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Ecological Genetics and Modern Problems of the Biosphere

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Abstract—This article considers problems of the biosphere: global warming, environmental pollution, the consequences of economic globalization, reduced biodiversity, the production and cultivation of genetically modified organisms, and related problems of environmental genetics, a scientific field that studies genetic processes in populations and takes into account environmental effects.

Keywords: ecological genetics, environment, populations, genetic processes, global warming, pollution, species extinction, genetically modified organisms

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INTRODUCTION

Earth is the only planet in the solar system on which life exists. The conditions of the space surrounding the Earth and the conditions on other planets—the presence of a vacuum, low or high temperatures, high levels of radiation—are not suitable for the appearance and preservation of life. Suitable conditions do not exist even in the deep layers of the Earth, with their darkness, high temperature, and high pressures. Thus, our planet is surrounded by a layer that is rather marshy, the only one suitable for living organisms: water and bottom sediments, a land surface, and the lower layers of the atmosphere. This layer is not only the habitat of all known organisms; it is literally saturated with them. Suffice it to say that the annual production of organic matter created by plants, animals, and microorganisms living in this layer reaches a colossal value, one that is significant on a geological scale: the total annual production of dry organic matter on Earth is about 2×10^{11} t. Living organisms not only maintain their existence in the surface layer of the Earth; they actively influence its properties, its structure and chemical composition. The surface layer of the Earth is the biosphere, the habitat of living organisms, which is constantly both processed by them and includes them.

The modern biosphere evolved as a result of evolution over many millions of years. In the course of this evolution, a harmony of nature arose that long astounded observers. If we approach the processes of the biosphere not from the position of emotional perception but from the perspective of scientific analysis, then we can say that these processes are perfectly balanced. They proceed stably, and, basically, an equilibrium in the absorption and release of substances and energy is maintained in the biosphere. We say "basically," since there is a certain storage of energy in the form of organic matter of oil, coal, and peat.

More precisely, however, one can say not that the equilibrium "is maintained" but that it "was maintained," because the situation that has existed for millions of years has changed significantly with the advent of humans. Even a primitive humans, armed with fire and primitive tools, significantly influenced nature; they exterminated certain species of animals or accelerated their death and destroyed the forest in some territories. While human activity did not quite fit into the natural balance, it did not disturb it very much until recently.

Nature began to change dramatically from the middle of the 20th century. The development of human civilization, which proceeds according to its own laws, has led to two phenomena. It first resulted in a rapid growth of the Earth's population from 100–230 million at the beginning of our era to 1 billion in 1850, 2 billion in 1930, 3 billion in 1960, 4 billion in 1975, and 6 billion people by 2000 (Kapitsa, 1999). Currently, 7756500000 people live on the Earth (https://www.worldometers.info/world-population/). A huge population requires food and has many other needs and produces a large amount of waste, much of which is difficult to process or is dangerous for living organisms. Second, mankind has turned out to be armed with powerful technology, the capabilities of which increase with each decade.

To satisfy the need for food, humans destroy more and more natural landscapes, replacing them with crops of cultivated plants. To satisfy the need for energy, they use the oil, gas, and coal that accumulated in past geological eras. Cities, industrial complexes, and roads occupy large territories and isolate from the natural biological cycle of substances and energy. As a result, large areas occupied by urbanized and technogenic landscapes cease to be suitable for the existence of animals and plants. The chemical composition of the biosphere is changing on an increasing scale due to the allocation of industrial, transport, and household waste and the use of chemicals in agriculture. The volumes of individual elements introduced into the biosphere, e.g., heavy metals, are comparable with the consequences of geological processes.

Certain species of animals and plants have disappeared, and others are threatened with death. The overall productivity of the biosphere decreases: oxygen production and the accumulation of organic matter decrease, and perhaps most importantly, the equilibrium, which until now has been characteristic of natural processes, is disturbed. Genetics must be involved in research on the consequences of these environmental phenomena.

Ecological genetics is a branch of science of heredity and variability. It studies processes in populations in connection with the ecological conditions of their existence. Naturally, when the ecological situation in many regions of the world or even globally changes as a result of anthropogenic influences, environmental genetics faces new challenges and interesting opportunities.

