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The Theriofaunistic Zoning of Northern Eurasia

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Abstract—For the purpose of zoning on the basis of theriofauna, Northern Eurasia was considered within the boundaries of the Soviet Union in 1991 and was divided into 245 mapping units. Mapping units were marked on the World Vegetation Map at a scale of 1 : 2000000. Each mapping unit occupied a territory within the limits of a natural subzone with a latitudinal distance of 10°. A list of mammal species was generated for each unit. Jaccard similarity coefficients were calculated for these lists; the coefficients were used as the basis for performing cluster analysis of theriofauna of the mapping units. The results of calculations were used to create a hierarchical classification, which includes three theriofauna regions divided into seven subregions. They were classified as island or mainland. All the subregions (except one) were delimited into 18 provinces and 17 districts; one of the districts was delimited into four subdistricts. Environmental factors that correlate with heterogeneity of theriofauna within the studied territory were described. The proposed zoning is 1.9–3 times more informative than previously developed schemes and takes into account 69% of the variance of the similarity coefficients of the faunas of specific regions (coefficient of multiple correlation is 0.83). The association with environmental factors and natural conditions may explain 83% of the heterogeneity of the theriofauna (correlation coefficient is 0.91). Comparing the results of zoning that were carried out for different classes of terrestrial vertebrates, we found significant similarity between causes of fauna heterogeneity (zonal features, remoteness, sun exposure, and their combined effect). In addition, the differences in tolerance to the environment among the studied animal classes resulted in substantial discordance of the boundaries of the described taxa and their hierarchy. This discordance was found during zoning. Because of this, general conclusions concerning the heterogeneity of the fauna of terrestrial vertebrates can be made only after the total analysis of their fauna is completed.

Keywords: zoning, fauna, mammals, Palaearctic, Northern Eurasia, cluster analysis, factors, correlation

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All methods, scientific approaches, and characteristics of the materials were described in [1–6]. For information about the areas, the "Biodat" database [A. Yu. Puzachenko, www.biodat.ru] was used with partial clarification on departmental data that was presented on the Internet and in literature sources [7]. Names for the species are presented according the Catalog of Mammals of the Soviet Union [8].

Some changes were introduced as a result of step-by-step analysis of different classes of vertebrate fauna. For example, some zones of habitat of amphibians, reptiles, and mammals (the Crimea, the Carpathians, and the Kurile Islands) were delimited into two parts due to significant faunal differences. The theriofauna of inland bodies of water was excluded from the review due to the lack of information about species richness. As a result, the total number of sites was reduced by five compared to the zoning for avifauna analysis.

As for bird fauna, the regions were not initially demarcated due to satisfactory (balanced) administrative division into provinces. For other vertebrates, averaging the subregion parameters gave additional information. After this, bird fauna regions were demarcated for comparison.

Ranks of subregions (island and mainland) were found only for mammals, because such ranks were not observed on the graphs for amphibians and reptiles. As for birds, the fauna of island subregions is more similar to that of the adjacent mainland than to other islands. Only for mammals was a more consistent similarity between island faunas observed on the graph in the form of consistent changes of the polar fauna and fauna of the eastern islands of the Palearctic ecozone.

It should be noted that, unlike seabirds, which are tied to the land, sea mammals were excluded from consideration.

RESULTS AND DISCUSSION

Theriofaunistic Zoning

In the classification given in the map legend, there are six levels of zoning: rank, region, subregion, province, district, and subdistrict (Fig. 1). The subregion level is the most significant. The subregion level is a

