Introduced, Mixed, and Peripheral: Conservation of Mitochondrial-DNA Lineages in the Wild Boar (*Sus scrofa* L.) Population in the Urals

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Abstract: Translocations and introductions are important events that allow organisms to overcome natural barriers. The genetic background of colonization success and genetic consequences of the establishment of populations in new environments are of great interest for predicting species' colonization success. The wild boar has been introduced into many parts of the world. We analyzed sequences of the mitochondrial-DNA control region in the wild boars introduced into the Ural region and compared them with sequences from founder populations (from Europe, the Caucasus, Central Asia, and the Far East). We found that the introduced population has high genetic diversity. Haplotypes from all the major phylogenetic clades were detected in the analyzed group of the animals from the Urals. In this group, no haplotypes identical to Far Eastern sequences were detectable despite a large number of founders from that region. The contribution of lineages originating from Eastern Europe was greater than expected from the proportions (%) of European and Asian animals in the founder populations. This is the first study on the genetic diversity and structure of a wild boar population of mixed origin at the northern periphery of this species' geographical range.

Keywords: wild boar; D-loop; translocation; colonization; founder population; haplotype diversity

1. Introduction

Translocations and introductions are important ecological and evolutionary events that allow organisms to overcome natural barriers and that disrupt the natural pace at which ecosystems have evolved through millennia [1]. As a consequence, the organisms introduced into a new environment may face difficulties with adaptation to novel habitats, and this problem may, in turn, reduce the success of species establishment. On the other hand, the introduction of organisms may often result in their rapid invasion of natural communities [2]. Given the evolutionary, ecological, and economic (in case of invasion) importance of animals' translocations and introductions, it is worthwhile to understand the factors that mediate the establishment and expansion of a species' population in a new region. Many studies have addressed the role of extrinsic factors (climate, habitat quality, and competitors) and intrinsic factors (propagule pressure, life history, and dispersal

abilities) in organisms' colonization success [3–6]. The most intriguing questions include the genetic background of colonization success and genetic consequences of the establishment of populations in new environments, which are often situated at the periphery of the species' geographical ranges. The most important factors affecting the establishment success via founders' genetic diversity are multiple introductions and intra- and interspecies hybridization [2,6,7]. Particularly, an intraspecific genetic admixture may benefit introduced populations via (1) an increase in genetic variation, which provides a larger pool of raw material for adaptive evolution; (2) the emergence of novel or transgressive phenotypes through previously unexplored allele and gene combinations [6,8,9]; (3) heterosis; and (4) the masking or purging of deleterious mutations; the latter process may reduce potentially negative effects of genetic bottlenecks and inbreeding [6,10,11]. The effect of multi-source introductions has been investigated for plants [12–14], mollusks [15,16], arthropods [17,18], and lizards [19–21]. Most of these studies indicate an increase in genetic diversity in introduced versus source populations, but some reports also show a decrease in genetic diversity in mixed populations resulting from the admixture of geographically distant populations [4,13,14]. In mammals, the genetics of introduced populations has been researched for some carnivores [22–24] and *Mus musculus* [25,26], but relatively few studies involved ungulates [27,28], even though many of these animals have been intentionally introduced into novel environments for hunting and conservation purposes [29]. Ungulates are of great economic and ecological importance [30–33] and understanding the genetic specific features of newly established populations could help with conservation of endangered species [34–36] and controlling species that could affect native ecosystems [37,38]. The latter issue is especially relevant for the wild boar, which is expanding in the areas of introduction [39–41] and is treated as a pest in a number of countries [42].

The wild boar is a species occurring across the whole Palearctic [43]. Despite its controversial role in ecosystems [44], it has been introduced for hunting purposes into the Americas [40,45–47] and Australia [48] and into many parts of North Eastern Europe and Northern Asia [49]. The taxonomy of the genus *Sus* is contradictory due to the variability of the species' morphological and genetic traits. According to Keuling O. et al. [43], 16 wild boar subspecies are recognized based on morphological parameters, such as the shape of the skull, size and proportions of the body, and hair color. Despite these differences, laboratory experiments have not revealed any limitations of crossbreeding between wild boar subspecies and between the wild boar and various breeds of the domestic swine [50].

Subspecies of wild *Sus scrofa* are divided into European, Asian, and South Asian groups [43]. Molecular systematics confirms these clades [51] but also includes the Near Eastern (NE) clade, which in turn consists of two subclades (NE1 and NE2) [52]. The genetics of wild and domestic *S. scrofa* have been extensively investigated [53–55] and references therein), and most studies on wild populations come from Western Europe (e.g., [55–59]), the Far East [60–63], and a few areas of Southern and Central Asia [64]. The information on genetic diversity in recently introduced populations of the wild boar is scarce and represented by a few studies from New Zealand [65] and the South [45] and North [66,67] Americas. There are also several reports [68–70] based on a relatively small number of samples. Many wild boar releases have been well documented, and there are sufficient data about the genetics of founders of an introduced wild boar, which is a good model for analyzing changes in genetic diversity in admixed populations. This problem sounds especially interesting given that often, these animals have been released in northern areas beyond this species' historical range. In particular, this is the case for the wild boar introduction into the Urals (Russia).