Further, I will consider several situations faced by the biosphere and humanity, and I will give examples of ecological and genetic studies in which the consequences of these new challenges were studied with genetic methods.

GLOBAL WARMING

Global warming is a long-term increase in the average temperature climate the system of the Earth. It has been observed for over more than a hundred years and has been especially pronounced in recent decades. It is usually considered to be caused by human activity, i.e., an anthropogenic factor. In addition to the change in average temperatures, warming causes, especially in the northern regions, and the destruction of the existing ecological environment (degradation of glaciers, thawing of permafrost, etc.).

Climatic changes caused by global warming lead to changes in the species composition of fauna and flora: the extinction of some species and the appearance of others that did not previously live in a particular territory.

We noticed that the coccinellid species *Adalia frigida*, which is numerous, even predominant, in Arkhangelsk, was not encountered after 2008; neither it nor a large number of the closely related species *A. bipunctata* (which usually lives in the middle lane) could be found on the Kola Peninsula or in Northern Norway (the cities of Tromso and Alta). It turned out that the ratio of mitochondrial haplotypes clinally changes to the north in the distribution of *A. bipunctata* (Palenko et al., 2018).

Climate-related genetic changes have been described in the study of the stoneflies *Lednia tumana* (Plecoptera, Nemouridae) in the mountains of Montana (United States); the larvae of this species live in the cold water of streams flowing from glaciers. The gene pools of populations collected in 1997, 1998, 2005, and 2010 were compared. A decrease in genetic diversity was found, in particular, the disappearance of one mtDNA haplotype that was quite common in old samples. A decrease in genetic diversity can indicate a decrease in the adaptive potential of the studied population (Jordan et al., 2016).

Studies conducted on the cosmopolitan form of Drosophila, *D. subobscura* clearly identified the effects of global warming. The authors compared the modern chromosomal polymorphism in populations of this species and those collected over the previous 24 years on three continents. In 21 of the 22 studied populations, the polymorphism changed in a direction characteristic of lower-latitude (southern) populations. The observed phenomenon may be the result of both adaptive rearrangement of the gene pool of the population existing in a given area and the migration of individuals from more southern populations (Balanyá et al., 2006). Similar changes in the gene pool have been described for populations of other Drosophila species (van Heerwaarden and Hoffmann, 2007).

The possibility of genetic adaptation of organisms to changing temperature conditions of habitat and the circumstances that impede such rapid adaptation are discussed in an article by Belgian authors (De Meester et al., 2018).

Global warming not only threatens many representatives of wild flora and fauna but also creates problems for agriculture in many regions. In an editorial in the magazine *Nature Genetics* (Genetics..., 2019) examined the problems of the genetics of cultivated plants in connection with a dramatic change in the conditions of their cultivation.

Global warming contributes to biological invasions: the resettlement of southern species and their rooting in new territories. The introduction of new species of insect vectors in a temperate climate region has already led to the appearance of tropical diseases where they did not appear before.

CHEMICAL AND RADIATION POLLUTION

One of the first studies in the field of ecological genetics examined the so-called industrial melanism in insects of the order Lepidoptera. Entomologists in England drew attention to the accumulation of dark-colored individuals in populations of the birch moth *Biston betularia* in cities and their environs, where industrial pollution of the atmosphere is most pronounced (Majerus, 1998).

Since the beginning of the 20th century, a huge number of works have studied the effect of environmental pollution on genetic processes in populations of various organisms. The following problems were developed: (1) the indirect effect of pollution—the composition of the organism of a model population changes in reaction to a change in the composition of biota in a polluted area (this refers to the classic case of melanism in the butterfly *B. betularia,* see below); (2) increased resistance to the toxic effect of the pollutant or the amount of pollution; (3) an increase in the frequency of mutations when chemical or physical mutagens enter the environment.

The appearance of dark individuals in populations of the birch moth *B. betularia* was noted in the middle of the 19th century. In the middle of the 20th century, it was experimentally shown that melanists and nonmelanists (light-colored butterflies) are victims of insectivorous birds at different frequencies. Numerous studies performed on *B. betularia* yielded the following main results (Majerus, 1998).

