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Large-scale variation in carabid assemblages, with special reference to the local fauna concept

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Thanks to pitfall trapping, carabid beetles form one of the most appropriate groups for comparative studies on community composition and variation, both at local and geographical scales. This paper focuses on the following conceptual points: (1) At a local level, two types of species assemblages can be distinguished, i.e. communities, separated on a habitat basis, and local faunas, defined as a list of species occurring in all habitats at a locality. The concept of a local fauna is intended to link the traditional faunistic phenomena with their possible explanatory variables, both ecological and biogeographical. (2) The environmental factors affecting the assemblage composition and spatial variation at larger geographical scales can be divided into two major groups: regional, caused mainly by historical reasons (isolations, glaciations) and zonal, caused by the recent climatic conditions. (3) The parameters of carabid assemblages can be derived from either species composition or species diversity. On a within-region scale, species composition and its derivatives appear to be more informative in reflecting the environmental gradients in comparison to species diversity. Above questions are illustrated on (i) the basis of literature survey on large-scale variation of ground-beetle communities, and (ii) an analysis of the changes in 61 local faunas of the genus *Carabus* L. scattered over the Russian Plain in relation to environmental factors.

1. Introduction

Over 40 years ago, Carl Hildebrandt Lindroth stated in his prominent work entitled “Die Fennoskandischen Carabiden, Bd. 3” that “It is misleading to wish to establish complex units before their components are sufficiently known. Before one is familiar with the autecology of the species, synecology is impossible” (Lindroth 1992, p. 24). The few decades following this statement have been marked with an increasing interest in synecological aspects of biotic organization, i.e. assemblages or communities. The community paradigm prevailing over the individualistic one culminated in the 1970’s until a back swing which has led us again to more species-orientated ecological studies or even, in the recent years, to an individual-based ecology. I do not intend to present a historical review here, but I would like to stress that my paper will be devoted to a synecological or, better to say, synbiogeographical phenomenon, that is, large-scale variation in local groupings of carabid species.

First, I would like to provoke a discussion on a definition of the local groupings of species, communities and faunas, with special emphasis placed on the local fauna concept. The second important question is, which environmental factors play a major role in the formation and spatial variation of carabid assemblages. Thirdly, it seems necessary to specify which assemblage parameters are the most informative for environmental quality assessments and predictions of ecological change. And finally, I shall try to illustrate the above conceptual points with examples from literature and original data. I feel that the above questions are important, because it is fruitful to summarise at larger, international scales, the databases accumulated in different countries. Thanks to pitfall trapping, the carabid beetles seem to be one of the best objects for this purpose.

2. An outline of the concepts

2.1. A definition of the carabid groupings: communities versus local faunas

All local groupings of carabids will be defined here as "assemblages". A ground-beetle assemblage sampled by means of pitfall trapping in a certain habitat can be termed as a "community". A list of the species occupying all the habitats at a geographical locality forms the latter's "local fauna". The discrepancy between "communities" and "local faunas" is not at all a matter of terminology or scientific approach only, as both major forms of biotic organisation, i.e. "synecological" and the "faunal" (Fig. 1), are controlled by factors different in nature (Chernov 1975, 1984). In contrast to biotic communities, which are usually distinguished on the basis of, and hence affected mostly by, both the properties of the habitat and biotic interactions, the local faunas can be regarded as more complicated products of zonal (recent climatic), regional (historical) and local (habitat conditions, biotic interactions) processes. In other words, biotic communities are synecological notions, whereas local faunas represent a crosspoint between classical faunistics and ecology.

The idea of a "local fauna" stemmed from the "concrete flora" concept proposed by the Russian botanist Tolmachev (1931). Initially, the basic goal of Tolmachev lay in a study of some traditional floristic phenomena, such as species composition, taxonomic and phytogeographical structure, at local scale. Later, the method of "concrete flora" was developed into a theoretical concept assuming that the species listed at a locality can be considered as a "floristic sample" reflecting the floristic composition of a larger region. According to some authors, Tolmachev's notion can be considered even as a "new paradigm in floristic research leading to the understanding of a flora as a hierarchical system based on elementary natural floras" (Shelyag-Sosonko, 1980).

Later, the "concrete flora" concept was extrapolated by Chernov (1975, 1989), who introduced the terms "concrete fauna" and "concrete biota" into biogeography. According to him, a concrete fauna is a list of the animal species, occurring in the habitats most characteristic of the biome encompassing a given locality. Respectively, a concrete biota is a list of both plant and animal species at a locality. The term "concrete fauna/biota" is not so popular as the analogous notion "local flora/fauna" which I prefer to use here.

One of the most crucial points of this concept lies in a definition of the area taken up by a local flora/fauna. For practical reasons, Tolmachev proposed a day-long botanical excursion along radial transacts across a locality as a unit of local flora representation. Later, Yurtsev (1975) suggested a standard area of 100 km^2, i.e. a circle with a radius of about 5–6 km. The latter idea seems convenient also because this is exactly the area of a 10 by 10 km UTM square. Due to pragmatic difficulties, however, areas of local floras or faunas can hardly be standardised when studying them over large regions, subcontinents for example. In such cases, some noise probably caused by differences in area has to be neglected in order to unravel large-scale factors of primary interest. In practice, every list of the animal species encountered in a well-explored nature reserve or at another faunistically well-documented locality can be regarded as a local fauna. Ideally, in case of a far-fetched research program, a transact for sampling of local faunas ought to look like Fig 2.

A strong support for the use of the local fauna concept lies in the fact that faunal units, such as "realms" or "provinces", are usually distinguished as based on larger regions. The environmental conditions there vary in space considerably and their average values can hardly be directly related to the faunal parameters. Yet, be they large-scale or local, the environmental factors act locally affecting a given

