
REVIEWS
AND THEORETICAL ARTICLES

*Blessed memory
of Yuri Petrovich Altukhov
and Nikolai Vasilievich Glotov*

Two Branches, Ecological and Genetic, in Studying the Species Population Structure: History, Problems, and Solutions

L. A. Zhivotovsky

Vavilov Institute of General Genetics, Russian Academy of Sciences, Moscow, 119991 Russia

e-mail: levazh@gmail.com

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Abstract—This paper presents a brief history of two different methods for studying the species population structure. The first method employs ecological markers that characterize population-specific environmental conditions, as well as biological features of populations. The second one involves genetic markers: DNA and RNA fragments, allozymes, etc. The problem of combining these two methods is discussed. A two-step approach is suggested for studying the species population structure using both the ecological and genetic markers. Firstly, the studied part of the species range is subdivided into so-called ecogeographic units (EGUs) according to environmental gradients, life strategies, and other characteristics that presumably associate with adaptation gradients and interpopulation gene flows. Secondly, the EGUs are tested genetically by using the data on multiple population samples that represent population segments within each of the ecogeographic units. The notion of representative samples with respect to the population structure, hierarchy of EGUs—populations, strategies of population management, and selection of the management units for optimizing exploitation, reproduction, and conservation of species fragments are discussed on the basis of this approach.

Keywords: species, population, structure, hierarchy, geography, ecology, DNA markers, sampling, representativeness, management unit

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INTRODUCTION

A species population structure is an aggregate of all its populations, taking into account their internal organization, hierarchical subordination, and migrations between them. Knowledge of the population structure is important not only for solving the theoretical problem of species organization but also for practical tasks of isolating protection units, reproduction units, and commercial units. In particular, this problem is relevant for species the majority of populations of which live in natural, wild conditions [1–4 and many others]. In the past, when isolating populations in zoological and botanical studies, criteria based on ecological data and morphophysiological features of the studied groups of individuals were used.

A giant leap in the study of wild populations of animals and plants which happened over the past half century was made possible through the use of the phenomenon of genetic polymorphism, from protein polymorphisms to DNA polymorphisms. The progress was so great that the question arose whether it was

possible to simply collect biological samples from different groups of a given species, genotype them by DNA markers, and reveal genetic clusters of individuals and samples, leaving behind a subordinate role for ecological characteristics. However, even the question itself is already fraught with a negative answer, for how without ecological data can one preliminarily identify groups in order to take their samples for molecular genetic research? Moreover, the variability of the overwhelming majority of DNA markers used today is usually selectively neutral and therefore clearly insufficient to identify the population organization of the species.

If we had in our hands DNA data on the variability of all those adaptive traits through which the groups studied were proved to be adapted to their environmental conditions, then perhaps this would be sufficient to identify the population structure. But the era of population studies using a complete set of population-specific adaptive DNA markers has not yet come. And so the question of interaction between these two

branches of population research, ecological and genetic, is still relevant.

In this paper, we trace in this perspective the history of population research, focusing on the work of Russian scientists.

GENETIC POLYMORPHISM IN POPULATIONS

The origins of the discovery of any phenomenon go back to the depths of time and any date is conditional. The beginning of studies of protein polymorphism can be dated to the discovery in 1949 by L. Pauling et al. [5] of chemical differences between normal and abnormal (causing sickle cell anemia) forms of hemoglobin. The next important step was taken in 1956 by V. Ingram [6], who, using his method of peptide maps, a kind of protein fingerprinting (cutting the protein chain into fragments and further their two-dimensional separation by electrophoresis), showed that the normal and anomalous variants of hemoglobin differ in charge on one of the peptide fragments. A year later, he found that the difference between hemoglobin variants for this fragment is due to the replacement in the beta chain of abnormal hemoglobin of negatively charged glutamine by electrically neutral valine, and thus it was demonstrated that the mutation process leads to hereditary changes in enzymes, unless it inactivates them [7]. A decade later, C. Shaw [8] showed that zonal electrophoresis makes it possible to distinguish between electrophoretic variants in enzymes. And a year later, three articles were published by H. Harris [9] and J. Hubby and R. Lewontin [10, 11], from which wide population studies of proteins began, and therefore 1966 can be considered the year of the beginning of broad studies on molecular polymorphism in populations.

