

# Role of Population Structuring in the Formation of Karyotypic Diversity of the Common Shrew *Sorex araneus* (Lipotyphla, Mammalia)

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**Abstract**—In this review, we describe karyotypic, morphological, and genetic structuring of population in the common shrew *Sorex araneus* (Lipotyphla, Mammalia), and try to explain some unclear and contradictory aspects of this structuring on the basis of population approach. The subdivision of this species into more than 76 parapatric chromosomal races does not correspond to its morphological and genetic structuring. Chromosomal hybrid zones are formed in the areas of contact between the races. The frequency of interracial F1 hybrids is low in nature, but we have shown that mating between different races in captivity occurs quite readily, although the postnatal survival of hybrids is reduced. We suggest that this species is subdivided into relatively small populations characterized by the unity of functioning, which is ensured by the predominant dispersal of individuals from each of the populations within their population space. It should also be emphasized that the main provisions set forth by Stanislav S. Shvarts in his conceptual monograph *The Evolutionary Ecology of Animals* are still relevant today.

**Keywords:** population, population structure, parapatry, chromosomal races, F1 hybrids, *Sorex araneus*

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The origin of parapatric forms is usually attributed to postglacial recolonization of suitable territory by individuals that survived in isolated refugia [1]. The number of such forms in the common shrew is obviously greater than the number of probable refugia: no less than 76 parapatric chromosomal races have been distinguished in this species, with their spatial distribution being often inconsistent with location of probable physical or ecological barriers [2]. The distribution of races and the interracial boundaries are not contingent on either these barriers or climatic and ecological conditions in the ranges of these races. To explain the diversity that emerged in the postglacial space, a model based on density-dependent processes has been proposed. According to this model, a form that appears to be at the front of expansion to vacant territory has higher reproductive potential and, hence, higher probability to successfully colonize it. This form occurs at the “leading edge” by chance and may have no selective advantage. Immigration of other forms to already colonized territory is blocked by residents under the competitive exclusion principle [3]. This model is universally applicable to explain the origin of parapatric forms on spatial scales ranging from microbial sectoring (division of microbial colonies into sectors occupied by different strains) to postglacial

recolonization, progressive island colonization, and human expansion [3].

The distribution of chromosomal races conforms to the pattern of rapid recolonization of the present species range from two refugia: periglacial (Baltic) and adjacent to Lake Baikal [2]. In the case of *S. araneus*, however, the proposed model can be implemented if applied not to an individual but to a population with a fixed karyotype. There are contradictions in estimation of gene flow through the hybrid zones. Judging from the distribution of karyotypes, this flow is limited, which may provide for the onset of speciation [4], while molecular markers do not confirm limitations to the gene flow [5]. Morphological variability and genetic (molecular) variability are not associated with karyotypic population structuring. In our opinion, the concept of population structuring of the species may markedly contribute to the understanding of evolutionary processes in *S. araneus*.

The Russian ecological school of thought has been forming with clear understanding of the idea of the population as a unit of biological community in which processes specific for this level of biological organization take place [6–8]. This approach is clearly reflected in studies by Stanislav S. Shvarts, who wrote in particular that “...ecology is a science of populations (...) ...the study of relationships and adaptive

reactions to the conditions of their existence should become the primary objective of ecology (...) ...population is an organization of individuals (a structural whole) outside of which they cannot exist" [6, pp. 5, 12]. Unfortunately, the interest of scientists in studies on specific features of interactions at the population level has been lost in the late 1990s, and a population is thought of as a random sample from a certain common space with certain properties. In such an approach, of primary importance is statistical analysis allowing the significance of differences to be verified. This approach is obviously sufficient for revealing both differences themselves and their trends, but it falls short of providing an in-depth insight into the mechanisms of processes accounting for these differences and trends.

Here we will discuss the known facts of population structuring in *S. araneus* and make an attempt to explain some unclear and contradictory aspects of this structuring on the basis of population approach. Quotations from the conceptual monograph by Shvarts [8] are used as epigraphs to sections of this review.