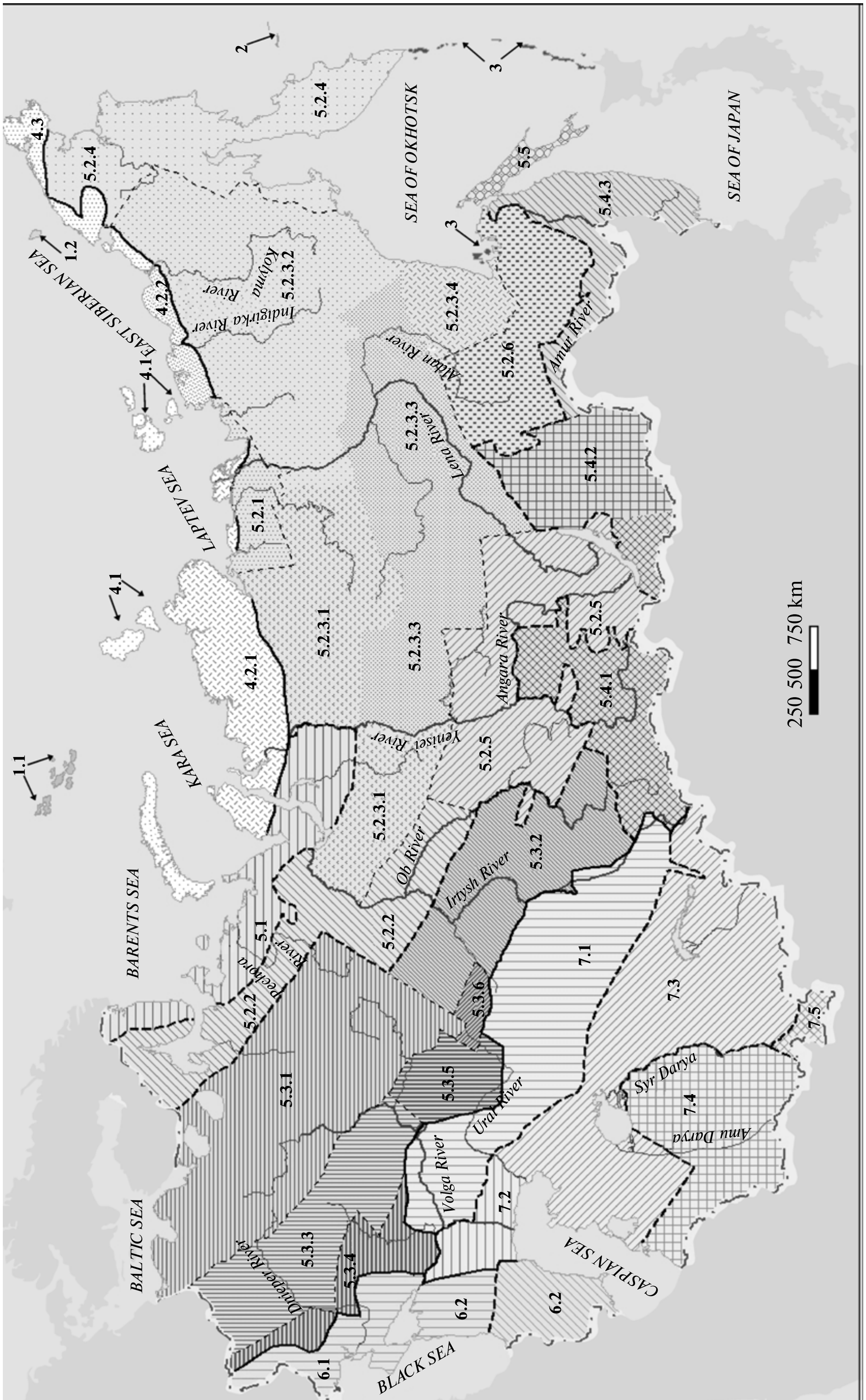

Fig. 1. Theriofauna Zoning of Northern Eurasia.