This was due to two circumstances. First, the three researchers (H. Harris, J. Hubby, and R. Lewontin) proposed an easily accessible method of electrophoresis for a wide range of proteins and enzymes in a polyacrylamide gel (or other carriers) followed by staining. Secondly, they showed that this method is used to study Mendelian traits that reflect intragenic polymorphism. Thirdly, data on the polymorphism of populations for a set of loci made it possible to apply the theoretical models of population and evolutionary genetics developed by that time and to evaluate population-genetic parameters.

The method of electrophoresis quickly entered the practice of population and evolutionary studies in laboratories around the world and led to amazing discoveries. High biochemical polymorphism of populations was confirmed for all taxonomic groups of plants, animals, and microorganisms studied. The tools of population genetics started working, which before used to be more of a theoretical toy, and now turned out to be practically powerful. It suffices to speak about the Jap-

anese scientist M. Kimura, whose theoretical works on the dynamics of mutations and genetic drift in populations immediately became an important foundation for molecular evolutionary and population genetics, and his theory of neutrality stood in one line with Darwin's theory of the origin of species [12].

These discoveries turned out to be revolutionary for the study of populations of animals and plants. Previously used in population studies, such genetic markers as blood groups, chromosome rearrangements, and morphological and physiological mutations, compared to open protein polymorphism, were only pieces of a huge layer of intraspecific genetic variability. Moreover, there was no need to crossbreed for searching intraspecific variability, which previously narrowed the range of natural taxa under study to a small number of model objects, such as *Drosophila*. It became possible to study genetic processes in natural populations of animals and plants, taking biological samples and examining them in the laboratory on simple electrophoresis machines, which work reliably even in the field. Let us add that the era of DNA fragment sequencing that started in the 1990s and the discovery of an even more tremendous class of microsatellite polymorphisms and then, at the end of the first decade of the 2000s, the genome-wide range of nucleotide substitutions (SNPs) quickly turned population genetics into a practically important discipline in all fields of knowledge: from gene mapping in medicine and forensic science to evolutionary and environmental research. This process has transformed population studies around the world. What was going in Russia?

THE MARKER POPULATION GENETICS

In Russia, the method of electrophoresis of proteins and enzymes spread widely owing to the enthusiasm and energy of Yuri Petrovich Altukhov. In the late 1960s, at the Institute of Marine Biology in Vladivostok organized by A.V. Zhirmunsky, he launched genetic studies on Pacific salmon and then continued them at the Institute of General Genetics, where he was invited by N.P. Dubinin. The activity of Yuri Petrovich was marked by the publication of the books *Population Genetics of Fish* [13] and *Genetic Processes in Populations* [14]. For many years, his laboratory was the center of attraction of biochemical polymorphism research in natural populations in Russia.

At first, it seemed that, with the use of protein polymorphisms, the secrets of evolution and adaptation of organisms were revealed. However, over time, it became increasingly clear that they were basically a selectively neutral or weakly selective part of intraspecific variability, and that not genes but markers of genes are studied, which are not the same thing. This branch of the genetics of populations, which deals with genome markers, I would call *the marker population genetics* (MPG). With the development of methods for analyzing DNA polymorphisms, population genetic



Yuri Petrovich Altukhov (left) and Nikolai Vasilievich Glotov (right) on expeditions with their staff (1970s); one studies the salmon population and the other the populations of oaks.

studies expanded even more. However, for natural populations, the situation largely remained the same—there was still the same MPG: mainly selectively neutral DNA variability was investigated, although over time, for economically important species such as Atlantic cod and Atlantic salmon, whose genomes were sequenced recently, it became possible to find some adaptively important segments of DNA.