When the introduction of the wild boar into the Urals was organized, representatives of four subspecies (*Sus s. scrofa*, *S. s. attila*, *S. s. nigripes*, and *S. s. ussuricus*) were translocated from their natural habitats and released in the eastern part of the region (Sverdlovsk Oblast; Figure 1). These subspecies differ in morphology [71,72] and polymorphism of blood group antigens [50]. These subspecies are geographically isolated in nature (except *S. s. attila* and *S. s. nigripes* [49,71]), but under experimental conditions, they crossbreed with each other [50].
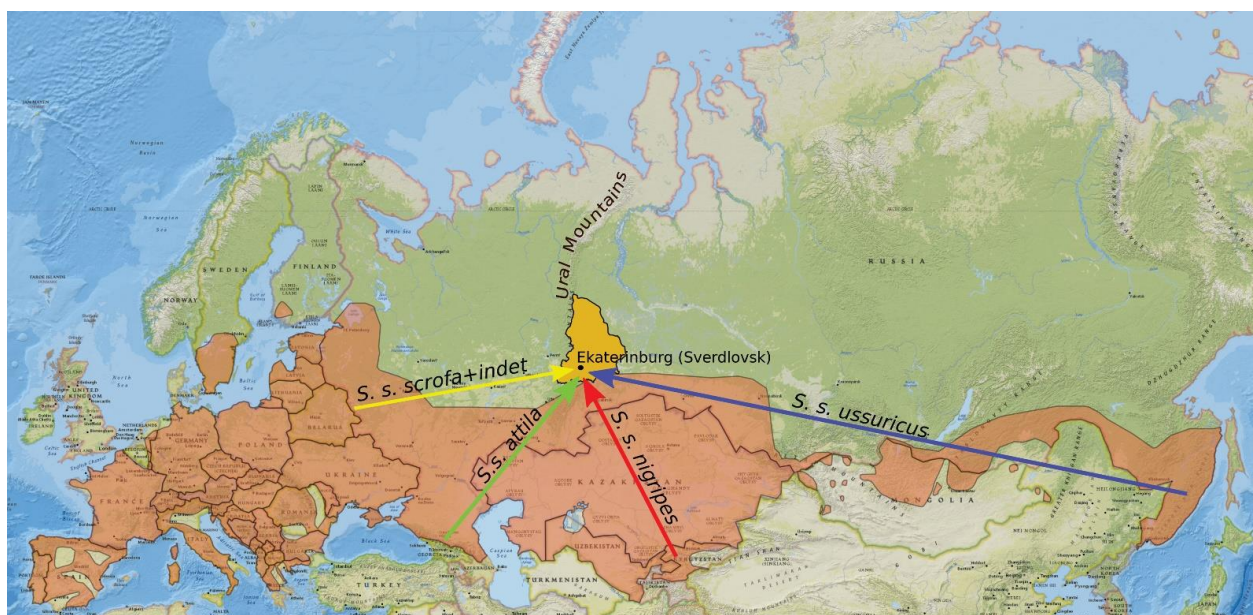
Figure 1. Origin and taxonomic status of the wild boars released in the Ural region. Arrows indicate the locations and taxonomic status of the animals released in the eastern part of the Ural region (orange polygon) in 1978–1984. The pink polygon denotes the wild boar's geographical range in Northern Eurasia in the middle of the 20th century [49,73]. The map was constructed by means of Natural Earth (free vector and raster map data @ naturalearthdata.com) using QGIS 3.8.

The European (*S. s. scrofa* and *S. s. attila*) and Asian subspecies (*S. s. ussuricus*) also differ substantially in their sequences of mitochondrial DNA (mtDNA) (the control region and cytochrome b gene) [51,74,75]. Additionally, wild boars have been translocated to the Urals from three regions of Central Russia, where the populations became established via natural expansion of European wild boars and via a few releases of the animals from Central Russia and the Caucasus [49]. The releases presumably took place between 1978 and 1984 [49,76,77] (Figure 1) and occasionally in the 2000s on private hunting grounds. At the beginning of the 1980s, the Ural region was at the north eastern periphery of the species' range [49]. In the northern parts of the geographical range, wild boar populations are affected by food availability and the weather conditions of winter and autumn [77–80]. The strategy of multi-source introductions is aimed at improving the animals' tolerance to the new harsh conditions via an increase in their genetic diversity [76].

In this study, we determined (1) whether all the genetic lineages present in founders were preserved in the current population; (2) whether the current genetic diversity in the Ural population is higher, lower, or the same as that in the founders' populations; and (3) how the current proportions (%) of various mitochondrial lineages are related to the proportions of genetically distinct founders. We addressed these questions by analyzing the diversity of haplotypes of the mtDNA control region. This genetic marker is widely used in the research on wild boar phylogeography and intraspecies taxonomy [55–59,61,64,81–84] and for investigation into *S. scrofa* domestication [51,85]. We examined haplotypic variation in the wild boar population from the eastern part of the Urals and compared it with the data from the founder populations. In particular, we, for the first time, characterized the haplotype composition and diversity of previously unsampled Central Asian wild boars. We also investigated data from the Caucasus Region (Republic of Dagestan, Russia). Data from this territory have already been reported in the literature [64,81], but the tested groups of animals included only a few individuals. Here, we employed a larger sample size (more than 20 specimens) to obtain more reliable results. The third founder population that we analyzed is the Far Eastern one. Furthermore, we used published data on the European wild boar and focused on East European populations that are known to contribute to the restoration of wild boar populations in European Russia and in the Urals [49,76].

We tested the following hypotheses: (1) the genetic diversity in the Ural population is equal to or greater than that in the founder populations; (2) all the main genetic lineages present in the founder populations were preserved in the newly established population; and (3) the proportions (%) of various genetic lineages in the current Ural population are similar to those in the founder populations. The first hypothesis is based on research that has shown higher genetic diversity in populations resulting from multiple introductions and intraspecies hybridization [2,3,20]. The second hypothesis derives from numerous studies where introduction history has been determined by means of the composition of mtDNA haplotypes decades after the beginning of expansion [86]. The third hypothesis originates from the lack (to the best of our knowledge) of research on the proportions of different lineages in mixed populations. To avoid type I error, i.e., looking for a phenomenon that probably does not occur, we assumed the absence of differences between the initial and current proportions of genetic lineages. We also discuss how our results can be interpreted in terms of theoretical concepts of invasive biology and genetics.

2. Materials and Methods

2.1. Sample Collection

In total, we collected 196 samples of wild boar muscle tissue from four regions: the Ural, Eastern Caucasus (Dagestan), Central Asia (Uzbekistan and Kazakhstan), and Russian Far East (Primorsky Krai) (Table 1, Supplementary Table S1). Tissue samples from the Ural population of wild boars were collected in Sverdlovsk Oblast (Russia). Tissue samples from the Caucasus region population (supposedly *S. s. attila*) were collected in the Eastern Caucasus (Republic Dagestan) from hunters. Muscle tissue samples representing the Central Asian wild boars (supposedly *S. s. nigripes)* were collected in 2018 in the western part of Uzbekistan and in Southern Kazakhstan. These two sampling regions represent the Tian Shan Mountains near Kyrgyzstan, from where the animals were brought to the Urals. The Far Eastern subspecies *S. s. ussuricus* was represented by tissue samples from north eastern Primorsky Krai.