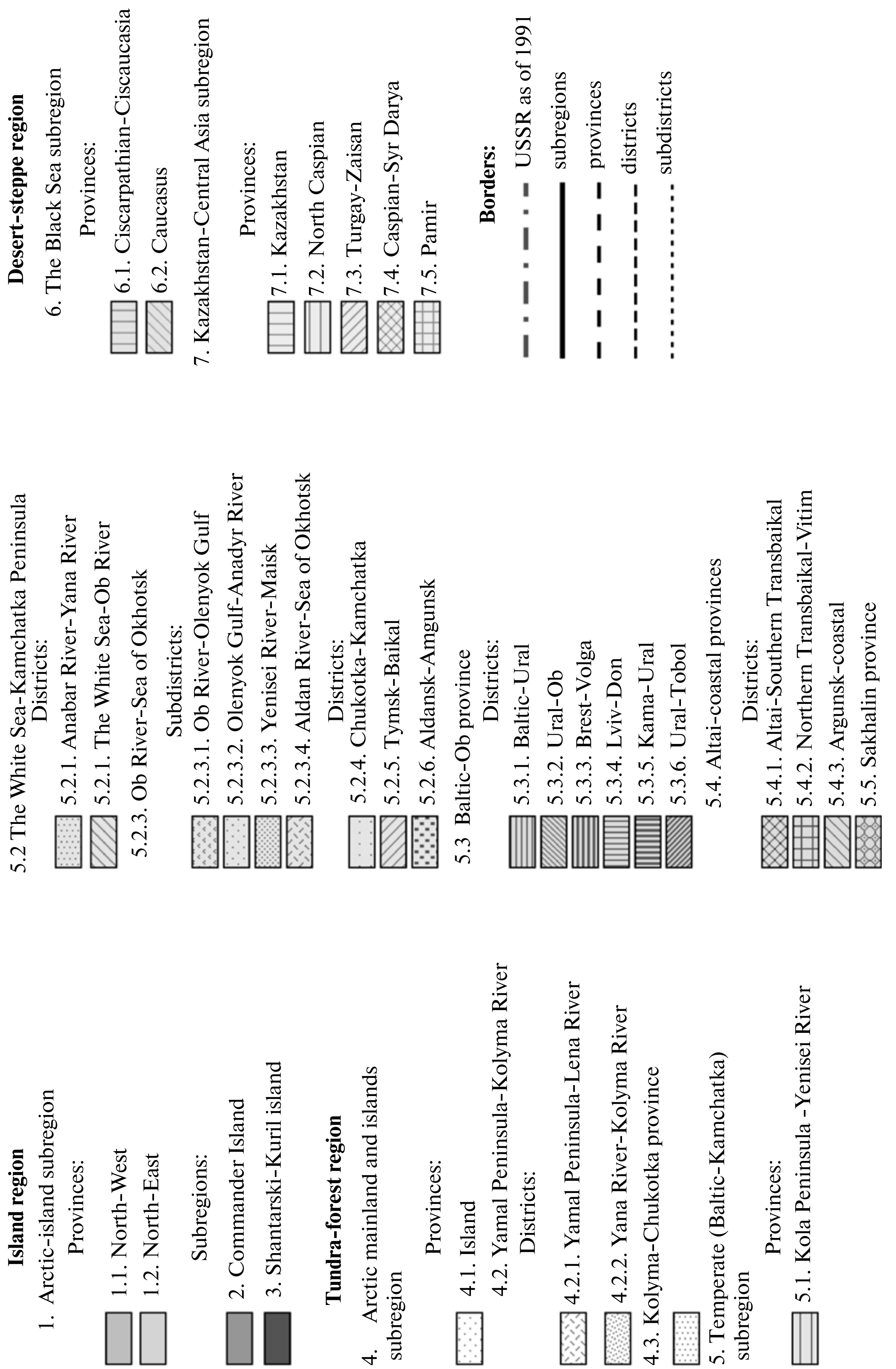
Island region
1. Arctic-island subregion
Provinces:
1.1. North-West
1.2. North-East
Subregions:
2. Commander Island
3. Shantarski-Kuril island
Tundra-forest region
4. Arctic mainland and islands subregion
Provinces:
4.1. Island
4.2. Yamal Peninsula-Kolyma River
Districts:
4.2.1. Yamal Peninsula-Lena River
4.2.2. Yana River-Kolyma River
4.3. Kolyma-Chukotka province
5. Temperate (Baltic-Kamchatka) subregion
Provinces:
5.1. Kola Peninsula -Yenisei River
5.2 The White Sea-Kamchatka Peninsula
Districts:
5.2.1. Anabar River-Yana River
5.2.1. The White Sea-Ob River
5.2.3. Ob River-Sea of Okhotsk
Subdistricts:
5.2.3.1. Ob River-Olenyok Gulf
5.2.3.2. Olenyok Gulf-Anadyr River
5.2.3.3. Yenisei River-Maisk
5.2.3.4. Aldan River-Sea of Okhotsk
Districts:
5.2.4. Chukotka-Kamchatka
5.2.5. Tymsk-Baikal
5.2.6. Aldansk-Angunsk
5.3 Baltic-Ob province
Districts:
5.3.1. Baltic-Ural
5.3.2. Ural-Ob
5.3.3. Brest-Volga
5.3.4. Lviv-Don
5.3.5. Kama-Ural
5.3.6. Ural-Tobol
5.4. Altai-coastal provinces
Districts:
5.4.1. Altai-Southern Transbaikal
5.4.2. Northern Transbaikal-Vitim
5.4.3. Argunsk-coastal
5.5. Sakhalin province
Desert-steppe region
6. The Black Sea subregion
Provinces:
6.1. Ciscarpathian-Ciscaucasia
6.2. Caucasus
7. Kazakhstan-Central Asia subregion
Provinces:
7.1. Kazakhstan
7.2. North Caspian
7.3. Turgay-Zaisan
7.4. Caspian-Syr Darya
7.5. Pamir
Borders:
USSR as of 1991
subregions
provinces
districts
subdistricts

Fig. 1. Contd.