But today, for the vast majority of species, it has not been possible to get close to the genes that control adaptive morphological, physiological, and behavioral traits that provide adaptation to the conditions of reproduction and life in the wild.

THE PHENOTYPIC POPULATION GENETICS

Beginning in the 1960s, another branch of population research was developed in Russia, which goes back to the works of Yu.A. Filipchenko, S.S. Chetverikov, A.S. Serebrovsky, F.G. Dobzhansky, N.P. Dubinin, and other scientists. In these years, thanks to N.V. Timofeev-Ressovsky, a powerful national school of evolutionary and population biologists was created. In the direction of studying natural populations, their activity from the very beginning was marked by the book *Essay on the Theory of Populations* written by N.V. Timofeev-Ressovsky together with his colleagues, A.V. Yablokov and N.V. Glotov [3], and the article by N.V. Glotov [15]. They developed, condi-

tionally speaking, *the phenotypic population genetics* (PPG), in which the priority was given to morphological traits presumably controlled polygenically and reflecting ecological interactions. Thus attention was paid to the characteristics of the habitat, as the population lives in certain environmental conditions and the variability of morphophysiological traits is an evolutionary reflection of these conditions. In particular, attention was paid to the allocation of biogeocenotic structures, which constitute any part of the range of the species.

The concept of PPG was developed especially intensively for natural plant populations owing to the geographically wide scope of the work of Nikolai Vasilievich Glotov, who organized such studies with his colleagues, L.F. Semerikov, M.M. Magomedmirzaev, L.A. Zhukova, and many others, in different parts of the country with both woody and herbaceous plants: in Dagestan, the Volga region, the Urals, Western Siberia, the Republic of Mari El, etc. Works on quantitative genetics in the country expanded to other objects. V.A. Dragavtsev [16, 17] in the fields of Siberia establishes the system for studying the inheritance of traits of spring wheat on the basis of diallelic crosses of various varieties and lines and shows a complex inheritance of these traits due to the high contribution of epistatic interactions, introduces the method of background traits to identify the direction of the shift of the selection trait in the direction of the shift of the cor-

relating background trait with zero genetic variance, and develops the theory of limiting environmental factors in relation to the development of quantitative plant traits. A.A. Zhuchenko [18] develops the ecological genetics of agricultural plants and together with A.B. Korol [19] the theory of recombination in the evolution and breeding of plants. Z.S. Nikoro and E.Kh. Ginzburg in the Novosibirsk Akademgorodok develop a theory of quantitative traits and on its basis the theory of breeding [20]. A.V. Yablokov [21] develops research on phenetics, which studies the distribution of discrete phenotypic traits (phenes) in populations, and L.A. Zhivotovsky [22] works on a multilocus theory.

The works in this direction emphasized the importance of the habitat in the formation of natural populations and the fact that the traits studied were associated with adaptive population variability. Such associations are typical of quantitative traits that, according to theory, have a polygenic basis and can be partly determined by adaptively loaded gene complexes formed by selection under appropriate environmental conditions and ecological interactions. However, in view of the difficulties of studying these characters in the field associated with the need for special experiments to establish their genetic conditionality and to collect specific indirect data on their inheritance, the analysis of quantitative traits in natural populations has not been widely adopted.

THE PROBLEM OF THE RELATIONSHIP BETWEEN GENETIC MARKERS AND ECOLOGICAL ADAPTATIONS

The concept of selectively neutral gene markers and the concept of polygenic traits as adaptive markers required the integration of MPG and PPG. In 1948, N.P. Dubinin [23] published a landmark article on the integration of hereditary diversity in the natural populations of *Drosophila*, but it was not developed further. In 1974, a book by R. Lewontin [24] was published, translated into Russian four years later, in which the answer to the question “What is the unit of selection?” was that such a unit is a multilocus system in which each individual gene is only an element of this system. A similar multilocus approach for evaluating the association of quantitative traits and monogenic markers was developed in [22].