Table 1. Sampling locations and haplotype distributions of wild boars (*S. scrofa*).

Geographical Region	n	H	D-loop Haplotypes 637-bp (Number of Individuals) *	Private Haplotypes **
Urals	116	11	Ss1(35), Ss2(57), Ss3(6), Ss4(2), Ss5(1), Ss6(3), Ss7(4), Ss8(1), Ss9(4), Ss13(2), Ss14(1)	Ss4, Ss5, Ss8, Ss13
Caucasus (Republic of Dagestan)	26	3	Ss1(11), Ss7 (14), Ss11(1)	Ss11
Central Asia (Kazakhstan and Uzbekistan)	16	4	Ss6 (8), Ss9 (1), Ss10(6), Ss12 (1),	Ss10, Ss12
Russian Far East	38	7	Ss15(4), Ss16(20), Ss17(1), Ss18(4), Ss19(4), Ss20(2), Ss21(3)	Ss15-21
Total	196			

* Some of these haplotypes have been described by other authors; see comments in the text and Supplementary Table S1. ** Haplotypes detected in only one of the regions in this study. Some of these haplotypes have been described by other authors; see comments in the text and Supplementary Table S1.

The experimental work was conducted with approval by the Institute of Plant and Animal Ecology, the Ural Branch of the Russian Academy of Sciences (UB RAS), where the wild boar DNA samples from this study were deposited. The Institute of Plant and Animal Ecology UB RAS does not have specific guidelines for wildlife sample collection but recommends following relevant laws about experiments involving wild animal specimens. The wild boar is classified as a game animal in all the countries and regions covered by the sampling in this study, and all the samples of wild boar muscle tissue were either donated by hunters holding a hunting license or collected from carcasses of accident-killed animals. Because no animals were killed specifically for the purpose of this research, we

did not attempt to seek approval from ethical review boards in the participating countries. Nonetheless, the procedures involving tissue samples from wild boars were in compliance with the laws of the countries involved in this study.

2.2. DNA Extraction, Amplification, and Sequencing

Total DNA was isolated from the muscle tissue samples using the DNA-Extran-2 Kit (Syntol LLC, Moscow, Russia).

Primers pDF/pDR [61] were used to amplify the mtDNA control region (approximately 1250 to 1350 bp). The variation of the amplicon length results from the number of tandem repeats in the control region in *S. scrofa* [40]. All polymerase chain reactions (PCRs) were carried out in a 25 μL reaction mixture consisting of 2.0 mM MgCl$_2$, 0.2 mM dNTPs, 0.27 μM each primer, 0.75 U *i*-StarTaq^{TM} DNA Polymerase (Syntol LLC, Moscow, Russia), and 50–60 ng of template DNA. For DNA sequencing, PCR products were purified with the ExS-Pure™ Enzymatic PCR Cleanup Kit (NimaGen, Netherlands). DNA sequencing was carried out on an ABI PRISM 3500xL Genetic Analyzer with the BigDye Terminator Chemistry v.3.1 Kit (Applied Biosystems, Foster City, CA, USA).

2.3. Data Analysis

We analyzed the left domain of the D-loop, examining the fragment situated upstream of the locus of tandem repeats that are present in the mtDNA control region of wild boars [87]. In addition, 60 sequences representing the haplotypes of animals classified as wild *S. scrofa* from Europe (n = 13) and Asia (n = 47) (see Supplementary Table S2) were retrieved from GenBank. A 637-bp fragment of the control region was utilized for estimating the genetic diversity and for phylogenetic reconstructions. This fragment contains 74.3% of the variable sites and 73.3% of the parsimony informative sites previously reported for the wild boar mtDNA control region [36]. Among the rest of the polymorphic sites, only five have been reported as variable in the Eurasian wild boar while the other eleven sites are polymorphic only in animals from Indonesia. Accordingly, the 637-bp fragment under consideration could be regarded as representative for samples from most regions of Eurasia. The number of haplotypes (h), haplotype diversity (H$_d$), nucleotide diversity (π), and neutrality indices (Tajima's D and Fu's Fs) were calculated using DnaSP v6.12.03 software [88]. The most appropriate model of nucleotide change was selected in jModelTest 0.1.1 [89], with a sequence of *Sus celebensis* as an outgroup (GenBank accession number KY911746.1). The best model, according to both the Akaike information criterion (AIC) and the Bayesian information criterion (BIC), was the HKY model [90], with Γ-distributed (G) rate variation across sites. Bayesian phylogenetic analyses were carried out in MrBayes 3.2 [91] using the HKY + G model of sequence evolution and two independent runs of four Markov chains (one cold and three heated) over 3,000,000 generations and sampling every 300 generations. The first 25% of the sampled trees and estimated parameters were discarded as burn-in.

The main aim of the phylogenetic analysis was not to present an exhaustive phylogeny of the wild boar but mostly to examine the position of the studied populations in the previously described main mtDNA lineages (European, Near Eastern, Pan-Asian, and South Eastern Asian). Therefore, we did not include in the phylogenetic analysis all available sequences of the wild boar control region but used the most recently published sets of data illustrating the above-mentioned clades. The main sources of data were the articles by Choi K.S. et al. [64] and Niedziałkowska M. et al. [59] presenting big sets of sequences from Asia and Europe, respectively. We also performed phylogenetic reconstructions based on a shorter fragment (548 bp), which enabled us to compare the data obtained in this study with published sequences from Iran [84]. Haplotypes downloaded from GenBank and identical to those sequenced in this study (Supplementary Table S2) were excluded from this analysis.

2.4. Collection of Data on Animals Released in the Urals

Information about the origin of wild boars released in the Urals was collected from available publications [49,76], the archives of local authorities responsible for game management, and interviews with their employees who participated in the releases during 1978–1984.