#### KARYOTYPIC STRUCTURING OF THE SPECIES *S. ARANEUS*. CHROMOSOMAL RACES

*The connection between these processes  
(intraspecific differentiation and speciation)  
is undoubted, and its establishment can be boldly  
classified as being among the most  
accomplishments of biology* [8, p. 10]

Divergence in the genus *Sorex* is almost not expressed morphologically, and relatively high conservatism of morphological characters is apparently connected with specific features of its ecological niche. The bulk of shrew diet consists of invertebrates, with most of them having a high survival capacity. This has determined basic structural features of the cranial skeleton, which have evolved so as to ensure the possibility to effectively catch and devour prey, and differences in the shape of cranial structures are therefore relatively slight [9]. The main variation concerns differences in body size between shrews preferentially feeding on larger or smaller invertebrates. Differential exploitation of food resources allows shrew species to optimize energy expenditures for catching prey and provides the possibility for them to exist in three basic "dimensional" niches [10].

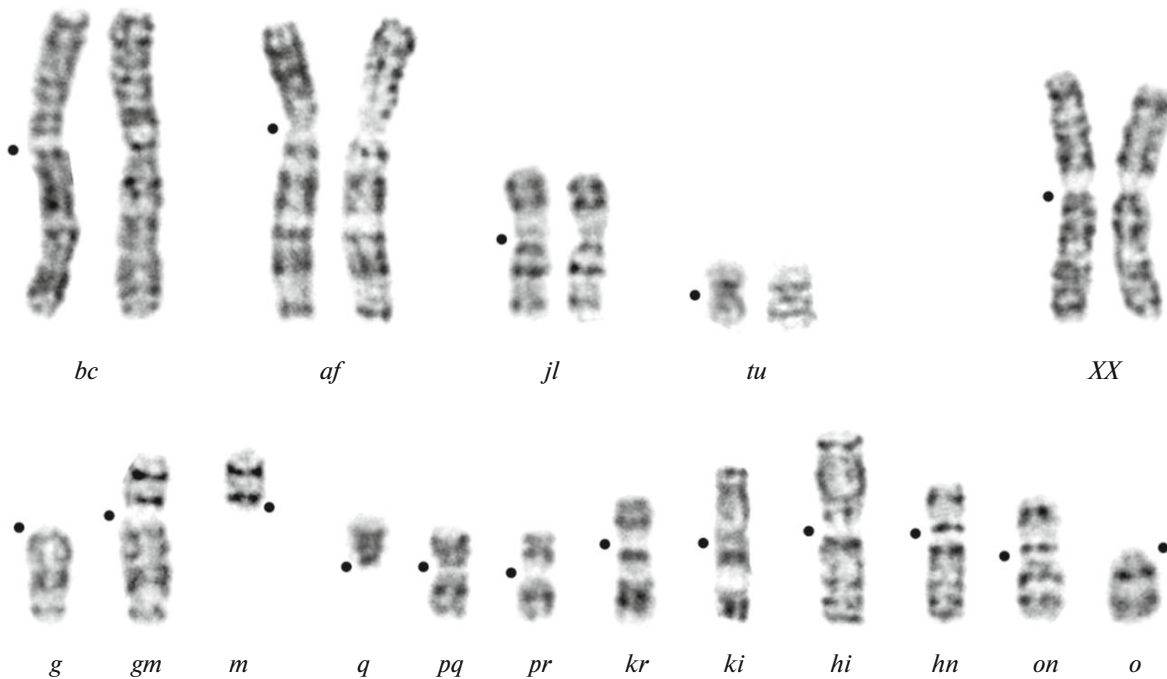
At the same time, shrews are characterized by a high rate of chromosomal evolution [11] with a tendency toward decrease in diploid chromosome number [12, 13]. The branching of species from the common stem can be traced by analyzing changes in karyotype and thereby reconstructing their karyological phylogeny. Such reconstruction has been performed for shrews of two karyotypic groups, minutus and araneus [14]. The most significant role in the evolution of shrew karyotype has been played by chromo-

somal rearrangements such as chromosome fusions, centromeric and noncentromeric fissions, and centromeric shift. The ancestral form of the araneus group appeared 3–2.5 million years ago, and *Sorex araneus* itself originated relatively recently, about 200 thousand years ago [15, 16].

