

Relationship between Morphological Disparity and Taxonomic Diversity in Rodent Communities in the Zone of Influence from the Eastern Ural Radioactive Trace in the Southern Urals

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Abstract—To test the hypothesis that morphological disparity increases while taxonomic diversity decreases in a radioactively contaminated environment, the relationship of these parameters was studied in communities (taxocenes) of rodents living in the Southern Urals in the zone of influence from the Eastern Ural Radioactive Trace (EURT) (2003–2008). Young of the year of six rodent species (98 samples) were examined in the background (control) area (0.2 Ci/km²) and in the impact area polluted with radionuclides from the EURT (750 Ci/km²). The dynamics of morphological disparity (*MD*), assessed with regard to average values of five exterior characters, was compared between the control and impact taxocenes. Taxonomic (taxocenotic) diversity was estimated with the Shannon index (*H*). Morphological disparity was found to increase significantly at low rodent abundance (in conditionally unfavorable years) and decrease at high abundance, with the value of *MD* in the impact taxocene being significantly higher. A negative correlation between *MD* and *H* was revealed ($r = -0.70$), in conformity with the above hypothesis. Discordance (difference in direction) of annual changes in the test parameters, with *H* increasing while *MD* decreases (or vice versa) was observed in unfavorable years; it can be used as an indicator of conditions unfavorable for rodent taxocenes.

Key words: morphological disparity, taxocene, technogenic environment, rodents.

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The problem of the relationship between manifestations of biological diversity, such as taxonomic diversity and morphological disparity, has been widely discussed in recent years (Foote, 1993, 1997; Ciampaglio et al., 2001; Navarro, 2003; Moyne and Neige, 2007). Paleontologists and paleoecologists have convincingly shown that during global biocenotic crises, which repeatedly occurred in the history of Earth, the taxonomic diversity of communities (*TD*) sharply decreased due to extinction of some taxa, while the remaining taxa displayed increasing morphological disparity (*MD*), which was due mainly to the emergence of new species (Moyne and Neige, 2007). Such studies scarce in neontological ecology (Neige, 2003; Shvarts, 2004), although their importance is obvious, especially in the light of Zherikhin's (2003) concept that signs of impending global biocenotic crisis are already visible against the background of increasing anthropogenic impact on the biota. Therefore, it appears promising to apply the morphospace concept (McGhee, 1999) to the study of communities at the level of taxocenes, i.e., groups of taxonomically related species with similar ecological functions within a community (such as the rodent taxocene).

The taxocenotic approach to studies on the emergence and functioning of communities is expedient because analysis of the community as a whole—including species and forms of microorganisms, fungi, plants, and animals—is extremely difficult, while its analysis by individual fragments (taxocenes) is quite feasible. Some initial skepticism toward the term “taxocenosis” (Arnol'di and Arnol'di, 1963; Zherikhin, 1994) is partly justified. It was caused by the fact that this term was initially applied to formal species lists of particular invertebrate orders, families, or subfamilies to which cenotic significance was often assigned arbitrarily, without special analysis. However, since an ecological guild usually includes taxonomically unrelated species that consume the same biotic resource and live in the same community, there should be a term to denote the special kind of guilds comprising only closely related species of a particular taxon that play a similar community role in utilizing the same set of resources. The term “taxocene,” understood as a single functional group within a community, appears quite adequate and is gradually gaining recognition (Nesterenko, 2000; Sergeev, 2003). This interpretation of the term *taxocene* makes it operational and allows it to be used for describing structural and

functional parts of communities as subjects for the study of morphological disparity.

McGhee (1999) introduced the notion of *morphospace*, a multidimensional space with each axis reflecting a certain morphological character. Each organism is represented in the morphospace as a point. Differences between groups of organisms are forms of intergroup diversity. Each group, occupying a part of the morphospace, accounts for a certain proportion of general disparity, which can be evaluated quantitatively. A number of different methods have been proposed for estimating the size and structure of morphospaces and measuring morphological disparity (Zelditch et al., 2004; Navarro, 2003; Pavlinov, 2008; Lisovskii and Pavlinov, 2008).