(1) Butterflies serve as food for insectivorous birds, who peck them from the tree trunks on which these night butterflies spend their daylight hours. Light butterflies are less noticeable on trunks covered with lichens, and dark ones are less visible on trunks lacking lichen.

(2) Lichens are sensitive to industrial pollution of the atmosphere, especially to SO_2 (sulfur dioxide). Thus, tree trunks in industrial areas are not covered with lichen, and the carbonaria form takes precedence.

(3) The composition of the population in a given area is determined by two factors: the magnitude of the selective advantage of one form or another in specific conditions and the migration of butterflies from areas with a different composition of populations.

Such a description of the history of the birch moth, however, turned out to be oversimplified. As a result of intensive studies conducted mainly in the United Kingdom, the interaction of genetic and environmental factors was shown to be a complex. It led to an increase in the proportion of melanists in populations, and, conversely, to their decrease in recent decades (Majerus, 1998).

Another mechanism is the phenomenon of the accumulation of melanists in populations of the ladybug *Adalia bipunctata* in some cities.

Lusis (1961) was the first to draw attention to the fact black forms are found significantly less in the immediate vicinity of Leningrad, in Peterhof and Gatchina, than in Leningrad itself (1961). We supplemented this observation by examining 17 populations of the suburbs of St. Petersburg and settlements of the Leningrad oblast over 10 years (Fig. 1). The correlation between the distance from the center of St. Petersburg and the proportion of melanists in the population (Fig. 2) is highly significant ($r = -0.75$, $P = 0.00036$).

The detected dependence may have a two causes. In Leningrad oblast, the largest industrial center is St. Petersburg. It should be the most polluted in terms of industrial and transport emissions. Air movements carry these contaminants spread into the vicinity, though their concentration decreases with distance from St. Petersburg. Conversely, one can expect the (passive and active) resettlement of ladybugs from the city to the oblast, and the melanization of the regional populations in this case is not a consequence of natural selection but of migration. Both mechanisms are likely to be operation, and the observed pattern is the result of the interaction of at least two factors: the spread of pollution and beetle migration.

Detailed studies by Creed (1966, 1971a) in the United Kingdom (more than 100 populations were examined) confirmed the link between the spread of melanism and industrial centers. The author obtained a high positive correlation between the frequency of melanists and the level of atmospheric pollution, in particular, the smokiness of the air.

In South Wales, which is characterized by a low concentration of melanists, Creed (1971b) found a population with a high frequency of melanists (53.7%) near one industrial enterprise, which gradually decreased as it moved away from the factory and amounted to only 10% at a distance of 35 km. The author considers this observation to be strong evidence that melanism in adalia is associated with industrial pollution of the atmosphere.

The above observations suggest that the high frequency of melanists in some large cities is really the result of the influence, not of climatic factors, but of anthropogenic influences, most likely, atmospheric pollution by industrial enterprises and stoves used to heat homes. It should be emphasized that ladybugs, unlike butterflies, are not often attacked by birds of prey and that the advantage of melanists cannot be explained by their better disguise. It is probably due to their greater physiological stability.

The accumulation of toxic heavy metals near metallurgical enterprises leads to the disappearance of vegetation cover with a high soil contamination; at a lower level, it stimulates plant adaptation to the toxic agent (Antonovics, 1975; Ernst, 2006).

Shevchenko (1979) showed that there is an increase in resistance to a physical factor, such as radiation, upon contamination. This was clearly shown in studies of unicellular algae (Shevchenko, 1979) and several species of flowering plants (*Centaurea scabiosa, Lilium martagon, Crepis tectorum,* etc.) collected at contaminated sites (Shevchenko and Pomerantseva, 1985; Shevchenko et al., 1992). In the first case, cell survival was increased upon external irradiation. In the second