In the araneus group, changes in karyotype occur mainly due to fusions, with the number of chromosome arms remaining unchanged. For convenience in describing the karyotype of this group, it has been proposed to designate chromosome arms, in order of decreasing size, by italicized Latin letters beginning with *a*, with pairs of letters designating chromosomes they form: e.g., *jl* for a metacentric chromosomes and *j* or so on for two homologous acrocentrics in the karyotype [17]. The invariable part of *S. araneus* karyotype consists of sex chromosomes—metacentric X (arms *d* and *e*), small acrocentric  $Y_1$  (arm *s*), and large acrocentric  $Y_2$ , a homologue of X-chromosome *d* arm [18, 19]—and four pairs autosomes (*af*, *bc*, *tu*, *jl*) with constant combinations of chromosome arms (for *jl*, polymorphism *j/l* or *j-l* has been described). The remaining ten initially separate chromosomes (*g*, *h*, *i*, *k*, *m*, *n*, *o*, *p*, *q*, *r*) combine with each other in different variants due to Robertsonian fusions (*Rb*) or whole-arm reciprocal translocations (*WART*). They may remain as individual chromosomes (acrocentrics) or fuse into metacentrics: *gm*, *gi*, *go*, *gr*; *hi*, *hk*, *hn*; etc. [20, 21]. "A chromosomal race (...) is a group of geographically contiguous or recently separated populations which share the same set of metacentrics and acrocentrics by descent" [22]. Some races retain free acrocentrics in their karyotype, but diversity in the territory of Russia is accounted for by races with completely metacentric karyotypes [2, 23].

So-called tension hybrid zones are formed in areas of contact between the ranges of different races [20]. They are maintained due to selection against hybrids with low fitness. The dependence between the width of hybrid zone (*w*) and level selection against such hybrids (*s*) is described by equation  $w = \sigma\sqrt{8/s}$  [24], where  $\sigma$  is standard deviation of dispersal distances. The coefficient of selection against hybrids at  $\sigma = 300$  has been estimated at 0.002 in case of minimum karyotypic differences between the parent races and at 0.08 in case of maximum differences, which is evidence for reduction of gene flow through the hybrid zone [5].

A fact in favor of relative isolation between the races is that all known hybrid zones are "bimodal"; i.e., the proportion of hybrids is lower than that expected under conditions of random breeding. This indicates that the parental forms have acquired some additional mechanisms preventing hybridization [25]. It should be noted, however, that there are no karyotypic limitations to hybridization between the parental races. Figure 1 shows the karyotype of F1 hybrid that we have obtained in captivity by crossing between the Moscow and Seliger races, whose karyotypes differ to



**Fig. 1.** G-banded karyotype of F1 hybrid between *S. araneus* races Moscow and Seliger with polymorphism for metacentric *m/q*. Dots indicate centromere locations, chromosomes are designated by Latin letters according to the accepted nomenclature [17]; XX are female sex chromosomes.

a maximum. The diagnostic component of the hybrid karyotype includes 12 unpaired chromosomes with monobrachial homology accounted for by additional polymorphism for metacentric *m/q*: *g/gm/m*, *q/pq/pr/kr/ki/hi/hn/no/o*. The low number of F1 hybrids in the zones of contact between chromosomal races may be regarded as evidence that they have entered the pathway of speciation.

**MORPHOLOGICAL STRUCTURING**

*A group of neighboring populations is not a single functional system. Their similarity is determined by development in a similar (or identical) environment and therefore is manifested even when there are no immediate ties among populations* [8, p. 17]

Chromosomal races in *S. araneus* appeared relatively recently: almost all specialists agree that they are of postglacial origin [22, 26, 27]. It could be expected that, due to isolation conditioned by karyotypic differences, these races would become morphologically and genetically segregated from each other, but analysis of morphological variation has revealed no such segregation [28, 29]. The impossibility of reliable differentiation based on morphological differences has been shown for shrews of the East European and West European karyotypic groups [30, 31]. Morphological division of *S. araneus* into subspecies in Ukraine has not been found to coincide with the distribution of chromosomal races [32]. Likewise, no correspondence between

morphological structuring and karyotypic differences has been revealed in European Russia [33–45].

However, the absence of association between morphological variability and karyotype in *S. araneus* does not indicate that morphological variation within the species is absent. The main role in morphological variation is attributed to biogeographic factors [36], and known tendencies in it are related to the latitudinal and altitudinal location of the sample under analysis. The body size of shrews is positively correlated with elevation [33, 36–38], with variation within the race sometimes being more significant than that between the races. Thus, the skull size in shrews of the Serov race collected at elevations of 300–600 m a.s.l. was significantly greater than in the sample from a lowland area [33, 38], and this parameter in the lowland sample was practically indistinguishable from that in the sample of the Sok race collected at approximately the same elevation, although shrews of the Sok race are on average smaller in body size. It should be noted that changes in skull shape were correlated with skull centroid size, which, in turn, was correlated with elevation [33].