By analogy with repeated changes in the ratio of taxonomic diversity and morphological disparity that took place during global and regional biocenotic crises in the geological history (see Moyné and Neige, 2007) and taking into account unfavorable long-term trends in recent community dynamics caused by increased anthropogenic pressure on the biota, we may expect the emergence of regional biocenotic crises leading to the acceleration of microevolutionary processes (Zherikhin, 2003; Vasil'ev and Vasil'eva, 2005).

In this context, the main problem may be formulated as to whether the morphological disparity of communities (taxocenes) increases under unfavorable ecological conditions, in an anthropogenic environment, wherein their taxonomic diversity decreases.

Evaluation of morphological disparity can be based on the method of morphophysiological indicators by Shvarts et al. (1968), who regarded dimensional parameters of the body and organs as principal morphophysiological indicators and believed that the size of an animal largely determines many of its physiological and ecological features. There is good reason to assess changes in morphological disparity of certain organisms primarily by exterior (*habitus*) characters, namely, individual size and weight. Taking this into account, our working hypothesis was that the morphological disparity of exterior characters in a taxocene increases when animals develop under unfavorable conditions (caused either by natural climatic or anthropogenic factors, including radioactive contamination).

The purpose of this study was to assess the dynamics of morphospace and morphological disparity in rodent taxocenes inhabiting background and radioactively contaminated areas in the zone of influence from the Eastern Ural Radioactive Trace (EURT) in the Southern Urals over several years differing in natural climatic conditions.

The study had the following objectives: to estimate probable dependence of parameters of morphological disparity (*MD*) on animal sex in species of the rodent taxocene; to assess the dynamics of morphospace and morphological disparity in the taxocene at different

population sizes and different phases of the population cycle; to compare the levels of morphological disparity in the background (control) area radioactively contaminated (impact) areas in the zone of EURT; to study the dependence of morphological disparity in the taxocene on its species composition and to estimate the degree of contingency between morphological disparity and taxonomic diversity; and to estimate the principal possibility of using parameters of morphological disparity for ecological indication of rodent communities (taxocenes) subject to destabilization in an anthropogenic (radioactively contaminated) environment.

MATERIAL AND METHODS

The study was performed with 1194 rodents of six species (*Sylvaemus uralensis*, *Apodemus agrarius*, *Clethrionomys rutilus*, *Microtus agrestis*, *M. oeconomus*, and *M. arvalis*) captured in August to early September, 2003–2008, in the background (control) area and in the area contaminated with radionuclides from the EURT, which formed after the accident at the Mayak Production Association (radiochemical plant) in 1957. The impact area was an old track road with an initial contamination density of 750–1000 Ci/km² (Il'enko and Krapivko, 1993; Tarasov, 2000); the control area was the environs of the village Metlino, outside the EURT, with a background contamination level of 0.2 Ci/km² (Grigorkina et al., 2006). The distance between the two areas was 10–12 km. Elementary samples included animals of the same species and sex captured in the same year and locality. A total of 98 such samples were studied; without differentiation by sex, their number decreased to 53.

The relative age of mice (*Sylvaemus uralensis* and *Apodemus agrarius*) was estimated from the degree of molar tooth wear on the occlusal surface, or masticatory abrasion (Kolcheva, 1992), that of northern red-backed voles (*Clethrionomys rutilus*), from the degree of tooth root development (Tupikova et al., 1970); and that of *Microtus* voles, from the general degree of skull sculpturing (Larina and Lapshov, 1974). Comparison were made between conditionally even-aged groups of conspecific young of the year (juvenile animals were not included in such samples).

The morphospace and morphological disparity (*MD*) of taxocenes were estimated by five exterior characters (in all species): body length (*L*), tail length (*C*), plantar length (*Pl*), body weight (*P*), and fatness index (*F*), or cubic root of body weight divided by body length. Logarithms of all measurements were taken and standardized relative to the overall mean for each character. Multidimensional ordination of the morphospace of the taxocene and individual species was performed by the principal coordinates method (PCO). The volume of the morphospace was estimated using the geometric mean of the range of values (max–min) of the first five principal coordinates

