

ECOLOGICAL NICHE EVOLUTION AND ITS RELATION TO PHYLOGENY AND GEOGRAPHY: A CASE STUDY OF ARVICOLINE VOLES (RODENTIA: ARVICOLINI)

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Relations between ecological niches, genetic distances and geographic ranges were analyzed by pair-wise comparisons of 43 species and 38 intra-specific phylogenetic lineages of arvicoline voles (genera *Alexandromys*, *Chionomys*, *Lasiopodomys*, *Microtus*). The level of niche divergence was found to be positively correlated with the level of genetic divergence and negatively correlated with the level of differences in position of geographic ranges of species and intraspecific forms. Frequency of different types of niche evolution (divergence, convergence, equivalence) was found to depend on genetic and geographic relations of compared forms. Among the latter with allopatric distribution, divergence was less frequent and convergence more frequent between intra-specific genetic lineages than between either closely-related or distant species. Among the forms with parapatric distribution, frequency of divergence gradually increased and frequencies of both convergence and equivalence gradually decreased from intra-specific genetic lineages via closely related to distant species. Among species with allopatric distribution, frequencies of niche divergence, convergence and equivalence in closely related and distant species were similar. The results obtained allowed suggesting that the main direction of the niche evolution was their divergence that gradually increased with time since population split. Some initial level of niche divergence was shown to be a necessary condition providing a possibility of co-occurrence and sympatric distribution of species, whereas moderate interspecific competition of sympatric species could be an effective driver of their further niche divergence.

ЭВОЛЮЦИЯ ЭКОЛОГИЧЕСКИХ НИШ И ЕЁ СВЯЗЬ С ФИЛОГЕНИЕЙ И ГЕОГРАФИЕЙ: ИССЛЕДОВАНИЕ СЕРЫХ ПОЛЁВОК (RODENTIA: ARVICOLINI)

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Взаимоотношения между экологическими нишами, генетическими дистанциями и положением ареалов проанализированы путём

попарных сравнений 43 видов и 38 внутривидовых филогенетических линий полёвок трибы Arvicolini (роды *Alexandromys*, *Chionomys*, *Lasiopodomys*, *Microtus*). Показано, что уровень дивергенции ниш положительно скоррелирован с уровнем генетической дивергенции и отрицательно — с уровнем различий в географическом положении ареалов видов и внутривидовых форм. Частоты различных типов эволюции ниш (дивергенция, конвергенция, стабильность) варьируют в зависимости от уровней генетических и географических различий сравниваемых форм. Дивергенция ниш отмечена реже среди аллопатрических форм, конвергенция ниш — чаще между внутривидовыми генетическими линиями, чем между как близко-, так и дальнеродственными видами. Среди парапатрических форм частота дивергенции постепенно возрастает, а частоты конвергенции и стабильности постепенно снижаются в ряду от внутривидовых генетических линий через близкородственные виды к дальнеродственным видам. Среди аллопатрических видов частоты дивергенции, конвергенции и стабильности ниш у близкородственных и дальнеродственных видов не различаются. Полученные результаты свидетельствуют о том, что основным направлением эволюции ниш является их дивергенция, уровень которой постепенно увеличивается со временем, прошедшим после разделения популяций. Определённый начальный уровень дивергенции ниш является необходимым предварительным условием, разрешающим сосуществование двух видов; межвидовая конкуренция умеренной интенсивности в условиях симпатрии видов может служить эффективным усилителем дальнейшей дивергенции их ниш.

1. Introduction

Ecological niche is one of the central but at the same time most controversial concepts in current ecology. Originally, the niche was considered as an attribute of the environment but later, after Hutchinson's (1957) introduction of the concept of multidimensional hyperspace of niche variables, the niche definitions progressively shifted to understanding niche as an attribute of population (or species) in relation to its environment (Colwell, 1992). Two aspects of the niche concept are usually distinguished based on the original definitions, Grinnellian and Eltonian niches. The Grinnellian niche (sometime referred to as habitat or ecotope, see Whittaker et al., 1973) is defined by environmental variables on a broad (geographic) scale, relevant to understanding coarse-scale ecological and

geographic properties of species (Grinnell, 1917; Vandermeer, 1972; Whittaker et al., 1973; James et al., 1984; Soberon, 2007). The Eltonian niche is defined by biotic interactions and resource variables at a local (intra-community) scale (Elton, 1927; MacArthur, 1968; Vandermeer, 1972; Leibold, 1995; Soberon, 2007).

Hutchinson (1957) had introduced an idea of recognition of fundamental and realized niches, and this became widely accepted by later authors. Fundamental niche was defined as “pre-interactive” describing potential distribution of a species (population) in multi-dimensional ecological space limited by the species' eco-physiological tolerances. Realized niche was defined as “post-interactive” describing actual distribution of a species (population) in multi-di-

mensional ecological space in the presence of its competitors. Pulliam (2000) expanded the concept of realized niche by including the influences of dispersal limitation and source-sink dynamics (together with inter-specific competition) in it. He demonstrated that the realized niche can be narrower or wider than the fundamental niche, depending on the combination of acting forces. Vandermeer (1972) defined the Grinnellian niche as pre-interactive (fundamental) and the Eltonian niche as post-interactive (realized), but Soberon (2007) insisted on application of the concepts of fundamental and realized niches to both Grinnellian and Eltonian niches.

The ecological niche describes eco-physiological aspects of the phenotypes of a population (Colwell, 1992). Each population contains a variety of ecologically specialized phenotypes, and individuals of each phenotype have maximal fitness within a specific part of a resource axis present in the environment (Roughgarden, 1972). Consequently, the shaping of niche characteristics can be viewed as an evolutionary phenomenon (Knouft et al., 2006). Niche evolution attracted increasing attention in the theoretical literature (Roughgarden, 1972; Holt, Gaines, 1992; Holt, 1996; Proulx, 1999; Ackermann, Doebeli, 2004), especially in relation to the problem of niche conservatism (Peterson et al., 1999; Graham et al., 2004; Knouft et al., 2006; Pearman et al., 2008; Warren et al., 2008). Most publications on this subject are devoted to comparison of niches among species of different phylogenetic relatedness.

It is well-known that analysis of intra-specific geographic variation is a powerful tool in evolutionary studies (Mayr, 1965), however, analyzes of intra-specific geographic variation of niche attributes are rare. At the same time, it was demonstrated that species' ecological niches, both fundamental and realized, can vary geographically

due to intra-specific niche differentiation and geographic changes in environmental conditions (James et al., 1984; Peterson, Holt, 2003; Devictor et al., 2010).

The ecological niche can be characterized by two parameters, the mean (niche position or centroid) and the variance of the resource use (niche breadth or width) (Hutchinson, 1957; Vandermeer, 1972). Theoretical models of niche evolution consider the both, i. e., evolution of niche width and niche shifts (Roughgarden, 1972; Holt, Gaines, 1992; Ackermann, Doebeli, 2004; Kawecki, 2008), whereas most empirical studies of niche evolution concentrate on shifts of niche centroids (Pearman et al., 2008).

The usual method of estimation of niche divergence is measuring niche overlap using values of environmental variables in the points of occurrence of compared species, either directly or through comparison of species distribution models (SDM) (Warren et al., 2008; Broennimann et al., 2012). However, environmental data are usually spatially auto-correlated, and differences in the values of environmental variables between any two sets of points should increase with geographic distance, thus over-estimating the true niche divergence. The tests revealed significant niche differentiation in the cases, in which background conditions were non-overlapping, though such conditions cannot be used as true evidence of niche differentiation (Peterson 2011). To avoid the confounding effect of environmental spatial auto-correlation, it is necessary to compare the observed niche differences with the differences in background environments (McCormack et al., 2009). Another problem of using the niche overlap measure for niche divergence estimation is its inability to distinguish between differences in the level of divergence for non-overlapping niches.