It has been found that body size is decreased in *S. araneus* shrews from northern populations, with this phenomenon being interpreted as an exception from Bergmann’s rule and attributed to the impossibility of physiological adaptation [39]. The correlation with latitude is apparently mediated by environmental factors. Thus, skull centroid size in some samples of the Manturovo and Sok races (inhabiting more south-

ern regions) proved to be smaller than in the northern sample of the Petchora race [33], whereas in general this size in samples of the two southern races was greater than in the Petchora race. It appears that morphometric changes mainly reflect differences between habitats from which the samples were taken. For example, comparisons of centroid sizes showed that shrews of the Moscow race from a moss spruce forests of taiga type in Tver oblast were significantly smaller than shrews of the same race from other habitats and those of the Mologa race sampled farther north [34]. Apparently, the main factor of variation in *S. araneus* is the size of main prey. Thus, mtDNA haplotypes (cyt b) of fossil giant shrews fit into the variation range characteristic of *S. araneus*, and their body size is considered to depend on food supply [40].

Since obvious karyotypic subdivision is not accompanied by similarly obvious morphological subdivision, it appears that the karyotypic diversity of *S. araneus* does not contribute significantly to divergence within this species. However, the absence of correlation with karyotypic structuring is due not to low interracial variation but rather to high interpopulation variation. It has been shown [35] that morphometric differences at the interpopulation level are markedly and significantly greater than those at the interracial and, sometimes, at the interspecific level. We have obtained similar results when analyzing the morphological variability of races in the northeast of European Russia [33, 34, 38]. The level of differences has not been found to correlate with distance in any of these studies. These facts suggest that morphological features of animals mostly reflect the specific mosaic pattern of local environmental conditions; i.e., each sample characterizes a certain population as an independent unit that functions under specific conditions of a given environment. As a result, differences between the races estimated from variances of characters prove to be obscured by interpopulation differences.

## GENETIC STRUCTURING

... *the population's genetic unity is always combined with its genetic diversity* [8, p. 20]

Mitochondrial DNA, autosomal microsatellites, and Y-chromosome microsatellites are the main markers that have been used in studies on *S. araneus* [41]. Differentiation between samples based on cytochrome *b* sequence similarity does not coincide with chromosomal differentiation and mainly reflects the geographic history of the species as a whole rather than differences between recently originated races: chromosomal mutations appeared not long ago and have been transmitted from one population to another [42]. The distribution of haplotypes by the least difference principle has a star-shaped pattern with one common haplotype in the center. The absence of phylogeographic structure suggests that the distribution of haplotypes may be indicative of rapid postglacial

expansion of ancestral forms, with populations retaining a high ancestral level of polymorphism. Analysis of cytochrome *b* gene sequences also suggests that the existing races have been formed within the area populated by the species after the glacial period was over [26]. Intrapopulation variation makes the largest contribution to haplotype diversity: over 70%, irrespective of race or karyotypic group [41]. About 75% of haplotypes have originated in situ and proved to be unique for the sample. The level of difference between populations within the races ( $F_{st}$ ) corresponds to the level of interracial differences [43]. This may be regarded as evidence for partial isolation of local populations, by analogy with races.

No significant geographic structuring has been revealed in "continental" races on the Scottish islands [44]. Haplotypes found on the islands are absent on the "continental" territory, but most of them have originated from the continental haplotype occupying the central position in the star-shaped network [44]. Such differences are attributed to the founder effect and genetic drift. The effect we observed in an insular population of the Sok race in the Transvolga region (Dyakovsky forest) appears to be similar: the most frequent haplotype in this population is one of "continental" haplotypes that rarely occur beyond its range [45].

Characterizing haplotype variation in the samples as a whole, a note should be made of a generally high level of diversity: about 70% of the samples are represented by unique or singular haplotypes scattered over the species range. Thus, haplotypes described in the British race Aberdeen and Polish race Drnholec were found on single occasions in Central Russia [45]. Against the background of such diversity and scattering, the observed differences are determined mainly by haplotypes incidentally occurring in the samples. As a result, significant local differences obscure those between samples representative of the races as the wholes.