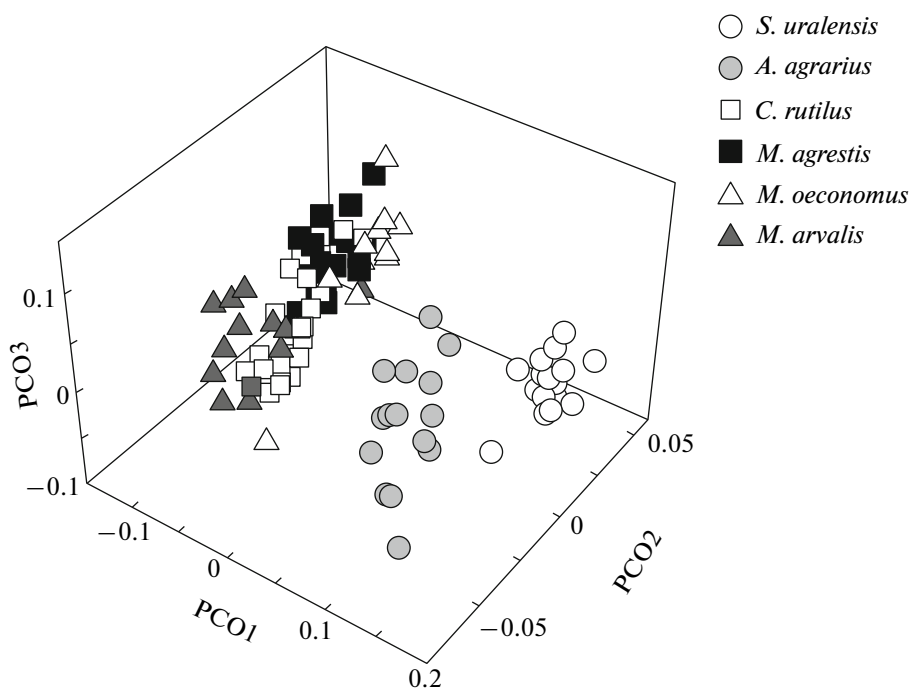


Fig. 1. Distribution of six species subspaces in the morphospace of the rodent taxocene in different years (2003–2008), without subdivision into control and impact subsamples (elementary groups are represented by samples of males and females from different localities), in the space of the first three principal coordinates (PCO1–PCO3).

(Navarro, 2003). The parameter characterizing the degree of morphological disparity (MD) was calculated as the mean square Euclidean distance between a given group of samples and the general centroid (Foote, 1993, 1997). The homogeneity of variance was estimated by Levene's test. Multiple comparisons were made using the nonparametric Kruskal–Wallis test and also the Walsh F -test and permutation test with 10000 iterations. The error of MD was also estimated by bootstrap resampling.

RESULTS AND DISCUSSION

Initially, we estimated the influence of animal sex on changes in the profiles of morphological disparity (MD) in the background (control) and impact areas in different years. The profiles of male and female samples were almost identical in the control area but differed slightly in the impact area, with these differences reaching the level of statistical significance in some years. We pooled the data obtained in different years into male and female groups from the control and impact areas and performed multiple comparisons of the resulting four samples. The Levene test showed that the variance of MD was similar in all samples ($p = 0.200$), and the Walsh test ($F = 1.07$, $df = 51$; $p = 0.369$) showed no significant differences between them; neither were they revealed in multiple pairwise comparisons by the Scheffé method: in either case, the values of S ratios varied from 0.21 to 1.51, not reaching the standard value 2.84. Thus, the influence of animal

sex on estimates of morphological disparity in rodent taxocenes proved to be negligible. Therefore, we subsequently refrained from dividing conspecific samples into male and female groups, except for ordination of the morphospace volume of each species.

Figure 1 shows the distribution of the subspaces of individual species in the morphospace of the rodent taxocene in general (without division into control and impact subsamples) in different years. The elementary samples were ordinated by the PCO method. The first three principal coordinates account for 97% of the total variance. The difference between mice and voles is distinctly visible along the first axis. The morphological subspace of voles is densely packed, while the subspaces of the two mouse species are segregated along the second and third axes, with ordinate scattering in the striped field mouse (*A. agrarius*) being significantly greater than in all other species, including the pygmy wood mouse (*S. uralensis*).

