Artículo de investigación

The history of the formation of the population structure of Juniperus communis L. (Cupressaceae) in the Cis-Urals and the Southern Urals

ИСТОРИЯ ФОРМИРОВАНИЯ ПОПУЛЯЦИОННОЙ СТРУКТУРЫ МОЖЖЕВЕЛЬНИКА ОБЫКНОВЕННОГО *JUNIPERUS COMMUNIS* L. *(CUPRESSACEAE)* В ПРЕДУРАЛЬЕ И НА ЮЖНОМ УРАЛЕ

Historia de la formación de la estructura de la población de Junger mushroom del juniperus communis l. (Cupressaceae) en la Ural y en los Urales del sur

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Abstract

The possible ways of the historical development of juniper (*Juniperus communis* L.) in the Cis-Urals and in the South Urals are considered. The main habitats and populations of the species are indicated. It is shown that the history of the settlement of *Juniperus communis* is consistent with the history of the development of pine forests in the region. The South Ural mountain population has the earliest origin (over 12 thousand years), the Cis-Ural forest-steppe population has the most recent (about 3-4 thousand years), the Cis-Ural forest population has an average formation time (about 10-12 thousand years).

Key words: *Juniperus communis*, Southern Urals, Cis-Urals, history of settlement, population.

Аннотация

Рассмотрены возможные пути исторического развития можжевельника обыкновенного (*Juniperus communis* L.) в Предуралье и на Южном Урале. Указаны основные районы обитания и популяции вида. Показано, что история расселения можжевельника обыкновенного согласуется с историей развития сосновых лесов в регионе. Наиболее раннее происхождение (старше 12 тысяч лет) имеет южноуральская горная популяция, наиболее позднее (около 3-4 тысяч лет) – предуральская лесостепная популяция, среднее по времени формирования (около 10-12 тысяч лет) – предуральская лесная популяция.

Ключевые слова: *Juniperus communis*, Южный Урал, Предуралье, история расселения, популяции.

Resumen

Se consideran las posibles vías del desarrollo histórico del enebro (Juniperus communis L.) en los Cis-Urales y en los Urales del Sur. Se indican los principales hábitats y poblaciones de la especie. Se muestra que la historia del asentamiento de Juniperus communis es consistente con la historia del desarrollo de los bosques de pinos en la región. La población de las montañas del sur de los Urales tiene su origen más temprano (más de 12 mil años), la población de estepas del bosque Cis-Ural tiene la más reciente (alrededor de 3-4 mil años), la población del bosque Cis-Ural tiene un tiempo de formación promedio (aproximadamente 10-12 mil años).

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Palabras clave: Juniperus communis, Urales del sur, Cis-Urales, historia del asentamiento, población.

Introduction

The history of the formation and settlement of *Juniperus communis* in the Cis-Urals and in the southern Urals is inextricably linked with the formation and settlement of pine forests in general. According to the generalized reference data (Maleev, 1949; Sokolov et al., 1977; Mamaev, 1983), the juniper is mainly a companion of pine, pine-larch, and less often - dark coniferous forests in the Urals. The species is found in 54 forest types in the mountain forests of the Middle Urals, and at the same time prefers P. hyloccmiosa (Kolesnikov et al., 1973; Tishkina, 2009; Kozhevnikov, Tishkina, 2014). At the southern tip of the Urals and in the northern part of Kazakhstan, it is part of the undergrowth of pine-steppe, or mixed with broad-leaved species.

In the Southern Urals, the species is located at the border of its distribution (The determinant…, 1988), characterized by irregularity and fragmentation of settlement. In the region under study, we identified several (Farukshina, Putenikhin, 2012; Putenikhin, Farukshina, 2013) relatively large habitats of *Juniperus communis*: 1) in the plain pine forests (including open spaces) of the Belaya-Kama-Ufa interfluve in northwest and northern parts of the Bashkir Cis-Urals and the adjacent part of the Udmurt Republic (Nikolo-Berezovskaya, Dyurtyulinskaya, Amzinskaya, Maksimovskaya and Mazuninskaya cenopopulations); 2) in dark coniferous forests in the central highly elevated part of the Southern Urals within the Republic of Bashkortostan and the Chelyabinsk Region (Katav-Ivanovsk cenopopulations); 3) in the central part of the South Urals (Shigaevskaya, Uzyanskaya, Burzyanskaya, Avzyanskaya cenopopulations).