Genetic differentiation of *S. araneus* populations from different locations in Switzerland was revealed by analyzing the distribution of autosomal microsatellites. It is noteworthy that differences in the frequency of these markers between populations of the same race were nonsignificant when the distance between them was 1.5 km but acquired statistical significance when this distance increased to at least 3 km [46].

Analysis of allozyme polymorphism in 12 *S. araneus* populations along a 36-km transect in the hybrid zone between the Guzowy Młyn and Łęgucki Młyn in Poland revealed significant differences in allozyme frequencies among all samples [47], regardless of distance between them. The samples were taken in different years over a period of up to 7 years, but there were no significant differences depending on the time of sampling. Thus, population structuring is stable over time.

It appears that spatial population structuring has most effect on the estimate of gene flow in hybrid

zones, which is based on the ratio between the variance in the frequency of a trait between different groups and the total variance for all groups ( $F_{st}$ ). When the gene flow is restricted, differences should be greater in hybrid zones with more complex heterozygotes (hybrids) and also between differently rearranged (compared to ordinary) chromosomes [5]. Analysis of five hybrid zones with different complexity of heterozygotes revealed a relatively small but highly significant  $F_{st}$  value (i.e., population structuring) for each zone. Differences between populations within the race ( $F_{sc}$ ) were significant, while those between the races as the wholes ( $F_{ct}$ ) were slight and lacked statistical significance in the majority of hybrid zones. No correlation was observed between the level of interracial differences and heterozygote complexity or between  $F_{ct}$  and position of the locus.

Such a result may be evidence that chromosomal rearrangements have no substantial significance for the formation and maintenance of hybrid zones in *S. araneus*. However, this contradicts the results of analysis of karyotype distribution in these zones. The authors [5] offer several probable explanations for this contradiction. In particular, restrictions to the gene flow may remain undetected because Robertsonian heterozygotes in *S. araneus* do not suffer from infertility as substantially as in other taxa; the impact of chromosomal rearrangements may depend on the location of markers on different chromosomes or their position within a chromosome, and, at the low level of genetic differentiation observed in the hybrid zones, it may be necessary to use markers with higher resolution to detect this impact; finally, demographic, geographic, or historical factors may have a stronger effect than chromosomes in structuring the hybrid zones [5].

The last explanation appears most credible, assuming that the population is a functional unity of individuals that maintains its own internal diversity.

#### ORIGIN OF CHROMOSOMAL RACES. RECOLONIZATION OF RECENT RANGE

*We regard the rules reflecting the interdependence between the dynamics of the structure of populations and the modification of their genetic makeup as the most important factor of the evolutionary process* [12, p. 13]

The distribution of chromosomal races over the present *S. araneus* range is regarded as an example of diversity formation in the course of postglacial recolonization [1, 26, 48, 49]. In refugia where the species survived the last glaciation, differences emerged that have been fixed in differentiated forms, interfering with their subsequent fusion. In the course of recolonization, these forms come into contact and produce hybrid zones of different types, depending on the level of differences between them. Tension hybrid zones are of special interest, because further divergence of forms

in this case is more probable than their fusion [50]. There is still no consensus as to the location of putative refugia and the origin of chromosomal races. Supposedly, the formation of these races or their ancestral forms has proceeded since the Late Pleistocene and Holocene and is still underway [15, 16, 51–55].

The majority of researchers agree that the initial *S. araneus* karyotype was represented by diagnostic chromosomes in the acrocentric state [12–14], with subsequent Rb fusions resulting in the formation of metacentric chromosomes [52, 54, 55, 57–59]. Further diversification occurs via WARTs [53, 56–59]. Based on minimization of distance between karyotypes and geographic distance between the races, a global network of chromosomal races has been constructed, where all possible interracial connections are shown [27]. In the territory of Russia, races with acrocentric chromosomes are widespread near the Baltic sea in the northwest and in the vicinity of Lake Baikal in the east (Fig. 2). Completely metacentric karyotypes begin to appear at a distance of less than 500 km from localities where acrocentrics concentrate.