The volume of the morphological subspace of each species was calculated as the geometric mean of its extent along the first five principal coordinates. Their comparison showed that the volume of morphospace was the greatest in the striped field mouse and the smallest in the pygmy wood mouse, a dominant species (Fig. 2). Interestingly, dominant species (*Sylvaeomys uralensis*, *Clethrionomys rutilus*, and *Microtus agrestis*) proved to have smaller morphospaces than subdominants. This fact may be cautiously taken as indirect evidence that the above species differ in the

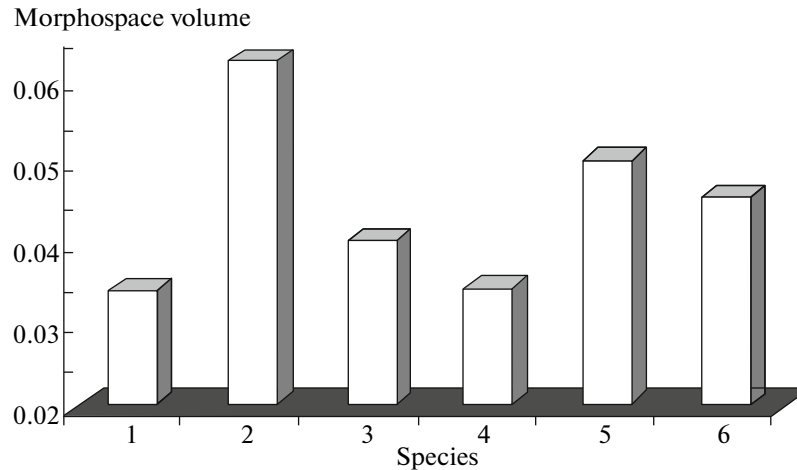


Fig. 2. Volumes of individual morphospaces (*MS*) of species forming the rodent taxocene in the EURT impact zone: (1) *Sylvae-mus uralensis*, (2) *Apodemus agrarius*, (3) *Clethrionomys rutilus*, (4) *Microtus agrestis*, (5) *M. oeconomus*, and (6) *M. arvalis*.

degree of adaptation to the habitats studied. A basis for such an assumption is provided by the results of Glo-tov's (1983) experiments with *Drosophila* lines and wheat cultivars. In these experiments, deterioration of developmental conditions (provocative background) was found to have a fan-spread effect on variability in test groups. Since some subdominant species (e.g., *A. agrarius*, *M. oeconomus*, and *M. arvalis*) are not permanent members of the taxocene and their abundance in some years decreased so strongly that they were absent in catches, the relatively greater volumes of their morphospaces reflect the higher level of their phenotypic plasticity (modification variability). By contrast, dominant species, especially the pygmy wood mouse, have smaller morphospaces, which is indicative of their general morphogenetic stability in the situation where individuals develop under environmental conditions changing from year to year.

The morphospace of taxocenes changed considerably from year to year both in the control and in the

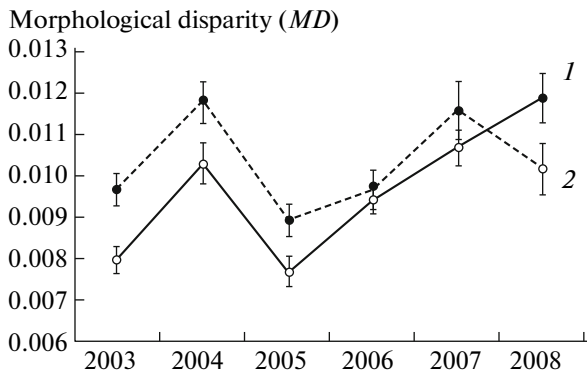


Fig. 3. Interannual dynamics of the morphological disparity index (*MD*) in (1) control and (2) impact rodent taxocenes (vertical bars show standard error).