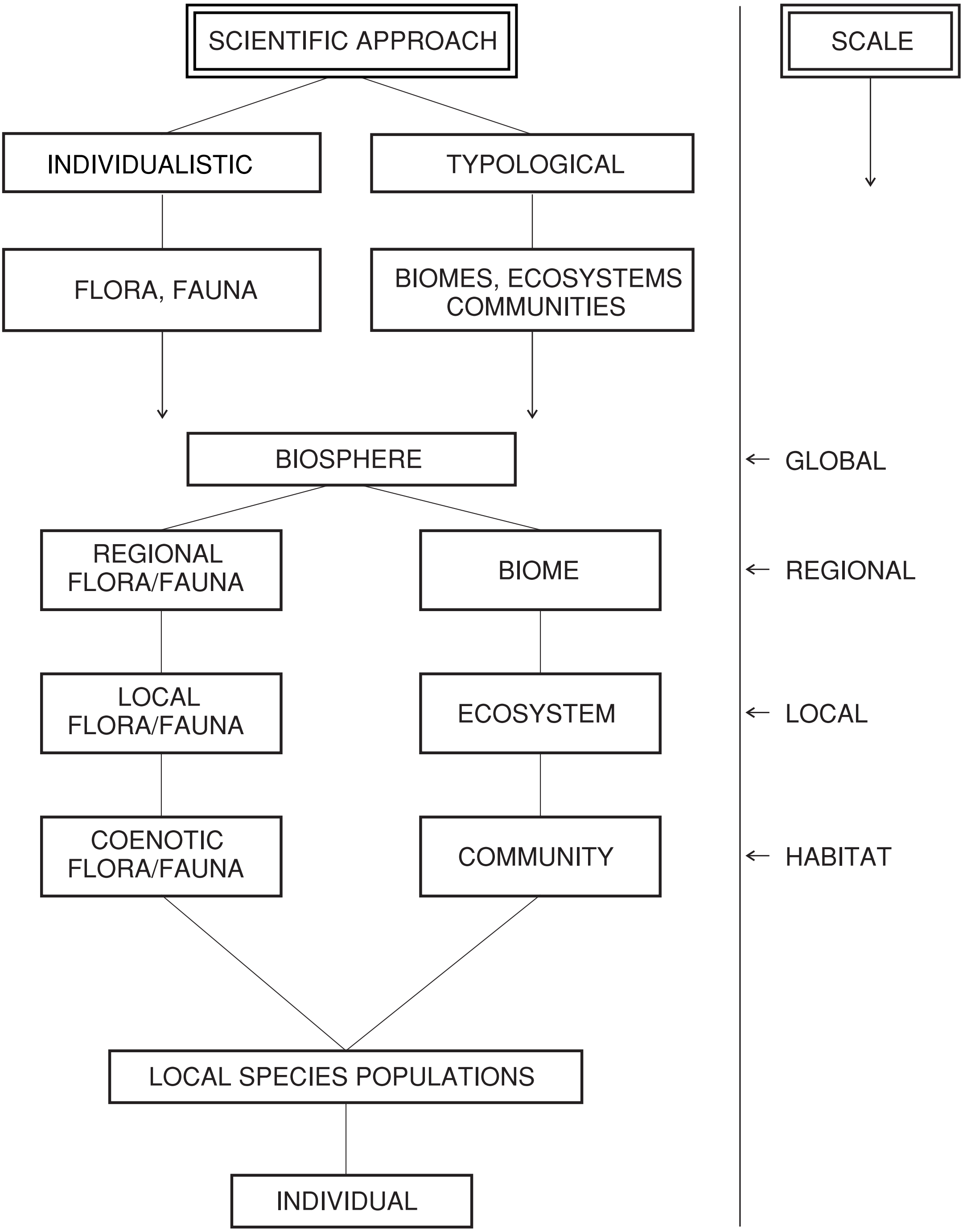

Fig. 1. Two parallel aspects, invidualistic and typological, in studying the organic life and their expressions at different spatial scales.

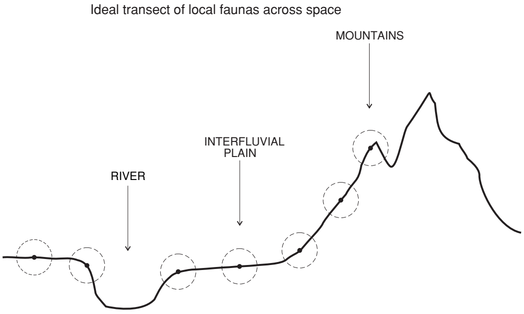

Fig. 2. An ideal transact for sampling of local faunas.

species population. Thus, the local faunas seem to be those natural units which parameters can be related both to ecological and biogeographical variables. Another reason for applying the local fauna concept lies in the fact, that if we want to predict the effect of global climatic change on the biota, we need a deep knowledge on the relationship between biotic and climatic parameters. There are, in my opinion, two choices to obtain such a knowledge at the assemblage level: (1) to use the changes in the composition of fossil/subfossil local faunas as an indirect monitor of the dynamics of past climates, and (2) to study the interactions between the climate and the biota at larger spatial scales, and after than, to extrapolate the revealed relationships on temporal scale.

2.2. A leading role of the environment: large-scale versus local factors

The species composition and assemblage characteristics of the local assemblages are a product of the combined effect of the following principal groups of factors:

1. Large-scale factors:
1.1. Between-region differences caused by historical processes
1.2. Macroclimatic gradients determining nature zonation within a certain geographic region
2. Local-scale factors:
2.1. Habitat properties
2.1.1. Altitude
2.1.2. Exposure
2.1.3. Landscape structure
2.1.4. Habitat diversity
2.1.5. Habitat composition
2.1.6. Soil properties
2.1.7. Vegetation cover
2.1.8. Land management (anthropogenic)
3. Temporal variation in the environment
3.1. Short-term periodicity and between-year dynamics
3.2. Long-term changes
4. Biotic (intra- and interspecific) interactions

The above scheme is simplified and often discussed in the literature (Brown & Gibson 1983, Chernov 1984, Penev 1992). I should rather focus on the more complex large-scale factors usually determined in carabidological works as “regional”. However, this term obviously needs further specification into regional sensu strictiore, caused by historical reasons, on one hand, and zonal, macroclimate-caused, on the other hand (Chernov 1975, Penev 1992, Chernov & Penev 1993). Indeed, a comparison between the carabid assemblages of the European and North American taiga forests (Niemelä *et al.* 1994) readily reveals regional differences in the community traits, whereas similar studies in the Finnish taiga (Niemelä 1990, Niemelä *et al.* 1994) demonstrate the effect of zonal, rather than regional, factors. Further, from the analyses of large-scale spatial variation, e.g. in the carabid communities of the grasslands of north-eastern Europe (Eyre & Luff 1992) or in the local faunas of the genus *Carabus* L. over the Russian Plain (Penev & Turin 1994), a combined impact both of regional and zonal factors can be expected. Studies on smaller geographical scales, for instance in Central Russia (Sharova, 1981, Gryuntal, 1985), illustrate a strong effect of nature zonation on carabid assemblages.

2.3. Indicatory value of the carabid assemblage parameters: species diversity versus species composition

A proper choice of biotic parameters is of paramount importance in predicting the consequences of global environmental change. The question is, which community parameters better reflect the spatial variation in environment and hence can be used to predict the effect of ecological change on the biota? In general, a response of the biotic assemblages — floras, faunas or communities — to variation in the environment is a product of the reactions of their constituent species populations. Yet an analysis of separate species as individual elements is bound to fail as a substitute of complex studies on the reaction of the biotic assemblage as a whole.

All assemblage parameters can generally be divided in two main groups (Hengeveld 1990, Penev 1992, Chernov & Penev 1993, Penev *et al.* 1994):

(1) Individualistic, dependent on the species identity, expressed as species listings, based either on presence/absence or abundance data. From these listings, several structural characteristics can be derived, such as taxonomic or zoogeographical structure of the assemblages;
(2) Typological, independent of the species identity, including a good number of synthetic quantitative characteristics of the assemblages as a whole, such as species richness, diversity, total sum of individuals, biomass, productivity, etc.

The fact that the difference between both above groups is essential can be exemplified as follows. Two analogous communities situated on different continents can be very similar (ideally, even equal) regarding their quantitative characteristics (Group 2 above) but completely divergent as to their species compositions (Group 1 above). Hence, the parameters insensitive to species identities would be more informative when comparing the communities between large, widely disparate faunistic regions, whereas the parameters related to the species composition may be expected to be more useful on a within-region scale. Yet the species composition and its derivative community characteristics seem much more promising as indicators of climatic impacts in comparison with species diversity, as has been shown on the basis of other animal groups (Penev 1992, Chernov & Penev 1993 Penev *et al.*1994).

