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Does mitochondrial haplotype diversity reflect the evolutionary history of the hybrid zone?

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ABSTRACT. Identifying the mechanisms that shape genetic variation within populations and contribute to the formation of reproductive barriers between species is one of the central goals of evolutionary biology. Here, based on mitochondrial cytochrome *b* gene sequences from two sibling species of grey voles (*Microtus arvalis* and *M. obscurus*) forming an extensive hybrid zone in the European part of Russia, we present the first analysis of mitochondrial variation within central part of the hybrid zone. The observed pattern of genetic variation in peripheral populations of *M. obscurus* is characterized by reduced haplotype diversity and signals consistent with recent demographic growth. These findings are discussed in the context of existing local physical and geographical barriers, as well as the previously proposed hypothesis of gradual westward expansion of *M. obscurus* into the range of *M. arvalis*.

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Изменчивость митохондриальных гаплотипов в гибридной зоне как отражение её эволюционной истории

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РЕЗЮМЕ. Определение механизмов, формирующих генетическую изменчивость внутри популяций и участвующих в формировании репродуктивных барьеров между видами, является одной из центральных задач эволюционной биологии. В данной работе на основе анализа последовательностей митохондриального гена цитохрома *b* двух близкородственных видов серых полёвок (*Microtus arvalis* и *M. obscurus*), образующих протяжённую гибридную зону в европейской части России, мы впервые исследуем митохондриальную изменчивость в центральной части этой зоны. Наблюдаемая картина генетической изменчивости в периферических популяциях *M. obscurus* характеризуется сниженным гаплотипическим разнообразием и признаками, согласующимися с недавним демографическим ростом. Полученные результаты обсуждаются в контексте существующих локальных физико-географических барьеров, а также ранее выдвинутой гипотезы о постепенном расширении ареала *M. obscurus* на запад, в пределы ареала *M. arvalis*.

КЛЮЧЕВЫЕ СЛОВА: *Microtus arvalis*, *Microtus obscurus*, цитохром *b*, Русская равнина.

Introduction

The evolutionary histories of most Palaearctic small mammal species include drastic reductions in distribution range during glacial periods, when species survived in small and isolated refugial areas, followed by dispersal and range expansion (Sommer & Nadachowski, 2006; Provan & Bennett, 2008; Stojak *et al.*, 2015). Such dispersals contributed to secondary contacts between allopatrically diverged lineages, which in some cases led to the formation of hybrid zones (Malygin *et al.*, 2020).

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To gain insight into a population's past dynamics, one can turn to molecular genetic data, which capture the underlying genetic variation. Expansions and drastic reductions in population density leave imprints in the genome that allow inferences to be made about the events accompanying the species' evolutionary history. When species come into secondary contact and form a hybrid zone, its characteristics and spatial position may change over time. In the case of hybrid zone movement driven by the invasion of one species into the range of another, genetic diversity in the growing and expanding populations of the invading species may be reduced because it derives from relatively few haplotypes. For more details on possible outcomes that can be inferred from genetic data in case of moving hybrid zones, see Buggs (2007) and Petit & Excoffier (2009). In case of the gradually displaced local species, by contrast, its genetic variability within the hybrid zone may remain relatively unchanged.