Following the logic of changing in karyotypes, we proposed a scheme of relationships among races inhabiting the territory of Russia. Four karyotypic “chains” of races were constructed based on the principle of minimum change (i.e., one Rb or WART mutation) between the karyotype of neighboring races. Transformation of karyotypes in three out of four chains—Ilomansi, Kirillov-Moscow, and Sok—can be traced in the northwest–southeast direction. All of them stem from the same root and terminate with the Novosibirsk race. The fourth, Baikal chain extends from the east of the species range (from Lake Baikal) and terminates with the Tomsk race in the Yenisei region. The karyotype of the Novosibirsk race is completely metacentric, and none of its diagnostic metacentric chromosomes occurs in the neighboring Tomsk race (Fig. 2). Therefore, these karyotypes cannot be derived from each other by means of a simple transformation [2].

The chains of karyotype transformations produced “fluxes” that, in the course of nature, converged and intersected with each other, which resulted in the formation of hybrid zones. In our opinion, it is in these zones where the main diversity of races has been formed in the Russian territory. It has been shown that new genetic variants, including chromosomal variants, occur especially frequently in the zones of contact between races [4, 60–62]. According to our data, approximately 95% of known cases of chromosomal polymorphism concentrate in the hybrid zones. In the zone between the Moscow and Seliger races, for example, a new variant of metacentric (*hm*) was described, which had not been previously found in any other race [4]. However, the hybrid zones can start forming only after at least one metacentric chromosome appears in the karyotype.





for shrews in the western part of the range were in periglacial regions [2]. In brief, our arguments in favor of this conclusion are as follows.

As all representatives of the genus, *S. araneus* shrews are unable to sustain starvation for a long time. Their way of foraging does not involve targeted search for prey: shrews catch food objects that they come upon while patrolling their home ranges. These animals have a polyphasic activity pattern and forage periodically throughout the day. The vast periglacial hyperzone, which existed in place of recent tundra, forest, and steppe zones, was characterized by an extra-arid environment [67]. Under such conditions, the activity of prey objects was limited, and they remained inaccessible to shrews for long periods of time. However, there still was a narrow band of diverse herbaceous vegetation along the glacier [68]. In places, this type of vegetation has been preserved to date in the northwestern part of *S. araneus* range and appears to be favorable for shrews, since their abundance in such biotopes is relatively high. The areas to the south and east of the band along the glacier were occupied by sparse steppe vegetation with pioneering communities on disturbed or underdeveloped soils [68]. Temperatures in the period of maximum cooling were 10–15°C lower in winter and 5–7°C lower in summer [69]. Such cooling is not critical for *S. araneus*, which is well adapted to cold. Analysis of these adaptations may be a subject matter of special review, and here we should only note that this species is still abundant in cold regions in the north of Arkhangelsk oblast, the Komi Republic, the Northern Urals, and Central Siberia. On the other hand, its distribution is confined to arid areas.

It is known that the last glaciation was characterized by alternating periods of warming and cooling [70]. Short warming periods could give rise to temporary streams with meadow vegetation developing along them (today, rich meadows are also formed in the floodplains). Thus, it is in this region that conditions arose for the fixation of individual metacentric chromosomes. As a result, completely metacentric races managed to be formed in the area between the positions of glacier boundary during the last glacial maximum (LGM) and the last glacial termination (LGT), which have subsequently expanded over the vacant territory. We have not revealed restrictions to their expansion due to the presence of physical barriers or unfavorable ecological conditions of the environment [2]. The occupation of territory by a certain chromosomal race of *S. araneus* is the only factor limiting the distribution of a neighboring race.

The model of expansion governed by density-dependent processes predicts reduction of diversity with increase in distance from the source region for expansion, the absence of specific adaptations to conditions in the occupied area, and consistent increase in the range of the form that has occurred by chance at

the leading edge of expansion [3]. The present distribution of races over the range within the territory of Russia perfectly corresponds to these predictions [2]. However, for this scenario to be implemented, a population where metacentric chromosomes have been fixed (rather than an individual with a certain specific karyotype) should occur at the leading edge.

#### POPULATION AS AN INDEPENDENTLY FUNCTIONING UNIT

*... the elementary unit of the evolutionary process is the population; a change in the genetic structure of a population is the initial stage of microevolution... [8, p. 9]*

All aspects of diversity formation considered above are readily explainable on the premise that the biological community is subdivided into units—populations—characterized by the unity of functioning and relatively independent of other such units. Is any data available that confirm such subdivision?

The main characteristic of a population is its size (abundance). Its maintenance at a certain level throughout the population range is provided for by two processes: reproduction and dispersal, with the unity of functioning being related particularly to dispersal [71]. It may be expected that independently functioning populations will have similar dynamics of abundance. The probability to reveal such independence is higher for species in which the rate of dispersal is correlated with genetic processes in the population. In such cases, individual patterns of dynamics in neighboring populations may be not coincident with each other.

