

Zoning of Northern Eurasia based on the fauna of pine flower, fungus and leaf-rolling weevils (Coleoptera: Nemonychidae, Anthribidae, Rhynchitidae, Attelabidae)

Районирование Северной Азии по фауне немонирид, ложнослоников и трубковертов (Coleoptera: Nemonychidae, Anthribidae, Rhynchitidae, Attelabidae)

Yu.S. Ravkin^{*,**}, I.N. Bogomolova^{*}, S.M. Tsybulin^{*}, A.A. Legalov^{*}
Ю.С. Равкин^{*,**}, И.Н. Богомолова^{*}, С.М. Цыбулин^{*}, А.А. Легалов^{*}

* Institute of Systematics and Ecology of Animals, Siberian Branch of Russian Academy of Sciences, Frunze Str. 11, Novosibirsk 630091 Russia. E-mail: zm@eco.nsc.ru.

** Институт систематики и экологии животных СО РАН, ул. Фрунзе 11, Новосибирск 630091 Россия.

** Tomsk State University, Prosp. Lenina 36, Tomsk 634050 Russia.

** Томский государственный университет, просп. Ленина 36, Томск 634050 Россия.

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Ключевые слова: районирование, Nemonychidae, Anthribidae, Rhynchitidae, Attelabidae, кластерный анализ, факторы, корреляция.

Abstract. Habitat data for 231 species of pine flower, leaf-rolling and fungus weevils were subjected to cluster analysis to develop a classification of fauna distribution, which encompasses five regions, seven sub-regions, eight provinces, and eight districts. The total information value of the model obtained equals 87% of Jaccard's similarity matrix variance for the given faunas ($r = 0.93$).

Резюме. По сведениям об ареалах 231 вида немонирид, трубковертов и ложнослоников с помощью кластерного анализа составлена фаунистическая классификация, в которой представлено пять регионов, семь подобластей и по 8 провинций и округов. Общая информативность полученных представлений равна 87 % дисперсии матрицы коэффициентов сходства конкретных фаун (коэффициент корреляции 0,93). Русский вариант статьи размещен на странице лаборатории зоомониторинга на сайте Института (<http://eco.nsc.ru/lab4.html>) в разделе «Публикации».

The goal of the present analysis was not so much to perform zoning of Northern Eurasia based on the habitats of leaf-rolling and fungus weevil species (for simplicity hereafter referred to as weevils) as to compare these zoning results with our earlier data obtained using exactly the same approach for the flora of woody plants, as well as for the fauna of vertebrate and invertebrate species [Ravkin et al., 2014a, b, 2015]. In doing so, we aimed at gaining insight into peculiarities and similarities between floristic and faunistic heterogeneity, which

may ultimately help establish a unified floristic and faunistic zoning of this territory.

Materials and methods

Habitat data for 231 species of leaf-rolling weevils and fungus weevils were taken from Legalov [2001a, 2001b, 2002a, b, c, 2004, 2005, 2006a, b, c, 2006d, e, 2007a, b, c, 2009a–e, 2010a, b, c, 2011a, b], Legalov, Korotyaev [2006]; Legalov, Legalova [2005]; Legalov, Opanassenko [2000]; Legalov, Shevnin [2007a, 2007b]; Legalov, Sitnikov [2000]; Legalov, Streltsov [2005]; Legalov et al. [2006]; Opanassenko, Legalov [1996]. Detailed description of the methods and approaches used in our analysis have been published elsewhere [Blinova, Ravkin, 2008; Ravkin, Livanov, 2008; Ravkin et al., 2010a, b, 2013, 2014a, b]. Briefly, habitat mapping data for select species of beetles were extracted for 597 sites curated by the Biodat database (www.biodat.ru) and converted into a binary format (if the species range covers > 50 % of the territory of the given site, it is assigned a value of 1, otherwise 0). Next, Jaccard's similarity coefficients were calculated across all pairs of sites for all species [Jaccard, 1902]. The matrix thus obtained was used for cluster analysis using factor classification algorithm [Trofimov, Ravkin, 1980]. The territories formed by the clusters thus obtained were operationally considered as subregions of the Palearctic region. Northern Eurasia is delimited by the borders of the former USSR as of 1991. Representative subre-

gion-level clusters were run twice through the same pipeline to obtain finer subdivision hierarchies. Results from the first run were defined as forming a province, whereas the second run produced district-level clusters. As a result, hierarchical classification was established. Additionally, using the same platform and inter-cluster similarity data, we performed merging of subregions and satellite districts into regions. This allowed joining of clusters that were weakly yet broadly linked with each other.