impact area. In years of population growth and peak, the morphospace of the taxocene was different from that in years of decline and depression. In general, the abundance of the impact taxocene was lower than that of the control taxocene, but the curves of population dynamics in both groups changed relatively synchronously (Krashaninina and Chibiriyak, 2007). Therefore, we categorized our material by years with high (2003, 2005, 2006, and 2008) and low (2004 and 2007) animal abundance and estimated differences in the value and variance of morphological disparity (*MD*) between the two pooled samples. According to the Levene test, the variance of *MD* was significantly higher in years with low abundance ($p = 0.0002$). The value of *MD* in years with low abundance was also significantly higher than in years with high abundance, as shown by the Walsh test ($F = 38.68$, $df = 1182$; $p \ll 0.0001$) and permutation test ($N = 10000$ iterations, $p \ll 0.0001$). In other words, morphological disparity increased significantly at low animal abundance (in conditionally unfavorable years) and decreased at high abundance. It should be noted that morphological disparity in the impact area was generally higher, both at different phases of population dynamics and in comparisons of samples from different years, except for the year 2008 when the control and the impact group reversed their positions (Fig. 3).

Generalized comparison of the morphological disparity of taxocenes in the control and impact areas showed that *MD* was higher in the impact than in the control area (the Walsh test: $F = 9.456$, $df = 2656$; $p = 0.0021$; permutation test at $N = 10\,000$ iterations: $p = 0.0025$), the same being true of its variance (the Levene test: $p = 0.0006$). It may be concluded that permanent radiation exposure leads to a significant increase in the general morphological disparity of the impact taxocene, which may be indirect evidence that condi-

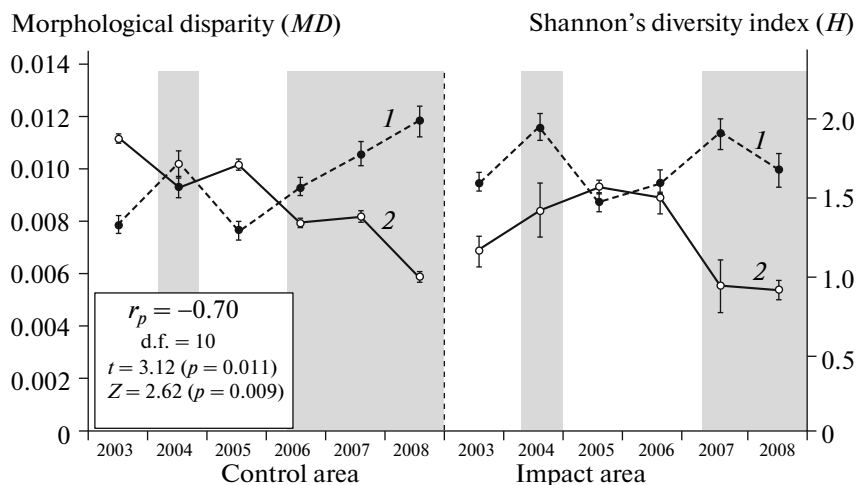


Fig. 4. Dynamics of (1) morphological disparity (MD) and (2) taxonomic diversity ($TD = H$) in the control and impact areas over several years (vertical bars show standard error). Shaded zones indicate areas of “negative” discordance (difference in direction) between changes in MD and TD .

tions in the area contaminated with radionuclides are unfavorable for the rodent taxocene as a whole.

A significant negative correlation was revealed between morphological disparity (MD) and taxocenotic diversity (TD) estimated by the Shannon index H : Pearson's correlation coefficient $r = -0.70$, with the correlation being significant according to Student's t -test, Z -statistics, and permutation test (Fig. 4). Morphological disparity decreases at high taxocenotic diversity and increases at low taxocenotic diversity.

We also analyzed the dynamics of relationship between morphological disparity (MD) and taxocenotic diversity (TD) in the control and impact areas in different years (Fig. 4). The standard errors of MD and H in this case was calculated by means of bootstrap resampling. “Positive” discordance, i.e. difference in the direction of changes of these parameters, was observed under “favorable” conditions, with TD increasing and MD decreasing. The shaded areas in the diagram show areas of “negative” discordance, with TD decreasing and MD increasing in “unfavorable” years.