However, there was no answer to the question of how to combine these two approaches, MPG and PPG, for the purpose of studying *natural populations*. And, as before, these two branches of research in Russia developed independently and in isolation from each other. One can only regret that productive scientific directions headed by the schools of Yu.P. Altukhov and N.V. Glotov and their colleagues actually did not cross and did not produce a fruitful hybrid.

And since the early 1990s, research on natural populations in Russia has dramatically declined because of the bottleneck in funding of scientific researches.

A NEW ERA IN POPULATION STUDIES: COMBINING GENETICS AND ECOLOGY

In the meantime, the search for joint approaches in order to combine environmental and genetic data in the study of natural populations, in particular, for environmental purposes, has intensified in world science. In 1991, R. Waples [25], discussing the notion of an evolutionary significant unit (ESU) introduced by O. Ryder [26], defined it by two criteria: it is reproductively isolated from other similar units; it is an important evolutionary component of the species (which is equivalent to the evolutionary interpretation in the definition of a population given by N.V. Timofeev-Ressovsky et al. [3]). On the basis of ESU, two concepts of preserving the natural biodiversity were considered [25, 27–29, etc.]: (1) preserving the existing intra- and interpopulation genetic diversity, which ensures the adaptation of populations to the conditions of their habitat; (2) preserving those evolutionary processes that generate genetic diversity and ensure the action of selection for adaptive traits.

However, the concept of evolutionarily significant units could not be directly applied in practice because it was impossible to directly assess adaptive genetic and evolutionary processes. Therefore, various approaches to the use of available environmental characteristics that could be associated with population adaptability were proposed. This can be achieved, for example, by identifying important ecological gradients in the range of the species and by dividing the species into the corresponding groupings [27]. Or one can use the approach of landscape genetics: outline geographic areas, the boundaries between which provide reproductive isolation between the populations inhabiting them, and link this information to population-genetic differentiation [30–32]. Or one can distinguish “projected units” [33]: first identify groupings of individuals by analyzing different traits (morphological, behavioral, neutral genetic markers, etc.) and then prove their phylogenetic and other significance and assess the difference in individuals of different units. The most suitable practical procedure for the isolation of ESU was developed by R. Waples et al. [34–36], according to which an evolutionarily significant unit was expressed in terms of genetics, life strategies, and environment. Accordingly, they proposed to analyze population data as follows: (1) first use genetic data and build a population tree (for example, from data on genetic distances between samples); (2) then subdivide this tree on the basis of the remaining characteristics, that is, on the basis of available demographic, environmental, and other data.

However, population trees and other graphical representations of the relative location of samples or their

constituent individuals, statistical methods for analyzing group and individual genetic variability, and other methods of analysis can give a biased location of separate groups of individuals in the space of genetic coordinates. This bias may be due to various reasons:

strong genetic drift due to the bottleneck effect or the founder effect;

interpopulation exchange of individuals;

artificial reproduction, if it altered the genetic composition of the reproducible part of the population, or the introduction of individuals from genetically different groups;

low representation of these populations among the samples studied (one or two samples instead of multiple samples);

a small number of DNA markers, because for each of them population-genetic processes such as mutations and drift proceed independently;

a small sample size, as a result of which the frequencies of alleles and genotypes in the samples may accidentally significantly deviate from real population profiles;

inadequacy of clustering and other methods of data analysis; etc.

All these factors can lead to large deviations in population-genetic estimates and to an inaccurate representation of the place of some populations in the population picture of the species.

ECOGEOGRAPHIC UNITS AS A POSSIBLE BASIS FOR IDENTIFYING A POPULATION STRUCTURE OF THE SPECIES

As already mentioned, a more complete understanding of the population structure is associated with studying the factors of population adaptation to the habitat and migratory relations between populations. At the same time, little is known about the genetics of adaptations, even for well-studied species. Therefore, we are compelled to be content with indirect data on adaptive hereditary differences between populations and their "surrogates." As such surrogates, the following two types of markers can be taken.