The common vole *Microtus arvalis* Pallas, 1778 is widespread in Europe, from the Atlantic coast in the west to central Russia in the east, and comprises six phylogroups that diverged during the last 100 kya (Stojak *et al.*, 2015). The range of the Altai vole *M. obscurus* Eversmann, 1841 extends from Ukraine, Asia Minor and central Russia to central Siberia. The two species differ in their karyotypes: although both have the same diploid number ($2n$ = 46), *M. arvalis* possesses eight small acrocentric chromosomes, whereas *M. obscurus*, originally described as a karyomorph of the former species, carries 20 acrocentrics (Malygin, 1974; Král & L'apunova, 1975; Vorontsov *et al.*, 1984). Recently, the debate over the taxonomic status of *M. obscurus* has gradually shifted towards general acceptance of its species rank (Tougard *et al.*, 2013; Mahmoudi *et al.*, 2017). Both species come into contact in the territory of the European part of Russia, which forms one of the longest hybrid zones among mammals in Europe stretching for more than 800 km in length in a north-south direction (Golenishchev *et al.*, 2001). Extensive studies based on chromosomal (Bulatova *et al.*, 2010a) and molecular genetic (Lavrenchenko *et al.*, 2023, 2024) data shed light on the structure of this zone in its different parts and have revealed patterns of interspecific introgression. Across the hybrid zone, its northernmost (Nizhny Novgorod oblast) and southernmost (Voronezh oblast) parts remain less studied, partly owing to the mosaic distribution of populations in the contact area. Within the well-studied central part, the structure of the hybrid zone varies. In the Lipetsk oblast, the extremely narrow hybrid zone is localized along the Voronezh River. By contrast, in the Vladimir oblast 400 km to the north, in the absence of pronounced geographical barriers the zone extends over tens of kilometers in width. Recent molecular genetic study based on a 190-km transect across the Vladimir part of the hybrid zone (Lavrenchenko *et al.*, 2023), showed that this part of the zone possesses characteristics consistent with the tension zone model (Barton & Hewitt, 1985). Observed asymmetric pattern of introgression as well as pronounced eastward shift of mitochondrial DNA (mtDNA) cline center (Lavrenchenko *et al.*, 2024) allowed to suggest pronounced asymmetry in dispersal of both species, mainly due to *M. obscurus* expansion into the area of *M. arvalis*. As a result, a substantial proportion of individuals carry the mitochondrial genome of the other species. However, all available data on mtDNA introgression are based on PCR typing of fragments of the mitochondrial cytochrome *b* gene (*Cytb* gene), which yield different fragment lengths for *M. arvalis* and *M. obscurus* (Bulatova *et al.*, 2010b). Little is known about the structure of mitochondrial haplotype diversity within populations of both species in close proximity to the hybrid zone. Available studies on the *M. arvalis* and *M. obscurus* phylogeography on the Russian Plain are scarce and based on samples collected outside the hybrid zone (Sibiryakov *et al.*, 2018; Zagorodniuk, 2019; Baskevich *et al.*, 2021; Mashkov *et al.*, 2023).

Here, using a representative set of *Cytb* sequences from individuals sampled both within the hybrid zone and in genetically non-admixed populations outside it, we aimed to assess whether mitochondrial haplotype diversity could provide insights into the formation and evolution of the hybrid zone, and whether the results would be consistent with the previously proposed hypothesis of westward movement of the hybrid zone driven by the *M. obscurus* expansion.

Material and methods

The study was based on *M. arvalis* and *M. obscurus* specimens collected in 2015–2016 along a 195-km-long transect across the hybrid zone in the Vladimir oblast (see details in Lavrenchenko *et al.*, 2023). In addition, we augmented the sample with specimens from several localities from both sides beyond the transect boundaries, as well as several sites located relatively close to the center of the hybrid zone. In total, the sample comprised 158 individuals (98 *M. arvalis* and 60 *M. obscurus*). Here and below, we assign individuals to either *M. arvalis* or *M. obscurus* based on the defined mitochondrial haplotype. However, given the pronounced level of introgression, the species assignment based on nuclear DNA data differs for some individuals (Fig. 1B–C). Therefore, our analyses primarily describe mitochondrial lineages rather than unequivocally nuclear-defined species. Total genomic DNA was extracted from tissues preserved in 96% ethanol using the Raissol GM-Tissue extraction kit (Raissol, Russia). Complete fragment of the *Cytb* gene was amplified using the forward primer L14723 (5'–CCAATGACATGAAAAATCATCGTT–3') and the reverse primer H15915 (5'–TCTCCATTTCTGGTTTACAAGAC–3') under the following conditions: initial denaturation at 95 °C for 3 min; 35 cycles of 95 °C for 30 s, 52 °C for 30 s, and 72 °C for 1 min; and a final extension at 72 °C for 5 min. For sequencing, additional internal primers, MicrBinF (5'–CTCACACGATTCTTTGCCTTCCACT–3') and MicrBinR (5'–GTTCAGTC-