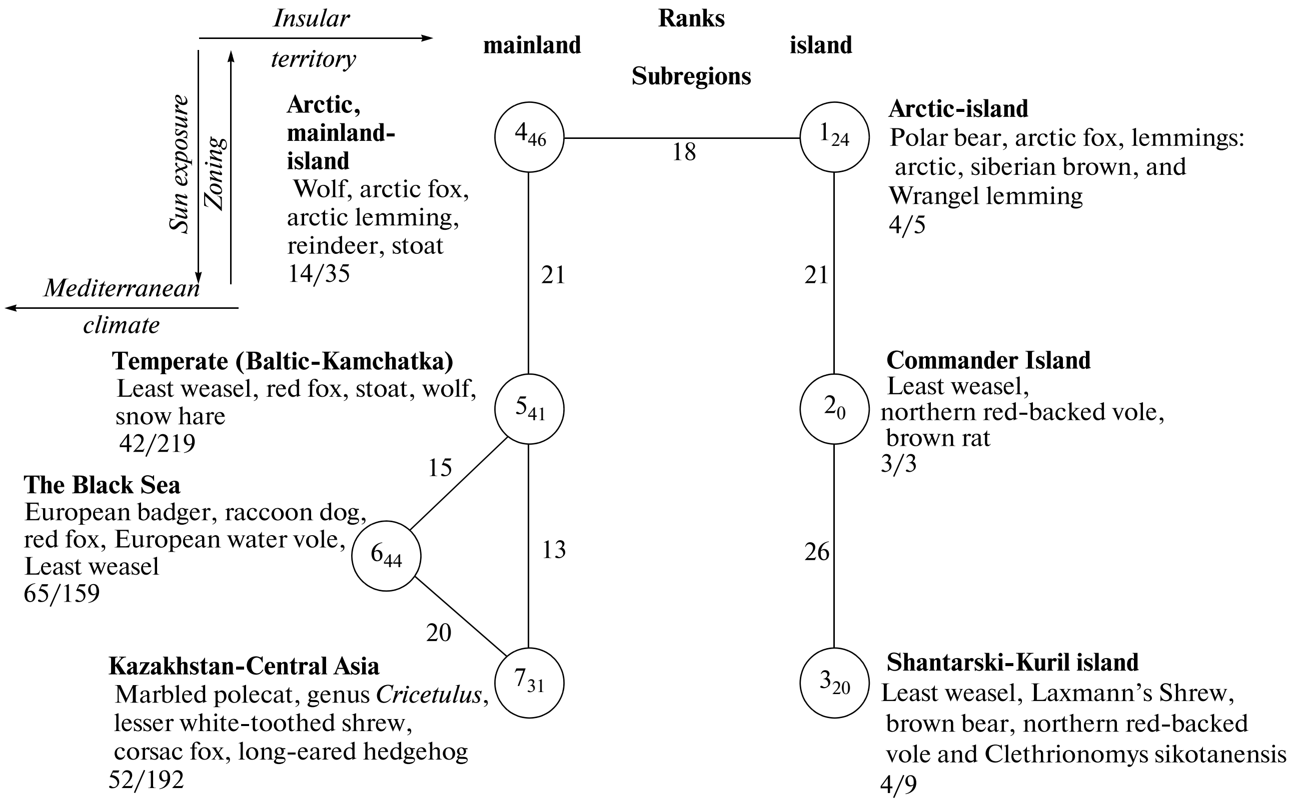

Fig. 2. Spatial-typological structure of theriofauna in Northern Eurasia on subregion level.

Note. The numbers of the inside icons are numbers of taxa represented at the appropriate classification; the index indicates similarity within the group. The lines between the icons mean suprathreshold substantial similarity. The similarities between groups are presented near the lines, species of high frequency of occurrence and total relative occurrence on site/ total number of identified species is shown near icons. Arrows located near main binding environmental factors indicate the direction of their increasing influence and theriofaunistic trends.

result of the initial zoning using cluster analysis. Reaggregation of subregions by similarity criteria allow one to delimit regions when the same program was used. A similarity graph built at the subregion level allowed us to identify the ranks: islands and mainland (Fig. 2). The zoning of large clusters at the subregion level gives provinces, while their further consecutive zoning gives districts and regions.