(1) *Ecological markers* (such as habitat parameters, as well as life strategies and division into races, features of behavior, nutrition and reproduction, migration relations between populations, and other biological characteristics of populations). The advantage of ecological markers is that they can be associated with population adaptation. Their disadvantage today is in almost complete lack of knowledge about their genetic associations.

(2) *Genetic markers* (DNA markers, sequenced fragments of genes, allozymes, blood groups, inherited epigenetic and transcriptome variations, etc.). Their advantage is that they represent a genome, and the disadvantage is that, at today's level of knowledge,

the intra- and interpopulation variability of available genetic markers in overwhelming mass is selectively neutral or almost neutral, that is, not associated with differential adaptation of populations (over time, as information accumulates, this disadvantage will decrease).

It is not enough to distinguish and compare populations only for ecological markers, since it is rarely possible to strictly scientifically prove that the differences revealed between populations are hereditary. To investigate only genetic markers is also insufficient because of the above-mentioned frequent shifts in the estimates of population-genetic parameters caused by the peculiarities of population-genetic dynamics and often the low representativeness of samples in relation to the species population structure.

We proposed the following two-step approach to studying the population structure of the species based on the joint use of ecological and genetic data [37, 38]:

(1) first, in the range of the species, the *ecogeographic units* (EGU) are allocated according to environmental gradients in the investigated part of the range, types of life strategies, allocated races and ecoforms, and other biological characteristics supposedly associated with adaptation gradients or interpopulation gene flows;

(2) the selected ecogeographic units are *genetically tested* on the basis of the data on multiple samples representative of different population segments in each of these EGUs by comparing genetic differentiation between populations within the EGU and between populations of different EGUs, as well as on the basis of other genetic parameters with the corresponding population-biological interpretation.

After genetic confirmation and final allocation of ecogeographic units, we can speak about the allocation of at least two hierarchically organized levels of the population structure in the species population structure: the level of ecogeographic units (EGU) and the level of their populations (Fig. 1). At the same time, even larger and smaller levels are not excluded. It is also possible that populations inside each EGU exchange significant gene flows between themselves.

Population management approaches may differ in accordance with these two levels. For example, let us consider the following management strategy within and between ecogeographic units:

(1) *within the EGU*: protection, commercial use, and reproduction of populations of one ecogeographic unit are regulated in a coordinated manner, taking into account environmental, ecological, and genetic characteristics of each constituent population, if necessary; restoration of an individual population should be based on the genetic resources of the population itself and, in the extreme case, involve the resources of populations of the same EGU, but not from other EGUs;

(2) *between different EGUs*: protection, commercial use, and reproduction must be carried out separately

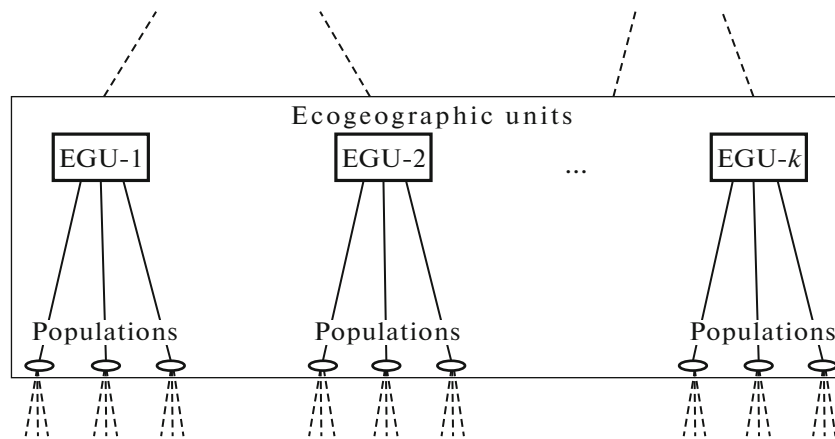


Fig. 1. Ecogeographic and population levels of the hierarchy.

in each of the EGUs, independently of each other; transport between populations of different EGUs is prohibited.