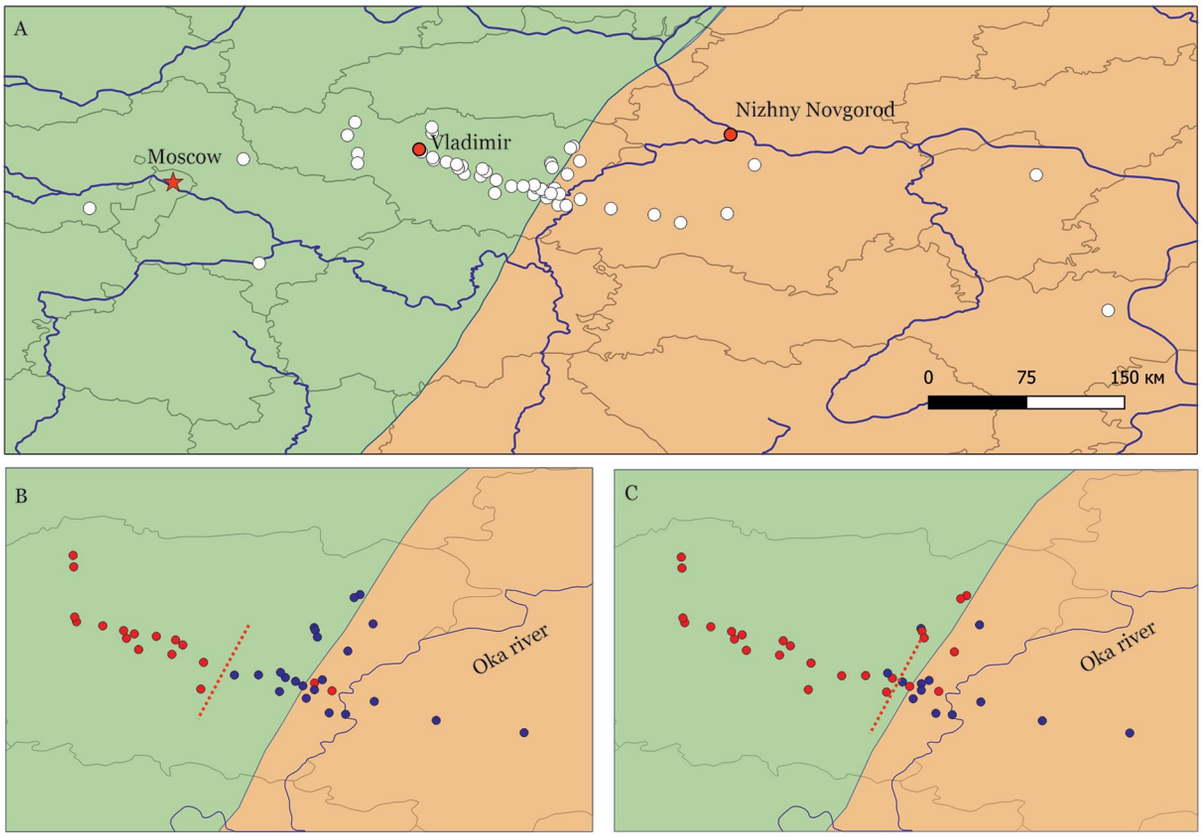


Fig. 1. General view of the hybrid zone (A) and enlarged map sections showing the structure of the hybrid zone based on the nuclear *tp53* marker (data from Lavrenchenko *et al.*, 2023; B) and the mitochondrial (*Cytb*) marker (this study; C). Note the pronounced eastward shift of the zone in the mtDNA data. Green indicates the range of *M. arvalis*, ochre — *M. obscurus*. Red circles — haplotypes of *M. arvalis*, blue — *M. obscurus*. The red dashed lines indicate the approximate centre of the hybrid zone for each marker.