If one thinks of the coefficient matrix as of a landscape, the first two clustering steps should produce «surface»-level differences, whereas downstream cluster-joining step visualizes underlying, «subsurface» features. These can only be uncovered when the strongest differences are removed or masked. Merging of two classifications is superficially similar to hierarchy-based visualization, wherein the region level corresponds to weak, yet overall general similarities, and the subregion level mirrors a strong, yet somewhat local degree of similarity. Therefore, zoning procedure uncovers gradual faunistic changes analogous to geobotanical series. These encompass weakly similar, yet related spatial groups. Subregional series, nonetheless, tend to display more pronounced intra- rather than inter-series similarity.

Aggregation algorithm used in our work joins the objects being classified into unspecified number of groups so that they cover maximal variance of the similarity matrix. Recomputation of the similarity matrix to evaluate the influence of clusterization on the variance is performed by subtracting average value from all similarity coefficients of the probes forming each class followed by adding the average value of interclass similarity to all the interclass coefficients. To uncover taxonomic hierarchy, we used information about the order of appearance of a given taxon when splitting the body of clusters according to their fauna and representativity of the lower-ranking clusters and taxons. The hierarchical classification obtained thus far includes four taxonomic levels.

1. Regions. These are the territories identified based on the secondary aggregation of primary clusters.

2. Subregions are defined as a result of primary clustering of the territory. We require that each of the subregions contains at least 8 clusters. Subregions come in two «flavors»: enclave (i.e. composed of isolated pieces of land sharing similar environmental features, such as islands), and non-enclave (those having common borders).

3. Provinces are the territories obtained upon secondary subdivision of subregions having sufficient numbers of clusters. Each of the provinces is set to have at least three clusters and be enclave or non-enclave-type.

4. Districts:

4.1 — autonomous (satellite) districts ranking-wise are equal to subregions, as they are obtained upon first-line subdivision. Importantly, each of them encom-

passes fewer than 8 clusters, i.e. they are less representative than subregions. Autonomous districts are part of a subregion or a province, whereas satellite districts are juxtaposed to subregions or provinces.

4.2 — non-autonomous districts are formed by territories obtained via secondary subdivision of province faunas, with each district encompassing at least 8 clusters.

To visualize linkage between faunistic heterogeneity of weevil species and major structural environmental and seasonal factors, hierarchical clustering and structure graph were used. Graph is constructed based on the estimates of subregion-level correlation degrees. Correlation between environmental factors and faunistic heterogeneity of the territory is estimated using linear quantitative approximation algorithm (quantitative analog of regression model) [Ravkin et al., 1978]. Environmental factors are expressed using a grading scale (for instance, «high–average–low» or «western–central/mid–eastern»). It must be kept in mind that both the classification as well as the classification-based map provide a very broad image of spatial heterogeneity of weevil species fauna. They serve to illustrate the concept as a whole, rather than to show the details of species habitats or faunistic composition.

Similarity graph is constructed using correlation pleiades approach [Terentjev, 1959]. This graph illustrates basic subregion-level trends in variability of weevil species fauna and shows greater degree of intra- rather than interregional similarity.

Results and Discussion:

Zoning

We used cluster analysis to identify five faunistic regions in Northern Eurasia, namely: Northern coastal region, Northern continental region, Central region, Southwestern region, and Southeastern region. Each region encompasses seven subregions, generally named according to the predominant zones and subzones that form them. Their number is provided in the end of the taxon description, beginning with subregion level (Fig. 1).

The classification obtained is given below.