3. Results

3.1. Genetic Diversity and Haplotype Composition of the Introduced versus Founder Populations

A total of 21 haplotypes based on 637-bp fragments of the mtDNA control region were identified in 196 wild boars sampled across the Far East, Central Asia, Caucasus, and Urals (Table 1, Supplementary Table S1). Sixteen of the haplotypes are identical to previously published sequences (Supplementary Table S2) [59,64], whereas five are described for the first time. Among the new haplotypes, one (Ss4) was found only in the Ural population, two (Ss10 and Ss12) only in Central Asia, and one (Ss11) only in the Eastern Caucasus (Republic of Dagestan, Russia). One of the new haplotypes (Ss9) has been found in the Urals and Central Asia. One of the haplotypes detected in the Russian Far East (Ss17) appeared to be identical to the haplotypes described for the Duroc and Landrace breeds of domestic pigs [83]. Thus, we suspected that this haplotype represents a hybrid between a male wild boar and a female domestic pig.

The most numerous haplotypes in the Ural population were Ss1 and Ss2 (92 of 116 studied individuals). Six haplotypes (Ss1, Ss2, Ss3, Ss7, Ss8, and Ss14) proved to be shared between the Urals and Eastern Europe [28], and two haplotypes (Ss1 and Ss7) were found in the Ural and in the Caucasus. Animals from the Ural populations also share two haplotypes (Ss6 and Ss9) with Central Asian populations, but there are no common haplotypes between the Urals and Russian Far East. One haplotype of the 11 (9%) was found in the Ural population (Ss4 has not previously been deposited in GenBank). This unique haplotype was found in two individuals, and according to a BLAST search (Ref. ID GH3TT16E013), it is 99.69% similar to haplotype H8 detected by Alves P. et al. [92] in Southern Europe and in house pigs from Portugal. Two other haplotypes (Ss5 and Ss13) (Ref. IDs GH4FUWX1016 and GH4P2E97016, respectively) proved to be identical to the haplotypes of domestic pigs. Therefore, these animals are most probably hybrids between a wild boar male and a female domestic pig. Haplotype Ss8 was previously reported as H11 in [92].

The values of the haplotype diversity (H_d) (Table 2) turned out to be similar among most of the tested populations. The highest values were noted in the Russian Far East, Central and Eastern Europe, and the Urals, whereas the group of animals from the Caucasus showed the lowest H_d (Table 2). Nucleotide diversity (π) is the highest in the Caucasian group of wild boars, whereas this index in Central Asia is the lowest among the analyzed populations. The haplotype diversity is higher in the Ural population than in the founders' populations from the Caucasus and Central Asia but similar to this parameter in Europe and the Russian Far East.

Table 2. Genetic diversity in the introduced (the Urals) and founding (the Caucasus, Central Asia, the Russian Far East, and Eastern Europe) wild boar populations, H_d: haplotype diversity, π: nucleotide diversity, Tajima's D and Fu's Fs are neutrality tests.

Location	H_d	π (%)	Tajima's D	Fu's Fs	Source
Urals	0.667 ± 0.033 (0.649 ± 0.034) [a]	0.00657 ± 0.0011 (0.0059 ± 0.0015) [a]	−0.78 (−0.77 [a]) [n. s.]	2.21 * (3.061 [a**])	This study
Caucasus (Republic of Dagestan)	0.551 ± 0.048	0.0099 ± 0.0009	2.42 ***	10.65 ***	This study
Central Asia (Kazakhstan and Uzbekistan)	0.642 ± 0.081	0.0024 ± 0.001	−1.6 *	0.718 [n. s.]	This study
Russian Far East	0.698 ± 0.072 (0.682 ± 0.074 [a])	0.0061 ± 0.001 (0.00514 ± 0.001 [a])	−0.77 (0.72 [a]) [n. s.]	2.36 (2.53) *.	This study
Central and Eastern Europe	0.65 [b]	0.00570 ± 0.0015 [b]	−1.503 [c, n. s.]	−5.051 [c, n. s.]	Niedziałkowska et al. 2021

[a] Excluding haplotypes identical to domestic pig breeds Ss5, Ss13, and Ss17; [b] data of Niedziałkowska M. et al. [59] adjusted for the analyzed 637-bp fragment; [c] from [59]; [n. s.]: $p > 0.1$; * statistically significant at $p < 0.1$; ** statistically significant at $p < 0.05$ ($p = 0.048$); *** statistically significant at $p < 0.01$.

Both the Ural (Fu's Fs) and the Caucasus (Tajima's D and Fu's Fs) populations demonstrate a statistically significant ($p < 0.05$) deviation from the neutral model in terms of an excess of rare alleles.

3.2. Phylogenetic Status of the Introduced versus Founder Populations

3.2.1. The Topology of Trees

We constructed phylogenetic trees based on the 637- and 547-bp fragments of the mtDNA control region. The phylogenetic tree based on the 637-bp fragment includes mtDNA samples (i.e., individuals) from Asia and the Eastern Caucasus (this study and [64]), Eastern and Central Europe [59], and the Ural region (this study). The phylogenetic tree based on the 547-bp fragment involves additional mtDNA samples from sequences from Iran [84]. The inclusion of mtDNA samples from Iran allowed assignment of our sequences to the Near Eastern clade described by Khalilzadeh P. et al. [84]. The topologies of both trees are the same. We then inspected the 637-bp-fragment-based tree (Figure 2). Interpretation of the Near Eastern cluster was performed in accordance with the 547-bp-fragment-based tree (Supplementary Figure S1).

All the mtDNA samples clustered into four big haplogroups (Figure 2): two clusters containing individuals from South Eastern Asia (SEA 1 and 2), one cluster with sequences from continental Asia (from the Far East to Caspian Sea) and Japan (hereafter, the Eastern clade), and the clade that could be tentatively named Western because the mtDNA samples in this group originate from the western part of the wild boar geographic range. The topology of the 637-bp tree supports some previously published phylogeographical reconstructions for the wild boar [51,61,64]. The SEA clade is basal to all the other groups, and the Eastern clade is basal to the Western clade. The Western clade, in its basal part, includes haplotypes from South Eastern Asia (Indonesia and Vietnam, SEA 3), but the connection of these haplotypes to the Western clade is poorly supported (53%). The haplotype network (Figure 3) unambiguously indicates that this group is related to the Eastern not the Western clade. The rest of the haplotypes within the Western clade split into two well-supported clusters. One exclusively contains mtDNA samples originating from the Urals and Caucasus region (W1). These sequences are similar to those from Iran [84] (see Supplementary Figure S1); thus, we interpreted this group as a Near Eastern clade. The second cluster in the Western clade (W2) includes individuals from the Urals, Caucasus, and Europe. These sequences group with mtDNA samples from Eastern Europe; therefore, we designated this group as the European clade. On the Bayes tree, W1 is a sister group to W2 (Figure 2) while the haplotype network (Figure 3) shows that W1 originates from W2. This result is in agreement with the network presented by Ashrafzadeh M. et al. [52].