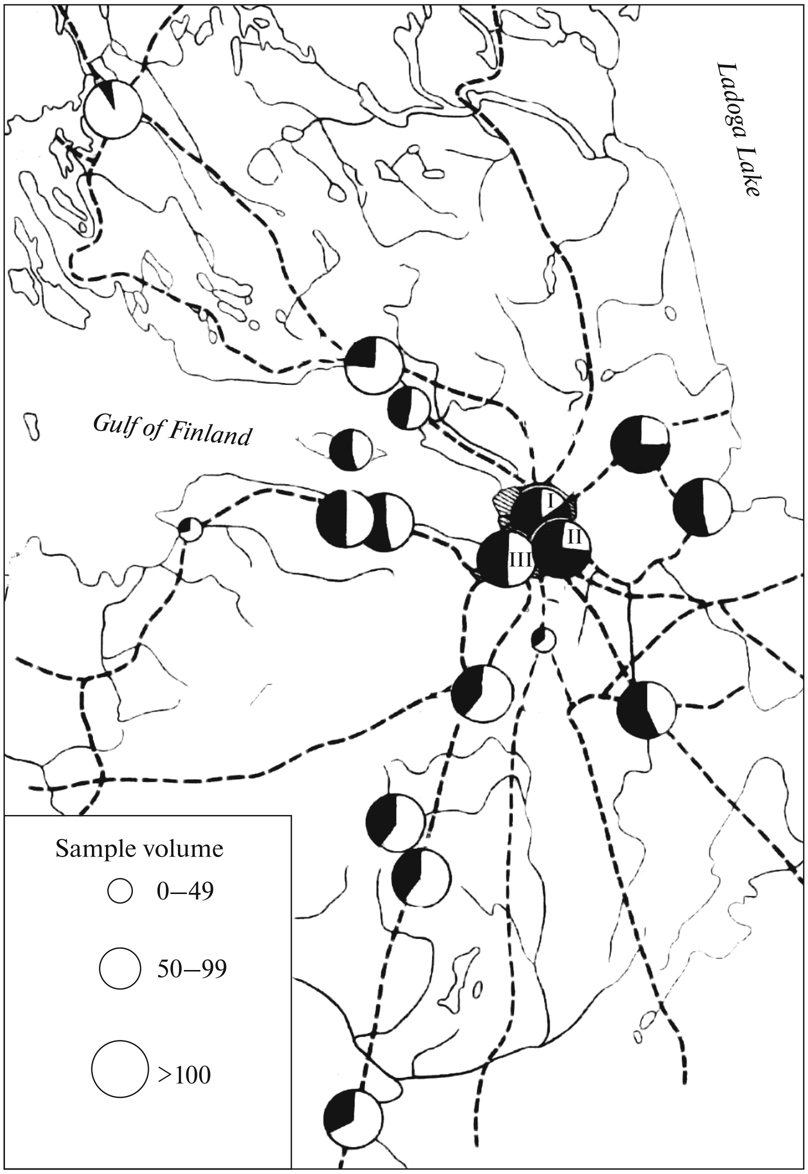

Fig. 1. Composition of *Adalia bipunctata* populations of Leningrad oblast (authors' data). The size of the black sector corresponds to the percentage of black forms in the population. I, II, III, districts of St. Petersburg (respectively, central, south, southwest).

case, it was demonstrated via the testing of chromosomal aberrations.

CONSEQUENCES OF ECONOMIC GLOBALIZATION

The manifestation and conditions of economic globalization are expansion of the network of transport routes and a sharp increase in the flows of transported goods. Both of these created favorable opportunities for the uncontrolled movement and resettlement of representatives of species of flora and fauna. The genetic study of aboriginal and invasive populations made it possible in some cases to establish the sources and routes of invasion.

In 2005, the appearance of an Asian yellow-legged wasp was noted *Vespa velutina* in France. This species has already occupied territories of 190000 square km for 5 years. Subsequently, the yellow-legged wasp was discovered in Spain, Portugal, Italy, and Belgium. A large predatory wasp began to cause noticeable harm to beekeeping. Its bites are also dangerous for humans. The natural range of the species is southeast Asia. In Asia, invasive populations have been found in Korea and Japan.

The mitochondrial DNA polymorphism (mtDNA) and nuclear markers (22 microsatellites) in individuals from the natural distribution and from invasive populations of France and Korea were studied by Arca et al. (2015). There was no diversity in mtDNAs in invasive populations: all wasps in France had mitotype F, those in Korea had mitotype K. There were many different mitotypes throughout southeast Asia; F and K were predominant in populations of southern China. It was concluded that it was this area that was the source of invasion both in Europe and in Korea. This conclusion was confirmed by the study of microsatellites. The authors also concluded that the French population originated from one (!) female fertilized by several (estimated two to four) males (Arca et al., 2015).

