BALTIC FORESTRY

https://balticforestry.lammc.lt
ISSN 1392-1355
eISSN 2029-9230

Baltic Forestry 2025 31(2): id 798
Category: Research article
https://doi.org/10.46490/BF798

Genetic variability of American mink (*Neogale vison*) introduced from different places of origin

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Paulauskas, A., Šakienė, D., Griciuvienė, L., Lipatova, I. Aleksandravičienė, A. and Vaitkevičiūtė, R. 2025. Genetic variability of American mink (*Neogale vison*) introduced from different places of origin. *Baltic Forestry* 31(2): id 798; https://doi.org/10.46490/BF798.

Received 5 May 2025
Revised 4 September 2025
Accepted 26 October 2025

Abstract

The American mink (*Neogale vison*; Patterson et al. 2021), a non-native species originally from North America, has successfully acclimatised and established wild populations across Europe, where it has largely displaced the native European mink (*Mustela lutreola*). Assessing genetic variability in invasive populations provides valuable insights into introduction history, colonisation dynamics, and the long-term viability of established populations. This study aimed to evaluate the genetic variability of different American mink subpopulations in Lithuania. Six microsatellite loci were analysed in 62 individuals sampled from three Lithuanian regions: Alytus, Šilutė, and Zarasai. The results revealed a total of 29 alleles across six loci, with heterozygosity levels varying among subpopulations. Šilutė showed the highest genetic diversity ($H_o = 0.712$; $H_e = 0.730$), while Zarasai exhibited a pronounced deficit of heterozygotes ($H_o = 0.333$; $H_e = 0.656$), consistent with a founder effect. STRUCTURE analysis identified the presence of two to four genetic clusters, suggesting that populations originated from multiple introduction sources and have undergone genetic admixture. These results highlight that introduction history and subsequent genetic mixing have increased the adaptive potential of this invasive species, thereby facilitating its successful establishment. Understanding these dynamics is crucial for developing management strategies to control mink populations and mitigate their impacts on the native biodiversity.

Keywords: American mink; *Neogale vison*; Lithuania; genetic variability; microsatellite loci; invasive species

Introduction

The deliberate or accidental introduction of species beyond their native range has been a historical consequence of human migration and trade, and this process has accelerated dramatically in recent times (Clout and Russell 2008). The spread of invasive non-native species has had a devastating impact on native biodiversity, locally and globally, and is considered one of the greatest threats to natural ecosystems (Vitousek et al. 1997). Invasive and colonizing species have been the subjects of considerable interest for decades, especially concerning the role of natural selection in facilitating species adaptation to new environments (Zalapa et al. 2010). Many introduced mammals are yet to attain the full extent of their distributions. Local genetic adaptation and even divergent evolution are also possible over long periods (Gleeson et al. 2006). At the same time, examining neutral genetic variation provides valuable insights into introduction history, colonisation processes, and the degree of admixture between different founding populations. Such information is critical for conservation, as the number and origin of introductions directly influence the genetic diversity and population structure of invasive species, which in turn shape their adaptive potential, ecological impacts, and management challenges (Frankham et al. 2002, Dlugosch and Parker 2008, Zalewski et al. 2010).

American mink (*Neogale vison*; Patterson et al. 2021) is a semi-aquatic carnivore native to North America that was successfully introduced throughout Europe through escapes from fur farms and intentional releases. As a result of mass and persistent escapes from fur farms, damage to farms caused by hurricanes and fires, as well as deliberate releases and accidental introductions, wild populations of American mink have become established in the aquatic ecosystems of many European countries (Bonesi and Palazon 2007, Lecis et al. 2008). The American mink has established itself as an invasive species across Europe, significantly affecting native wildlife, particularly in areas once inhabited by the native European mink (*Mustela lutreola*) (Bonesi and Palazon 2007, Jernelöv 2017). Due to its impact on native species, their habitats, and the overall structure of the ecosystem, the American mink is considered one of the most significant threats to biodiversity, as it can alter species populations and reduce the distribution range of their habitats (Van Leeuwen et al. 2024). American mink can transmit diseases such as Aleutian Disease Virus (ADV) and COVID-19 through fur farms and

exchange parasites with other mustelids, potentially impacting native predators (Zaleska-Wawro et al. 2021, Vahedi et al. 2023, Suita et al. 2025).

The American mink is a valuable fur-bearing animal (Brzeziński and Marzec 2003), whose breeding on fur farms in Europe began in the 1920s (Michalska-Parda et al. 2009). In Lithuania, such farms were established in the 1930s, near Kaunas. After World War II, the American mink naturally spread from fur farms in the Kaliningrad region to the lower reaches of the Nemunas River (Prūsaitė et al. 1988, Balčiauskas 1996). Since the 1950s, cases of deliberate introduction have also been recorded, viz. 37 individuals were released from farms into the wild in two areas, the Utena and Zarasai districts. In 1953, another 46 individuals were introduced to southeastern Lithuania (Ukmergė and Anykščiai districts) from Tatarstan. While the density, distribution, conservation, and impact of American mink populations on native fauna have been studied in Lithuania (Mickevičius and Baranauskas 1992, Balčiauskas 1996, Balčiauskas et al. 1997, Prūsaitė et al. 1988), the changes in population genetic structure and dynamics during the biological invasion process have not been investigated. However, various genetic studies on American mink populations have been conducted in European countries such as Denmark (Brusgaard et al. 1998), Spain (Lecis et al. 2008), Poland (Michalska-Parda et al. 2009, Zalewski et al. 2010, Horecka 2019), Ireland (Mullins 2010), and France (Van Leeuwen et al. 2024), to assess their genetic diversity, population structure, and spatial distribution, as well as to compare them with farmed mink and other Mustelidae species. Nevertheless, in certain regions of Europe, including Lithuania, detailed information on the current genetic status of this invasive species is still lacking, particularly in populations where individuals have been introduced from different sources.