I. Northern coastal region.

1 — Northern coastal subregion (no weevil species recorded; 56 tundra clusters, 7 polar desert clusters, 1 sparse woodland).

II. Northern continental region.

2. Northern continental sparse-woodland subregion (prevailing species: *Byctiscus populi* (Linnaeus, 1758), *B. betulae* (Linnaeus, 1758), *Gonotropis crassirostris* (Sharp, 1891); average total occurrence 2; number of species 3; sparse-woodland species 52¹).

¹ Hereafter, these values follow the same order, with their names omitted. Prevailing/leader species are listed in order of decreasing occurrence; when equal in occurrence, the species are listed alphabetically.

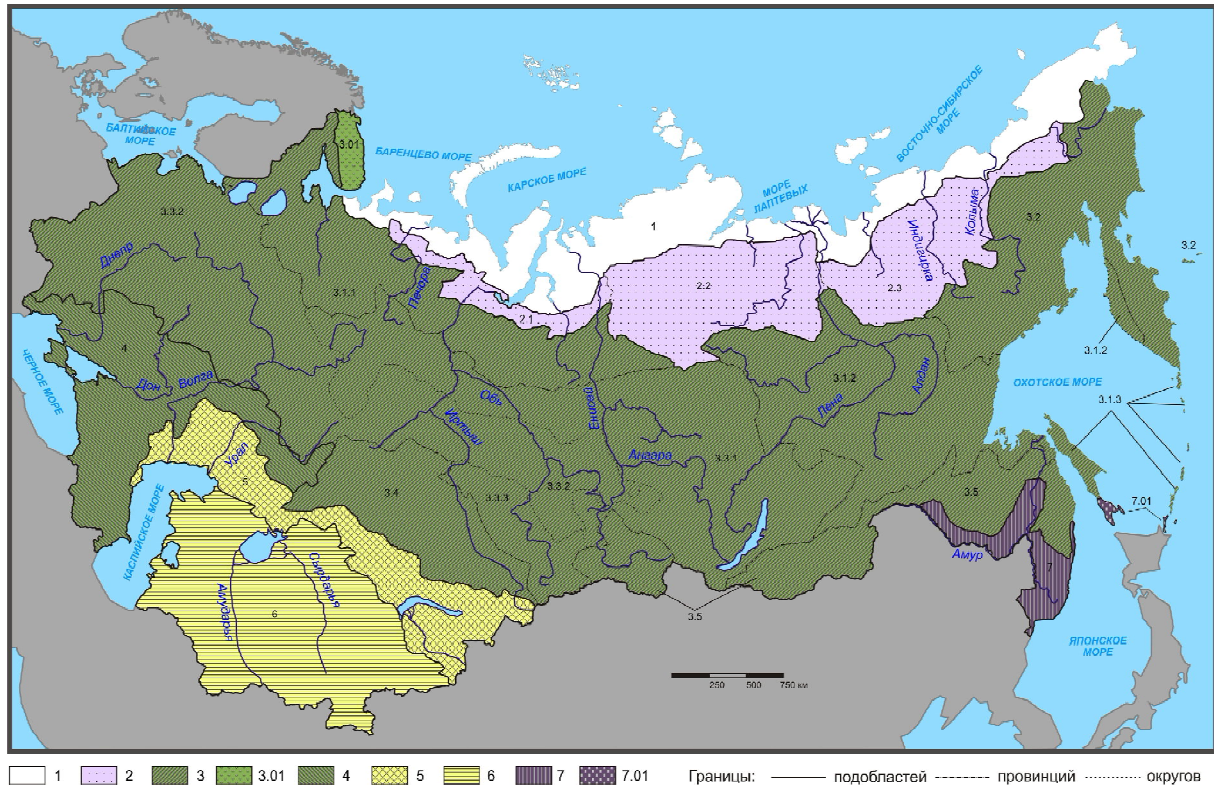


Fig. 1. Zoning of Northern Eurasia based on the fauna of weevil beetle species. Regions are color-coded on the map. Subregions and provinces are delimited by a dashed line, districts are denoted with a numerical code and are separated with borders. Subregions and provinces are numbered from 1 to 4; provinces are named using decimal numbering wherein the first digit is the number of the subregion they belong to and the second digit is the number of the subregion or province (for instance, 4.2). Three-digit numerical coding is used for naming non-autonomous districts: the first and second digits denote the subregion and province numbers it maps to, and the third digit denotes the district number (for instance, 3.2.2). Naming of the autonomous (satellite) districts is composed of the number of the subregion it maps to or borders, which is followed by the zero and the individual district number (for instance, the code 2.01 should be read as the first autonomous district adjacent to the second subregion). Non-autonomous districts are labeled with three-digit indices and are delimited by borders.