Paleobotanical materials for junipers are currently extremely inadequate. Based on the available data, it is very difficult to determine the paths of settlement and the importance of junipers in the vegetation cover, in some specific segments of the geological history. The few fossil remains of some species of the Oxycedrus and Sabina sections are found in various areas of the range, the most ancient of which are found in Upper Cretaceous sediments (Gorchakovsky, 1969; Ismailov, 1974).

Materials on the history of the settlement of juniper show that *Juniperus communis* had an extensive range covering most of North America and Eurasia up to the Tertiary period of Cenozoic; according to paleobotanical data, the species is known from the Tertiary sediments of Altai, the Pleistocene sediments of North America and the post-Pleistocene sediments of Northern Europe (see: Ismailov, 1974). The juniper habitat in glacial and interglacial epochs underwent repeated changes. In the postglacial period, the juniper, moving after the retreating glacier, restores large areas of the former range in the north. According to M. I. Ismailov (1974), the modern juniper is either a “cold-resistant mutant” that appeared in the Ice Age and later spread, or a pre-glacial old look, which “had hidden features” in the period of “cryophilization”.

This report analyzes the historical development paths of the *Juniperus communis* in the Cis-Urals region and in the southern Urals.

Material and methods

Within the Southern Urals and the Cis-Urals (Belaya – Kama interfluve), 10 main cenopopulations were identified (Table 1). Geographically, the juniper research area covers the northwestern, northern, and northeastern parts of the Bashkir Cis-Urals (with the adjacent southeastern part of the Udmurt Cis-Urals), the entire mountain belt of the Southern Urals (including the northern edge of the Zilair Plateau in the south) and the territory of the Urals adjacent to the east.

Table 1. Test areas in juniper cenopopulation in the Urals and in the southern Urals

Cenopopulation (trial plot)	Geographical position	Composition of the three stand*
Bashkir and Udmurt Cis-Urals (Belaya-Kama-Ufa plain-hilly interfluve)		
Mazuninskaya	"Udmurt" Cis-Ural (south-east; right bank of the Kama river)	–
Amzinsky	Bashkir Cis-Ural (north-west; the interfluve of the rivers Kama and Buy)	9P1B+S rarely L
Maksimovskaya	Bashkir Cis-Ural (northern forest-steppe part)	–
Nikolo-Berezovskaya	Bashkir Cis-Ural (north-west; between the rivers Kama and Belaya)	9P1B
Dyurtyulinskaya	Bashkir Cis-Ural (north-west; upper course of the Belaya River)	10P
South Ural (mountain forest zone)		
Katav-Ivanovskaya	North of the central part (Katav River)	3F2S5P
Shigaevskaya	Central part (North Kraka range, eastern slope)	10P+L rarely B
Uzyanskaya	Central part (Middle Kraká ridge, western slope)	10P rarely L
Avzyanskaya	Central part (Bashtau ridge, southern slope)	2P8P rarely L
Burzyanskaya	South central part (South Kraká ridge, western slope)	10P

Note. * The composition of the stand (on the test plot), to which the cenopopulation of *Juniperus communis* is confined; - "forest-steppe" cenopopulations growing in open space or edge; P - pine, B - birch, S - spruce, L- linden, F - fir, L - larch.

To study the population structure, a three-level hierarchical sampling system was implemented (Mamaev, 1973; Putenikhin et al., 2004, 2005): 1) sample areas in cenopopulations (one for the cenopopulation), 2) randomly selected

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individuals in the test areas (15 female and 15 males), 3) individual samples of generative organs with 15 females and 1-3 vegetative sprouts from all 30 individuals. From each individual sample, 10-20 cones and seeds were randomly taken (Mamaev, 1973; Putenikhin et al., 2004, 2005). 10 signs of generative organs and 7 morphological signs of vegetative organs were studied.