Such a strategy was proposed for the purposes of protection and reproduction of a Red List species of salmonids, the Sakhalin taimen [37].

REPRESENTATIVENESS OF SAMPLES WHEN STUDYING THE SPECIES POPULATION STRUCTURE

The most important stage in the study of the species population structure is the collection of primary material and biological samples. In accordance with the approach presented here, sampling can be schematically represented in two stages. The first stage is the preliminary subdivision of the investigated part of the species range into ecogeographic units (EGU), and the second stage is the collection of samples from these EGUs (Fig. 2).

In this case, the *representativeness of samples with respect to the species population structure* is important, that is, so that the number of different samples is large enough and that the samples cover all the allocated ecogeographic units. Ideally, each explored population of each EGU would be represented not by one but several samples, better if not less than three. This would cover the possible temporal and spatial heterogeneity and would also be a certain safeguard against random deviations to which one-time sampling may be subjected. (It goes without saying that the representativeness of each individual sample in terms of its size is also desirable, although not always feasible, for example, for rare or hard-to-reach species.) At the same time, the representativeness of samples in relation to the species population structure is the most important requirement in planning the material collection in the field, in particular, by targeting the collection of samples from different parts of the territory or water area occupied by the population, taking into account the horological structure of the range, eco-

logical features, and migratory relations between different populations.¹

ECOGEOGRAPHIC UNIT AND MANAGEMENT UNIT

An ecogeographic unit may be a convenient start to solving the practical task of allocating a management unit that would include close populations in order to develop a unified management strategy for these populations. With the currently increasing anthropogenic pressure on nature, this must be done both for economically important species and for endangered rare and protected species of animals and plants. Let us define a management unit as follows:

A management unit is a grouping of individuals of a given species consisting of one or more neighboring populations combined by common environmental conditions; similar biological features; a unified management plan (a plan for reproduction, commercial use, and protection).

An ecogeographic unit that combines populations on the basis of common ecological and geographic features and possible migratory exchanges between these populations may be a practical object for the allocation of management units. Indeed, on one hand, the ecogeographic unit biologically substantiates why these populations are grouped together into one management unit. On the other hand, it delineates the geographical boundaries of the management unit, which is convenient for practical purposes of implementing the management strategy of this management unit: its operation, reproduction, and protection. Accordingly, different management units can be controlled and regulated independently of other management units of this species.

¹ We leave beyond this discussion the sufficient representation of males and females, individuals of different ages, etc., in the samples, which is very important for many problems of population biology [4].