CONCLUSION

As a result of this study, we have revealed the phenomenon of interannual changes in the morphospace of the rodent taxocene (based on exterior characters) and the dependence of these changes on the total abundance of rodents. The relatively high volume of the morphospace of certain species may indirectly indicate their lower morphogenetic stability and lower degree of adaptation to environmental conditions and also possibly reflect the level of their phenotypic plasticity. Statistically significant differences in the value of MD exist between taxocenotic samples corresponding to years with high (2003, 2005, 2006, and 2008)

and low (2004 and 2007) rodent abundance. In years with low abundance (conditionally unfavorable), morphological disparity (MD) and its variance have proved to be significantly higher than in years with high abundance. The value of MD in the EURT zone is significantly higher in the impact area than in the background (control) area; this difference is observed at different phases of population dynamics as well as in comparisons of pooled samples and by years (except for of 2008). The negative correlation revealed between the levels of morphological disparity (MD) and taxonomic diversity (H) agrees well with the above hypothesis and with the fact that the “negative” discordance of annual changes of these parameters (with TD decreasing while MD increases) was observed in unfavorable years with low rodent abundance. The latter provides indirect evidence that “morphogenetic stress” in such years affects all species components of the taxocene.

Thus, the results described above do not contradict our initial hypothesis and agree with the paleoecological phenomenon of discordance between changes in taxonomic diversity (TD) and morphological disparity (MD) in taxocenes during global and regional biocenotic crises in the geological history of the Earth, i.e., during processes with far greater characteristic times (Moyné and Neige, 2007). We may therefore conclude that this approach applied to studies on recent animal communities gives an opportunity to reveal signs of an impending regional biocenotic crisis caused by increasing anthropogenic impact on the biota. A warning about the possibility of such a crisis was given in the works of Zherikhin (2003). The proposed method of assessing a taxocene as part of community is neither labor-intensive nor expensive and may be used in synecology for indicating unfavorable states of taxocenes.