The ladybug *Harmony axyridis*, another Asian species, has spread in recent decades over four continents: Europe, North and South America, and Africa.

In 1988, it was reported that the Asian ladybug was found in southeastern Louisiana and eastern Mississippi. It was proposed that the introduction of *H. axyridis* into the state by sea was of a random nature, since the six coccinellid species (including *H. axyridis*), which were foreign to the United States until the beginning of the 1990s, were all found in close proximity to the seaports of the east coast. A second invasive population was discovered in the 1980s on the northwestern Pacific coast of the United States. This population is thought to have emerged independently of the earlier population. By 1994, *H. axyridis* was found in 24 states, most of which were adjacent to the western and eastern coasts of the United States. By 2007 the number of states where they found consonance had increased to 45. At present, the species has not been identified only in Wyoming and Alaska (Andrianov et al., 2018).

Invasive populations of *H. axyridis* appeared in Europe in 2000, and they quickly consolidated and spread. By 2005, the species appeared in 27 states of western and eastern Europe, including Germany, Belgium, the Netherlands, England, Switzerland, and France. In subsequent years *H. axyridis* was recorded in almost all countries of western and central Europe: in Italy, Poland, the Czech Republic, Austria, Denmark, Norway, Spain, Sweden, Hungary, Serbia, Croatia, Slovakia, Latvia, Romania, Ukraine, Bulgaria, Montenegro, and Slovenia. The northernmost finds of *H. axyridis* were recorded in Norway in 2010. The breeding of *H. axyridis* was observed by the author of this article in 2018 in Finland (Oulu).

H. axyridis was first found in Russia by us, in Kaliningrad in 2010. After that, findings were reported in other regions: Krasnodar krai in 2011 and the Crimea in 2013 (Andrianov et al., 2018).

The study of the polymorphism of indigenous and invasive populations made it possible to determine the paths of the global settlement of *H. axyridis*. The development of microsatellite genotyping techniques and statistical processing of the obtained results significantly expanded the possibilities of the study of the genetic structure of populations and their origins. The genetic structure of native, invasive, and biocontrol populations (artificially bred and used to control pests) of *H. axyridis* was studied with the use of selectively neutral markers, 18 microsatellite loci (Lombaert et al., 2010, 2014). Based on the obtained data, the probability of various scenarios of *H. axyridis* settlement was assessed.

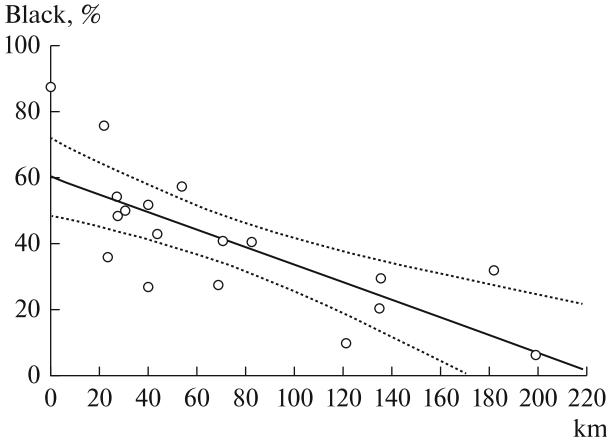

Fig. 2. Dependence of the frequency of black forms in the populations of the Leningrad oblast on the distance of the collection sites to the center of St. Petersburg. The 95% confidence interval of the regression line is indicated.

The analysis clearly supported the scenario in which North America was the first continent to be invaded by *H. axyridis* as a result of two independent events from the Asian region, most likely, from northeast China (Fig. 3). The first infestation took place in 1988 in the eastern United States (ENA), and the second occurred in 1991 in the western United States. There was a significant mixing of the gene pools of the western and eastern bridgehead populations in the zone of their contact in the states of Utah and Colorado. The eastern bridgehead has become the likely source of four invasions of other continents (South America, Africa, and Europe). In South America, at least two invasive populations, Brazil/Argentina and Chile, formed as a result of two independent introductions from ENA. One of the ENA offshoots penetrated and established itself in the western Europe, in Belgium and France, and the rooting was accompanied by mixing with the European biocontrol line. The bridgehead population of western North America, the WNA population, has been the source of at least two independent introductions to Europe. The consequence of one of them was the rooting of the "wild" *H. axyridis* population in northern Italy, while the second probably led to mixing with the western European invasive population in the distribution of both populations, ENA and WNA offshoots, to the eastern and northern parts of the mainland: Germany, Poland, the Czech Republic, Hungary, Denmark, and Norway. It is likely that additional introductions could have taken place in the mixing area.