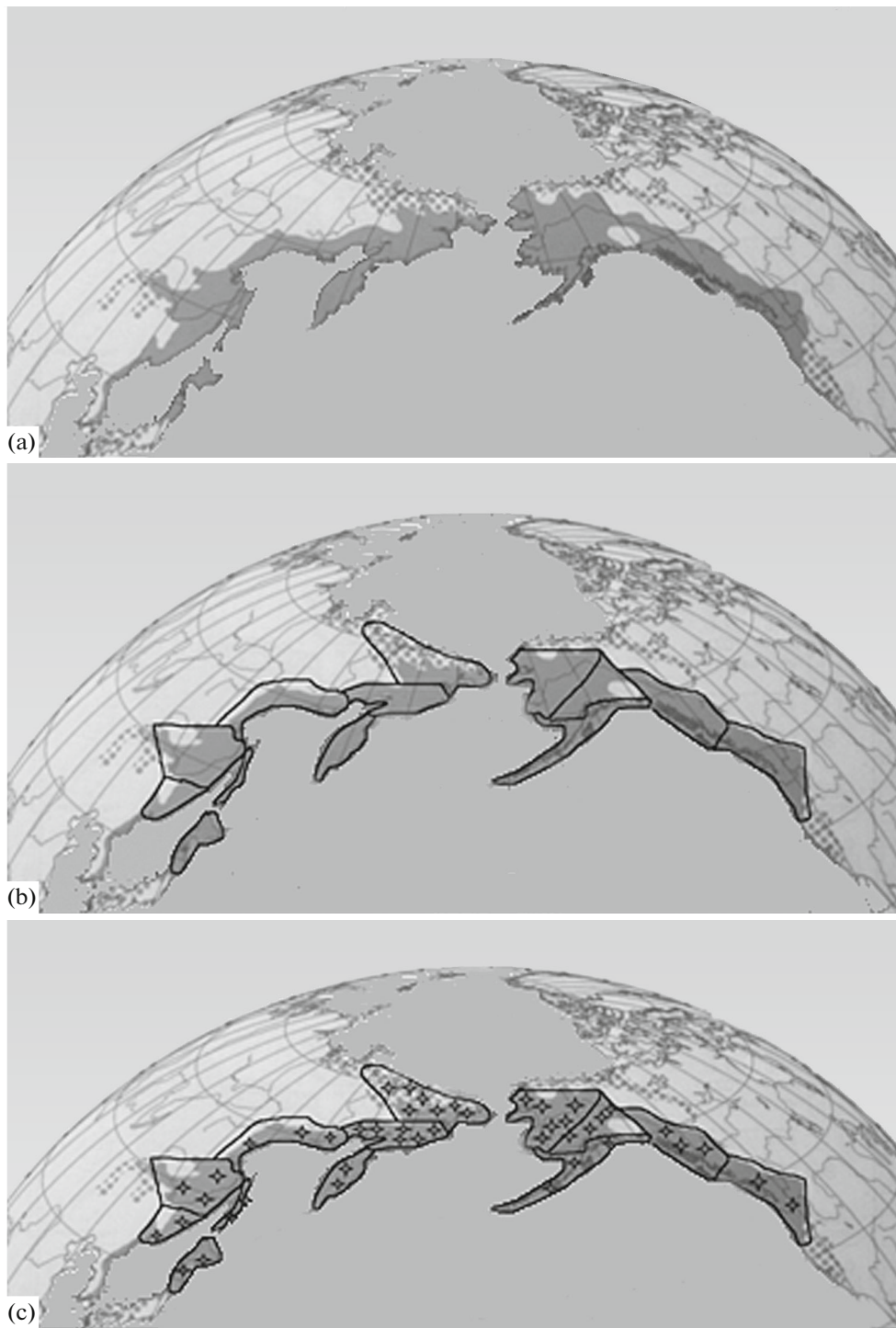


Fig. 2. Scheme of the study of the species population structure: (a) the range of the conventional species (shadow coastal strip); (b) subdivision of the range into ecogeographic units; (c) samples from ecogeographic units taken for their analysis by DNA markers and morphophysiological and other traits (shown by asterisks).

CONCLUSIONS

Undoubtedly, the approach to studying the species population structure on the basis of the allocation of ecogeographic units and the resulting condition for the representativeness of samples require an in-depth

study of species biology and long-term detailed field-work, which is difficult to achieve in field expeditions. However, this approach orients the researcher to the breadth, depth, and duration of the study of the investigated part of the range of the species. This also dic-

tates the importance of accessing archival data that can provide additional information for the allocation of ecogeographic units and even provide material for DNA analyses in the form of preserved biological samples. Organizationally, this requires the specialists in various disciplines, ecologists, geneticists, zoologists, botanists, biogeographers, and others, to study the population structure of the species and solve both the theoretical problems of organizing a biological species and the practical problems of optimizing the efforts for commercial use, conservation, and reproduction of its constituent populations.

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