3.2.2. Positions of Founder Populations on the Phylogenetic Tree

The mtDNA samples from the Russian Far East (Primorsky Krai) ended up in the Eastern clade. Two haplotypes (Ss16 and Ss20) grouped into a highly supported cluster: The others clustered with individuals from Mongolia and Japan. All the mtDNA samples from Central Asia fall into the Eastern clade with no structure within it. The mtDNA samples from the Eastern Caucasus (Dagestan) ended up in the Western clade, with two haplotypes in the Near Eastern cluster and one in the European cluster.

3.2.3. Positions of Haplotypes from the Introduced Population on the Phylogenetic Tree

The haplotypes from the Ural population are affiliated with all clades except SEA (Figure 2). Two haplotypes (Ss6 and Ss9) fall into the Eastern clade. Both proved to be identical to haplotypes typical for Central Asia (Table 1). Nine haplotypes are unique to the Western clade. Two of them (Ss7 and Ss11) are identical to the haplotypes found in the Eastern Caucasus and are affiliated with the Near Eastern (W1) clade.
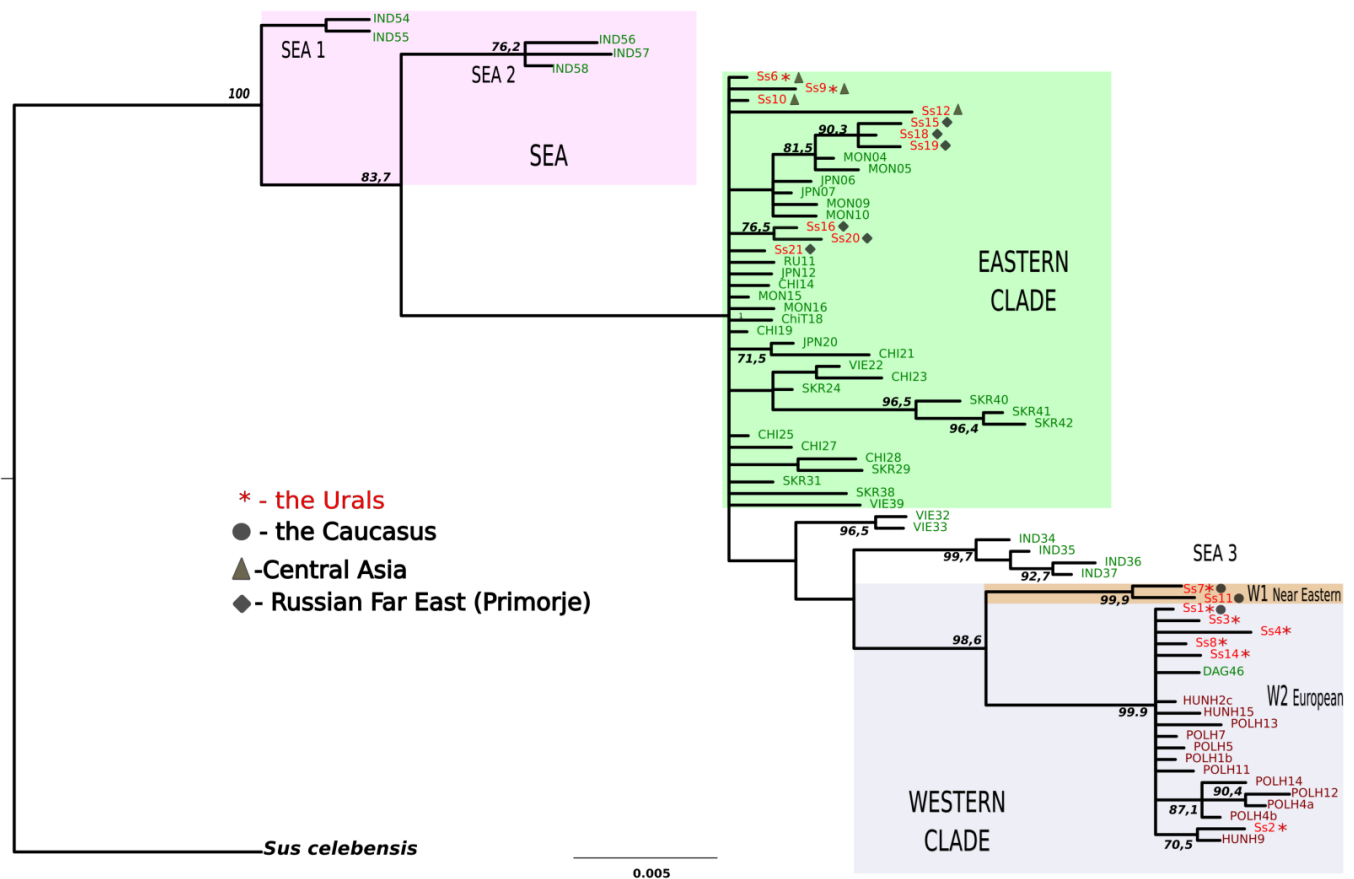
Figure 2. Positions of the studied populations (Urals, Caucasus, Central Asia, and Russian Far East) on the phylogenetic tree of the main wild boar mtDNA lineages. The Bayesian (MCMC) haplotype tree is constructed from the partial sequences of the mtDNA control region (637 bp) from the Eurasian wild boar. The tree reconstruction is based on the 18 haplotypes of wild boars sequenced in this work (haplotypes suspected to originate from hybrids between a wild boar and domestic pig—Ss5, Ss13, and Ss17—were excluded from the analysis) and 51 sequences (representing the haplotypes of animals classified as wild *S. scrofa* from Europe (n = 13) and Asia (n = 38)) downloaded from GenBank. The haplotypes sequenced in this study begin with Ss and are shown in red. The haplotypes reported by Choi K.S. et al. [64] are shown in green. The haplotypes presented by Niedziałkowska M. et al. [59] are shown in a brown color. The haplotypes retrieved from GenBank and identical to those sequenced in this study were excluded from this analysis. The HKY + G model was implemented. The Bayesian posterior probability is shown for branches with over 70% support. Major clades are indicated with different colors. Cluster W1 was named NE (Near Eastern) because on the tree based on 547-bp fragments, these sequences grouped with mtDNA samples from Iran (Supplementary Figure S1). The phylogeny was calculated in MrBayes 3.4 [44] with the default values of priors. See Table 1, Supplementary Table S1, and Figure S1 for details. The illustration was created in FigTree 1.4.4 [93].