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REFERENCES

- Arnol'di, K.V. and Arnol'di, L.V., On Biocenosis as a Basic Concept of Ecology: Structure and Scope, *Zool. Zh.*, 1963, vol. 42, no. 2, pp. 161–183.
- Ciampaglio, C.N., Kemp, M., and McShea, D.W., Detecting Changes in Morphospace Occupation Patterns in the Fossil Record: Characterization and Analysis of Measures of Disparity, *Paleobiology*, 2001, vol. 27, no. 4, pp. 695–715.
- Foote, M., Contributions of Individual Taxa to Overall Morphological Disparity, *Paleobiology*, 1993, vol. 19, pp. 403–419.
- Foote, M., The evolution of Morphological Diversity, *Annu. Rev. Ecol. Systematics*, 1997, vol. 28, pp. 129–152.
- Glotov, N.V., Genetic Heterogeneity of Natural Populations with Respect to Quantitative Traits, *Extended Abstract of Doctoral (Biol.) Dissertation*, Leningrad: USSR Acad. Sci., Leningr. Gos. Univ., 1983.
- Grigorkina, E.B., Olenev, G.V., Pashnina, I.A., et al., Reproductive Strategy of Murine Rodents in a Radioactively Contaminated Biogeocenosis, *Izv. Chelyabinsk. Nauch. Tsentra*, 2006, issue 4 (34), pp. 101–105.
- Il'enko, A.I. and Krapivko, T.P., Ecological Consequences of Radioactive Contamination for Small Mammals Involved in Strontium Transfer, in *Ekologicheskie posledstviya radioaktivnogo zagryazneniya na Yuzhnom Urale (Ecological Consequences of Radioactive Contamination in the Southern Urals)*, Sokolov, V.E. and Krivolutskii, D.A., Eds., Moscow: Nauka, 1993, pp. 171–180.
- Kolcheva, N.E., Dynamics of Ecological Structure of the Common Field Mouse in the Southern Urals, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Yekaterinburg: Inst. Plant Anim. Ecol., Ural Division, Russ. Acad. Sci., 1992.
- Krashaninina, Yu.V. and Chibiryak, M.V., Analysis of Rodent Fauna Structure and Dynamics in Radioactively Contaminated Environment, *Ekologiya ot Arktiki do Antarktiki: Mat-ly konf. molodykh uchenykh (Ecology from the Arctic to Antarctica: Proc. Young Sci. Conf.)*, Yekaterinburg, 2007, pp. 149–154.
- Larina, N.I. and Lapshov, V.A., On Methods for Distinguishing Age Groups in Some Voles, in *Fiziologicheskaya i populyatsionnaya ekologiya zhivotnykh (Physiological and Population Ecology of Animals)*, Saratov, 1972, issue 2 (4), pp. 92–97.
- Lisovskii, A.A. and Pavlinov, I.Ya., On the Study of Morphological Diversity in Cranial Metric Characters of Mammals: 2. Scalar and Vector Parameters of Group Variation, *Zh. Obshch. Biol.*, 2008, vol. 69, no. 6, pp. 428–433.
- McGhee, G.R., *Theoretical Morphology: The Concept and Its Applications*, New York: Columbia Univ. Press, 1999.
- Moyne, S. and Neige P., The Space–Time Relationship of Taxonomic Diversity and Morphological Disparity in the Middle Jurassic Ammonite Radiation, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 2007, vol. 248, pp. 82–95.
- Navarro, N., MDA: A MATLAB-Based Program for Morphospace–Disparity Analysis, *Comp. Geosci.*, 2003, vol. 29, pp. 655–664.
- Neige, P., Spatial Patterns of Disparity and Diversity of the Recent Cuttlefishes (Cephalopoda) across the Old World, *J. Biogeogr.*, 2003, vol. 30, pp. 1125–1137.
- Nesterenko, V.A., Shrews in the South of the Russian Far East and Organization of Their Taxocenoses, *Extended Abstract of Doctoral (Biol.) Dissertation*, Vladivostok: Inst. Biol. Soil Sci., Far East Div., Ross. Acad. Sci., 2000.
- Pavlinov, I.Ya., Morphological Disparity: General Concepts and Basic Characteristics, in *Zoologicheskie issledovaniya. Sb. tr. Zool. Muzeya MGU (Zoological Studies. Collected Works of the Zoological Museum, Moscow State University)*, Moscow: Mosk. Gos. Univ., 2008, vol. 49, pp. 343–388.
- Sergeev, V.E., Ecological–Evolutionary Factors of Community Organization in Shrews of Northern Eurasia, *Extended Abstract of Doctoral (Biol.) Dissertation*, Novosibirsk: Inst. Anim. System. Ecol., Ross. Acad. Sci., 2003.
- Shvarts, E.A., *Sokhranenie bioraznoobraziya: soobshchestva i ekosistemy (Biodiversity Conservation: Communities and Ecosystems)*, Moscow: KMK, 2004.
- Shvarts, S.S., Smirnov, V.S., and Dobrinskii, L.N., *Metod morfofiziologicheskikh indikatorov v ekologii nazemnykh pozvonochnykh (The Method of Morphological Indicators in the Ecology of Terrestrial vertebrates)*, Sverdlovsk: UFAN SSSR, 1968.
- Tarasov, O.V., Radioecology of Terrestrial Vertebrates in the Head Part of the Eastern Ural Radioactive Trace, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Ozersk–Yekaterinburg: Inst. Plant Anim. Ecol., Ural Division, Russ. Acad. Sci., 2000.
- Tupikova, N.V., Sidorova, G.A., and Konovalova, E.A., Kay for Determining the Age of Forest Voles, in *Materialy k poznaniyu fauny i flory SSSR (Materials for Studies on the Fauna and Flora of the Soviet Union)*, Moscow, 1970, issue 45 (60), pp. 160–167.
- Vasil'ev, A.G. and Vasil'eva, I.A., Epigenetic Rearrangements in Populations As a Probable Mechanism Causing a Biocenotic Crisis, *Vestn. Nizhegorod. Gos. Univ., Ser. Biol.*, 2005, issue 1(9), pp. 27–38.
- Zelditch, M.L., Swiderski, D.L., Sheets, H.D., et al., *Geometric Morphometrics for Biologists: A Primer*, Amsterdam: Elsevier, 2004.
- Zherikhin, V.V., Evolutionary Biocenology: The Choice of Models, in *Ekosistemnye perestroiki i evolyutsiya biosfery (Ecosystem Rearrangements and Biosphere Evolution)*, Moscow: Nedra, 1994, pp. 13–20.
- Zherikhin, V.V., *Izbrannye trudy po paleoekologii i filotsenogenetike (Selected Works in Paleoecology and Phytocenogenetics)*, Moscow: KMK, 2003.