Peterson et al. (1999) hypothesized that ecological niches evolve little at or around the time of speciation events, whereas niche differences accumulate later. Many estimates of niche divergence/conservatism, using comparison of SDM, have been published in recent years. The results of these estimates are quite controversial, and some of them contradict the hypothesis that the level of niche divergence is related to time passed after post-speciation period (for example, Warren et al., 2008; Kalkvik et al., 2012). It should be noted that SDM-based tests demonstrating significant niche similarity/identity can be considered as a true indication of niche conservatism (although without discriminating between niche equivalence and convergence). However, the tests that have demonstrated significant niche differentiation in cases, when background conditions were non-overlapping, cannot be taken as true evidence of niche differentiation (Peterson, 2011). Nevertheless, a review of SDM-based tests of niche conservatism/differentiation published between 1999 and 2008 (Peterson, 2011) demonstrated that niche conservatism was found in more than 70% of cases of within-species and between sister species comparisons, but in less than 50% of cases in comparisons among closely-related (but not sister) species and across monophyletic lineages of species.

Patterns of geographic distribution of species can considerably modify the patterns of their niche evolution. Widely accepted in ecology and evolutionary biology is the statement that “complete competitors cannot coexist, or ecological differentiation is the necessary condition for coexistence”, which is known as “the competitive exclusion principle”, “Gause’s principle”, or “Grinnell’s axiom” (Hardin, 1960). This principle pro-

duced an idea that the niche divergence is a consequence of ecological segregation of species during their secondary contact following allopatric speciation event (Diamond 1973, McCormack et al., 2009), although interaction between interspecific competition and niche divergence theoretically may be not so unequivocal (Abrams, Cortez, 2015).

In this paper, I shall test the two hypotheses concerning niche divergence. The first hypothesis is that niche divergence increases with time since speciation events, so niche divergence should be positively correlated with the genetic distance between compared taxa. The second hypothesis is that niche divergence should be higher between sympatric than between allopatric taxa. I shall test these hypotheses using data on the grey voles (Arvicolini).

2. Material and Methods

Species were selected for the analyses based on the following two criteria: 1) existence of at least 16 known points of occurrence allowing distribution modeling and niche shift analysis and 2) existence of available mitochondrial DNA data for estimation of genetic distances. Based on these criteria, 43 species and 39 intraspecific genetic lineages were selected for the analyses. Information on selected species and the number of record points used for the present analyses are provided in the Table 1*.

Distributional and environmental data. Records of occurrences were taken from previously published source (Shenbrot, Krasnov, 2005) and were supplemented with museum records and publication data that became available later. Data on most museum records were obtained using Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>). Additional information was

*See all tables at the end of the article.

obtained directly from Zoological Museum of Moscow University, Naturhistorisches Museum Wien, Prirodoslovni muzej Slovenije (Ljubljana), Kemerovo State University Museum (<http://museum.kemsu.ru/catalog>) and from M.V. Vinarski personally (Omsk State Pedagogical University). Most of these data had no original GPS coordinates, so they were geo-referenced using Geographic Names Gazetteers (available at http://earth-info.nga.mil/gns/html/cntry_files.html) and checked subsequently for suitable habitats using Google Earth. Data that could not be geo-referenced precisely, such as those provided by Mitchell-Jones et al. (1999) as presence/absence in a grid 50×50 km, were excluded from the analysis.

Environmental data for SDM and niche divergence analyses were used as 30 arc-second grids (1 km resolution approximately) and were represented by climate, relief, and vegetation variables. The climate variables (annual mean temperature, mean monthly temperature range, mean temperatures of coldest and warmest quarters, maximal temperature of warmest month, minimal temperature of coldest month, temperature annual range, annual precipitation, and precipitation of wettest quarter) were obtained from WORLDCLIM Version 1.4 (Hijmans et al., 2005) available at <http://www.worldclim.org>. Slope data were derived from altitude (extracted from GTOPO30 data set distributed with ArcGIS) using the Spatial Analyst module of ArcMap. The data on Normalized Difference Vegetation Index (NDVI) were obtained from VEGETATION Programme (<http://www.spot-vegetation.com>; now <http://www.vito-eodata.be>; data for 1998–2007, each a ten-day estimate) and averaged by seasons (winter, spring, summer, and autumn) across all available years. The NDVI is an index of greenness that is directly correlated with productivity and green vege-

tation biomass and is widely used in ecological studies (Pettorelli et al., 2005).

DNA data and estimation of genetic distances. Mitochondrial DNA, especially *cytb*, is traditionally the most popular genetic source used for phylogenetic reconstructions in rodents generally and in Arvicolinae particularly (Jaarola et al., 2004; Buzan et al., 2008). Of course, phylogenetic reconstructions based on mitochondrial genes only can be biased due to ancient mtDNA introgressions, so it is preferable to use a set of both mitochondrial and nuclear DNA (Kohli et al., 2014). However, the data on *cytb* are available for more than 80% of arvicoline species, whereas available data on other genes cover a very limited number of species. So that I used *cytb* data for phylogenetic reconstruction and genetic distance estimations.

For most of the analyses of genetic distances of within-species lineages, phylogeographic structure was borrowed from the following sources: Bannikova et al. (2010) and Lissovsky et al. (2010) for *A. middendorffii*; Brunhoff et al. (2003) for *A. oeconomus*; Bannikova et al. (2013) for *Ch. gud* and *Ch. roberti*; Castiglia et al. (2009) and Bannikova et al. (2013) for *Ch. nivalis*; Petrova et al. (2015) for *L. gregalis*; Jaarola, Searle (2002, 2004) and Herman, Searle (2011) for *M. agrestis*; Conroy, Neuwald (2008) for *M. californicus*; Conroy, Cook (2000) for *M. longicaudus*; Tryfonopoulos et al. (2008), Rovatsos, Giagia-Athanasopoulou (2012) and Thanou et al. (2012) for *M. thomasi*. For *M. leverniedii* and *M. subterraneus*, *cytb* sequences were retrieved directly from GenBank.

I used both complete *cytb* sequences (1143 bp) and partial sequences no less than 800 bp. One specimen per species and up to five for within-species genetic line were selected at random and used for the analysis. Alignment of sequences was performed with

ClustalW algorithm (Higgins et al., 1994) implemented in MEGA 6 (Tamura et al., 2013) with default parameters. The best model of nucleotide substitution was selected based on maximum likelihood estimation using Bayesian Information Criterion and corrected Akaike Information Criterion, the procedure implemented in MEGA 6. According to both criteria, the best model for Arvicolini appeared to be the General Time Reversible model with discrete Gamma distribution of evolutionary rates among sites and a certain fraction of evolutionarily invariable sites (GTR + G + I), which corresponds to previous findings (Jaarola et al., 2004; Buzan et al., 2008). The (GTR + G + I) model with parameters estimated by MEGA 6 software was used to calculate K2P distances with MEGA 6.

Geographic range distance/dissimilarity measurement. To estimate distance between two geographic ranges, an overlap-based metric calculated as $d = 1 - O$, where O is overlap measure, is used usually in biogeographic analyses. As overlap measure, Jaccard (Dennis et al., 1998) or Kulczynsky (Hausdorf, Henning 2003) indices are used most frequently. Overlap-based distances vary from 0 for completely overlapping geographic ranges of the same size to 1 for non-overlapping ranges independently of how far ranges are from each other. Moreover, these distances increase as the size differences between two ranges increase. To overcome these problems, Krasnov et al. (2010) proposed a standardized distance measure, $D_{St} = D_C / (D_C - D_E)$, where D_C is the distance between geometric centers of the two geographic ranges, and D_E is the distance between the edges of these geographic ranges. D_C values were measured directly on the projected maps constructed using the ArcGIS Desktop 10.3 software. For non-overlapping geographic ranges, D_E

values were measured directly as the minimal of the distances between each point of occurrence of the first species and each point of occurrence of the second species. For overlapping geographic ranges, D_E values were calculated as $D_C - D_{CE1} - D_{CE2}$, where D_{CE1} and D_{CE2} are the maximal of the distances between geometric centers and points of occurrences of the corresponding species in the area of overlap of their ranges. D_{St} equals 0 for geographic ranges with identical position of geometric centers, varies from 0 to 1 for overlapping geographic ranges, equals 1 for non-overlapping ranges that abut each other, and is greater than 1 for non-overlapping and non-abutting ranges. Due to possible errors in parameter estimates, I accepted arbitrarily that values between 0 and 0.85 indicated sympatric distribution, from 0.85 to 1.15 indicated parapatric distribution, and values exceeding 1.15 indicated allopatric distribution.