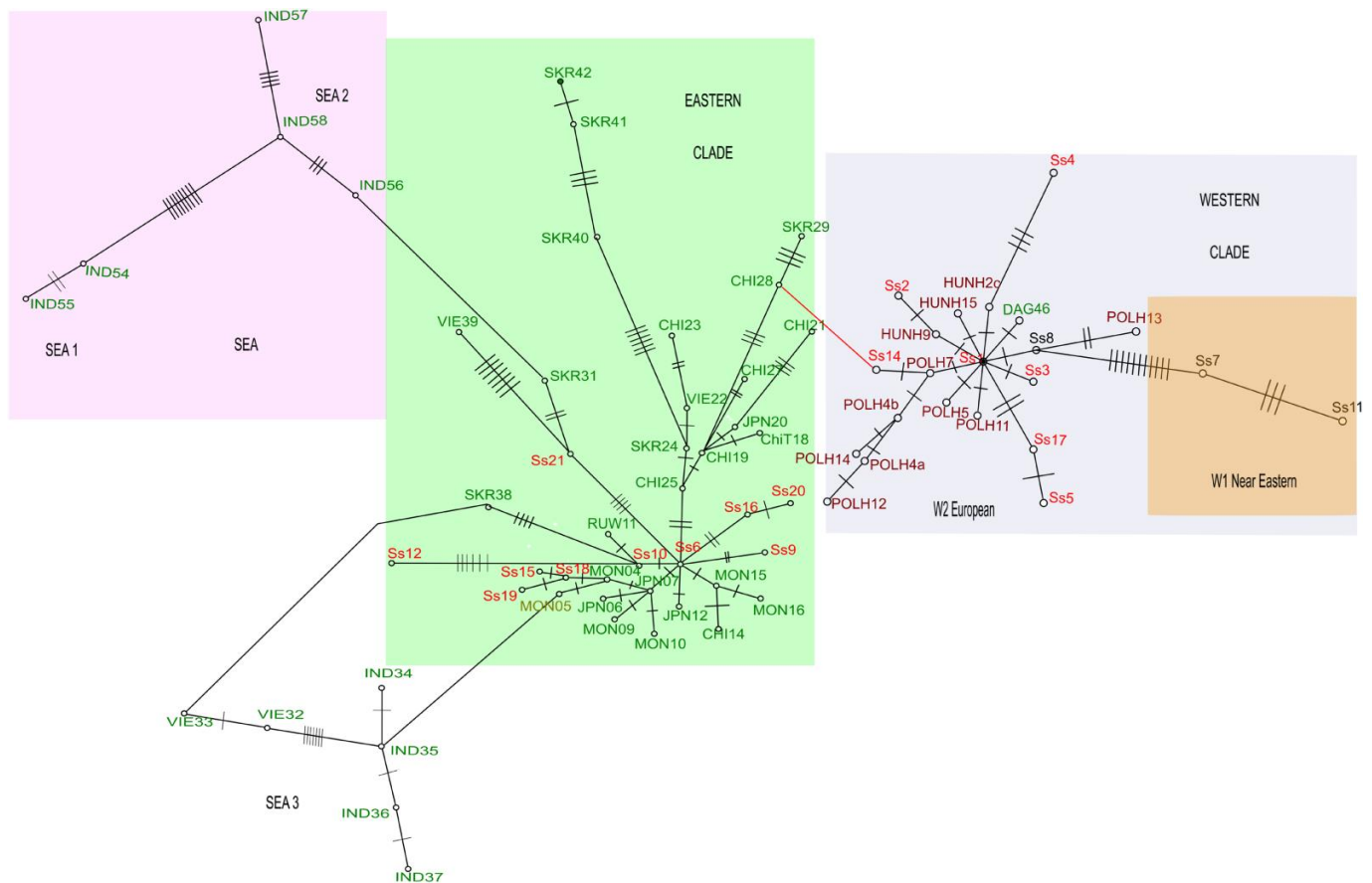
Figure 3. The haplotype network based on the 21 haplotypes of wild boars sequenced in this work and 51 sequences (representing the haplotypes of animals classified as wild *S. scrofa* from Europe (n = 13) and Asia (n = 38)) downloaded from GenBank. The network was created in R package *pegas* Paradis E [94] via an infinite site model (i.e., uncorrected or Hamming distance) of DNA sequences [95]. The haplotypes sequenced in this study begin with Ss and are highlighted in red. The haplotypes reported by Choi K.S. et al. [64] are shown in green. The haplotypes presented by Niedziałkowska M. et al. [59] are highlighted in brown. The haplotypes downloaded from GenBank that were identical to those sequenced in this study were excluded from the analysis.

3.3. Proportions of MtDNA Lineages in the Current Wild Boar Population of the Urals in Comparison with the Proportions of Released Subspecies

Twenty-six percent of the animals released in the Ural region originate from the Caucasus (supposedly representing subspecies *S. s. attila*) or Eastern Europe (Belarus) (*S. s. scrofa*) (Table 3) and hence belong to the Western clade (Figure 2). The proportion of wild boars translocated from Asia (Central Asia: *S. s. nigripes* and Far East: *S. s. ussuricus*) was found to be 23%. The remaining 51% of the wild boars released in the Urals were taken from mixed populations [41]. The ratios of European, Near Eastern, and Asian haplotypes in Western Russia were borrowed from [69]. After recalculation of the data from mixed populations, the proportions of representatives of the Western and Eastern clades in the releases were 0.66 and 0.34, respectively. The proportions of Western (European and Near Eastern) and Eastern haplotypes in the current population turned out to be 0.92 and 0.08; therefore, the proportion of Western haplotypes is 1.41 times higher while that of Eastern haplotypes is 4.25 times lower as compared to the founder population.

