18	4.52	4.07	2.23	2.32	3.35	2.69	2.21	1.76	2.57	2.57	1.73	1.59	6.03	6.48	2.74	2.56	4.87	1.96	
Alatalo's evenness (F)	0.71	0.47	0.94	0.85	0.83	0.90	0.88	0.69	0.62	0.77	0.72	0.91	0.54	0.73	0.54	0.65	0.69	0.79	0.84	0.81	0.66	0.77	0.41	
Molinari's evenness (G)	0.36	0.10	0.72	0.55	0.52	0.63	0.60	0.33	0.24	0.44	0.37	0.66	0.16	0.38	0.15	0.27	0.33	0.45	0.53	0.49	0.29	0.44	0.07	
Brillouin's diversity index (HB)	1.43	0.76	1.24	0.51	0.68	1.21	1.25	0.59	0.73	1.12	0.87	0.72	0.41	0.85	0.88	0.50	0.38	1.64	1.77	0.83	0.84	1.47	0.60	
Brillouin's evenness (HBeven)	0.69	0.45	0.90	0.71	0.60	0.84	0.84	0.71	0.44	0.74	0.70	0.72	0.47	0.65	0.52	0.49	0.53	0.80	0.81	0.67	0.61	0.73	0.31	