Figure labels: Regions (I–V), subregions 1–9. I. Polar: 1 — Polar desert/tundra (no bark beetles present); II. Tundra/sparse woodland: 2 — Western sparse woodland, 3 — Eastern sparse woodland, III. Kuril-Kamchatka-Okhotsk sparse woodland/tundra; IV. Central: 5 — Central temperate forest, 6 — Caucasus temperate forest, 7 — Southeast Sakhalin-Ussuri temperate; V. Central Asian semidesert-desert: 8 — Caspian northwest semidesert-steppe, 9 — Central Asian semidesert-desert. Borders of: Regions, subregions, districts.

Рис. 1. Районирование Северной Евразии по фауне немоихид, трубковёртов и ложнослоников (характеристики таксонов см. в классификации). Регионы обозначены тональностью, подобласти и провинции выделены штриховкой, округа — цифровым кодом и отделены друг от друга границами. Подобласти имеют простую нумерацию (от 1 до 4), провинции — двузначный код, составленный из номера подобласти и провинции, разделённых точкой (например, 4.2). Неавтономным округам присвоен трёхзначный цифровой код. Первая цифра в нём означает номер подобласти, вторая — номер провинции, к которой он относится, третья — номер округа (например, 3.2.2). Код автономных (спутниковых) округов включает номер подобласти, в которую он входит или к которой примыкает, и через ноль — собственный двоичный номер (например, код 2.01 означает первый автономный округ, соседствующий со второй подобластью). Неавтономные округа на карте помечены трёхзначным цифровым индексом и выделены только границами.

Provinces:

2.1 — European West Siberian (*Byctiscus populi*, *B. betulae*; 1; 2; sparse-woodland species 9),

2.2 — Central Siberian (*Byctiscus populi*, *B. betulae*; 1; 2; sparse-woodland species 22),

2.3 — East Siberian (*Byctiscus populi*, *Gonotropis crassirostris*; 2; 2; sparse-woodland species 21).

III. Central region.

3. Baltic-Pacific woodland subregion (sites 2, 3) (*Platystomos albinus* (Fabricius, 1758), *Byctiscus populi*, *B. betulae*, *Anthribus nebulosus* Forster, 1770, *Gonotropis crassirostris*; 16; 78; taiga and woodland

species 210, sparse-woodland species 25, subarctic tundra species 16, forest-steppe and steppe species 20 and 34, respectively).

3.1 — (Northeastern transeurasian province (*Gonotropis crassirostris*, *Platystomos albinus*, *Anthribus nebulosus*, *Byctiscus populi*, *Apoderus coryli* (Linnaeus, 1758); 9; 28; taiga species 85).

Districts:

3.1.1 — Northern European–Central Siberian (*Byctiscus populi*, *Gonotropis crassirostris*, *Platystomos albinus*, *Anthribus nebulosus*, *Apoderus coryli*; 7; 8; Northern- and mid-taiga species, 30 and 10).

3.1.2 — East Siberian/Okhotsk (*Byctiscus populi*, *Gonotropis crassirostris*, *Platystomos albinus*, *Anthribus nebulosus*; 10; 22; taiga species 39).

3.1.3 — Northern Sakhalin/Kuril (*Attelabus cyanellus* Voss, 1925, *Deporaus betulae* (Linnaeus, 1758), *Caenorhinus mannerheimi* (Hummel, 1823), *Auletobus sanguisorbae* (Schrank, 1798), *Byctiscus rugosus* (Göbler, 1830); 10; 18; mid- (3)- and Southern taiga (3) species).