Regarding the population functioning in terms of dispersal rate, three groups of species can be distinguished by this criterion: (1) species capable of changing the dispersal rate, (2) species with a consistently high dispersal rate, and (3) species with a low level of dispersal and unable to enhance its rate [72]. Group 1 is divided into two subgroups: (1a) species capable of enhancing the dispersal rate in direct response to an impact, and (1b) species in which this response is delayed. Intensification of dispersal in the latter case is mediated by genetic processes within populations. The emergence of intraspecific genetically different forms is most probable in group 3 and subgroup 1b, with species of the latter subgroup being more stable in an unstable environment [72]. If the unity of population functioning is mediated by dispersal processes, it may be expected that independence of the dynamics of abundance can be revealed in an independently functioning population of species from subgroup 1b in the absence of synchronizing external influences.

We have observed such a phenomenon at the biological station in Tver oblast, where long-term population monitoring is performed [73]. The distance between the plots with asynchronous population dynamics was approximately 3 km, and they were not

separated by any physical or environmental barriers. Observations were performed in different habitats, but the abundance of shrews in different biotopes within the same plot changed synchronously [73]. Since independence of the dynamics was supposedly due to the absence of significant migration between these populations, we estimated the probability of transition from one population to another using as markers spores and colony-forming units of microscopic fungi transferred in the fur of shrews. A total of 108 micro-mycete species were found (846 positive tests). The results showed that their frequencies were similar in different biotopes of the same plot but sharply differed between samples from different plots. It is noteworthy that the level of differences proved to be the highest in the putative “boundary region” [73]. Apparently, shrews that carried background micromycete species (used to distinguish between populations) were prevalent at the periphery of populations, while the occurrence of more rare species in this zone was less probable.

If populations are functioning independently, the frequencies of inherited traits may also change independently. Samples from the same plots were analyzed for genetic diversity. As in previous cases, haplotype frequencies (D-loops) were compared in samples from different habitats and different populations. The results showed that difference in these frequencies lacked statistical significance when comparing different habitats within the plot inhabited by one population, but all of them differed significantly from those in the sample from the other population [74]. The results of morphometric analysis were similar: data on the skull shape obtained by methods of geometric morphometrics showed the absence of significant differences among samples from the same population and confirmed statistical significance of differences between samples from different populations [34].

Thus, there are grounds to believe that the species *S. araneus* is divided into relatively small populations characterized by the unity of functioning, which is provided for by predominant dispersal of shrews from each population within their own population space. Such an idea of the species structure largely explains contradictions in the results of assessing the spatial distribution of trait frequencies and karyotype. Morphological differences accumulate in each individual population, and, since these population are small, their accumulation may occur rapidly. In this case, morphological and genetic variation between local populations is independent of their belonging to a certain chromosomal race. When interpopulation variation is high, we may simply fail to discern the phylogeographic signal.

Special attention should be devoted to the vast genetic diversity of samples. According to Altukhov [75], even slight restriction of free migration between populations united into a system leads to genogeographic structuring, and, although allele frequencies

in local populations may differ significantly, diversity in the system as a whole is maintained in the initial level. As a result of genetic drift, an allele may increase or decrease in frequency; it may disappear from one population but prove to be fixed in another population and appear again in the former population as a result of genetic drift; etc. When isolation of local populations is sufficient for noticeable manifestation of drift processes but these populations are interconnected by migration, a population system is formed [76]. As follows from the results of computer modeling [77], subdivision in a population prevents the loss of genetic diversity: a panmictic population of a certain size becomes completely degenerate (i.e., homozygous) after a certain period of time, whereas a subdivided population of the same size retains the initial level of diversity during the same period. A population system in nature may arise in the absence of physiographic barriers interfering with panmixia [75]. Assuming the formation of such a system in *S. araneus*, it is possible to explain both the abundance of rare alleles and high diversity of samples.

It should be noted in conclusion that population studies in the field are labor-intensive, require long-term observations, and are currently not popular. However, it is impossible to understand the essence of relevant processes without in-depth analysis of interactions at the population level. It would be unfortunate for the Russian ecological school of thought if research in the direction so successfully and fruitfully developed by our predecessors were to come to a halt.

#### COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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