Coordinates of a range geometric center were identified using species distribution modeling (SDM). The SDMs were built with MAXENT 3.3.3k software (Phillips et al., 2006). The extent of study area or “landscape of interest” affects significantly the results of SDM (Anderson, Raza, 2010; Elith et al., 2011). To define study area of a species, I calculated first the kernel density of occurrence points of this species (using Kernel Density option in ArcGIS Desktop 10.3.1) with search radius equal 4° , and then reclassified obtained raster so that the original values of kernel density equal to or higher than 0.01 were converted to 1, while values lower than 0.01 were converted to “NoData”. This reclassified raster was used as the mask for clipping environmental variables to the study area. Models were constructed with default MAXENT settings, as these settings were demonstrated to be most appropriated for wide-ranging data (Phillips, Dudik, 2008;

Warren, Seifert, 2011). I used MAXENT logistic output which provides estimates of relative habitat suitability (Elith et al., 2011).

To delineate the areas of real species occurrence, the original model values, ranging continuously from 0 to 1, were transformed to binary 0 or 1 using a threshold value. The latter was chosen equal to the minimum training presence for species with 50 or less points of occurrence and equal to 10 percentile training presence for the species with more than 50 occurrence points. After reclassification of the original raster according with the chosen threshold value, the reclassified raster was transformed to polygons. Only polygons containing occurrence records were considered as areas of occurrence. Areas of these polygons were calculated using command “calculate geometry” in sq km, and the sum of areas of these polygons was used as estimation of geographic range size. Geographic coordinates of a range geometric center were calculated with the command “mean center” of Spatial Statistics Tools (ArcMap 10.3) with the polygons weighted by area.

Estimation of niche differentiation. I used the procedure described in detail by Shenbrot (2013) and Shenbrot et al. (2016) which is not based on SDM comparisons. To estimate the level of niche differentiation relative to the differences in background environments, I performed canonical discriminant analysis based on values of 15 environmental variables drawn from four samples: two sets of occurrence points in two regions and two sets of random points in these regions; the number of random points was equal to the number of occurrence points in each region.

As a metric for pair-wise comparisons, Shenbrot (2013) used the ratio of Mahalanobis distance (DM) between occurrence points of species A and B to Mahalanobis distance between random points (a and b) in

their geographic ranges ($R_M = DM_{A-B}/DM_{a-b}$). Mahalanobis distance is the normalized distance between group centroids in the canonical space. A ratio greater than 1 indicates true niche divergence, whereas a ratio less than 1 indicates true niche convergence. In case of allopatry, when environmental differences are high enough, this metric works well. However, in the case of sympatric populations, when the environment of the two populations is the same (the difference is close to zero), the index value become extremely high, even if the absolute values of niche differences (DM_{A-B}) are very low. To avoid this problem, Shenbrot et al. (2016) modified the above index of relative niche differentiation to $\check{R}_M = (\log_2(DM_{A-B} + 2))/(\log_2 DM_{a-b} + 2)$. As with the original index, a value greater than 1 indicates niche divergence and a value less than 1 indicates niche convergence, while in the case of identical niches and identical environments the value is equal to one. Statistical significance of this metric was assessed with 100 bootstrap replicates of occurrence and background samplings points.

In between-species comparisons, all available occurrence points were used. However, in comparisons of within-species genetic lineages, the number of genetically dated points usually was too small. To increase the number of points included in the analyses, I build minimal convex polygons (MCP) around genetically verified points for each genetic lineage. All known points of occurrence of the species that fall into the part of MCP of a given genetic lineage that was not intersected with MCPs of other genetic lineages, were considered as belonging to this lineage.

It is necessary to note that the estimations of niche shifts may reflect changes in both niche position and niche width. In the case when niche centroids are placed far from one another, niche shift (divergence or con-

vergence) may be the result of shifts of centroids, or changes in width of niches, or both. In the case when niche centroids are close to one another, niche shift will be mainly the result of the shifts of niche centroids.

All operations with maps were performed with ArcMap 10.3 including Hawth's Tools application. Statistical analyses were carried out in STATISTICA (StatSoft Inc. for Windows Release 7.0 package).

3. Results

Results of estimations of niche divergence for within-species genetic lineages are presented in the Table 2. Estimations varied from 0.788 in *M. californicus* to 1.204 in *M. longicaudus*. Among 49 pair-wise comparisons, 14 cases were classified as divergence, 13 as equivalence and 22 as convergence. Results of pairwise comparisons of Nearctic and Palearctic species are presented in Tables 3–5. In the Nearctic species, estimations varied from 0.736 between *M. longicaudus* and *M. montanus* to 1.702 between *M. pennsylvanicus* and *M. xanthoghathus*. Among 152 pairwise comparisons of the Nearctic species, 29 cases were classified as convergence, 19 as equivalence and 104 as divergence. In the Palearctic species, estimations varied from 0.592 between *M. agrestis* and *M. subterraneus* to 1.789 between *L. gregalis* and *A. oeconomus*. Among 220 pairwise comparisons of the Palearctic species, 48 cases were classified as convergence, 48 as equivalence and 124 as divergence.

Analysis of all quantitative data pooling together demonstrated that the level of niche divergence was correlated positively with the level of genetic divergence and negatively with the level of differences in position of geographic ranges. These relations are well described by the next linear regression equation: $Nd = 1.0158 + 0.5766 \pm 0.1213 \times Gd - 0.0218 \pm 0.0038 \times Rd$, where Nd is the niche

divergence, Gd is genetic divergence, and Rd is geographic range difference. The regression is highly significant: $r = 0.331$, $r^2 = 0.109$, adjusted $r^2 = 0.105$, $F(2,420) = 25.783$, $p < 00000$.

Frequency of qualitative types of niche evolution (divergence, convergence, equivalence) was found to differ depending on genetic and geographic relations of the compared forms (Fig. 1). Among forms with allopatric distribution, divergence was less frequent, while convergence was more frequent between intra-specific genetic lineages than between closely-related or distant species. Among forms with parapatric distribution, frequency of divergence gradually increased and frequencies of convergence and equivalence gradually decreased from intra-specific genetic lineages via closely-related to distant species. Among species with allopatric distribution, frequencies of divergence, convergence and equivalence in closely-related and distant species pairs were similar.

4. Discussion

Results of the presented analysis generally support the first of the tested hypotheses that niche divergence increases with time since speciation events. It was demonstrated above that the level of niche divergence was positively correlated with genetic distance between compared taxa. Original hypothesis (Peterson et al., 1999) postulated that ecological niches evolve little at or around the time of speciation events, whereas niche differences are accumulated subsequently. Nevertheless, I found that statistically significant niche divergence at intra-specific level, i. e. before speciation events, occurred approximately in one third of the cases analyzed. In most of these cases, the level of divergence was relatively low (index values less than 1.1) and only in three cases it was significantly higher. Two of the last three

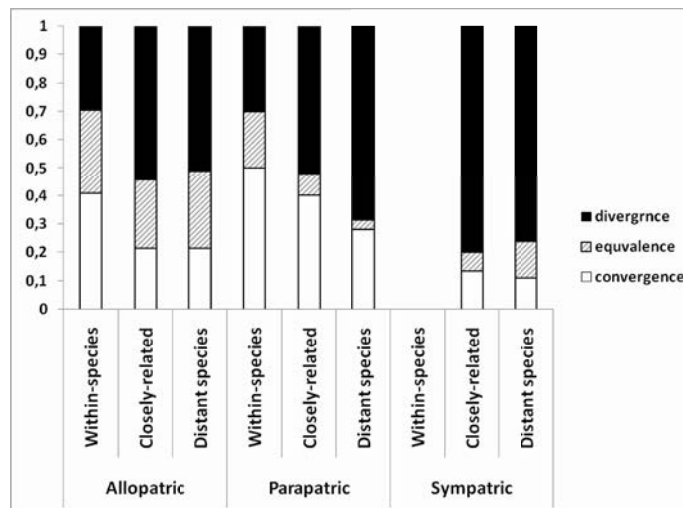


Fig. 1. Frequency distribution of different types of niche evolution in the groups with different levels of genetic and geographic differentiation.