Results and its discussion

Previously, on the basis of multidimensional methods, phenotypic differentiation of *Juniperus communis* was assessed using a set of 17 morphological features of generative and vegetative organs in the Cis-Urals and the Southern Urals (Farukshina, Putenikhin, 2016b). Three phenotypically differing local biological populations were identified (figure 1): Cis-Ural forest (Amzinskaya, Nikolo-Berezovskaya and Dyurtyulinskaya cenopopulations; all of them are cenopopulations growing under a canopy), Cis-Ural forest-steppe (Maksimovskaya and Mazuninskaya cenopopulations; confined to open habitats), South Ural Mountain (cenopopulations of the mountain forest zone of the Southern Urals). Within the last population, two subpopulations were distinguished - forest (Avzyanskaya, Burzyanskaya, Uzyanskaya) and forest edge (Shigaevskaya, Katav-Ivanovskaya cenopopulations).

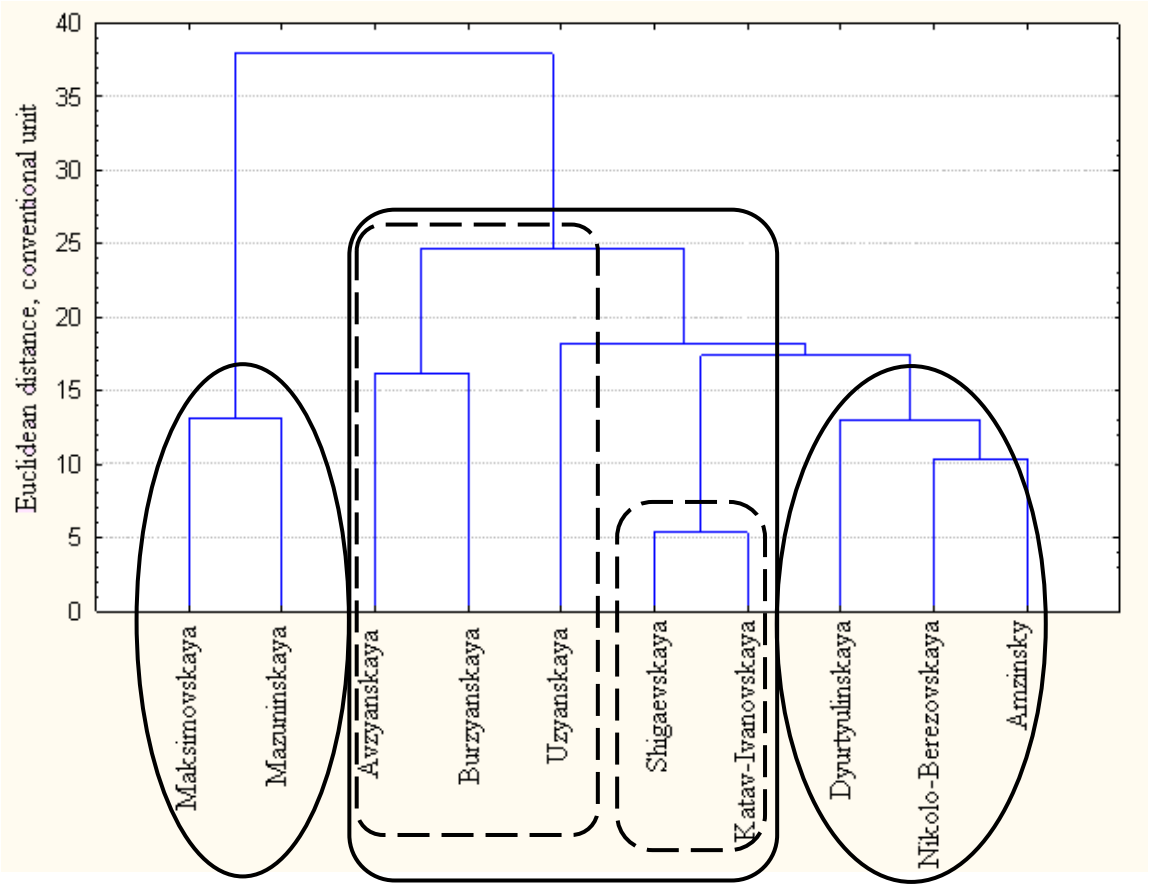

Figure 1. Dendrogram of differences and similarities of coenopopulations of *Juniperus communis* based on signs of vegetative and generative organs

The cis-Ural forest population is completely confined to the flat pine forests of the northwestern part of the Bashkir Cis-Urals. The Cis-Ural forest-steppe population is localized in the north-west of the Bashkir Cis-Urals and in the south-eastern part of the Udmurt Cis-Urals. The mountainous South Ural population is located in the central part of the Southern Urals and is mainly associated with mountain pine and dark coniferous forests. The forest subpopulation is represented by typically sub-forested locations, and the forest edges subpopulation is represented by areas on open steppe slopes or forest edges.