Table 3. Affiliation of animals released in the Urals with the mtDNA clades.

Year of Release	Number of Individuals	Origin	Clade
1978	30	Central Asia (Kyrgyzstan)	Eastern
1979	171	Belarus (Brest region) and Caucasus (Kabardino-Balkaria)	Western
1981	123	Far East of Russia (Primorsky Krai)	Eastern
1982	94	Western Russia (Smolensk Oblast)	Mixed (67% Western, 33% Eastern) *
1983	101	Western Russia (Smolensk Oblast)	Mixed (67% Western, 33% Eastern) *
1984	97	Western Russia (Kaluga Oblast)	Mixed (89% Western, 11% Eastern) *
1984	50	Western Russia (Vladimir Oblast)	European*

* According to [69].

4. Discussion

We, for the first time, analyzed the modern haplotypic composition of a wild boar population introduced at the northern edge of the species' range and tested three hypotheses about the genetic consequences of establishing a population originating from numerous introductions of different subspecies. Below, we discuss each hypothesis and outline questions arising from our results.

4.1. Genetic Diversity in the Introduced Population

Dlugosch K.M. and Parker I.M. [2] reported that the loss of allele diversity in the populations of plants and animals established via multiple introductions is ~7.9% of that in the source populations. When their data were recalculated for mammals, the average loss was approximately -9.8% of allele richness. In our case, H_d of the Ural population equals the average haplotype diversity in the founder populations. It is obviously high in comparison with the Caucasus, where the diversity could be low due to a strong decline in the wild boar population in 2010–2011 resulting from an outbreak of African swine fever [96]. The recent bottleneck in the Caucasus is clearly supported by the obtained Tajima's D and Fu's Fs statistics (Table 2). The haplotype diversity in the Urals is 35% lower than that reported for Western Europe on the basis of a shorter fragment (0.902) [97] and 12% lower than the value (0.71) reported for Eastern and Central Europe on the basis of complete D-loop sequences [59]. Moreover, it is lower than the values reported for introduced populations in the USA (0.825) [67] and Argentina (0.827) [98]; these populations are mainly of European origin.

The reason for the relatively low values of H_d is the distribution of haplotype frequencies that is strongly biased toward haplotypes Ss1 and Ss2. These two haplotypes were detected in 79% of the Ural wild boars. They are shared between the Urals and Eastern Europe [59]. Of note, in the study population of Niedziałkowska M. et al. [59], Ss1 dominated over Ss2 (302 versus 90 individuals), whereas in our study population, the proportion of Ss2 is higher than that of Ss1 (57 versus 35 individuals). The current value of H_d indicates that most of the wild boar population in the Ural originates from a relatively small number of genetically similar founders with the European haplotypes. Multi-source introductions have not resulted in an increase in haplotype diversity as reported by other authors for plants and lizards [13,19,20]. The low haplotype diversity compared to the American population of introduced feral pigs could be explained by the high proportion of domestic swine haplotypes in the USA and a smaller sample size in comparison with both the USA and Argentina [67,98].

4.2. Phylogenetic Lineages in the Natural and Introduced Populations

Our phylogenetic tree is similar to other published phylogenies based on the mtDNA control region [51,64,84] in terms of the splitting of the whole dataset into South Eastern Asian, Eastern, and Western (including Near Eastern) clades. Our analysis was aimed at

determining the positions of previously unsampled (or poorly sampled) populations within the reported clades. It yielded several interesting results. First, the Central Asian mtDNA samples are unambiguously positioned within the Eastern clade. Most of these haplotypes are situated on the basal branch and do not cluster together. Khalilzadeh P. et al. [84] found the Eastern haplotypes in eastern Iran while in Southern and Western Iran, the Western (therefore Near Eastern and European) haplotypes were predominant. After combining this finding with our data, we propose that the east coast of the Caspian Sea is the western boundary of the Eastern clade. Half of the haplotypes found in the Central Asian samples were the new haplotypes, which is no surprise given this region has never been sampled before. Far Eastern haplotypes are also (expectedly) in the Eastern clade, and three of them group into a highly supported cluster within this clade. The history of Far Eastern wild boar populations has been discussed previously in several articles [61,64]; for this reason, we did not focus on this topic in this work.

The MtDNA samples from the Eastern Caucasus ended up (in equal proportions of individuals) in the European and Near Eastern clades. Particularly, the newly described haplotype Ss11 is in the Near Eastern clade. Khederzadeh S. et al. [81] revealed that the Dagestanian haplotypes are distant from all other European individuals and suggested possible gene flow from the Caucasus to Southern Europe. Most likely, the haplotypes analyzed in that study belong to the Near Eastern clade because other haplotypes found in the Eastern Caucasus grouped well with the mtDNA samples found by Niedziałkowska M. et al. [59] in Central and Eastern Europe. The presence of highly distant haplotypes in the Eastern Caucasus may reflect both historical processes (hypothesized presence of *S. s. attila* in the northern and *S. s. lybicus* in the southern part of the Caucasian region, as reported by Groves (1981) [99]) and recent processes (an outbreak of African swine fever and decline in the wild boar population [96]) that shape this species' genetic diversity. The Eastern Caucasus (like Central Asia) is characterized by a high proportion of the newly described haplotypes since only few sequences have been previously published for this region. The newly described haplotype Ss11 is closer to Near Eastern Ss7 than to European Ss1 (99% and 97.6% identity, respectively)

Finally, the haplotypes from the Urals (the introduced population) proved to be affiliated with the Eastern, Near Eastern, and European clades. The current haplotypes found in the Urals could have originated from representatives of different subspecies brought from the Caucasus, Central Asia, and Eastern Europe (Belarus and Western Russia) but also from mixed populations transferred to the Urals from Central Russia [48]. The Near Eastern haplotype found in the Urals is identical to that registered in the Eastern Caucasus. Two Asian haplotypes detected in the Ural region are identical to those found in Central Asia (Uzbekistan and Kazakhstan). Our results show that the Near Eastern and some Asian mtDNA haplotypes did not go extinct during colonization of the region that is situated at the north eastern periphery of the geographical range. Of note, in the Urals, we did not find haplotypes identical to those from the Far East, although 123 individuals were released there, and wild boars from the Central Russian populations could also possess these haplotypes. There may be two explanations. First, the Far Eastern animals could have migrated from the site of the release to the unsampled parts of the Urals. Second, they could have become locally extinct while expanding to new territories. Testing the first supposition would require wider sampling in the Ural region. The second supposition will be discussed in the subsection where we compare the proportions of Western and Eastern haplotypes among the released animals to those in the current population.