The numerous literature sources exploring the applicability of the different diversity statistics (i.e. Jarosik 1991, Baev & Penev 1993, Booij 1994) leave the general impression of a non-monotonous and unstable response of their values to variation in the environment. Moreover, the various diversity statistics can often yield contradictory results from a viewpoint of their biological interpretation. Species diversity measured as number of species can be regarded as a discrete community parameter influenced by a large number of stochastic factors. On the contrary, changes in species composition along large-scale gradients summarise the reactions of the individual species. An unimodal model of species responses to environmental gradients proved for local scales (Whittaker 1975, Ter Braak & Prentice 1988) may be extended to a far larger geographical scale as well Hengeveld 1985, 1990, Chernov 1989). On the other hand, the climatic parameters also vary continually and therefore should be better indicated by continually varying biotic parameters, such as species composition, rather than by discrete ones, such as species richness.

3. Some implications

3.1. Large-scale variation in carabid assemblages

The pitfall sampling data obtained so far in various regions of Europe challenge the carabidologists with an exceptional chance to attempt large-scale studies on carabid communities.

Numerous papers have long proved the utility of carabid beetles and their communities as indicators of local habitat conditions (Thiele 1977). However, are these beetles equally good also as markers of large-scale variation in the environment? The question is the more important as the global warming of the climate makes a search of suitable monitors increasingly topical not only at the species but also at the community level.

At this stage of our knowledge, a simplified scheme of the combined effect of environmental factors on large-scale variation in carabid assemblages looks like in Fig 3. Large-scale studies on carabid communities based on pitfall trapping data and concerning several biomes seem to have first been applied since the 1970's by a research team headed by Sharova (Sharova & Matveeva 1974, Sharova 1981, 1984, Gryuntal 1985, 1987, Sharova & Dushenkov 1986). Those papers, covering vast geographical distances often measured in thousands of kilometres over the Russian Plain, focused on variation in carabid communities across natural zones, first of all in species composition, composition of dominant species, life-form structure, relative abundance of ecological and zoogeographical groupings, etc. However, due to the lack of an appropriate software available at that time, the works of those Russian carabidologists have been performed mostly on

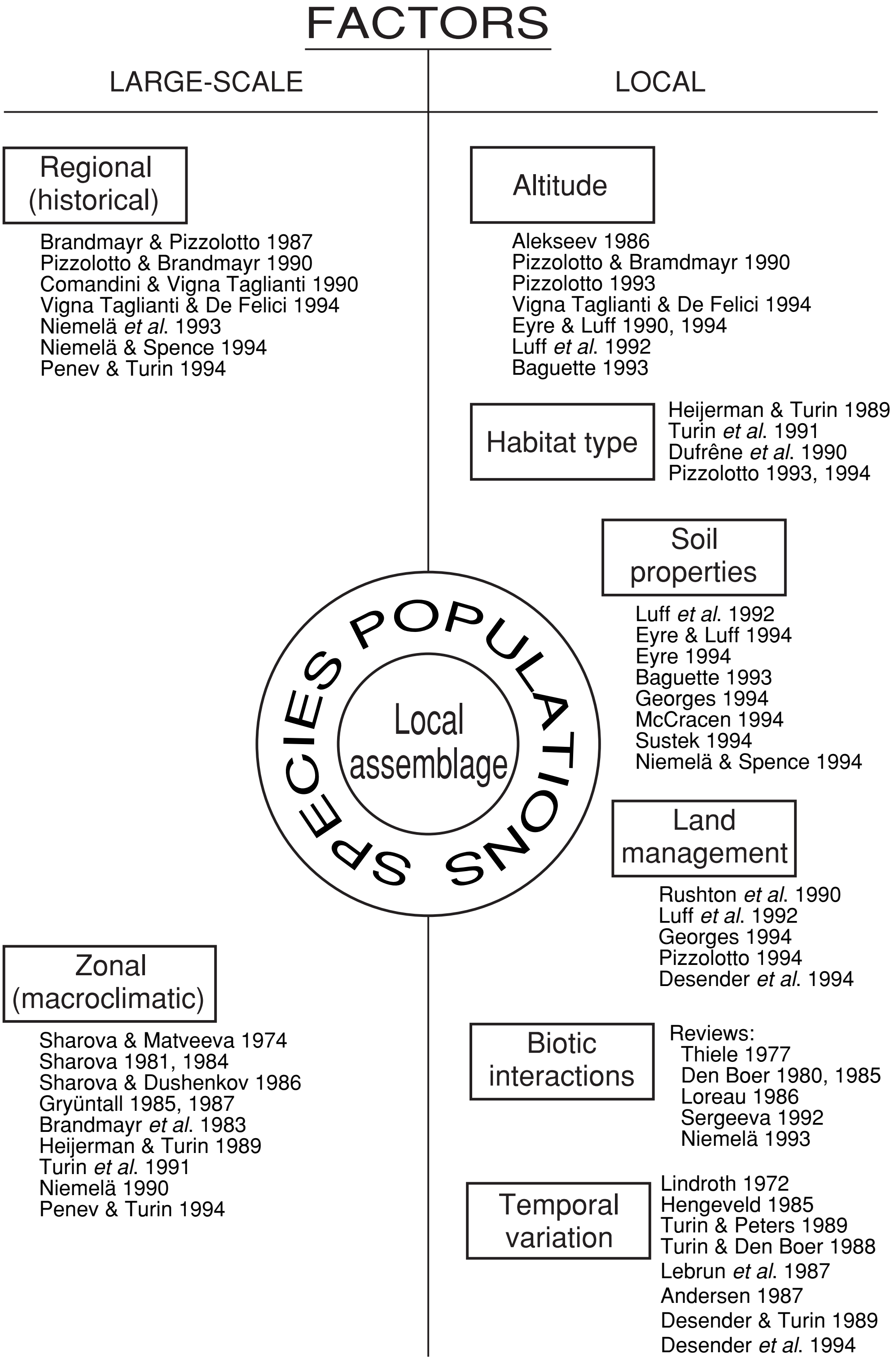

Fig. 3. Factors affecting the composition and variation of local ground-beetle assemblages.

a descriptive basis, without directly relating the variation in communities to the environment.

Large-scale comparisons of pitfall data as based on classification and ordination procedures have just been started by five independent research groups, namely in the Netherlands (Turin *et al*. 1991), United Kingdom (Luff *et al*. 1989, 1992, Eyre & Luff 1990), Belgium (Dufrêne *et al*. 1990, Baguette 1993), Finland (Niemelä 1990, Niemelä *et al*. 1993, 1994, Niemelä & Spence 1994), and Italy (Brandmayr *et al*. 1983, Brandmayr & Pizzolotto 1987, Pizzolotto 1993, Comandini & Vigna Taglianti 1990, Vigna Taglianti & De Felici 1994) (Fig. 3). However, most of these studies are operated only with local environmental variables, if any, such as altitude, habitat type, vegetation cover, soil properties, and land management. The influence of large-scale factors has only been suggested by some authors under the quite obscure term "regional differences" (i.e. Heijerman & Turin 1989, Niemelä 1990, Turin *et al*.1991). To the best of my knowledge, there are no papers as yet focusing on the effect of truly large-scale variables on the variation in carabid communities, except for those dealing with temporal changes in carabid faunas during the last century with respect to climate (Lindroth 1972, Hengeveld 1975, Turin & Peters 1986, Andersen 1987, Turin & Den Boer 1988; Desender *et al*. 1994, Müller-Motzfeld 1995). There are, however, attempts to seek for both historical and ecological explanations of the variation in local carabid assemblages, an approach used by some Italian workers (Brandmayr & Pizzolotto 1987, Pizzolotto & Brandmayr 1990, Vigna Taglianti & De Felici 1994). A special attention deserves a recently published paper by Niemelä *et al*. (1993) comparing ground-beetle communities of Canadian and European taiga. Such projects exploring the phenomenon of "natural experiments", i.e. parallel evolution of analogous communities on different continents are of key interest for understanding the community structure and composition, and have already been carried out on the basis of other organisms, such as plants and birds (Cody & Mooney 1975, Wiens 1992).