Рис. 1. Частотное распределение различных типов эволюции ниш в группах с различными уровнями генетической и географической дифференциации.

cases (genetic lineages of *M. longicaudus*) can be considered as belonging to not within-species level but rather to different cryptic species, because genetic distances between compared forms are noticeably higher than it is typical for intra-specific forms of mammals (Baker, Bradley, 2006). Only in one case (genetic lineages of *Ch. nivalis*) this level was established for definitely within-species level. These findings allow suggesting that niche evolution can start with population differentiation and that speciation events are not critical thresholds in this process.

Some authors (Wiens, Graham, 2005; Kalkvik et al., 2012) did not distinguish convergence and equivalence of niches considering both as niche conservatism, which may be correct at least in some cases. For example, realized niches of two closely related allopatric forms with relatively small geographic ranges can represent only minor parts of a large fundamental niche. In this case, convergence of realized niches corre-

sponds to equivalence of fundamental niches. Probably, this explanation can be applied to the cases of high level of niche convergence between different within-species genetic lineages (as it was found in *M. californicus* and *M. agrestis*). However, cases of the high level of niche convergence between sympatric species in pairs (*M. longicaudus* — *M. montanus*), (*M. pennsylvanicus* — *M. pinetorum*), (*Ch. gud* — *M. daghestanicus*), and (*M. agrestis* — *M. subterraneus*) seem to represent the true deep convergence of fundamental niches.

Results of this analysis also support the second of the tested hypotheses that niche divergence is higher between sympatric than between allopatric taxa. It was demonstrated above that the frequency of niche divergence was higher among species with allopatric distribution than among species with sympatric or parapatric distribution. The finding that the level of niche divergence was negatively correlated with the standardized distance be-

tween geographic ranges of compared taxa also may be considered as a support for this hypothesis. However, only increase of the niche divergence with decrease of standardized distances between geographic ranges from 1 to 0 is the real hypothesis support. From the other hand, decrease of the niche divergence with increase of standardized distances between geographic ranges from 1 to higher positive values is an obvious result of spatial auto-correlation of environments, when any niche divergence became low relative to progressively increasing differences in the background environments.

All these results together indicate a significant role of interspecific competition and competitive exclusion in ecological niche and geographic range evolution. It seems clear that some initial level of niche divergence is a necessary condition providing possibility of co-occurrence and sympatric distribution of a pair of species. Before achieving this level of niche divergence, strong interspecific competition prevents co-occurrence by competitive exclusion. On the other hand, moderate interspecific competition at sympatry can be effective driver of any further niche divergence.

The cases of high level of niche convergence between sympatric species can be explained by niche divergence in other respects not detected by the current analysis. As all species considered here have similar foraging adaptations, divergence of their trophic niches seems unlikely. The most probable explanation of this phenomenon is differentiation by micro-habitat use: for example, rocky and meadow micro-habitats in the case of *M. longicaudus* and *M. montanus* or meadow and forest micro-habitats in the case of *M. pennsylvanicus* and *M. pinetorum*. Unfortunately, this ecological feature cannot be detected at the spatial scale applied in this study.

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Table 1. Characteristic of data included in the analyses.**Табл. 1.** Характеристика данных, включённых в анализ.

Species	Number of occurrence points	Number of genetic lineages
<i>Alexandromys middendorffii</i>	119	3
<i>Alexandromys oconomus</i>	2526	3
<i>Chionomys gud</i>	159	2
<i>Chionomys lasistanius</i>	17	1
<i>Chionomys nivalis</i>	830	2
<i>Chionomys roberti</i>	105	2
<i>Lasiopodomys (Stenocranius) gregalis</i>	432	6
<i>Lasiopodomys (Stenocranius) kossogolicus</i>	124	1
<i>Lasiopodomys (Stenocranius) raddei</i>	95	1
<i>Microtus (Agricola) agrestis</i>	8843	6
<i>Microtus (Agricola) levernedii</i>	2199	2
<i>Microtus (Agricola) rozianus</i>	43	1
<i>Microtus (Aulacomys) californicus</i>	1315	2
<i>Microtus (Aulacomys) mexicanus</i>	808	1
<i>Microtus (Aulacomys) richardsoni</i>	468	1
<i>Microtus (Herpethomys) guatemalensis</i>	16	1
<i>Microtus (Herpethomys) oaxacensis</i>	19	1
<i>Microtus (Mynomes) canicaudus</i>	56	1
<i>Microtus (Mynomes) longicaudus</i>	3432	5
<i>Microtus (Mynomes) montanus</i>	1839	1
<i>Microtus (Mynomes) oregoni</i>	594	1
<i>Microtus (Mynomes) pennsylvanicus</i>	5887	1
<i>Microtus (Mynomes) townsendii</i>	440	1
<i>Microtus (Orthriomys) chrotorrhinus</i>	194	1
<i>Microtus (Orthriomys) miurus</i>	261	1
<i>Microtus (Pedomys) ochrogaster</i>	1840	1
<i>Microtus (Pedomys) xanthognathus</i>	138	1
<i>Microtus (Pitymys) pinetorum</i>	1006	1

Табл. 1. Ending.

Table 1. Окончание.

Species	Number of occurrence points	Number of genetic lineages
<i>Microtus (Pitymys) quasiater</i>	120	1
<i>Microtus (Terricola) brachycercus</i>	33	1
<i>Microtus (Terricola) daghestanicus</i>	163	1
<i>Microtus (Terricola) duodecimcostatus</i>	742	1
<i>Microtus (Terricola) felteni</i>	26	1
<i>Microtus (Terricola) fingeri</i>	27	1
<i>Microtus (Terricola) gerbei</i>	294	1
<i>Microtus (Terricola) liechtensteini</i>	111	1
<i>Microtus (Terricola) lusitanicus</i>	263	1
<i>Microtus (Terricola) majori</i>	301	1
<i>Microtus (Terricola) multiplex</i>	249	1
<i>Microtus (Terricola) savii</i>	161	1
<i>Microtus (Terricola) subterraneus</i>	4408	3
<i>Microtus (Terricola) tatricus</i>	144	1
<i>Microtus (Terricola) thomasi</i>	163	2

Table 2. Estimations of geographic range differences, niche divergence (mean \pm SD) and genetic divergence between phylogenetic lineages intra-specific in Arvicolini.

Табл. 2. Оценки различий в положении ареалов, дивергенции ниш (среднее \pm стандартное отклонение) и генетической дивергенции между внутривидовыми филогенетическими линиями Arvicolin.

Pairs of compared forms		Genetic distance	Niche divergence mean \pm SD	Range standardized distance
<i>A. m. middendorffi</i>	<i>A. m. hyperboreus</i>	0.02	1.0642 \pm 0.0308**	1.469
<i>A. m. middendorffi</i>	<i>A. m. rypheus</i>	0.027	1.0099 \pm 0.0195 ^{NS}	1.218
<i>A. m. hyperboreus</i>	<i>A. m. rypheus</i>	0.031	1.0419 \pm 0.0204**	2.501
<i>A. oeconomus</i> C Eur	<i>A. oeconomus</i> N Eur	0.027	0.9305 \pm 0.0087***	1.17
<i>A. oeconomus</i> C Eur	<i>A. oeconomus</i> C As	0.042	0.9215 \pm 0.0054***	1.663
<i>A. oeconomus</i> C Eur	<i>A. oeconomus</i> Bering	0.042	0.9689 \pm 0.0051***	3.714
<i>A. oeconomus</i> N Eur	<i>A. oeconomus</i> C As	0.04	1.0328 \pm 0.0154**	1.042
<i>A. oeconomus</i> N Eur	<i>A. oeconomus</i> Bering	0.044	0.8578 \pm 0.0133***	2.62
<i>A. oeconomus</i> C As	<i>A. oeconomus</i> Bering	0.031	1.0585 \pm 0.0138***	0.933
<i>Ch. gud</i> NW	<i>Ch. gud</i> SE	0.04	0.9763 \pm 0.0189*	1.046
<i>Ch. nivalis</i> Eur	<i>Ch. nivalis</i> W As	0.014	1.1335 \pm 0.0178***	1.149
<i>Ch. roberti</i> NW	<i>Ch. roberti</i> S	0.023	0.9781 \pm 0.0415 ^{NS}	1.287
<i>L. (S.) gregalis</i> A1	<i>L. (S.) gregalis</i> A2	0.035	1.0398 \pm 0.0157**	0.905
<i>L. (S.) gregalis</i> A1	<i>L. (S.) gregalis</i> A3	0.033	0.9360 \pm 0.0248**	1.116
<i>L. (S.) gregalis</i> A1	<i>L. (S.) gregalis</i> A4	0.033	0.9943 \pm 0.0169 ^{NS}	1.119
<i>L. (S.) gregalis</i> A1	<i>L. (S.) gregalis</i> A5	0.027	0.9762 \pm 0.0040***	1.438

Табл. 2. Continuing.
Table 2. Продолжение.