Provinces:

3.2 — Okhotsk (*Platystomos albinus*, *Attelabus cyanellus*, *Gonotropis crassirostris*, *Byctiscus populi*, *Compsapoderus erythropterus* (Gmelin, 1790); 4; 8; subarctic tundra and sparse-woodland species: 16 and 25).

3.3 — Southwestern European / Central Siberian (*Byctiscus populi*, *Deporaus betulae*, *Caenorhinus mannerheimi*, *Anthribus nebulosus*, *Temnocerus caeruleus* (Fabricius, 1798); 22; 54; taiga and woodland 103, forest-steppe 20, and steppe 6).

Districts:

3.3.1 — Southern European–Central Siberian (*Apoderus coryli*, *Byctiscus populi*, *Deporaus betulae*, *Caenorhinus mannerheimi*, *Temnocerus caeruleus*; 15; 28; mid-, Southern-, and mountainous taiga 50).

3.3.2 — European — West Siberian (*Apoderus coryli*, *Rhaphitropis marchica* (Herbst, 1797), *Byctiscus populi*, *Deporaus betulae*; 28; 47; Southern taiga and woodland, 17 and 32, woodland-steppe, 20).

3.3.3 — Subaltai/Altai (*Byctiscus populi*, *B. betulae*, *Deporaus betulae*, *Caenorhinus mannerheimi*, *Temnocerus caeruleus*; 21; 30; steppe 6, mountainous taiga 4).

Provinces:

3.4 — Tobol-Irtysh (*Neocoenorhinus germanicus* (Herbst, 1797), *Temnocerus nanus* (Paykull, 1792), *Epirhynchites auratus* (Scopoli, 1763), *Byctiscus populi*, *B. betulae*; 14; 24; steppe 18).

3.5 — Baikal-Amur (*Byctiscus populi*, *Deporaus betulae*, *Caenorhinus mannerheimi*, *Auletobus sanguisorbae*, *Byctiscus rugosus*; 22; 48; taiga 22, steppe 10).

3.01 — Kola satellite (*Apoderus coryli*, *Deporaus betulae*; 2; 2; tundra 2, sparse-woodland 1).

4. Black Sea subregion (*Epirhynchites auratus*, *Aletinus akinini* (Faust, 1885), *Byctiscus populi*, *Neocoenorhinus germanicus*, *Temnocerus nanus*; 28; 62; steppe 47, woodland 13, semidesert 3).

IV. Southwest region.

Subregions:

5. Kazakhstan desert/semidesert (*Byctiscus populi*, *B. betulae*, *Epirhynchites auratus*, *Bruchela orientalis* (Strejcek, 1982), *Nemonyx canescens* Solsky, 1881; 6; 19; semidesert 28, desert 11, mountain-steppe 1).

6. Central Asian desert/mountain-steppe (*Epirhynchites auratus*, *Aletinus akinini*, *Nemonyx canescens*, *Epirhynchites sarafschanicus* (Voss, 1929), *Eurostanletes rubrorufus* (Solsky, 1880); 4; 23; desert 40, semidesert 6, mountain-steppe 12).

V. Southeast region.

7. Southeastern continental woodland subregion (cluster 6) (*Apoderus coryli*, *A. jekelii* Roelofs, 1874, *Compsapoderus erythropterus*, *Neocoenorhinus interruptus* (Voss, 1920), *Deporaus unicolor* (Roelofs, 1874); 53; 101; woodland 9, Southern taiga 2).

7.01 — Southeastern insular Sakhalin-Kuril Southern taiga satellite district (cluster 5) (*Apoderus coryli*, *A. jekelii*, *Neocoenorhinus interruptus*, *Deporaus unicolor*, *Byctiscus puberulus* (Motschulsky, 1860); 68; 94; Southern taiga 2).

As it follows from the above classification, there is incomplete overlap between the borders of subzones and distribution of species. This is likely due to the widespread distribution of species beyond their typical zones and subzones.