It was found that the mountainous South Ural population with a relatively increased intrapopulation phenotypic (genetic) diversity according to hereditarily determined signs of the generative organs is at the same time less variable, i.e. phenotypically more homogeneous in vegetative indicators. Cis-Ural populations are characterized by an inverse pattern (Farukshina, Putenikhin, 2016b).

It is possible to determine the possible ways of settlement in the Urals based on the history of the settlement of pine forests (see above), of which it is a satellite. For the Scots pine during the repeated Pleistocene glaciations, the Southern Urals region became one of its refuge in landscapes of larch-pine-birch forest-steppe (Blagoveshchensky, 1943; Krasheninnikov, 1939; Panova, 1982; Filippova et al., 2006; Frenzel, 1960). Akchagyl marine ingression had a significant influence on the change in the vegetation cover of the Cis-Urals at the end of the Pliocene and the beginning of the Pleistocene, when the region of the Belaya-Kama depression was flooded (Gorchakovsky, 1969; Fedorova, 1970). Since that time, the pine forests isolated in the Cis-Urals have their own history (Krasheninnikov, 1939; Popov, 1980).

In general, the historical age of the South Ural pine forests is significantly greater than that of the pine in the main, more northern part of the range (Frenzel, 1960). The forest vegetation of the plain Belaya-Kama interfluve (Cis-Ural), in particular, pine and spruce forests have an age not older than the end of the Pleistocene, and possibly Holocene (Popov, 1980; Shalandina, 1998). If flat pine forests spread to this territory from the northwest, mountain pine forests penetrated into the Southern Urals from Eastern Siberia through the Kazakh low mountain (Gorchakovsky, 1969; Popov, 1980), therefore, these two groups of forests have not only different ages, but also origin.

In the xerothermic phase of the Holocene (4.5-2.5 thousand years ago), warming and drying of the climate led to a shift of vegetation zones; Steppe vegetation, especially in the Cis-Ural region, strongly advanced to the north, increasing the spatial isolation of the cis-Ural pine forests from the South Urals (Krasheninnikov, 1939; Igoshina, 1963; Gorchakovsky, 1969). At the end of the Holocene, the range of pine trees in the region underwent more significant disjunctions not only due to the expansion of deciduous forests and forest-steppe vegetation, but also due to intensive anthropogenic activities (Popov, 1980). In the past two centuries, the area of pine forests in the region, especially in the Cis-Urals, has decreased significantly. Juniper squares decreased in the wake of pine. In the western part of the Republic of Bashkortostan, the juniper is a relic of the former boron vegetation (Putenikhin, Farukshina, 2013). The distribution of *Juniperus communis* in the two parts of the habitat under consideration (in the Cis-Ural and in the southern Urals), apparently, was closely related to the Pleistocene-Holocene settlement of Scotch pine.

Given the above, the differentiation of the juniper populations in the study area can be represented as follows. The mountainous South Ural population was probably formed in the pre-Pleistocene and Pleistocene time as a result of the settling of Scots pine from Siberia to the Southern Urals, as well as in the process of Holocene expansion of the South Ural pine refuge. In the Holocene, as the climate is xerophytic, the juniper partly leaves the pine forests under the canopy to the edges and open spaces, and, on the other hand, is introduced into the composition of dark coniferous forests. The initial stages of differentiation of the South Ural population with the formation of an edge - forest subpopulation may be associated with these processes. Thus, the age of the mountainous southern Ural population of juniper is more than 12 thousand years. Microevolutionary processes aimed at the divergence of the mountain population itself into subpopulations probably began no earlier than 1-2 thousand years ago and so far have not led to the formation of independent local populations. Therefore, the only local biological population represents *Juniperus communis* in the mountains of the Southern Urals.

As it was shown earlier with the phenotypic characteristics of populations (Farukshina, Putenikhin, 2016b), according to some signs of vegetative organs, as well as the density of individuals in cenopopulations, the mountainous South Urals population deviates towards the Siberian and northern populations of common juniper. According to the parameters of the generative organs, together with the cis-Ural populations, the mountainous South Ural population is intermediate between Eastern European and Siberian habitats. This may be a consequence of the processes of historical development of the species in the region, which we have mentioned above.