Pairs of compared forms		Genetic distance	Niche divergence mean ± SD	Range standardized distance
<i>L. (S.) gregalis</i> A1	<i>L. (S.) gregalis</i> A6	0.04	1.0440±0.0062***	1.508
<i>L. (S.) gregalis</i> A2	<i>L. (S.) gregalis</i> A5	0.029	0.9719±0.0091***	2.591
<i>L. (S.) gregalis</i> A3	<i>L. (S.) gregalis</i> A4	0.031	0.7276±0.0465***	0.854
<i>L. (S.) gregalis</i> A4	<i>L. (S.) gregalis</i> A6	0.04	1.0431±0.0150**	1.207
<i>L. (S.) gregalis</i> A	<i>L. (S.) gregalis</i> B	0.086	0.8832±0.0100***	1.034
<i>L. (S.) gregalis</i> B	<i>L. (S.) gregalis</i> C	0.141	0.9778±0.0421 ^{NS}	1.009
<i>M. (A.) agrestis</i> C	<i>M. (A.) agrestis</i> E	0.015	0.9525±0.0055***	0.993
<i>M. (A.) agrestis</i> C	<i>M. (A.) agrestis</i> N Br	0.011	0.9970±0.0032 ^{NS}	1.495
<i>M. (A.) agrestis</i> C	<i>M. (A.) agrestis</i> Scan	0.011	0.9058±0.0079***	1.025
<i>M. (A.) agrestis</i> C	<i>M. (A.) agrestis</i> W	0.014	0.8204±0.0051***	0.898
<i>M. (A.) agrestis</i> E	<i>M. (A.) agrestis</i> N Br	0.014	0.9416±0.0019***	1.638
<i>M. (A.) agrestis</i> E	<i>M. (A.) agrestis</i> Scan	0.014	0.8586±0.0093***	0.934
<i>M. (A.) agrestis</i> Fr	<i>M. (A.) agrestis</i> N Br	0.009	0.9897±0.0020***	2.654
<i>M. (A.) agrestis</i> Fr	<i>M. (A.) agrestis</i> W	0.013	0.9570±0.0121***	1.035
<i>M. (A.) agrestis</i> N Br	<i>M. (A.) agrestis</i> Scan	0.01	0.9994±0.0026 ^{NS}	2.549
<i>M. (A.) agrestis</i> N Br	<i>M. (A.) agrestis</i> W	0.012	1.0506±0.0045***	0.899
<i>M. (A.) agrestis</i> Scan	<i>M. (A.) agrestis</i> W	0.013	0.9421±0.0039***	1.919
<i>M. (A.) levernedii</i> E	<i>M. (A.) levernedii</i> W	0.008	1.0042±0.0072 ^{NS}	1.187

Табл. 2. Ending.
Table 2. Окончание.

Pairs of compared forms		Genetic distance	Niche divergence mean \pm SD	Range standardized distance
<i>M. (Au.) californicus</i> N	<i>M. californicus</i> S	0.046	0.7879 \pm 0.0093***	0.893
<i>M. (M.) longicaudus</i> Ariz	<i>M. longicaudus</i> C	0.043	1.0137 \pm 0.0029***	7.08
<i>M. (M.) longicaudus</i> Ariz	<i>M. longicaudus</i> Isl	0.026	0.9869 \pm 0.0021***	6.65
<i>M. (M.) longicaudus</i> Ariz	<i>M. longicaudus</i> NW	0.023	0.9729 \pm 0.0058***	2.054
<i>M. (M.) longicaudus</i> Ariz	<i>M. longicaudus</i> SRoc	0.054	1.1085 \pm 0.0093***	2.567
<i>M. (M.) longicaudus</i> C	<i>M. longicaudus</i> Isl	0.041	1.0101 \pm 0.0023***	3.237
<i>M. (M.) longicaudus</i> C	<i>M. longicaudus</i> NW	0.037	0.9587 \pm 0.0059***	1.248
<i>M. (M.) longicaudus</i> C	<i>M. longicaudus</i> SRoc	0.056	1.0175 \pm 0.0055***	1.791
<i>M. (M.) longicaudus</i> Isl	<i>M. longicaudus</i> NW	0.02	1.2043 \pm 0.0265***	0.895
<i>M. (M.) longicaudus</i> Isl	<i>M. longicaudus</i> SRoc	0.061	1.0010 \pm 0.0011 ^{NS}	3.992
<i>M. (M.) longicaudus</i> NW	<i>M. longicaudus</i> SRoc	0.057	0.9990 \pm 0.0021 ^{NS}	1.961
<i>M. (T.) subterraneus</i> NWEur	<i>M. subterraneus</i> S Eu	0.034	1.0041 \pm 0.0107 ^{NS}	0.944
<i>M. (T.) subterraneus</i> NWEur	<i>M. subterraneus</i> Tur	0.041	0.9958 \pm 0.0261 ^{NS}	2.175
<i>M. (T.) subterraneus</i> SEur	<i>M. subterraneus</i> Tur	0.039	0.9985 \pm 0.0423 ^{NS}	1.122
<i>M. (T.) thomasi thomasi</i>	<i>M. thomasi atticus</i>	0.026	1.0182 \pm 0.0249 ^{NS}	1.07

Significance levels of differences from 1: * – $p < 0.05$, ** – $p < 0.01$, *** – $p < 0.001$, NS – nonsignificant.
Уровни значимости отличий от 1: * – $p < 0.05$, ** – $p < 0.01$, *** – $p < 0.001$, NS – незначимо.

Table 3. Estimations of niche divergence (below diagonal, mean \pm SD), genetic divergence (first row above diagonal) and geographic range difference (second row above diagonal) among Nearctic species of Arvicolini.

Табл. 3. Оценки дивергенции ниш (ниже диагонали, среднее \pm стандартное отклонение), генетической дивергенции (первая строка выше диагонали) и различий в положениях ареалов (вторая строка выше диагонали) между Неоарктическими видами Arvicolini.