Local habitat conditions appear to be the most thoroughly studied at the community level (Fig. 3). Among these, soil water content, soil properties, elevation and land management practices have proved to be significantly correlated with the main trends in variation in community composition. Soil moisture has been shown to be an important factor in almost all such papers. Another factor of key value is the altitude even when the sites are scattered over plains. Even not so big differences in altitude cause changes in carabid assemblages, probably through other habitat variables such as soil properties and vegetation cover. This is one more evidence that altitude appear as important as both other geographical characteristics of a locality, latitude and longitude.

For a deeper understanding of community variation, however, a link between the patterns at the community level and the data on ecophysiological characteristics of individual species is required. In this respect, we are still at the beginning.

3.2. Spatial variation in the local faunas of the genus *Carabus* L. over the Russian Plain

The combined effect of large-scale and local factors on the species composition has been studied as based on 61 local faunas of the genus *Carabus* L. situated throughout on the Russian Plain, including a part of Fennoscandia (Karelia), the Urals and the Crimea (Fig. 4, Table 1). Data have been gathered from numerous literature sources, museum collections and personal observations. Variation in both diversity and species composition has been analysed in relation to the following groups of factors:

(1) Recent climatic factors: mean annual temperature, mean temperatures of the coldest and warmest months, annual temperature amplitude, mean number of frostless days, annual precipitation rate, precipitation for the warm and cold periods;
(2) Historical factors: (a) presence of the Valdai (= Würm) Glaciation, and (b) distance of the site from the glaciation border presented as a rough 4-grade scale: 0 – under the glaciation cover; 1 — near the glaciation border (periglacial zone); 2 — intermediate; 3 — far from the glaciation border (data on the Valdai Glaciation range after Velichko 1993);
(3) Local habitat conditions expressed as (a) presence/absence of six main habitat types: tundra, coniferous forests, deciduous forests, natural steppes, open water pools, sea shore, and (b) "synthetic variable" expressed as site scores on the first and second ordination axes extracted by means of Detrended Correspondence Analysis (DCA) from the local compositions of the above habitat types.

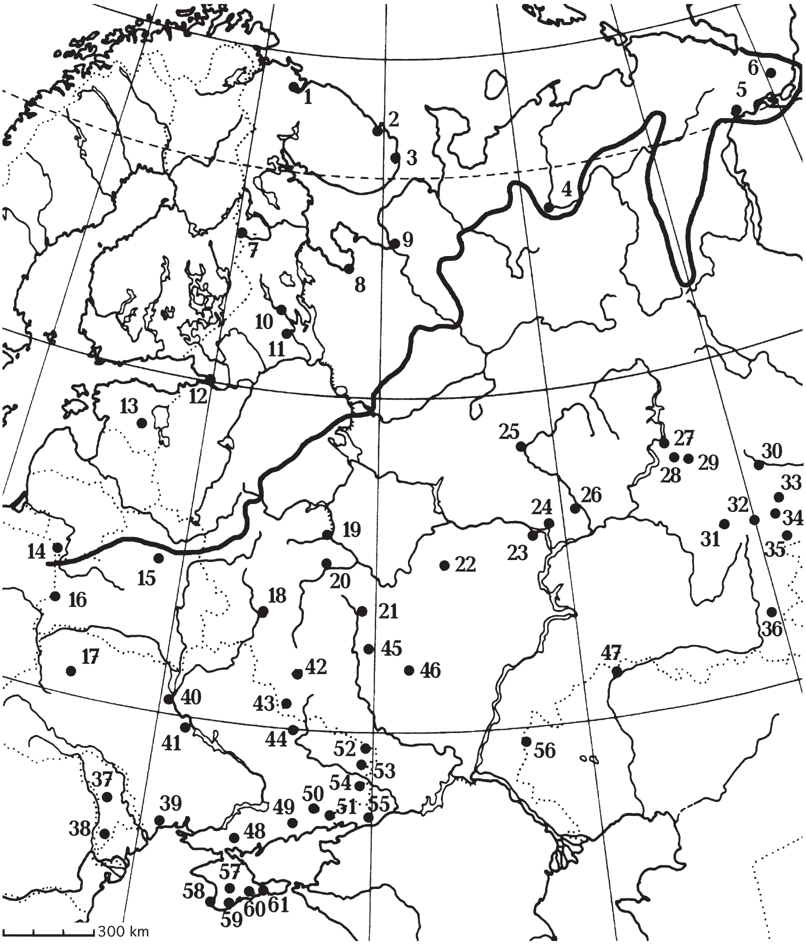

Fig. 4. Distribution map of local faunas of the genus *Carabus* over the Russian Plain. For locality names see Table 1. The thick line shows the maximal phase of the Valdai (= Würm) Glaciation (after Velichko 1993).

I am able to immediately pinpoint two controversies in my own analysis. First, the areas of the local faunas vary and cannot be standardised. This is a major but unavoidable obstacle in studies of large-scale variations. On the other hand, the upper limit in local species richness is quite strongly determined by both zone and region where the locality is situated. Thus, selecting 61 well-studied local faunas from an initial dataset of 133 localities, I expect to operate with indeed representative and comparable data.

The second problem arises from the multicollinearity of the environmental variables, that is, the well-known problem of autocorrelation. Correlations among the climatic parameters and other climate-affected factors makes it difficult to separate them from each other in assessing their impact on the biota.

The species listings (presence/absence data) were ordinated using Detrended Correspondence Analysis (DCA) performed with CANOCO (Ter Braak 1988) (Fig. 5). After that I calculated the Spearman rank correlation between DCA axes and the environmental variables (Table 2). The first DCA axis (eigenvalue 0.72) clearly expressed a north-south gradient which can be related to both the distance from the Würm glaciation border and macroclimatic temperature factors, in the first line the mean temperatures of warmest month and the year, as well as the number of frostless days. The first DCA axis correlated also with the presence of steppe habitats, and to a lesser extent with the presence of tundra, open water sources and sea shore. The dominant compositional gradient on the second DCA axis (eigenvalue 0.36) is orientated from west to east and correlated positively with the annual temperature amplitude and the mean temperature of the coldest months, thus in-

Table 1. Localities with well-known faunas of the genus *Carabus* L. For geographical locations of the sites see the map on Fig. 4.