CAGTTGGGTTGTT–3'), were used. PCR products were visualized on 2% agarose gels and purified for Sanger sequencing by ethanol precipitation with ammonium acetate. Sequencing was performed according to the manufacturers' protocols using the NovaDye Terminator Cycle Sequencing Kit (GeneQuest, Russia) on a Nanophor 05 Genetic Analyzer (Syntol, Russia) at the Core Centrum "Genomic Technologies Group" of the Koltzov Institute of Developmental Biology, Russian Academy of Sciences. The obtained sequences were aligned in SeqMan v11.2.1 (DNASTAR, USA) and then trimmed to an equal length of 1 143 bp. Haplotype network reconstruction was performed separately for datasets of both species using Hapsolutely v0.2.3 (Vences *et al.*, 2024) with the TCS algorithm. Mitochondrial diversity statistics and neutrality tests were calculated in DnaSP v6 (Rozas *et al.*, 2017). For each dataset, we estimated the number of haplotypes (*Nh*), haplotype diversity (*h*) and nucleotide diversity (π). To test for deviations from neutrality, we applied Tajima's D (Tajima, 1989), Fu's Fs (Fu, 1997), and the R2 statistic (Ramos-Onsins & Rozas, 2002), the latter being particularly suitable for small sample sizes. Analyses were performed separately for the whole datasets of *M. arvalis* and *M. obscurus* as well as for *M. obscurus* subsamples collected on the left (western) and right (eastern) banks of the Oka River. Representative sequences for each haplotype (22 for *M. arvalis* and 20 for *M. obscurus*) were deposited in GenBank under the accession numbers QB225508–QB225549.

Results

The obtained results revealed distinct patterns of mitochondrial variation for the populations of studied species. The *M. arvalis* dataset comprised 98 individuals and 22 haplotypes and showed little geographical structure (Fig. 2, Upper plot). Two common haplotypes, represented by 61 and 13 specimens, occurred in individuals regardless of their proximity to the hybrid zone. The remaining haplotypes are minor variants differing from the two major ones by one or two substitutions and found in single individuals. By contrast, mitochondrial diversity in *M. obscurus* (Fig. 2, Lower plot) is notably structured, and the resulting haplotype network can be tentatively divided into two groups, oc-

curring either on the left (western) or on the right (eastern) banks of the Oka River. Whereas haplotypes from the right bank exhibit a relatively diverse structure, with several haplotypes shared among multiple specimens, the population from the left bank displays a star-like structure: one predominant haplotype is shared by 34 specimens, while the remaining rare haplotypes differ from it by only one or two substitutions. Note, however, that this division is not absolute, as certain haplotypes were found on both sides of the river.

The observed pattern is further supported by estimates of genetic diversity indices and the results of neutrality tests (Table 1). Thus, haplotype and nucleotide diversity estimates are largely similar between *M. arvalis* and