	1	2	3	4	5	6
1		0.155 1.196	0.161 1.311	0.146 1.08	0.149 1.818	0.12 1.783
2	0.9809 \pm 0.0015***		0.143 1.128	0.167 1.026	0.136 3.67	0.132 3.515
3	1.0040 \pm 0.0023*	1.0891 \pm 0.0055***		0.152 1.065	0.152 1.19	0.137 0.981
4	1.1475 \pm 0.0069***	1.0776 \pm 0.0083***	0.9771 \pm 0.0057***		0.125 3.142	0.14 3.317
5	0.9862 \pm 0.0064***	0.9856 \pm 0.0065***	1.0634 \pm 0.0242**	0.9762 \pm 0.0036***		0.108 2.045
6	1.0345 \pm 0.0105***	1.0161 \pm 0.0110*	1.1566 \pm 0.0368***	0.9880 \pm 0.0032***	1.0476 \pm 0.0196**	
7	0.9117 \pm 0.0081***	0.9070 \pm 0.0107***	0.9848 \pm 0.0028***	1.0529 \pm 0.0133***	1.0006 \pm 0.0014 ^{NS}	0.9990 \pm 0.0010 ^{NS}
8	1.3410 \pm 0.0076***	1.2272 \pm 0.0077***	0.9232 \pm 0.0086***	1.2349 \pm 0.0290***	0.8995 \pm 0.0137***	1.0036 \pm 0.0206 ^{NS}
9	1.0054 \pm 0.0017***	1.2336 \pm 0.0071***	0.9910 \pm 0.0082*	1.4622 \pm 0.0327***	0.9836 \pm 0.0062**	1.0083 \pm 0.0121 ^{NS}
10	1.0022 \pm 0.0039 ^{NS}	1.1988 \pm 0.0134***	0.9969 \pm 0.0023**	1.0396 \pm 0.0167**	0.9909 \pm 0.0028***	1.0028 \pm 0.0031 ^{NS}
11	1.2341 \pm 0.0097***	1.1761 \pm 0.0052***	1.0634 \pm 0.0073***	1.5479 \pm 0.0176***	0.9680 \pm 0.0090***	1.0385 \pm 0.0167**
12	0.9385 \pm 0.0045***	1.0151 \pm 0.0080*	1.0103 \pm 0.0018***	1.1570 \pm 0.0138***	0.9982 \pm 0.0020 ^{NS}	0.9991 \pm 0.0017 ^{NS}
13	1.1644 \pm 0.0188***	1.0153 \pm 0.0020***	0.9829 \pm 0.0029***	1.0444 \pm 0.0039***	1.0003 \pm 0.0032 ^{NS}	1.0098 \pm 0.0035**
14	1.0857 \pm 0.0182***	1.0006 \pm 0.0016 ^{NS}	1.0040 \pm 0.0024*	1.0494 \pm 0.0053***	1.0025 \pm 0.0042 ^{NS}	1.0161 \pm 0.0033**
15	1.0810 \pm 0.0035***	1.0690 \pm 0.0022***	1.0230 \pm 0.0049***	1.1902 \pm 0.0113***	0.9815 \pm 0.0058***	1.0199 \pm 0.0085**

Table 3. Continuing.**Табл. 3.** Продолжение.

	1	2	3	4	5	6
16	1.3436± 0.0611***	1.0210± 0.0018***	1.0262± 0.0034***	1.1030± 0.0079***	1.0087± 0.0040**	1.0157± 0.0031**
17	0.9974± 0.0041 ^{NS}	1.0061± 0.0011***	1.0141± 0.0025***	1.0595± 0.0038***	1.0545± 0.0063***	1.0309± 0.0061***
18	1.0712± 0.0075***	1.0710± 0.0063***	1.1719± 0.0260***	1.0066± 0.0016***	1.0076± 0.0117 ^{NS}	1.2842± 0.0577***

	7	8	9	10	11	12
1	0.148 1.176	0.161 0.87	0.18 1.065	0.187 1.11	0.182 0.792	0.149 1.074
2	0.155 1.032	0.197 0.674	0.161 0.616	0.186 0.648	0.155 1.227	0.156 0.938
3	0.138 1.726	0.172 0.912	0.144 0.909	0.184 1.472	0.17 0.925	0.131 1.538
4	0.152 0.943	0.158 0.463	0.134 0.394	0.167 0.672	0.158 0.595	0.147 0.724
5	0.171 6.417	0.176 1.703	0.163 2.6	0.171 4.705	0.172 1.615	0.158 4.885
6	0.133 8.876	0.166 1.656	0.152 2.65	0.162 5.432	0.155 1.737	0.133 5.385
7		0.152 0.846	0.102 1.042	0.142 0.143	0.111 1.16	0.05 0.523
8	0.9866± 0.0151 ^{NS}		0.153 0.513	0.169 0.591	0.16 0.465	0.157 0.563
9	0.9124± 0.0079***	0.7358± 0.0076***		0.151 0.831	0.081 0.613	0.088 0.937
10	1.1714± 0.0352***	1.0496± 0.0114***	1.1644± 0.0092***		0.175 0.976	0.138 0.265
11	0.9561± 0.0124***	1.6178± 0.0110***	1.0568± 0.0044***	1.1370± 0.0075***		0.102 1.007
12	1.0616± 0.0332*	1.0796± 0.0100***	1.0789± 0.0084***	1.1170± 0.0353***	1.0421± 0.0064***	
13	1.0118± 0.0051**	1.1336± 0.0093***	1.0101± 0.0029***	1.0120± 0.0034***	1.2264± 0.0300***	1.0087± 0.0037**

Table 3. Continuing.

Табл. 3. Продолжение.

	7	8	9	10	11	12
14	0.9904± 0.0023***	1.3905± 0.0175***	1.0271± 0.0026***	1.0037± 0.0028*	1.2479± 0.0152***	0.9982± 0.0026 ^{NS}
15	0.9986± 0.0038 ^{NS}	1.2432± 0.0070***	1.0831± 0.0043***	1.0426± 0.0021***	1.0002± 0.0067 ^{NS}	1.0248± 0.0018***
16	0.9859± 0.0027***	1.5550± 0.0270***	1.0464± 0.0044***	1.0395± 0.0039***	1.7019± 0.0387***	1.0311± 0.0042***
17	0.9906± 0.0060*	1.0432± 0.0029***	1.0110± 0.0014***	0.9970± 0.0016***	0.8402± 0.0066***	0.9926± 0.0019***
18	1.0044± 0.0014***	1.1327± 0.0140***	1.0446± 0.0047***	1.0149± 0.0014***	1.1689± 0.0148***	1.0070± 0.0012***

	13	14	15	16	17	18
1	0.122 1.223	0.152 0.281	0.167 1.093	0.224 0.79	0.16 1.279	0.13 1.68
2	0.149 2.807	0.166 2.284	0.143 1.773	0.172 1.586	0.159 2.077	0.15 2.75
3	0.132 1.625	0.165 2.184	0.164 0.95	0.162 1.705	0.163 1.183	0.15 0.88
4	0.15 1.503	0.165 0.718	0.166 0.855	0.167 1.014	0.15 1.419	0.13 2.6
5	0.152 2.075	0.167 4.851	0.171 1.817	0.149 3.764	0.137 2.446	0.14 1.76
6	0.108 2.16	0.137 5.151	0.138 1.892	0.236 3.868	0.124 2.162	0.12 1.1
7	0.134 2.181	0.153 2.41	0.159 1.488	0.145 1.711	0.168 2.338	0.15 5.9
8	0.158 1.329	0.174 0.849	0.191 0.849	0.152 0.729	0.196 1.119	0.17 1.66
9	0.143 1.474	0.172 1.465	0.163 0.816	0.148 1.121	0.169 1.198	0.16 2.1
10	0.168 1.95	0.165 1.864	0.182 1.274	0.168 1.289	0.189 2.148	0.18 4.1
11	0.148 0.577	0.156 0.774	0.169 0.411	0.159 0.519	0.189 0.59	0.16 1.47

Table 3. Ending.**Табл. 3.** Окончание.

	13	14	15	16	17	18
12	0.127	0.156	0.157	0.132	0.175	0.16
	2.051	1.613	1.301	1.322	2.229	4.19
13		0.145	0.14	0.223	0.149	0.15
		2.387	1.055	1.268	0.812	2.03
14	1.0848±		0.162	0.247	0.159	0.13
	0.0071***		1.503	0.637	2.284	4.31
15	0.9870±	1.0745±		0.235	0.169	0.17
	0.0099*	0.0039***		1.072	0.498	1.64
16	1.0926±	1.0538±	1.1045±		0.271	0.24
	0.0228***	0.0443*	0.0123***		1.483	3.31
17	1.1163±	1.0543±	1.0855±	1.0461±		0.1
	0.0261***	0.0038***	0.0139***	0.0069***		1.65
18	1.0004±	1.0013±	1.0445±	1.0142±	1.0303±	
	0.0026 ^{NS}	0.0026 ^{NS}	0.0038***	0.0026***	0.0031***	

Species / Виды. 1 – *A. oeconomus*, 2 – *M. (Au.) californicus*, 3 – *M. (Au.) mexicanus*, 4 – *M. (Au.) richardsoni*, 5 – *M. (H.) guatemalensis*, 6 – *M. (H.) oaxacensis*, 7 – *M. (My.) canicaudus*, 8 – *M. (My.) longicaudus*, 9 – *M. (My.) montanus*, 10 – *M. (My.) oregoni*, 11 – *M. (My.) pennsylvanicus*, 12 – *M. (My.) townsendii*, 13 – *M. (O.) chrotorrhinus*, 14 – *M. (O.) miurus*, 15 – *M. (Pe.) ochrogaster*, 16 – *M. (Pe.) xanthognathus*, 17 – *M. (Pi.) pinetorum*, 18 – *M. (Pi.) quasiater*.