No on the map	Locality	Abbreviation	Country/Province	Number of Carabus species
1	Murmansk Coast	MURM	Murmansk	4
2	Iokanga	IOKA	Murmansk	3
3	Ponoi	PONO	Murmansk	3
4	Ust'-Tsilma	UTSL	Komi	7
5	Salekhard	SALE	Yamal	4
6	Khadyta Field Station	KHAD	Yamal	3
7	Kostomuksha Reserve	KOST	Karelia	2
8	Onega	ONEG	Arkhangelsk	2
9	Arkhangelsk	ARKH	Arkhangelsk	2
10	Kivach Reserve	KIVA	Karelia	2
11	Petrozavodsk	PTRZ	Karelia	5
12	St. Petersburg	SPET	St. Petersburg	9
13	Tartu (=Yurev)	TART	Estonia	7
14	Zhuvintas Reserve	ZHUV	Litva	5
15	Berezina Reserve	BRZN	Minsk	9
16	Belovezha Reserve	BLVZ	Brest	10
17	Kivertsy nr. Lutsk	KIVE	Volynsk	10
18	Bryansk Forest Game	BRYA	Bryansk	13
19	Moscow	MOSC	Moscow	11
20	Prioksko-Terrasny Reserve	PRIO	Moscow	9
21	Gremyachka nr. Dankov	GREM	Ryazan	10
22	Mordov Reserve	MORD	Mordov	10
23	Raifa Reserve	RAIF	Tartar	9
24	Kazan	KAZA	Tartar	10
25	Kotelnich	KOTE	Vyatka (= Kirov)	5
26	Malmyzh	MALM	Vyatka (= Kirov)	8
27	Perm	PERM	Perm	10
28	Spasskaya Gora Reserve	SPAS	Perm	7
29	Preduralye Reserve	PRED	Perm	9
30	Ekaterinburg (=Sverdlovsk)	EKAT	Ekaterinburg	12
31	Ai-River	AIRI	Bashkiria	9
32	Ilmen Reserve	ILME	Chelyabinsk	13
33	Bolshoi Kuyash Lake	BKUV	Chelyabinsk	9
34	Chelyabinsk	CHEL	Chelyabinsk	6
35	Troitskii Game Nr. Berlin	TROI	Chelyabinsk	6
36	Bolotovsk	BLTV	Orenburg	5
37	Kodry Reserve	KODR	Moldova	14
38	Roshu	ROSH	Moldova	4
39	Odessa	ODES	Odessa	5
40	Kiev	KIEV	Kiev	16
41	Kanev Reserve	KANE	Cherkassy	12
42	Streletskaya Steppe nr. Kursk	STRE	Kursk	11
43	Les-na-Vorskle Reserve	LESV	Belgorod	8
44	Kharkov	KHAR	Kharkov	11
45	Voronezh Reserve	VORR	Voronezh	10
46	Tellerman Forestry	TELL	Voronezh	8
47	7 Km N of Uralsk	URLK	Uralsk	5
48	Askania-Nova Reserve	ASKA	Kherson	2
49	Andreevka	ANDR	Donetsk	2
50	Veliki Anadol	VELI	Donetsk	2
51	Khomutovskaya Steppe	KHOM	Donetsk	3
52	Streltsovskaya Steppe	STRL	Lugansk	2
53	Derkul	DERK	Lugansk	8
54	Provalskaya Steppe	PROV	Lugansk	5
55	Rostov-na-Donu	RSTV	Rostov	12
56	Dzhanybek Field Station	DZHA	Uralsk	1
57	Simferopol	SIMF	Crimea	6
58	Sevastopol	SEVA	Crimea	5
59	Karadag Reserve	KARA	Crimea	4
60	Yalta	YALT	Crimea	4
61	Feodosiya	FEOD	Crimea	4

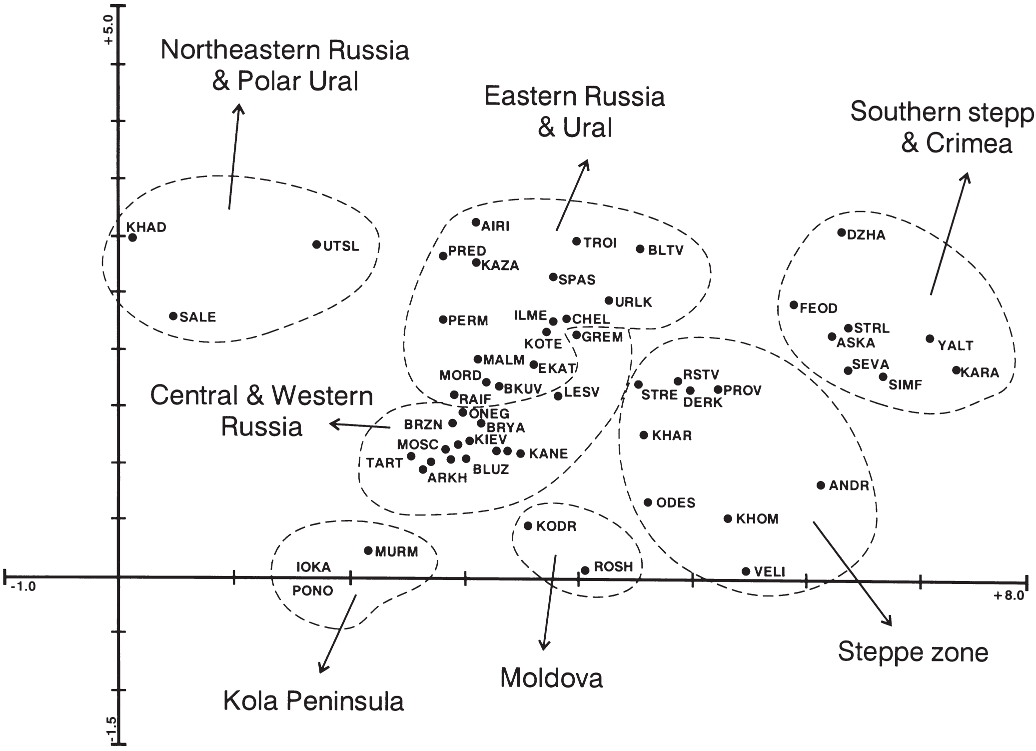

Fig. 5. Detrended Correspondence Analysis (DCA) diagram of 61 local faunas of the genus *Carabus* L. of the East European Plain. For site abbreviations see Table 1.

Table 2. Spearman's rank correlation of DCA axes and species richness with environmental variables. Only values significant at $P \leq 0.05$ are shown.

Factors	Axis 1	Axis 2	Species richness
Mean annual temperature	0.74	–	–
Mean temperature of the coldest month	0.48	– 0.54	–
Mean temperature of the hottest month	0.81	–	–
Number of frostless days	0.73	–	–
Annual temperature amplitude	–	0.70	–
Annual precipitation	– 0.55	– 0.37	–
Precipitation for the warm period	– 0.56	–	0.44
Presence of Valdai (= Würm) Glaciation	– 0.69	–	0.40
Distance from Valdai Glaciation border	0.88	–	–
Presence of steppe habitats	0.80	–	– 0.39
Presence of tundra habitats	– 0.43	–	–
Presence of coniferous forests	–	–	–
Presence of deciduous forests	–	–	0.55
Presence of open water sources	– 0.51	–	–
Presence of sea shore	– 0.50	–	– 0.37
Habitat composition (DCA axis 1)	–	–	– 0.42
Habitat composition (DCA axis 2)	– 0.47	–	–

dicating a major role of longitudinal gradients in climate continentality and severity.