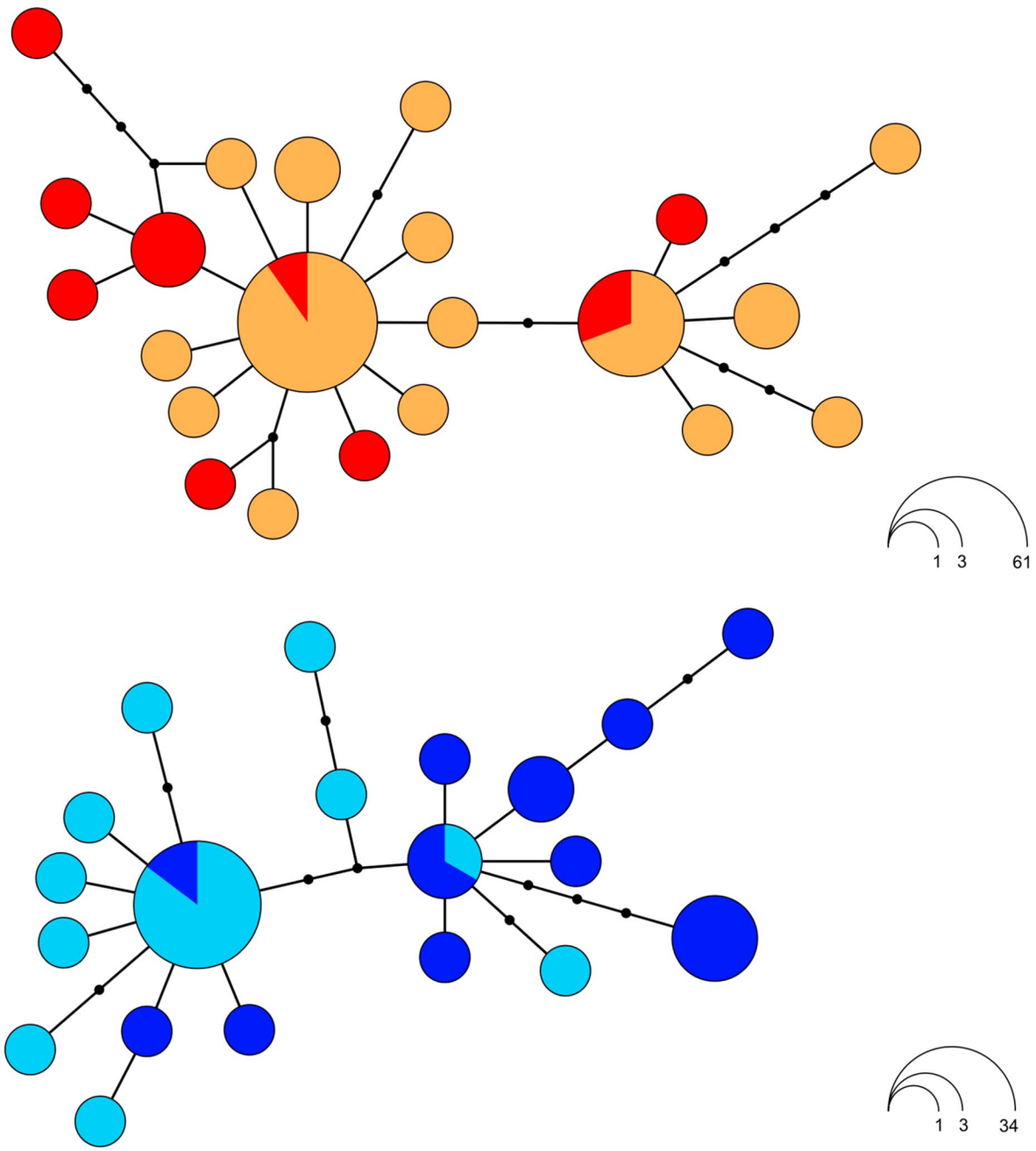


Fig. 2. Upper plot: haplotype network based on *Cytb* gene sequences for *M. arvalis*. Red colour marks haplotypes, found in individuals outside the hybrid zone (to the west of Vladimir), orange — to the east of Vladimir. Lower plot: haplotype network based on *Cytb* gene sequences for *M. obscurus*. Colours marks haplotypes found in individuals sampled in the left (Cyan) or right (Blue) banks of the Oka River. Circle size is proportional to haplotype frequency.

Table 1. Mitochondrial (*Cytb*) diversity statistics and neutrality test results for *M. arvalis* and *M. obscurus* populations. *n*, number of individuals; *Nh*, number of haplotypes; *h*, haplotype diversity; π, nucleotide diversity per site; Tajima's D, Tajima's D statistic; Fu's Fs, Fu's Fs statistic; R2, Ramos-Onsins & Rozas R2 statistic. Asterisks indicate statistical significance: * $p < 0.05$, ** $p < 0.01$.

Sample	*n*	*Nh*	*h*	π	Tajima's D	Fu's Fs	R2
M. arvalis	98	22	0.598	0.001	−2.10*	−15.86	0.033
M. obscurus (all)	60	20	0.675	0.002	−1.78	−9.43	0.045
M. obscurus (left bank)	40	12	0.479	0.001	−2.20**	−6.77	0.045
M. obscurus (right bank)	20	10	0.884	0.003	−0.075	−1.52	0.124

M. obscurus, but differ substantially when the latter species is subdivided into two groups. Tajima's D analysis indicated an excess of rare variants in all samples except the right-bank *M. obscurus* population. However, this deviation was statistically significant only in the left-bank *M. obscurus* population and in *M. arvalis*. Fu's Fs and R_2 statistics showed a broadly similar pattern, with stronger signals consistent with demographic expansion in the left-bank *M. obscurus* population than in its right-bank counterpart.