We detected three haplotypes (Ss5, Ss13, and Ss17) that appeared to be identical to sequences previously reported for the domestic pig [92,100,101]. These haplotypes were found in the Urals (Ss5 and Ss13) and in the Russian Far East (Ss17). We suspect these animals to be hybrids between a male wild boar and a female domestic pig. The proportion of these (possibly) hybrid haplotypes was 14.3% (3 of 21), which is similar to the average proportion of wild boar × domestic pig hybrids in European populations [102,103]. On the other hand, the proportion of individuals carrying these haplotypes did not exceed

2.5% in each population (the Urals and Russian Far East). It is quite possible that the level of introgression is much higher, but the mitochondrial DNA marker for identifying hybrid individuals can be a useful marker for identifying hybrid individuals, although it underestimates their frequency [104].

4.3. Predominance of the Western Clade and a Decline in Eastern Mitochondrial Lineages in the Introduced Population of Wild Boars

We demonstrated that in the Ural population, the proportions of Eastern and Western haplotypes changed in comparison with those at the time of the introduction. The strong increase in the proportion of European haplotypes and a respective decrease in Asian haplotypes could be explained in three ways:

- Animals from Asia were not detected in the sampled region because they dispersed to some other territories. Validation of this explanation requires wider sampling across the whole Ural region.
- The proportion of European haplotypes increased due to unofficial releases in the 2000s. Neither the number of individuals released during such unofficial introductions nor their origin are known. It is unlikely that wild boars were brought to the Urals from distant regions of Russia (such as the Russian Far East or Caucasus) or from Central Asia. Most probably, they were taken from local populations or brought from mixed populations of Central Russia, where the European lineage is more prevalent than the Asian one [69]. They could also be hybrids between wild boars and domestic pigs. All these factors could affect the genetic composition of the introduced population in some way. On the other hand, the current population of wild boars was established well before the 2000s. Thus, we believe that the haplotype frequencies in the current population are mainly a consequence of natural processes.
- Our third explanation is that animals carrying Western mitochondrial haplotypes are better adapted for survival and expansion in a new environment than those from the Eastern haplogroup. The lower survival rate of Eastern (particularly Far Eastern) haplotypes could be caused by two processes. First, the animals from the Caucasus, Central Asia, and Russian Far East could disperse across long distances from the release site. A possible reason is a difference in the habitat composition between the Urals and the regions of the animals' origin (natal habitat preference induction hypothesis [105]). More distant dispersal could lead to higher mortality [106] and hence to a decrease in the proportion of Asian haplotypes. The second process is related to the genetic diversity in the founder populations. Recently, Kostyunina O. et al. [70] showed lower genomic variation in Far Eastern wild boars than in European ones. It is possible that the low genetic variation could cause low adaptability of Far Eastern wild boars, which, in turn, leads to the elimination of their mitochondrial haplotypes. Moreover, Tsai T.S. et al. [107] demonstrated that domestic pigs with European mitochondrial haplotypes produce significantly larger litters, whereas the haplotypes that cluster with Asian mitochondrial haplotypes have the lowest reproductive efficiency rates. The higher proportion and adaptability of the European lineage could also be attributed to a relatively high level of hybridization with domestic pigs in many European populations [108].

The prevalence of European haplotypes in the mixed populations of wild boars in Western Russia has been reported by Davidova E.E. et al. [69], but their sample sizes in many regions did not exceed two individuals, and they did not compare data from mixed populations to those from the founder populations.

4.4. The Wild Boar in the Urals as a Model of Genetic Processes in Expanding (or Invading) Populations

The scenario of wild boar expansion in the eastern Urals appears to be similar to the scenarios of this species' expansions after the Last Glacial Maximum. According to the contraction–expansion hypothesis [109,110], the postglacial expansion of the species proceeded from the few refugia that were typically characterized by high genetic diversity

in comparison with the continent in general. In the case of the wild boar in the eastern Urals, the sites of releases could be compared to the refugia where many genetic lineages were present before the expansion. Expansion with one lineage dominating the others is similar to the scenarios of expansion of *S. scrofa* [55,58] and other mammalian species, e.g., the red deer *Cervus elaphus* and the European roe deer *Capreolus capreolus* [111,112], and is in agreement with the postglacial leading edge expansion hypothesis [113,114]. Consequently, the genetic processes in this population could be used for clarifying the temporal dynamics of expanding populations on a larger spatial and temporal scale. Especially interesting is the monitoring of the spatial and temporal variation of proportions of dominant and rare genetic lineages and investigation of the factors that could shape this variation.

In conclusion, in our analysis based on reliable mtDNA samples from both founders' and introduced populations, we demonstrate that 38 years after the introductions of various subspecies of the wild boar into the eastern part of the Urals, the current population (1) has genetic diversity similar to or higher than that in the founders' populations, thus supporting hypothesis 1; (2) retains haplotypes from all the major mtDNA lineages (European, Near Eastern, and Asian), thereby supporting hypothesis 2 that the main genetic lineages present in founder populations were preserved in the newly established population; and (3) the proportion of the European haplogroup increased while proportions of other haplogroups decreased in comparison with those suggested for the released individuals, thus refuting hypothesis 3. The last result allows us to theorize that the European genotypes are better adapted for expansion and survival in a new harsh environment in comparison with the Asian genotypes. In particular, this state of affairs could result from wild boar × domestic pig hybridization in many European populations. Additional studies using short-tandem-repeat and single-nucleotide-polymorphism markers are needed to test this hypothesis and reveal the proportion of hybrid individuals in the Ural population.

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