The above analysis demonstrated that, on a subcontinental scale, with the Russian Plain taken as an example, nature zonation is a major factor affecting species distributions and the variation in their assemblages. Hence the genus *Carabus* on the Russian Plain is one more evidence of a long-term effect of current nature zonation on species distributions, in spite of the surely great perturbations caused by Pleistocene glaciations. My results support the hypothesis that the Middle Russian biota could have largely survived those glaciations, including the last one, not only in the bigger south-western (Carpathian, Balkans) and/or south-eastern (South Urals) refugia (cf. Esjunin *et al.* 1993), but also in individual forest patches situated along some rivers in the south of the Plain (Lavrenko 1938, Arnoldi 1961). One can hardly believe that almost all the biota of the Russian Plain might have been completely destroyed during the Würm Glaciation (i.e. Grosset 1971), while further postglacial recolonizations realised from faunal sources preserved only in the Carpathians, Balkans, Crimea, and Caucasus. If this were true, one would expect that the west-east or southwest-east gradients in the spatial variation of the biota would prevail over the north-south ones due to the prevailing direction of the main recolonization routes. Both major factors, the recent climatic gradients, on one hand, and recolonizations from the Pleistocene refugia in the south (Lavrenko 1938), on the other hand, must have participated in the formation of the recent faunistic situation on the Russian Plain.

The second major gradient of variation in local faunas is longitudinal and can be related both to the increasing climatic continentality and the influence of faunal sources in Central Europe in the western, and of Siberia in the eastern, regions of European Russia. The species composition of *Carabus* changes not only from west to east, but also in the opposite direction, from the Ural Mountains to the central regions of Russia. In other words, the local faunas loose several western (nemoral and steppe) species, but gain in Siberian ones, towards the Urals. The regional differences are especially apparent within one biome, for example in the North. The local faunas of the Kola Peninsula are composed of European species, such as *C. violaceus* L. *C. problematicus* Hbst., *C. granulatus* L., and *C. glabratus* Payk., whereas those of north-eastern regions are dominated by Siberian species, such as *C. truncatellus* Eschsch., *C. henningi* Fisch.-W., *C. odoratus* Motsch., *C. aeruginosus* Fisch.-W. A similar pattern can be revealed in a latitudinal direction in the southernmost European Russia, Crimea and, especially, Ciscaucasian Plain: changes in the species composition caused by zonal gradients in climate and habitat composition are reinforced by the appearance of endemics, such as *C. gyllenhali* Fisch.-W. and *C. tauricus* Bon. in the Crimea and *C. exaratus* Quens. and *C.cumanus* in Ciscaucasia.

Such large-scale factors as the present-day climate and the past climatic events generally determine the composition of the regional species pool which are always and everywhere modified by the local habitat conditions. The ordination techniques revealed the presence of natural steppes, tundra habitats and open water-bodies as important factors. Both extreme biomes on the Russian Plain, i.e. tundra and steppe, support only impoverished local faunas of *Carabus* usually represented by as few as 2–3 species per locality. It can be stated that the species lists change gradually within the forested biomes but display a “hiatus”, or gap, at the border between the forest-steppe and steppe zones and, to a lesser extent, between the taiga and the tundra. In both tundra and steppe, the local faunas can clearly be divided into ones typical for those largely forestless zones and into intrazonal ones characteristic of forest and shrub riverside habitats. In the steppe, as a limiting factor appears also the absence of open water sources and, especially, of bigger rivers serving as “invasion channels” from the north. In other words, the local habitat composition plays a more significant role in the zones with extreme conditions than in those with moderate ones. The local faunas of the southernmost localities are composed both of eurytopic species, such as *C. convexus* F., *C. granulatus* L., *C. cancellatus* Ill., and steppe elements, like *C. bessarabicus* Fisch.-W., *C. hungaricus* F., *C. planus* Geh., once their habitats are situated along rivers. At the same time, the local faunas of the neighbouring steppe habitats are characterised by impoverished and highly specific steppe forms.

The ordination methods used in the present study allow a direct relation to be made of the main trends in the species composition of the local faunas to the underlying environmental gradients. In order to prove the difference between the two groups of parameters outlined above, I correlated the species richness to the same environmental variables (Table 2). Indeed, species richness correlated mostly with habitat factors, in the first line the presence of deciduous forests indicating that the richest *Carabus* faunas are concentrated in the middle regions of the Russian Plain. Species richness showed also a negative correlation with the presence of Würm Glaciation. Among the climatic variables, only the precipitation rate for the warm period correlated with species richness, which can be explained again with the concentration of the diversity in the middle part of European Russia.

4. Conclusions

1. Studies on the spatial variation in carabid communities as based on pitfall sampling data obtained in different regions of Europe have obviously advanced during the last few years. Such explorations are considered highly promising both in a theoretical aspect and from a viewpoint of large-scale environmental quality assessments and predictions of global ecological change at the community level.
2. At a local level, two types of species assemblages can be distinguished, i.e. communities, separated on a habitat basis, and local faunas, defined on a locality basis. Communities are thought to be affected mostly by both the properties of the habitat and biotic interactions, whereas local faunas both by biogeographical factors and local habitat composition. The idea of a local fauna seems to be a useful concept bridging the traditional faunistics and ecology at a local scale.
3. The environmental factors affecting the assemblage composition and spatial variation at larger geographical scales can be divided into two major groups: regional and zonal. The former factors are caused by historical reasons (isolations, barriers, glaciations), and the latter by recent climatic conditions.
4. The parameters of carabid assemblages can be derived from either species composition or species diversity. On a within-region scale, species composition and its derivatives appear to be more informative in reflecting the environmental gradients in comparison to species diversity.
5. Papers exploring the large-scale variation of ground-beetle assemblages deal in fact with local factors and rarely, with large-scale variables. Among the factors studied, most significantly correlated with variation in carabid communities appear to be the habitat type, soil properties and altitude. Studies both on local and large-scale factors, combined with knowledge of ecophysiological characteristics of the species and the biotic interactions among them, can yield a better understanding of the community structure and dynamics.
6. An analysis of the local faunas of the genus *Carabus* on the Russian Plain illustrated the applicability of the local fauna concept in reflecting the variation in zonal, regional and local factors. The main trend in variation in local faunas can be associated with latitudinally varying temperature factors, the second trend with both longitudinal changes in climatic continentality and regional differences caused by historical reasons. The local habitat composition appears to be also of importance, especially the presence of extreme-type habitats, such as tundra and steppes.

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References

Alekseev, S. K. (Алексеев, С. К.) 1986: (Habitat distribution of herpetobiont Coleoptera in the Tsei gap). — In: Fauna i ekologiya bespozvonochnykh zhivotnykh v zapovednikakh RSFSR: 49–56. — Moscow. (In Russian.).

Andersen, J. 1987: Qualitative changes in the Norwegian carabid beetle fauna during the present century. — In: Den Boer, P. J., Lövei, G. L., Stork, N. E. & Sunderland,

K. D. (eds.), Acta Phytopath. Ent. Hung. 22: 35–34.

Arnoldi, K. V. (Арнольди, К. В.) 1965: (The forest-steppe of the Russian Plain and an attempt of its zoogeographical and coenological characterisation based on a study of insects). — Tr. Tsentr.-chernoz. zap-ka 8: 138–166. (In Russian.).

Baev, P. & Penev, L. 1993: BIODIV – a program for calculating biological diversity parameters, similarity, niche overlap, and cluster analysis. — Exeter Software, N.Y.

Baguette, M. 1993: Habitat selection of carabid beetle in deciduous woodlands of southern Belgium. — Pedobiologia 37: 365–378.

Booij, K. 1994: Diversity patterns in carabid assemblages in relation to crops and farming systems. — In: Desender, K., Dufrêne, M., Loreau, M., Luff, M. L. & Maelfait, J.-P. (eds.), Carabid beetles: ecology and evolution: 425–432. — Kluwer, Dordrecht.