Significance levels as in Table 2 / **Уровни значимости** как в Табл. 2.

Table 4. Estimations of niche divergence (below diagonal, mean±SD), genetic divergence (first row above diagonal) and geographic range difference (second row above diagonal) among species of *Chionomys*, *Agricola*, and *Terricola*.

Табл. 4. Оценки дивергенции ниш (ниже диагонали, среднее ± стандартное отклонение), генетической дивергенции (первая строка выше диагонали) и различий в положении ареалов (вторая строка выше диагонали) между видами *Chionomys*, *Agricola* и *Terricola*.

	1	2	3	4	5	6	7
1		0.136 1.66	0.15 0.99	0.146 0.228	0.211 1.461	0.198 2.101	0.205 7.565
2	1.0433± 0.0325*		0.158 0.881	0.143 0.125	0.217 1.707	0.226 2.193	0.227 8.545
3	1.0829± 0.0223***	1.0613± 0.0333*		0.116 0.806	0.197 0.672	0.179 0.403	0.183 0.93
4	1.1775± 0.0593**	1.3077± 0.1050**	1.0159± 0.0193 ^{NS}		0.168 1.427	0.167 2.068	0.172 7.444
5	1.1050± 0.0120***	1.5421± 0.1050***	1.1333± 0.0078***	0.9975± 0.0162 ^{NS}		0.066 1.002	0.07 1.136
6	1.1536± 0.0156***	1.0953± 0.0148***	1.0310± 0.0154**	1.0321± 0.0140**	0.7684± 0.0038***		0.04 1.01
7	1.0003± 0.0028 ^{NS}	0.9940± 0.0060 ^{NS}	0.9709± 0.0217*	0.9962± 0.0050 ^{NS}	0.9849± 0.0119*	1.0051± 0.0185 ^{NS}	
8	0.9974± 0.0056 ^{NS}	1.0257± 0.0122**	1.1405± 0.0217***	1.0131± 0.0083*	0.9981± 0.0197 ^{NS}	1.0987± 0.0211***	1.0047± 0.0119 ^{NS}
9	0.7969± 0.0319***	1.0561± 0.0605 ^{NS}	1.1797± 0.0291***	0.9411± 0.0511*	1.0646± 0.0103***	1.0356± 0.0099***	0.9938± 0.0057*
10	0.9886± 0.0025***	1.0021± 0.0095 ^{NS}	1.1103± 0.0126***	1.0078± 0.0071*	0.8852± 0.0045***	0.9271± 0.0171***	1.0318± 0.0287*
11	1.0420± 0.0107***	0.9931± 0.0124 ^{NS}	1.3231± 0.0688***	1.0267± 0.0228*	1.0305± 0.0186*	1.2141± 0.0340***	0.9916± 0.0100 ^{NS}
12	0.9988± 0.0116 ^{NS}	1.1059± 0.0363**	1.4783± 0.0473***	1.0032± 0.0252 ^{NS}	0.9279± 0.0246**	0.9384± 0.0202***	1.0037± 0.0094 ^{NS}
13	1.0032± 0.0032 ^{NS}	0.9940± 0.0111 ^{NS}	1.0874± 0.0107***	1.0135± 0.0082*	0.9329± 0.0075***	1.0050± 0.0212 ^{NS}	0.9784± 0.0132*
14	1.0269± 0.0109**	1.0373± 0.0180**	1.0144± 0.0208 ^{NS}	0.9696± 0.0170*	1.0506± 0.0093***	1.2755± 0.0281***	0.9991± 0.0042 ^{NS}
15	0.9857± 0.0034***	0.9865± 0.0091*	1.0461± 0.0123***	0.9773± 0.0046***	0.9300± 0.0076***	1.0362± 0.0208*	0.9946± 0.0386 ^{NS}

Table 4. Continuing.
Табл. 4. Продолжение.

	1	2	3	4	5	6	7
16	1.1720± 0.0423***	1.2625± 0.0815***	1.2901± 0.0236***	0.8280± 0.0397***	0.9636± 0.0126**	1.0115± 0.0091*	0.9829± 0.0055***
17	0.9961± 0.0075 ^{NS}	1.0356± 0.0221*	0.8834± 0.0208***	0.9460± 0.0117***	1.0432± 0.0081***	1.3850± 0.0428***	0.9920± 0.0093 ^{NS}
18	1.0132± 0.0065**	1.0599± 0.0142***	1.1687± 0.0223***	1.0202± 0.0088**	1.0239± 0.0083**	1.2237± 0.0239***	1.0093± 0.0089*
19	1.1742± 0.0256***	1.1669± 0.0294***	1.0990± 0.0135***	0.9984± 0.0211 ^{NS}	0.5927± 0.0045***	0.7743± 0.0047***	0.9945± 0.0186 ^{NS}
20	1.0407± 0.0077***	1.0138± 0.0179 ^{NS}	1.1080± 0.0168***	0.9958± 0.0074 ^{NS}	1.3036± 0.0168***	0.9287± 0.0090***	0.9993± 0.0027 ^{NS}
21	1.0308± 0.0057***	1.0221± 0.0157*	1.5225± 0.0391***	0.9973± 0.0069 ^{NS}	1.0342± 0.0095***	1.1362± 0.0115***	1.0067± 0.0074 ^{NS}

	8	9	10	11	12	13	14
1	0.204 4.496	0.207 0.137	0.207 3.109	0.216 3.996	0.218 1.831	0.208 5.985	0.2 3.782
2	0.201 4.065	0.202 0.249	0.188 3.213	0.2 4.073	0.211 1.01	0.185 6.867	0.198 3.904
3	0.16 0.701	0.169 0.74	0.149 0.677	0.165 0.39	0.196 0.867	0.158 0.681	0.14 0.512
4	0.175 3.473	0.166 0.2	0.148 2.966	0.173 3.351	0.163 0.84	0.146 6.067	0.14 3.456
5	0.176 1.228	0.172 1.472	0.165 1.017	0.154 1.118	0.164 1.301	0.161 0.93	0.151 0.892
6	0.155 1.616	0.162 2.101	0.15 0.413	0.134 1.276	0.157 1.701	0.14 0.305	0.13 0.601
7	0.17 5.261	0.16 7.52	0.154 0.716	0.137 9.831	0.153 6.268	0.139 1.288	0.132 4.173
8		0.15 4.452	0.107 1.661	0.115 1.306	0.135 2.522	0.103 3.242	0.098 1.811
9	1.0111± 0.0077*		0.132 3.083	0.132 4.115	0.107 1.184	0.112 5.857	0.108 3.686
10	1.0061± 0.0288 ^{NS}	0.9705± 0.0042***		0.098 2.273	0.131 2.517	0.082 0.504	0.079 1.3
11	1.0184± 0.0125*	1.0544± 0.0158***	1.0848± 0.0196***		0.08 6.202	0.121 2.27	0.083 1.484

Table 4. Continuing.
Табл. 4. Продолжение.