Spatial structure and organization of the weevil fauna

Spatial variance of similarity between the taxons identified in our classification is visualized by the structure graph, which is constructed using a matrix of Jaccard's coefficients calculated for average values found in subregions and satellite districts. The major vertical trend is coincident with increased heat availability and lower moisture availability as one moves southwards. This trend is illustrative of a gradual change in the fauna of weevils from their zero prevalence in polar deserts, most of the tundra and sparse woodlands to woodland and woodland-steppe regions and to steppes and deserts. Horizontal bars denote provincial changes east- and westwards within central temperate territories.

As is shown in the graph, the total number of weevil species and their total occurrence decrease as one moves south- or northwards, away from the central taxons. As a rule, these parameters also tend to increase eastwards, except for one case, where Kazakhstan subregion encompasses fewer species than the Central Asian subregion. The degree of faunistic similarity between the columns of subregions in the upper (northern) part of the graph is lower compared to the subregions found in its lower (southern) part.

We estimated the coefficient of informativity of the hierarchical classification and the structure graph, as well the correlation with environmental factors and combinations thereof using variance of Jaccard's similarity coefficients. To do so, we implemented a method of linear quantitative approximation using graded values [Ravkin et al., 1978]. This approach is a quantitative analog of regression model and allows performing quantitative comparisons between past and present classifications used for zoning purposes.

In the context of weevil species inhabiting Northern Eurasia, the most pronounced correlation was observed for their faunistic heterogeneity and heat availability (which was calculated as a combined estimate of similarity in terms of zonality, provinciality, and altitudinal zonality) and regionality (56 and 53 %, respectively).