Brandmayr, P. & Pizzolotto, R. 1987: Aspetti zoocenotice e biogeografici dei popolamenti a Colleotteri Carabidi nella fascia alpina delle Vette di Feltre (Belluno). — Biogeographia 13: 713–743.

Brandmayr, P., Colombetta, G. & Polli, S. 1983: Waldcarabiden des Triester Karstes als Indikatoren des makroklimatischen Überganges vom kontinentalen Europa zur Mediterraneis (Coleoptera, Carabidae). — Zool. Jb. Syst. 100: 201–220.

Brown, J. H. & Gibson, A. C. 1983: Biogeography. — C. V. Mosby, St. Louis.

Chernov, Yu. I. (Чернов, Ж. И.) 1975: (The nature zonation and the terrestrial animals). — Mysl, Moscow. (In Russian.).

— 1984: (Flora and fauna, plant and animal population). — Zhurn. obshch. biol. 45(6): 732–748. (In Russian.).

— 1989: (The thermal conditions and the Arctic biota). — Ekologiya 2: 49–57. (In Russian with English summary.).

Chernov, Yu. I. & Penev, L. D. (Чернов, Ж. И. & Пенев, Л. Д.) 1993: (Biological diversity and climate). — Uspekhi sovr. biol. 113(5): 515–531. (In Russian.).

Cody, M. L. & Mooney, H. A. 1978: Convergence versus nonconvergence in Mediterranean-climate ecosystems. — Annu. Rev. Ecol. Syst. 9: 265–321.

Commandini, F. & Vigna Taglianti, A. 1990: Ground beetle communities in a Mediterranean area (Tolfa Mountains, Central Italy). — In: Stork, N. E. (ed.), The role of ground beetles in ecological and environmental studies: 171–179. Intercept, Andover.

Den Boer, P. J. 1980: Exclusion or coexistence and the taxonomic or ecological relationship between species. — Neth. J. Zool. 30(2): 278–306.

— 1985: Exclusion, competition or co-existence? A question of testing the right hypothesis — Zeitschr. Zool. Syst. Evol. 23: 259–274.

Desender, K., Dufrêne, M. & Maelfait, J.-P. 1994: Long term dynamics of carabid beetles in Belgium: a preliminary analysis on the influence of changing climate and land use by means of a database covering more than a century. — In: Desender, K., Dufrêne, M., Loreau, M., Luff, M. L. & Maelfait, J.-P.(eds.), Carabid beetles: ecology and evolution: 247–252. Kluwer, Dordrecht.

Desender, K. & Turin, H. 1989: Loss of habitats and changes in the composition of the ground- and tiger beetle fauna in four West-European countries since 1950 (Coleoptera: Carabidae, Cicindelidae). — Biological Conservation 48: 277–294.

Dufrêne, M., Baguette, M., Desender, K. & Maelfait, J.-P. 1990: Evaluation of carabids as bioindicators: a case study in Belgium. — In: Stork, N. E. (ed.), The role of ground beetles in ecological and environmental studies: 377–381. Intercept, Andover.

Esjunin, S. L., Golovatch, S. I. & Penev, L. D. 1993: The fauna and zoogeography of spiders (Arachnida: Aranei) inhabiting oak forests of the East European Plain. — Ber. nat.-med. Verein Innsbruck 80: 175–249.

Eyre, M. D. 1994: Strategic explanations of carabid species distributions in northern England. — In: Desender, K., Dufrêne, M., Loreau, M., Luff, M. L. & Maelfait, J.-P. (eds.), Carabid beetles: ecology and evolution: 267–276. Kluwer, Dordrecht.

Eyre, M. D. & Luff, M. L. 1990: A preliminary classification of European grassland habitats using carabid beetles. — In: Stork, N. E. (ed.), The role of ground beetles in ecological and environmental studies: 227–236. Intercept, Andover.

— 1994: Carabid species assemblages of Northeast England woodlands. — In: Desender, K., Dufrêne, M., Loreau, M., Luff, M. L. & Maelfait, J.-P. (eds.), Carabid beetles: ecology and evolution: 277–282. Kluwer, Dordrecht.

Georges, A. 1994: Carabid beetle spatial patterns in cultivated wetlands. The effect of engineering works and agricultural management in Marais Poitevin (western France). — In: Desender, K., Dufrêne, M., Loreau, M., Luff, M. L. & Maelfait, J.-P. (eds.), Carabid beetles: ecology and evolution: 283–294. Kluwer, Dordrecht.

Grosset, G. E. (Гроссет, Г. Я.) 1971: (Extinction of the biome of deciduous forests in Europe caused by the periglacial climate of the upper Plestocene, and the age of the relicts of that formation). — Byull. MOIP, Otd. biol. 67(3): 94–109. (In Russian.).

Gryuntal, S. Yu. (Гржнталь, С. Ж.) 1985: (Landscape-zonal peculiarities of ground-beetle distribution (Coleoptera, Carabidae) in forests of the Central Regions of the European part of the USSR). — Byull. Mosk. obshch. ispyt. prir., otd. biol. 90(5): 15–25. (In Russian.).

— 1987: (Carabid distribution in coniferous forests of the European part of the USSR). — In: Pochvennaya fauna Severnoi Evropy: 51–59. Nauka, Moscow. (In Russian.).

Heijerman, Th. & Turin, H. 1989: The Carabid Fauna of Some Types of Forests in the Netherlands: a numerical comparative analysis. — Tijdschr. Ent. 132: 279–305.

Hengeveld, R. 1985: Dynamics of Dutch beetle species during the twentieth century (Col. Carabidae). — J. Biogeography 12: 389–411.

— 1990. Dynamic biogeography. — Cambridge University Press, Cambridge.

Jarosik, V. 1991: Are diversity indices of carabid beetle (Col., Carabidae) communities useful, redundant, or misleading? — Acta Entomol. Bohemoslov. 88: 273–279.

Lavrenko, E. M. (Лавренко, Е. М.) 1938: (History of the flora and the vegetation of the USSR according to data on the recent distribution of plants). — In: Vegetation of the USSR: 235–396. Izd-vo AN SSSR, Moscow-Leningrad. (In Russian.).

Lebrun, Ph., Baguette, M. & Dufrêne, M. 1987: Species diversity in a carabid community: comparison of values estimated at 23 years interval. — In: Den Boer, P. J., Lövei, G. L., Stork, N. E. & Sunderland, K. D. (eds.), Acta Phypopath. Ent. Hung. 22: 165–173.

Lindroth, C. H. 1972: Changes in the Fennoscandian ground-beetle fauna (Coleoptera, Carabidae) during the twentieth century. — Ann. Zool. Fennici 9: 49–64.

— 1992: Ground beetles (Carabidae) of Fennoscandia. A zoogeographic study. Part. III. — Smitsonian Institution Libraries & The National Science Foundation. Washington DC.

Loreau, M. 1986: Niche differentiation and community organisation in forest carabid beetles. — In: Den Boer, P. J., Lövei, G. L., Stork, N. E. & Sunderland, K. D. (eds.), Carabid beetles. Their adaptations and dynamics: 465–487. Gustav Fisher, Stuttgart.

Luff, M. L., Eyre, M. D. & Rushton, P. 1992: Classification and prediction of grassland habitats using ground beetles (Coleoptera, Carabidae). — Journ. Envir. Manag. 35: 301–315.