Three theriofauna regions were identified for North Eurasia (within the boundaries of the Soviet Union in 1991): island, tundra–forest, and desert–steppe. Each region was divided into two subregions. Some regions were delimited into smaller units, viz., provinces, and a few were also divided into districts and subdistricts. The relative frequency of occurrence was defined as the number of sites that were populated by particular species divided by the total number of sites covered by this taxon (similar to the species abundance in population analysis). This approach allowed us to reduce the effect of the size of the area occupied by the taxon. The top five species with the highest relative frequency of occurrence measured as a percentage of the sum of these parameters for all species (similar to the density of population) were considered as the leading species. These species cannot be viewed as characteristic species, because they can be found in different taxa. It should be remembered that the classification was created without regard to the specifics of prevailing, differential, constant companion, or endemic species. For the purposes of analysis, all species were considered as equal; the zoning was based on attributed similarity coefficients using the previously mentioned algorithm. Also, the level of similarity based on zoning parameters (similar to dendrogram method) was not used. The zoning was conducted with regard to the largest part of the variance matrix of similarity coefficients.

The proposed theriofauna zoning of studied part of the Palearctic ecozone are 1.9–3 times more consistent with the heterogeneity of the mammalian fauna of this territory than previously proposed schemes of theriogeographical, zoogeographical, and biogeographical, as well as landscape zoning (Table 1).

A.P. Kuzyakin [12] was convinced that administrative zoogeographical zoning is inappropriate and that zoning should be done only in the context of landscape demarcation. Because of this, he considered that his

Table 1. Informativeness of theriofauna (1), zoo- and biogeographic (2, 3), as well as landscape zoning (4) with respect to the heterogeneity of theriofauna of the studied part of North Eurasia

Characteristics of zoning (1–4), author	Variance accounted for, %	Correlation coefficient
1. Yu. S. Ravkin, I. N. Bogomolova, and O. N. Nikolaeva	69	0.83
3. A. G. Voronov, V. V. Kucheruk [9]	36	0.60
1. B. A. Kuznetsov [10]	29	0.54
1. Yu. A. Mekaev [11] 4. A. P. Kuzyakin [12]	27	0.52
2. I. I. Puzanov [13], 3. B. G. Mordkovich [14] 3. N. F. Reimers [15], 4. Atlas of the Soviet Union [16]	23	0.47

Table 2. Evaluation of the most important parameters related to heterogeneity of theriofauna and fauna diversity of terrestrial vertebrates of Northern Eurasia, matrix variance accounted for of similarity coefficients, %

Class	Number of species	Factor, mode										
		Sun exposure**	Zoning, subzoning	Remoteness	Postglacial dispersal	Insular territory	Climatic zonality	All factors	All factors and modes	Diagonal rend at least	Complete evaluation	
											Sun exposure	Other factors
Amphibians*	41	30	19	22	12	1	3	43	84	41	71	13
Reptiles*	167	30	21	12	5	0.5	2	36	93	57	87	6
Mammals	332	45	34	21	20	12	4	63	83	20	65	18
Birds*	691	75	52	15	46	11	4	80	81	1	76	5

* See Tables 2 and 3 in [1–5]; ** Total assessment result for zoning, subzoning and remoteness, without diagonal trend.

zoning of the Soviet Union was not only the landscape, but also zoogeographical.

Spatial-typological structure and theriofauna

The structure of theriofauna for this part of North Eurasia was described at the level of subregions. The threshold value for the subregion similarities/differences was eight units (see Fig. 2) Both the scheme and the map clearly shows the effect of zones (differences in thermal conditions and moisture from North to South) and the effect of insular territory (the distance from the mainland), as well as the effect of the Mediterranean climate. In addition, the average total occurrence of species and their diversity in different subregions decreased toward the North. A deviation from the trend was observed for the Kazakhstan-Central Asia desert-steppe subregion (decrease in occurrence) and for the Black Sea steppe subregion (decrease in diversity). The maximum number of species were observed in the temperate subregion, which includes most of the forest and forest–steppe zones. This can be explained by the optimal hydrothermal conditions in the subregion as well as by the subregion's area, which is the largest of all areas.