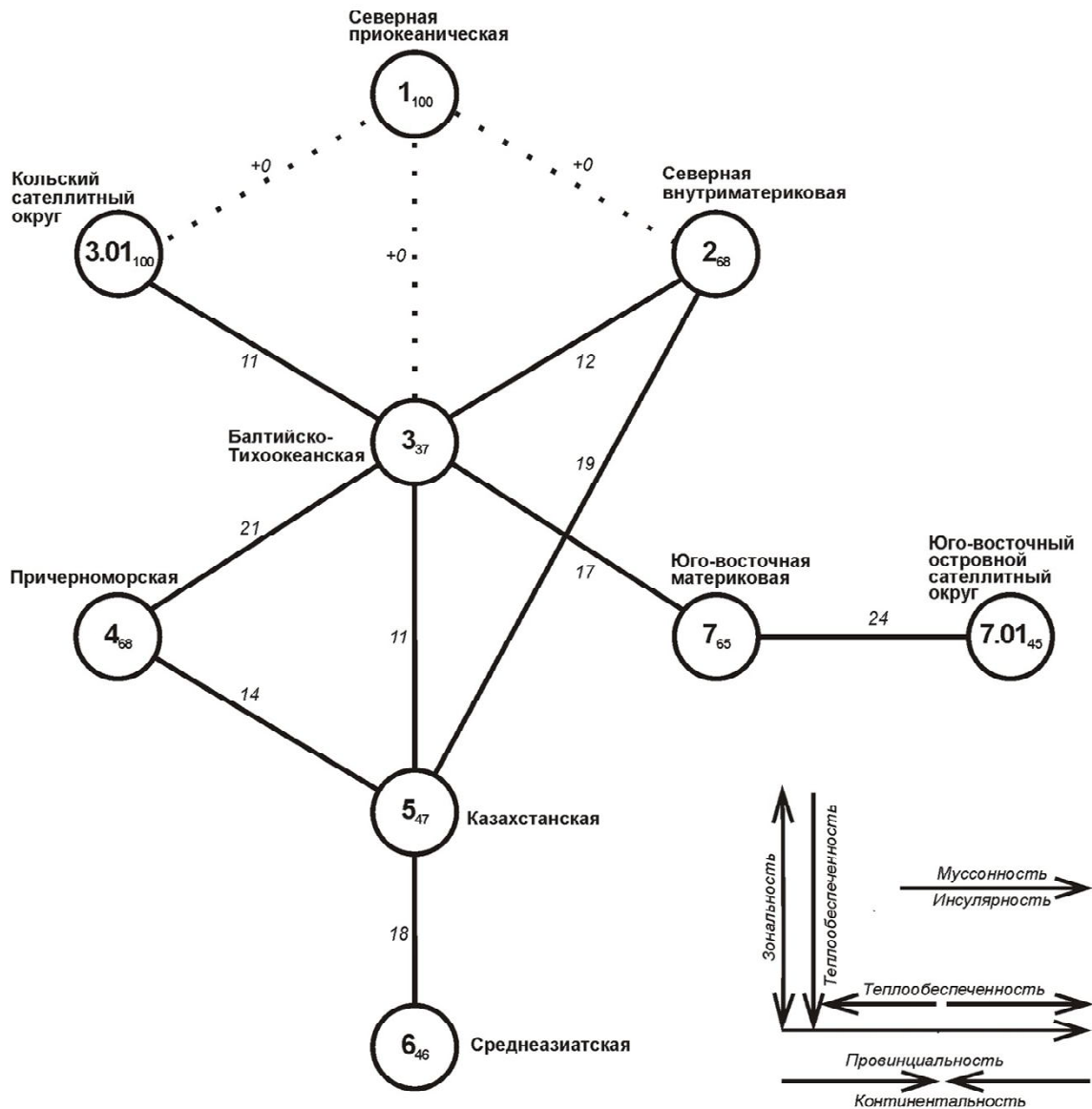


Fig. 2. Subregion-level spatial and typological structure of the fauna of weevil beetle species in Northern Eurasia. Numbers of the taxons are shown inside the circles; indices denote intragroup similarity. Similarity above the significance level is shown by solid connecting lines; dashed lines indicate similarity below significance level. Numbers near the connecting lines correspond to the estimates of intergroup similarity. Arrows by the major structural environmental factors indicate the direction of their increasing influence as well as faunistic trends.

Рис. 2. Пространственно-типологическая структура фауны немонирид, трубковёртов и ложнослоников Северной Евразии на уровне подобласти. Внутри значков приведены номера таксонов соответствующей классификации, индексом — внутригрупповое сходство. Сплошные линии между значками означают существенное сверхпороговое сходство, пунктирные — запороговое. Около этих линий обозначены значения межгруппового сходства. Около значков, кроме наименования подобластей, приведены названия трёх лидирующих видов указанных групп жуков, средняя суммарная встречаемость и общее число отмеченных видов. Стрелки около перечня основных структурообразующих факторов среды указывают направление увеличения их влияния и фаунистические тренды.

Individual correlation with zonality reached 51 % of the variance (Table 1). As for post-glaciation expansion and provinciality, the degrees of correlation are two- and six-fold lower. The influence of insularity and altitudinal zonality is little to moderate, because islands and mountain systems having distinct weevil species faunas are typically small in size.

If one turns to alternative zoning strategies, such as approximation of similarity matrices obtained for beetle species fauna [Semenov-Tyan-Shanskiy, 1936], using biogeography data ([Udvardy, 1975], lateron refined by Voronov and Kucheruk, 1977), climatic or physiographic data [The Atlas of the USSR, 1983] the estimates obtained are slightly lower. Notably, compared to our

approach, all the above-listed zoning variants accommodate 2- to 4-fold weaker variance in Jaccard's similarity coefficients obtained for weevil species fauna inhabiting Northern Eurasia.

Thus, faunistic heterogeneity of weevil species correlates most strongly with heat availability, much as was reported for terrestrial groups of animals and woody plants. For bark beetle fauna, regionality shows the highest correlation, as provinciality values decrease. When all factors are taken into account, data on bark beetle fauna heterogeneity result in the highest estimates (as compared to those of woody plants, terrestrial vertebrates, fishes and cyclostomes, and weevils (1.6-, 1.2, 1.3 and 1.3-fold less, respectively).