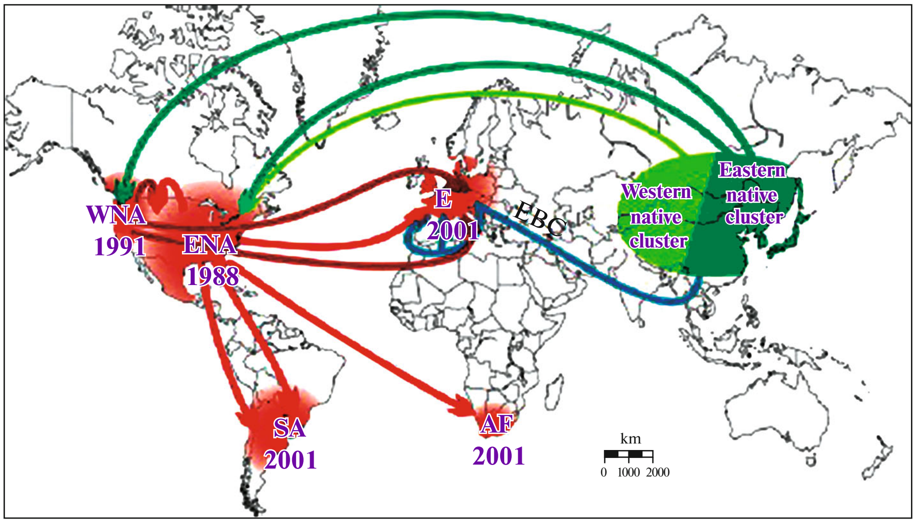

Fig. 3. Possible scenario of global invasion of *Harmony axyridis* according to microsatellite analysis. Indicated years of the first appearance *H. axyridis*. AF, Africa; E, Europe; EBC, European biocontrol population; ENA, eastern North America; SA, South America; WNA, western North America (from Andrianov et al., 2018, according to Lombaert et al., 2014).

It was repeatedly shown that the introduction of a large and aggressive Asian ladybug to new territories causes a decrease in the number of native species of coccinellids, which compete with the invading species.

The settlement paths of *H. axyridis* shown in Fig. 3 coincide well with the main global trade routes, along which goods are transported along with living organisms that are accidentally caught in containers.

GENETICALLY MODIFIED ORGANISMS

The widespread use of genetically modified organisms (GMOs) in agriculture is causing considerable public concern. There is no compelling scientific evidence on the dangers of GMOs to human health. Nevertheless, it is necessary to study and evaluate the possible impact of GMOs grown on wild flora and fauna, i.e., on the state of the environment, in those regions where genetically modified crops are grown.

This concern is primarily due to the possible adverse effect of GM plants on beneficial (or harmless) insects. Assessment of the dangers of GMOs for biodiversity showed that these concerns are exaggerated. The genes of the crystalline protein toxin from the genome of different strains of the bacteria *Bacillus thuringiensis* are used in the creation of plants that are resistant to insect pests. This so-called Bt-toxin is highly specific, and its variants act on representatives of some, but not other, insect orders. Bt Toxins are lethal for representatives of the order Lepidoptera or Coleoptera but harmless to hymenoptera, in particular, for bees (Duan et al., 2008).

Even with their potential toxicity, GMO plants do not damage insects that do not feed on them. Larvae of the popular monarch butterfly *Danaus plexippus* in the United States do not feed on corn leaves, but on cotton wool plants of the genus *Asclepias* spp. (Apocynaceae family). The pollen of Lepidoptera maize plants may fall on other plants growing close to the corn field. However, the most widely cultivated corn hybrids cultivated in the United States do not form a noticeable amount of toxin in pollen (although there are forms in which the toxin is present in pollen). In general, there are no data indicating that GMO corn has harmful effects on monarch butterflies, the larvae of which feed on forage plants growing near corn fields (Sear et al., 2001).