The most important parameter that is related to theriofauna heterogeneity is sun exposure, which was considered as a combination of zoning and remoteness. The differences in sun exposure allow one to explain the variability of 45% of the similarity coefficients (Table 2). When the effects of zoning and remoteness were assessed individually, it allowed us to explain the reduction in heterogenety by factors of 1.3 and 2.1, respectively. The smaller part of theriofauna dispersion (2.2 times) is associated with postglacial dispersal rather than with sun exposure.[1] The relationship between the distance of the territory from the mainland and with altitudinal climatic zonality is quite small on average. All of the above factors explain 63% of the variance in the similarity coefficients of specific theriofauna zones. The structural and classification modes are associated with 48 and 70% of the variance, respectively. The overall informativeness of representations is 83%, which is very close to the coefficient of multiple correlation of 0.91.

Calculations of magnitude and degree of correlation for environmental factors and theriofauna heterogeneity of Northern Eurasia were performed not only individually, but also cumulatively, while sequentially integrating the most important factors and removing

[1] When post-glacial dispersal is taken into consideration, it is commonly accepted that it causes all of the differences in the fauna of Eastern and Western areas.

Table 3. Comparative characteristics of the zoning results of Northern Eurasia for different classes of terrestrial vertebrates

Class	Number of species	Number of taxa					Descriptiveness, variance accounted for, %		
		regions	subregions	provinces	districts	total	classifications	all factors and modes	minimal increment compare to previously published classifications
Amphibians	41	3	4	7	23	37	75	84	21
Reptiles	167	4	7	18	14	43	91	93	67
Mammals	332	3	7	18	17	45	65	83	36
Birds	691	3	7	10	22	39	61	81	28

the less important ones. The result revealed that the zoning and subzoning completely correlate with sun exposure. When the remoteness parameter was included in the calculation, the variance accounted for an increase by 12%. When the distance from the mainland parameter was included, it increased by an additional 7%. Postglacial dispersal correlates with sun exposure and remoteness, while climatic zonality correlates with all of the mentioned environmental factors. The resulting variance increased by 19% when the classification mode was included in the calculation, but it was not affected by the structural mode.

For classes of terrestrial vertebrates, three to four regions and four to seven subregions were allocated (Table 3). The minimum number was allocated for amphibians, while the number of subregions was almost double for the other vertebrate classes. The number of provinces varies from 7 to 18. As for amphibians, this number is also minimal. It is higher for birds (10) and almost three times higher for reptiles and mammals. The smallest number of districts was allocated for reptiles (14), a little more for mammals (17), and almost 1.5 times more for birds and amphibians. In total, the number of taxa for all classes ranges between 37 and 45. It is less for amphibians and birds (37 and 39) and higher for reptiles and mammals. Typically, more classification taxa were allocated to the class of vertebrates, which has a higher average similarity for specific fauna species and higher species diversity. During zoning, an exception was noticed for birds, which have the highest number of species, but a very low number of taxa. The total variance accounted for is greater if the species diversity is lower. However, these parameters are lower for amphibians than for reptiles, while amphibian diversity is smaller. For pairwise comparison (poikilothermic and homeothermic animals), the observed differences had no exceptions. On average, there were more taxa in classifications for homoeothermic animals than for poikilothermic animals, while the total informativeness was lower. This result may be due to the fact that the similarity of zero options was taken as 100%.

For all the studied vertebrate classes, the heterogeneity of fauna was most strongly associated with the sun exposure (30–75% of the variance of similarity coefficients). The assessment of its magnitude and degree of correlation is highest for bird fauna. It is 1.7 times lower for mammals and 2.5 times lower for poikilotherms (see Table 2). The observed association of these parameters with the zonal–subzonal differences was smaller (19–52%), but the ratio of the values was similar. The association with remoteness was almost three times lower, but it was higher (22 and 21%) for amphibians and mammals than for birds and reptiles (15 and 12%). Postglacial dispersal correlates with differences in avifauna (46%) and it is 2 and 3 times lower for mammals and amphibians (20 and 12%). It is also minimal for reptiles. The distance from the mainland correlates with the heterogeneity of homeothermic fauna by 11–12% and with the heterogeneity of poikilotherms by 0.5–1%. For the altitudinal climatic zonality of Northern Eurasia in general, these values are minimal (2–4%). All described factors allow us to approximate 36–80% of the variance of the similarity coefficient matrix. The maximum value of variance was found for avifauna, a lower one was found for theriofauna (63%) and for poikilotherms in particular (43 and 36%). Informativeness of classifications varies between 61 and 91%. It is the highest for reptiles and amphibians (91 and 75%), but it is lower for birds and mammals (61 and 65%). An integrated assessment of the completeness of the explanation for the heterogeneity of vertebrate classes is very similar (93% for reptiles and 81–84% for other classes).