Diagonal shift of natural zones vegetation-wise is well-known. Significant difference in bird distribution as well as the diagonality of the forest zone subdivision, are clearly visible on the map plotted by Shtegman [1938]. It must be noted that since he observed widespread interpenetration in the distributions of certain types of fauna, he chose not to perform zoning and attributed these differences to the expansion of bird species from their centers of origin or glacial refugiums. We are inclined to explain this difference (i.e. distinct angle formed by the borders vs zonality angle) to post-glacial repopulation of original habitats and to similarity in the total present-day contribution of heat availability, as one moves northwards or away from the seas and oceans, i.e. we attribute this to a combination of zonality and continentality. As a result, the diagonal we observe for the terrestrial vertebrate dataset crosses the map from the Kola Peninsula to the Lake Baikal, whereas it is shifted south- and west-wards (from the Baltics to Altai) when we consider other groups, such as woody plants, bark beetles, fishes, and cyclostomes.

Total coefficient of determination of the model obtained equals 87 % of Jaccard's similarity matrix variance for these faunas (which translates to the correlation coefficient, $r = 0.93$).

Conclusion

When comparing the zoning results of Northern Eurasia for woody plant flora, and weevil species terrestrial vertebrate fauna, the numbers of the regions identified are the same (3), which is in contrast to the number obtained for weevil species (5). Notably, the borders obtained for these groups of animals and plants show poor overlap. Northern region does not appear to follow this rule, though. The differences observed here are as follows: for woody plants, the Northeastern-most part is merged with the Eastern region, whereas for terrestrial vertebrates and beetles, this part is joined with the Northern polar region. Interestingly, this region appears as a thin stripe in the coastal part, extending down to Kamchatka, and even further south to the Kuril Islands. No such north-to-south interdigitation is observed for the weevil species. We speculate that this interplay may stem from quite a peculiar habitat distri-

bution of reptiles. Namely, the northern border of both reptile and bark beetle species occurrence (in contrast to the rest of terrestrial vertebrates) is significantly shifted southwest [Ravkin et al., 2010a].

Western border of the Eastern region, as derived from the woody plant species dataset, is also significantly shifted southwestwards. This results in the separation of southern and northwestern parts of North Eurasia, thereby forming a Western region. Accordingly, the diagonal border inferred from the woody plant analysis stretches from the Gulf of Finland to Altai, whereas it is positioned differently (from the Kola Peninsula to Baikal), if one considers terrestrial vertebrate data. Notably, this border delimits territories ranked as regions, as applied to plants, fishes, and cyclostomes, in contrast to the subregional or provincial status, if one considers terrestrial animals. As for the bark beetles, the borders of the regions resemble zonal borders, and the diagonal thus formed stretches from the southern part of the Baltic states //southern Baltic Sea coast// to Altai.

We attribute these differences to distinct dispersal strategies: animals are known to resettle actively, whereas plants disseminate passively and so some groups and species of plants expand slower. Clearly, another important contributing factor is warm-bloodedness of terrestrial vertebrates, which mediates their overall greater tolerance to the deficit of heat. Additional opportuni-

Table 1. Estimates of correlation between environmental factors and faunistic heterogeneity of weevil species in Northern Eurasia

Таблица 1. Оценка связи факторов среды с неоднородностью фауны немонирид, трубокóвертов и ложнослоников Северной Евразии

Factor, regime	Contributing variance, %
Heat availability (zonality, provinciality and altitudinal zonality combined)	56
Regionality	53
Zonality	51
Post-glacial expansion	26
Provinciality	9
Insularity	0.6
Altitudinal zonality	0.2
All factors combined	68
Classification-based regimes	71
Structure-based regimes	64
All regimes	77
Total	87
Zoning based on beetle species fauna	30
Climatic zoning	34
Biogeographic zoning	29
Physiographic zoning	16

ties to travel north and east are actively used by seasonally migrating birds as well as several mammalian species. They take advantage of the northern territories in summer and travel south for the winter. Nonetheless, the overall south-to-north trend is common for all the groups of species examined so far.

Non-homogeneity of the woody plant flora slightly exceeds that of the fauna species (73 and 64 %), and unified values are the same (80 and 81 % variance). Variance for appropriate similarity matrices is taken into account by biogeographic and climatic zoning of the fauna distribution, with physicochemical data providing lower variance values. Most likely this is due to highly subjective delimiting of the regions by different authors.

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