McCracken, D. 1994: A fuzzy classification of moorland ground beetle (Coleoptera: Carabidae) and plant communities. — Pedobiologia 38: 12–27.

Müller-Motzfeld, G. 1995: Klimatisch bedingter Faunenwechsel am Beispiel der Laufkäfer (Coleoptera: Carabidae). — Angew. Landschaftsökologie 4: 135–154.

Niemelä, J. 1990: Spatial distribution of carabid beetles in the southern Finnish Taiga: the question of scale. — In: Stork, N. E. (ed.), The role of ground beetles in ecological and environmental studies: 143–155. Intercept, Andover.

— 1993: Interspecific competition in ground-beetle assemblages (Carabidae): what we have learned? — Oikos 66: 325–335.

Niemelä, J. & Spence, J. R. 1994: Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. — Ecography 17: 166–175.

Niemelä, J., Spence, J. R., Langor, D., Haila, Y. & Tukia, H. 1993: Logging and boreal ground-beetle assemblages on two continents: implications for conservation. — In: Gaston, K. J., Samways, M. & New, T. (eds.), Perspectives on insect conservation: 29–49. Intercept, Andover.

Niemelä, J., Tukia, H. & Halme, E. 1994: Patterns of carabid diversity in Finnish mature taiga. — Ann. Zool. Fennici 31: 123–129.

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

Penev, L. D., Esjunin, S. L. & Golovatch, S. I. 1994: Species diversity versus species composition in relation to climate and habitat variation: a case study on spider assemblages (Aranei) of the East European oak forests. — Arthropoda Selecta 3(1–2): 65–99.

Penev, L. & Turin, H. 1994: Patterns of distribution of the genus Carabus L. in Europe: approaches and preliminary results. — In: Desender, K. Desender, K., Dufrêne, M., Loreau, M., Luff, M. L. & Maelfait, J.-P. (eds.), Carabid beetles: ecology and evolution: 37–44. Kluwer, Dordrecht.

Pizzolotto, R. 1993: Carabid beetle (Coleoptera, Carabidae) coenoses for evaluation of faunal resources and impact assessment on the Aspromonte National Park of Calabria (Italy). — Coenoses 8(2): 69–79.

— 1994: Ground-beetles (Coleoptera, Carabidae) as a tool for environmental management: a geographical information system based on carabids and vegetation for the Karst near Trieste (Italy). — In: Desender, K., Dufrêne, M., Loreau, M., Luff, M. L. & Maelfait, J.-P. (eds.), Carabid beetles: ecology and evolution: 343–352. Kluwer, Dordrecht.

Pizolotto, R. & Brandmayr, P. 1990: The carabid groupings of the Nebrodi mountains in Sicily: ecological and historical indicators. — In: Stork, N. E. (ed.), The role of ground beetles in ecological and environmental studies: 201–207. Intercept, Andover.

Rushton, S. P., Eyre, M. D. & Luff, M. L. 1990: The effects of management of some carabid species in grassland. — In: Stork, N. E. (ed.), The role of ground beetles in ecological and environmental studies: 209–216. Intercept, Andover.

Sergeeva, T. K. (Сергеева, Т. К.) 1992: (Serological diagnostics of trophic interrelations and resource partitioning in predatory ground-beetle assemblage). — Uspekhi sovr. biol. 112(5–6) :758–773. (In Russian.).

Sharova, I. Ch. (Шарова, И. Х.) 1981: (Life forms of ground-beetles (Coleoptera, Carabidae)). — Nauka, Moscow. (In Russian.).

— 1984: (Zonal regularities of ecological and faunistic distribution of ground-beetles (Coleoptera, Carabidae) in field agrocoenoses). — In: Fauna i ekologiya bespozvonochnykh zhivotnykh: 62–69. Moscow. (In Russian.).

Sharova, I. Ch. & Dushenkov, V. M. (Шарова, И. Х & Душенков, В. М.) 1986: (Zonal peculiarities of changes of ground-beetle life forms (Coleoptera, Carabidae) in agrocenoses). — In: Ekologiya zhiznennykh form pochvennykh i nazemnykh chlenistonogikh: 32–38. Mosk. gos. pedagog. inst., Moscow. (In Russian.).

Sharova, I. Ch. & Matveeva, V. G. (Шарова, И. Х & Матвеева, В. Г.) 1974: (Ground-beetle complexes of floodland meadows in the landscape zones of the European part of USSR). — In: Fauna i ekologiya zhivotnykh: 3–17. Moscow. (In Russian.).

Shelyag-Sosonko, Yu. R. (Шеляг-Сосонко, Ж. Р.) 1980: On a concrete flora and the method of concrete floras. — Bot. zh. 65(6): 791–774. (In Russian with English summary.).

Šustek, Z. 1994: Classification of the carabid assemblages in the floodplain forests in Moravia and Slovakia. —

In: Desender, K., Dufrêne, M., Loreau, M., Luff, M. L. & Maelfait, J.-P. (eds.), Carabid beetles: ecology and evolution: 377–382. Kluwer, Dordrecht.

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.

Ter Braak, C. J. F. & Prentice, I. C. 1988. A theory of gradient analysis. — Adv. Ecol. Res. 18: 271–317.

Thiele, H. U. 1977: Carabid beetles in their environments. A study on habitat selection by adaptations in physiology and behaviour. — Springer Verlag, Berlin.

Tolmachev, A. I. (Толмачев, А. И.) 1931: (On the methods of comparative floristic investigations. 1. On the term “flora” in the comparative floristics). — Zhurn. Russ. botan. obshch., 16(1): 111–124. (In Russian.).

Turin, H., Alders, K., den Boer, P. J., van Essen, S., Heijerman, Th., Laane, W. & Penterman, E. 1991. Ecological characterisation of Carabid species (Coleoptera, Carabidae) in the Netherlands from thirty years of pitfall sampling. — Tijdschr. Ent. 134: 279–304.

Turin, H. & Peters, H. 1986: Changes in the distribution of carabid beetles in the Netherlands since about 1880. I. Introduction. — In: Den Boer, P. J., Luff, M. L., Mossakowski, D. & Weber, F. (eds.), Carabid beetles: 489–495.

Turin, H. & den Boer, P. J. 1988: Changes in the distribution of carabid beetles in the Netherlands since 1880. II. Isolation of habitats and long-term time trend in the occurrence of carabid species with different powers of dispersal (Coleoptera, Carabidae). — Biological Conservation 44: 179–200.

Velichko, A. A. (Величко, А. А.) (ed.) 1993: (Evolution of landscapes and climates of the Northern Eurasia. Late Pleistocene — Holocene. Element of prognosis. I. Regional palaeogeography). — Nauka, Moscow. (In Russian.).

Vigna Taglianti, A. & De Felici, S. 1994: Ground beetle communities in Central Appenines beech woods. — In: Desender, K., Dufrêne, M., Loreau, M., Luff, M. L. & Maelfait, J.-P. (eds.), Carabid beetles: ecology and evolution: 71–78. Kluwer, Dordrecht.

Whittaker, R. H. 1975: Communities and ecosystems. — Macmillan Publishing Co., New York.

Wiens, J. A. 1991: Ecological similarity of shrub-desert avifaunas of Australia and North America. — Ecology 72(2): 479–495.

Yurtsev, B. A. (Жрцев, В. А.) 1975: (Some trends in the development of the concrete flora method). — Bot. zh. 60(1): 69–83. (In Russian with English summary.).