It is known that the migratory abilities of birds are the highest, these abilities are smaller in mammals and in reptiles and amphibians in particular. On the basis of substantive considerations, it can be assumed that for the fauna class in general, the greater uniformity of distribution and lower degree of randomness with respect to the occupied territory correlate with higher migratory ability and relative independence from the environment.

Some contradictions were noted during the assessment of the magnitude and degree of the correlation between the heterogeneity of fauna and environmental factors. Thus, sun exposure and zonal–subzonal characteristics mostly correlate with the heterogeneity of fauna of homeothermic animals. The most significant contradictions were noted when estimates for birds and other classes were compared (1.7–2.5 fold difference). In contrast, it assumed that the dependence of birds from the environmental temperature should be lower due to the temperature of their bodies and their migratory abilities. The same contradictions were more significant when these parameters were compared with the migratory abilities of animals. Correlation with postglacial dispersal was higher for birds than for other classes of terrestrial vertebrates, especially for amphibians and reptiles. During these evaluations, it was found that the correlation with the distance from the mainland is significantly higher for homeothermic animals than for poikilothermic ones. According to objective logic, this should be the opposite. Correlation with environment factors, including sun exposure and the availability of water, as well as with the distance of islands from the mainland, should be more significant for amphibians, less significant for reptiles followed by mammals, and minimal for birds. Under the conditions of heat deficiency for the development of eggs and tadpoles and/or under the extreme conditions of winter tundra, poikilothermy of amphibians and reptiles results in the almost complete absence of these vertebrates. Homeothermic animals are less dependent on low temperatures. Birds in particular are capable of seasonal migrations, which allow them to avoid extreme winter conditions. But the heat deficiency increases not only from south to north (due to the latitude changes), but also from west to east (due to an increase in the characteristics of the continental climate when moving from the Atlantic coast to the center of the continent). The effect of the Pacific Ocean is less significant because of its cold currents. This results in a diagonal trend in zoning in both areas that are occupied by individual species and in territories occupied by taxa. It is also a cause of lower (compared to expected) magnitude and degree of correlation with zonality for poikilotherm and greater degree of correlation for homeotherms. Due to a lower dependence on the environment homeotherms have better dispersal through the continent than amphibians and reptiles. This explains the higher correlation between the heterogeneity of zone–subzonal fauna and climate change compared to poikilotherms. As mentioned before, this is due to the fact that the similarity of zero options was taken as 100%.

According to these assessments, the diagonal trend blurs the individual impacts of zoning and remoteness and reduces the degree of correlation with them. The difference between the total assessment of the correlation with all environmental parameters and total informativeness of representations (which take the diagonal trend into account; see Table 2) can be used as an evaluation criterion for the total effect of zoning and remoteness (which define the diagonal trend). Such estimates of the diagonal effect are much higher for amphibians and reptiles than for homeotherms.

The diagonal trend is a well-known phenomenon and can be observed in vegetation zones in relation to the latitude, as well as for the fauna of birds and small mammals in relation to vegetation subzones [11, 17]. This trend is more significant for animal populations. It displaces at a greater angle relative to the latitude than natural zones and subzones. Therefore, we can say that the consequences of differences in zoning and remoteness are associated with differences in sun exposure. Similar to the angle of trim, this phenomenon could be given the name “trimming.” This “trim” is clearly observed in the zoning of amphibian fauna of Northern Eurasia [3]; as well, it can be seen on climate maps of Northern Eurasia [18].

The paradoxical discrepancy, which was noted for the assessed degree of correlation between fauna heterogeneity and the distance of the island from the mainland for various classes of vertebrates, is determined by other factors. First, because of the small number of poikilotherm vertebrate species that populate islands, the similarity coefficient for their fauna is insignificant. For mammals and birds, which possess significant migration abilities, the island fauna is richer and more similar on different islands. Because of this, the similarity coefficient defines the largest part of the variance of the similarity matrix. Therefore, the assessed degree of correlation is higher for mammals and birds than for amphibians and reptiles. This is caused by a drawback of the Jaccard similarity coefficient, which does not account for the similarity in the absence of sample sets. In this case, the calculations that use correlation coefficients as a measure of similarity are likely to give better results.