	8	9	10	11	12	13	14
12	1.0123± 0.0188 ^{NS}	1.0798± 0.0255 ^{***}	1.0016± 0.0138 ^{NS}	1.0516± 0.0065 ^{***}		0,112 4.841	0.11 2.466
13	1.0623± 0.0118 ^{***}	1.0043± 0.0047 ^{NS}	1.1512± 0.0233 ^{***}	0.9948± 0.0271 ^{NS}	1.0325± 0.0119 ^{**}		0.064 2.442
14	1.0183± 0.0101 [*]	0.9746± 0.0169 [*]	0.9846± 0.0078 [*]	1.1056± 0.0140 ^{***}	1.0119± 0.0156 ^{NS}	1.1239± 0.0260 ^{***}	
15	1.0101± 0.0167 ^{NS}	0.9795± 0.0043 ^{***}	1.4328± 0.0425 ^{***}	1.0087± 0.0100 ^{NS}	1.0103± 0.0140 ^{NS}	0.8889± 0.0211 ^{***}	0.9997± 0.0033 ^{NS}
16	1.0232± 0.0079 ^{***}	1.3902± 0.0656 ^{***}	0.9819± 0.0041 ^{***}	1.1189± 0.0304 ^{***}	0.9654± 0.0242 [*]	1.0060± 0.0045 [*]	1.0108± 0.0211 ^{NS}
17	1.0638± 0.0183 ^{***}	0.9577± 0.0081 ^{***}	0.8974± 0.0114 ^{***}	1.1577± 0.0387 ^{***}	0.9558± 0.0171 ^{**}	1.0109± 0.0080 [*]	1.1437± 0.0307 ^{***}
18	1.1640± 0.0477 ^{***}	1.0078± 0.0081 ^{NS}	0.9314± 0.0116 ^{***}	1.1198± 0.0132 ^{***}	1.0174± 0.0224 ^{NS}	1.0622± 0.0069 ^{***}	0.9724± 0.0255 [*]
19	1.0798± 0.0174 ^{***}	1.0653± 0.0152 ^{***}	0.9578± 0.0072 ^{***}	1.2202± 0.0420 ^{***}	0.8738± 0.0338 ^{***}	1.0215± 0.0103 ^{**}	1.1132± 0.0181 ^{***}
20	1.0115± 0.0043 ^{**}	1.0010± 0.0078 ^{NS}	0.9894± 0.0029 ^{***}	1.0466± 0.0123 ^{***}	1.0193± 0.0063 ^{***}	1.0009± 0.0026 ^{NS}	0.9845± 0.0121 [*]
21	1.0139± 0.0195 ^{NS}	1.0617± 0.0087 ^{***}	1.0302± 0.0087 ^{***}	1.1181± 0.0708 [*]	1.0433± 0.0375 [*]	1.0431± 0.0053 ^{***}	1.0374± 0.0073 ^{***}

	15	16	17	18	19	20	21
1	0.211 4.513	0.185 0.189	0.198 4.434	0.212 4.712	0.211 1.3	0.205 2.659	0.21 4.08
2	0.19 4.701	0.183 0.325	0.179 4.81	0.202 4.67	0.224 1.596	0.202 2.953	0.186 3.238
3	0.159 0.778	0.146 0.664	0.128 0.654	0.167 0.648	0.18 0.309	0.156 0.625	0.155 0.567
4	0.17 4.329	0.144 0.078	0.15 4.285	0.18 4.068	0.165 1.31	0.155 2.66	0.157 2.77
5	0.169 1.058	0.168 1.337	0.173 1.007	0.19 1.012	0.165 0.424	0.18 0.824	0.184 1.176
6	0.159 0.639	0.139 1.958	0.153 0.456	0.167 1.025	0.153 0.47	0.143 1.24	0.166 1.207

Table 4. Ending.**Табл. 4.** Окончание.

	15	16	17	18	19	20	21
7	0.163	0.138	0.157	0.165	0.157	0.149	0.165
	0.336	6.838	3.188	3.258	1.3	5.645	4.908
8	0.118	0.138	0.114	0.054	0.145	0.119	0.109
	2.596	3.925	1.642	1.026	1.235	5.315	1.242
9	0.146	0.125	0.128	0.156	0.096	0.145	0.133
	4.473	0.185	4.372	4.622	1.306	2.587	3.955
10	0.052	0.108	0.094	0.108	0.137	0.107	0.107
	0.261	2.893	0.869	1.028	0.84	1.967	1.803
11	0.094	0.125	0.082	0.108	0.123	0.086	0.081
	3.886	3.785	2.852	2.296	0.761	2.134	0.546
12	0.138	0.126	0.128	0.134	0.054	0.123	0.116
	3.678	1.028	3.243	3.008	1.064	1.946	2.057
13	0.088	0.103	0.079	0.109	0.111	0.084	0.077
	0.608	5.316	1.335	1.67	0.854	3.645	3.116
14	0.086	0.102	0.058	0.098	0.106	0.083	0.074
	2.124	3.311	1	0.643	0.582	2.365	1.138
15		0.108	0.1	0.115	0.137	0.112	0.099
		4.21	1.53	1.681	1.053	3.086	2.716
16	0.9697± 0.0034***		0.119 3.944	0.145 4.095	0.121 1.214	0.117 2.272	0.135 3.006
	0.9567± 0.0065***	0.9741± 0.0108**		0.115 0.437	0.12 0.671	0.085 2.21	0.077 1.777
18	1.0087± 0.0075*	1.0326± 0.0087***	1.2029± 0.0382***		0.145 0.717	0.113 2.225	0.11 1.527
	0.9415± 0.0130***	1.0085± 0.0138 ^{NS}	1.0906± 0.0202***	1.1350± 0.0113***		0.13 0.302	0.119 0.774
20	0.9792± 0.0035***	1.0554± 0.0116***	0.8394± 0.0407***	1.0217± 0.0040***	1.1631± 0.0212***		0.091 2.307
	0.9984± 0.0066 ^{NS}	1.1017± 0.0093***	1.1017± 0.0140***	1.0661± 0.0117***	1.2263± 0.0141***	1.0328± 0.0039***	

Species / Виды. 1 – *Ch. gud*, 2 – *Ch. lasistanius*, 3 – *Ch. nivalis*, 4 – *Ch. roberti*, 5 – *M. (A.) agrestis*, 6 – *M. (A.) levernedii*, 7 – *M. (A.) rozianus*, 8 – *M. (T.) brachycercus*, 9 – *M. (T.) daghestanicus*, 10 – *M. (T.) duodecimcostatus*, 11 – *M. (T.) felteni*, 12 – *M. (T.) fingeri*, 13 – *M. (T.) gerbei*, 14 – *M. (T.) liechtensteini*, 15 – *M. (T.) lusitanicus*, 16 – *M. (T.) majori*, 17 – *M. (T.) multiplex*, 18 – *M. (T.) savii*, 19 – *M. (T.) subterraneus*, 20 – *M. (T.) tatricus*, 21 – *M. (T.) thomasi*.

Significance levels as in Table 2 / **Уровни значимости** как в Табл. 2.

Table 5. Estimations of niche divergence (below diagonal, mean \pm SD), genetic divergence (first row above diagonal) and geographic range difference (second row above diagonal) among some Palaearctic species of Arvicolini.

Табл. 5. Оценки дивергенции ниш (ниже диагонали, среднее \pm стандартное отклонение), генетической дивергенции (первая строка выше диагонали) и различий в положении ареалов (вторая строка выше диагонали) между некоторыми палеарктическими видами Arvicolini.

	1	2	3	4	5
1		0.102 0.15	0.165 1.811	0.171 0.353	0.151 0.533
2	1.1511 \pm 0.0243***		0.151 1.011	0.166 0.233	0.156 0.297
3	0.9426 \pm 0.0038***	1.0951 \pm 0.0060***		0.176 1.179	0.197 0.672
4	1.2930 \pm 0.0506***	1.7887 \pm 0.0429***	0.9486 \pm 0.0065***		0.218 0.348
5	1.1653 \pm 0.0202***	1.5690 \pm 0.0185***	1.1333 \pm 0.0078***	1.7646 \pm 0.0424***	

Species/Виды. 1 – *A. middendorffi*, 2 – *A. oeconomus*, 3 – *Ch. nivalis*, 4 – *L. (S.) gregalis*, 5 – *M. (A.) agrestis*.

Significance levels as in Table 2. / **Уровни значимости** как в Табл. 2.