The discussion of the environmental dangers of the cultivation of transgenic agricultural plants indicates the possibility of the distribution of alien, resistance-enhancing genes among wild relatives of cultivated plants. As a result, herbicides intended for weed control may be ineffective (Tsatsakis et al., 2017). Such a danger does exist, but its scope has not yet been determined. The environmental consequences of an increase in the amount of pesticides (herbicides) used are more real, the possibility of which is created by the resistance to herbicides of GM crops. An increase in the release of pesticides into the environment poses a threat to human health and violates the existing structure of biota. The review cited above also provides important information on the legislative regulation of the use of GMOs in the European Union and Russia (Tsatsakis et al., 2017).

REDUCED BIODIVERSITY AND EXTINCTION OF SPECIES

All of the processes discussed above, which occur under the influence of human activity in the biosphere, lead to a reduction in biodiversity. Such a reduction undermines the balanced functioning of the biosphere and can lead at some stage to its degradation with the most unfortunate consequences for humanity. It is believed that several thousand to 100000 species disappear on Earth every year. The extinction of a particular species can be quick, but this is not an instant process. The obvious stages are a decrease in the total number of individuals and a reduction and fragmentation of the range. These stages are accompanied by changes in the genetic characteristics of the population/populations: a decrease in genetic diversity and an increase in homozygosity and inbredness. In the last stages of population decline, an increase in the frequency of inbreeding in the case of cross-fertilizing organisms itself becomes a factor that contributes to or causes population death. Small populations may disappear for stochastic reasons.

Spielman et al. (2004) compared the heterozygosity level of 170 populations of endangered species with populations of related species that are not threatened with extinction. The objects of comparative analysis were plants, vertebrate, and invertebrate animals. It turned out that the threatened species in 77% of the compared pairs showed lower heterozygosity, by 35% on average, than their related partners species in good condition. Thus, a decrease in genetic diversity not only accompanies the movement of a population (species) towards extinction but is also probably a factor contributing to extinction.

The role of genetic factors in the conservation and extinction of a species was reviewed by Frankham (2005).

Genetics not only describes the processes that occur during extinction but can also recommend means to slow or prevent it while maintaining the viability of the population. The corresponding direction of population genetics was named "conservation genetics" by Altukhov (1995, 2002).

CONCLUSIONS

This article briefly examined the particularly acute problems of environmental genetics in connection with the changes taking place in the biosphere. I drew attention to some of these problems as early as 1984 (Zakharov, 1984). Each of the issues briefly discussed here could be the subject of a separate large article. Here, my task was only to outline key issues and give examples of how they are discussed or solved in the literature.

The genetic study of natural populations was simultaneously begun by the Russian scientists S.S. Chetverikov in Moscow and F.G. Dobrzansky in the United States. Both researchers worked with wild-type Drosophila species. While S.S. Chetverikov failed to develop his research, F.G. Dobrzhansky, who studied populations in vast areas of North and Central America, proceeded to analyze the influence of living conditions on the genetic structure of natural populations, i.e., to the study of environmental genetics. Beginning in the mid-1920s in the Soviet Union, Lusis (1961) conducted classical studies of ecological genetics using beetle populations *Adalia bipunctata*. Beginning in the 1920s, various objects of research that can be attributed to the field of environmental genetics were carried out in the United Kingdom and other Western countries. Their significance especially grew and was recognized with an understanding of the dysfunctional and alarmingly worsening state of the biosphere.

Under the influence of an ever-increasing anthropogenic press, it is not only the biosphere that is degraded. Humans dramatically accelerate the pace of evolution of the Earth's biota. This acceleration is insignificantly associated with the mutagenic effects of anthropogenic pollution and, to a decisive extent, with the emergence of new factors of natural selection. Under these conditions, the task of environmental genetics is to analyze the genetic processes occurring in populations of as many species as possible and to develop a forecast on this basis for the development of the evolutionary process in the biosphere.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflicts of interest.

Statement on the welfare of humans or animals. This article does not contain any studies involving animals performed by any of the authors.

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