Secondly, the Jaccard similarity coefficient is not just a parameter of similarity for specific fauna, because it is a ratio of intersection (species, which are common to both compared sets) and the size of the union of the sets for both individual faunas. The union of the sets includes both species that are common to both compared sets (intersection), and complement sets, which are unique for particular fauna. It is impossible to account for only unique species, because in this case, completely similar sets would not be 100% similar. Thus, the Jaccard coefficient does not reflect similarity/difference, but it is a conditional measure of heterogeneity. The similarity, which accounts for this coefficient, appears only during classification, when samples with similar coefficients are combined in clusters (in faunas, in this case). This is why it should be named the coefficient of heterogeneity. It also should be noted that in the case of assessing the magnitude and degree of correlation between environmental factors and differences in faunas, the environmental importance of these factors for animals are not assessed. Only the degree of agreement between two kinds of heterogeneity, viz., the environment and the fauna, is considered. It also should be noted that these calculations are carried out under the condition of "understanding" the factors that were used in the calculations [19]. This is why the total assessments of sun exposure (by gradation) that was considered separately from zoning and remoteness were lower than total assessments that were evaluated with regard to the diagonal trend. These better correlate with the total annual temperature or minimum winter temperatures for those species whose distribution is limited by them. However, it is possible to obtain an individual assessment of the effect of sun exposure on the heterogeneity of analyzed groups of vertebrate fauna in a different way. For this purpose, the assessments of the correlation with diagonal trend and with the total effect of zoning and remoteness (as simple combination of these factors by gradations) should be summarized. In this case, the increase of the informativeness due to other factors is maximal for mammals and reptiles (18 and 13%) and is approximately 3–4 times lower for amphibians and birds.

CONCLUSIONS

When comparing zoning maps, considerable overlap may be noted in the configuration of mapping units for amphibians and mammals, and significant deviations for birds and especially for reptiles [1–5]. Rank bands for subregion and/or region can be described as arctic, temperate, subarid, and arid. They also can be described as tundra, forest, steppe, and desert. In this case, differences among classes of vertebrates within those bands are clearly observed. For reptile fauna, the arctic band has the greatest territory among all the classes of vertebrates, especially in the northeast. In the temperate band, these vertebrates occupy the lowest territory, followed by greater territory for mammals and amphibians. The territory for birds is the largest. The subarid and arid bands for reptiles merged and include much of the temperate band and occupy the largest territory. For amphibians this territory is significantly smaller. The subarid band for birds almost completely overlaps with the temperate band and is only differentiated as an individual unit for mammals. The arid band (as an individual unit) occupies a larger territory for bird fauna and a smaller one for mammals.

The varying degrees of tolerance to the environment exhibited by the different groups of animals are the causes of these differences. Thus, the heat deficit is most significant factor for reptiles. This is why the arctic band for reptiles occupies the largest area. At the same time, the environmental conditions of arid and subarid areas are sufficiently attractive for them. The same degrees of tolerance to the environment were found for amphibians in drylands and in significant parts of the temperate areas for birds and mammals. Arid territories are better delimited for homeothermic animals, while subarid territories are also delimited for mammals. Bird dispersal into arid regions (broadleaf and floodplain forest in South) has some significance. It is lower for dispersal into northern parts, due to a heat deficit (steppe landscape).

In conclusion, we can state that the causes of heterogeneity of faunas of different classes of terrestrial vertebrates considerably overlap. The most important causes are zonality, remoteness, and the diagonal trend. However, due to differences in the degree of tolerance to these factors and their inseparable combinations, the taxon boundaries found during zoning do not match each other and have a trend toward the southeast compared to the borders of natural geographic subzones. As a result, it is impossible, as previously thought, to draw a conclusion about taxa (common for all vertebrate) based on the zoning results that were obtained for individual classes of studied animals [9, 19–21]. Apparently, total zoning can be made only when all species (or most of them) were taken into consideration, similar to what was done during the comparison of individual and total zoning for amphibians and reptiles [2]. The results from the zoning for all types of terrestrial vertebrates will be discussed in a future paper.

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