Discussion

Here, we provide the first detailed picture of mitochondrial haplotype variation in the *M. arvalis–M. obscurus* hybrid zone. The revealed patterns of mitochondrial variation differ markedly between the two species. In *M. arvalis*, mtDNA diversity pattern show no geographical structure, whereas obtained for *M. obscurus* haplotype network is clearly structured and splits into two groups, apparently associated with the left and right banks of the Oka River. The left-bank population possesses less genetic variation, whereas the right-bank population retains substantially higher haplotype diversity (Table 1). Notably, this difference is observed despite the larger sample size on the left bank ($n = 40$ vs. $n = 20$), indicating that it is not an artefact of sampling.

Reduced haplotype and nucleotide diversity, together with an excess of rare variants and signals of demographic expansion in neutrality tests, generally characterize populations that have undergone a recent founder event or range expansion. The observed star-like topology, with a single dominant haplotype surrounded by minor variants, is also consistent with recent expansion from a small number of founders (Excoffier & Ray, 2008). This suggests that *M. obscurus* individuals from the left bank may represent a relatively young, recently established population, whereas the right-bank population likely corresponds to an older, more stable part of the species' range.

It should be noted that our sampling covers only a small part of the both species ranges, primarily from the contact zone and adjacent areas. Peripheral populations are often characterized by reduced diversity and may show signals of local expansion or founder events that do not necessarily reflect the demographic history of the species as a whole. At the same, the observed on our data pattern is consistent with the previous result based on molecular genetic data and provides further support for the hypothesis of westward expansion of *M. obscurus* into the range of *M. arvalis*. The Oka River appears to act as a substantial, though not absolute, barrier to vole dispersal, which may contribute to the lower genetic diversity of *M. obscurus* on its left bank. Notably, the river also limits gene flow in the opposite direction: both mitochondrial (Fig. 1C) and nuclear (Lavrenchenko *et al.*, 2023, 2024) alleles introgressed from *M. arvalis* into populations of *M. obscurus* on the left bank spread as far as the river but do not cross it, leaving *M. obscurus* populations on the right bank genetically 'pure' in both mitochondrial and nuclear genomes.

At the same time, the reduced mitochondrial diversity of *M. obscurus* on the left bank of the Oka River may reflect not only, and perhaps not primarily, the river's barrier effect, but also selection against hybrids in the context of contact with *M. arvalis* populations. Such selection, in its turn, may operate through two distinct mechanisms. On the one hand, selection may act against hybrids due to intrinsic incompatibilities, typically involving nuclear loci and arising from Bateson-Dobzhansky-Muller incompatibilities. As a by-product, this selection may also impede mitochondrial introgression and, consequently, the spread of mitochondrial haplotypes across the hybrid zone. On the other hand, since the mitochondrial genes play key roles in cellular respiration (Gershoni *et al.*, 2009), their interactions with nuclear-encoded oxidative phosphorylation (OXPHOS) genes may be disrupted following the introgression of certain 'incompatible' mitochondrial haplotypes (Hill, 2016). In this case, selection would act directly against the introgression of specific mitochondrial haplotypes. Extending Hill's (2016) definition of a biological species as a population reproductively isolated by incompatibilities in uniquely co-adapted mitochondrial and nuclear-mitochondrial (N-mt) genes, we can hypothesize that at least some mtDNA haplotypes of *M. obscurus* may have acquired mutations that prevent them from functioning properly in the nuclear background of *M. arvalis*.

However, the available data are apparently insufficient to fully explain the processes underlying the observed genetic pattern. Further efforts to disentangle them will require larger sample sizes, complete mitochondrial genomes analyzed alongside nuclear genomic data, and, ideally, fitness-related phenotypic measurements.

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