The cis-Ural populations of common juniper, coenotic associated with relatively young pine forests that penetrated into the Cis-Urals from the northwest as the glacier receded, are probably of

late Pleistocene or Holocene age (not older than 10–12 thousand years). Consequently, the formation of juniper populations in the Cis-Urals took place during a shorter time (in the post-glacial), moreover, at a distance from the South Ural part of the range. In the cis-Ural part of the area, during the Holocene (as the climate warmed), intense microevolutionary processes took place, which led to the division of the originally single cis-Ural population into two independent local populations — the forest and the forest-steppe. Based on the time of intensive advance of the steppe and forest-steppe to the north (middle Holocene) (Gorchakovsky, 1969), the age of the forest-steppe of the Cis-Ural population can be approximately determined in about 3-4 thousand years.

Some indicators of cis-Ural populations — juniper density, signs of vegetative organs (Farukshina, Putenikhin, 2012, 2016b) indicate a certain phenotypic similarity with Eastern European populations of juniper (as already mentioned, the populations are intermediate position between European and Siberian populations). Perhaps this confirms the origin of the cis-Ural populations from the Eastern European populations that settled along with the common pine after the retreating glacier. The established nature of the population structure of common juniper, which corresponds to the "colonial type" (Grant, 1991), is consistent not only with the history of the development of pine forests, but, to a certain extent, with the phenotypic differentiation of the pine tree populations in the region (Putenikhin, 2000).

Estimation of intrapopulation variability showed (Farukshina, Putenikhin, 2016b) that the mountainous South Ural population is characterized by a higher phenotypic (and genetic) diversity compared to the cis-Ural populations. This is consistent with the larger range of the mountain population. At the same time, this indicates active processes of natural selection (probably stabilizing), maintaining a high level of intrapopulational diversity and providing a certain degree of stability of the species in mountain conditions (Schmalgauzen, 1946; Timofeev-Resovsky, etc., 1969; Grant, 1991). However, the initial stages of divergence of this population into separate subpopulations indicate the intensification of other forms of selection (for example, moving and / or disruptive) in conditions of significant climate warming in the modern era.

Cis-Ural populations are inferior in terms of the phenotypic variability of genotypically determined morphological features of the generative organs of the mountain populations, and in this respect, they are similar to each other. It can be assumed that the pre-Ural forest-steppe population in the xerothermic epoch was distinguished from the originally single Early Holocene population of the Cis-Urals. The juniper ordinary, still confined mainly to the pine forests of Kama and Belaya, began simultaneously to master the steppe areas that had advanced from the south. Under the action of disruptive selection, a differentiation of the initial population occurred with the formation of the forest-steppe cis-Ural population that was phenotypically (and genetically) different from the forest cis-Ural population. Due to this separation, intrapopulation "genetic" variability could be reduced to a certain extent.

In the forest-steppe population in the process of its development, the predominant role was acquired by the driving selection, thanks to which it acquired strong phenotypic differences from the original cis-Ural population. Interestingly, the cis-Ural forest-steppe population (Farukshina, Putenikhin, 2016b) is distinguished by the highest level of variability due to the labile traits of vegetative organs, as well as by high shaped diversity (Farukshina, Putenikhin, 2016a). In our opinion, this confirms the active action of a moving selection in it, leading to a shift in the phenotypic status of the population and the "chipping" of various forms according to the habit of the plants.

In general, the colonial nature of the population structure of a species in the region (including the disjunction of populations into more or less large isolates) does not exclude the effect of gene drift in populations, especially cis-Ural, occurring against the background of other microevolutionary factors.

Conclusion

The South Ural mountain population has the earliest origin (older than 12 thousand years), the most cis-Ural forest-steppe population is the latest (about 3-4 thousand years), and the cis-Ural forest population is about the average formation time (about 10-12 thousand years). Populations differ in the level of intrapopulation diversity and the directions of microevolutionary processes occurring in them. These differences, as well as the reduction of the ranges of populations throughout the second half of the Holocene, the formation of a colonial-type population structure determine the need to preserve the gene pool and the selective use of

juniper in the Ural and South Urals on a population basis.

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