Considering that the *N. vison* population in Lithuania has not been investigated from a genetic perspective and given the great importance of studying genetic structure for nature conservation, the objectives of this study were: (i) to evaluate the level of genetic diversity within and among mink subpopulations from different regions of Lithuania, (ii) to assess population differentiation and gene flow using microsatellite markers, and (iii) to identify possible introduction sources and admixture patterns shaping current genetic structure.

Material and methods

Sample collection and DNA isolation

A total of 62 spleen samples from legally hunted American mink were collected between 2018 and 2020 (Figure 1). Three feral subpopulations were studied: feral subpopulation 1 – north-eastern Lithuania (Zarasai subpopulation, $n = 22$), feral subpopulation 2 – southern Lithuania (Alytus subpopulation, $n = 29$), and feral subpopulation 3 – western Lithuania (Šilutė subpopulation, $n = 11$)

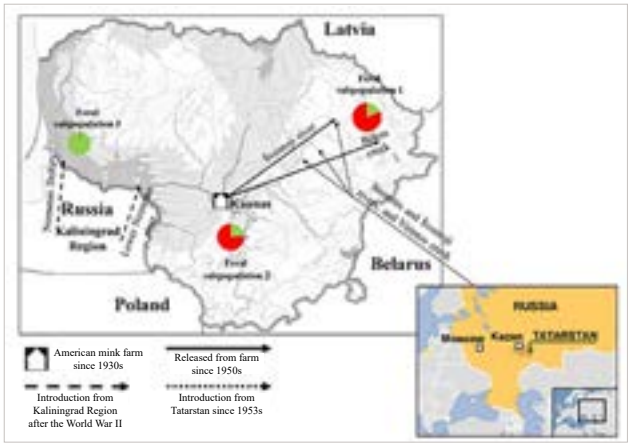

Figure 1. Map showing the introduction sites of *Neogale vison* in Lithuania

The pie chart illustrates the sampling locations of American minks and the proportion of STRUCTURE clusters at $K = 2$ for each subpopulation. Clustering structure: Cluster 1 in red, *and* Cluster 2 in green). Approximate assignment proportions were as follows: Zarasai – 79% of Cluster 1, 21% of Cluster 2; Alytus – 65% of Cluster 1, 35% of Cluster 2; Šilutė – 90% of Cluster 1, 10% of Cluster 2. Feral subpopulation 1 – Zarasai subpopulation (north-eastern Lithuania), feral subpopulation 2 – Alytus subpopulation (southern Lithuania), feral subpopulation 3 – Šilutė subpopulation (western Lithuania).

(Figure 1). All spleen samples were placed in 2 ml tubes containing 70% ethanol and stored at –20°C until genomic DNA extraction. Although the overall sample size is relatively small, it provides representative data of the main feral mink subpopulations across Lithuania.

DNA was extracted from spleen tissue using the Genomic DNA Purification Kit (Thermo Fisher Scientific Baltics, Vilnius, Lithuania) according to the manufacturer's standard protocol. DNA quality and quantity were assessed using a NanoDrop 2000 spectrophotometer (Thermo Scientific, Wilmington, DE, USA). The extracted DNA samples were stored at −20°C until the PCR amplification.

Microsatellite analysis

Total genomic DNA was extracted from tissue samples using the Genomic DNA Purification Kit (Thermo Fisher Scientific, Lithuania), following the manufacturer's instructions. To assess the genetic diversity of American mink, 10 primers (Mvi232, Mvi54, Mvi57, Mvi111, Mvis192, Mvi219, Mvis072, Mvis075, Mvis586, Mvis027) were used, of which only six produced successful amplification. These microsatellite loci were used further the analysis. Detailed information regarding the microsatellite loci characteristics and amplification profile can be found in Table 1.

The PCR amplification of each microsatellite locus was performed separately in a 10 µl reaction volume according to the protocol described by Lecis et al. (2008). Each reaction mixture contained 0.1 mM dNTPs, 1× buffer, 0.3 µM of each primer, 0.8 mM $MgCl_2$, 0.5 units of

Locus	Primer Sequence (5'–3')	Range of allele size (bp)	Ta (°C)	Source
Mvi232	F: GACGATTCACAAACCTATACC R: TCACCAGGGACCAACAGGT	145–161	55	O'Connel et al. 1996
Mvi54	F: CCCTCCTTGGCTCCGCAC R: AGAGTCTGTATACCTCCACC	91–129	56	
Mvi57	F: GAACAGGACCAGCCCTGC R: GTTGGAAATGAGGATCTCAC	92–102	58	
Mvi586	F: GTGAGCACTTATTCAGAGCTG R: GAAGAAAGAGACCCAATTAAC	125–145	52	Brusgaard et al. 1998
Mvis075	F: GAAATTTGGGGAATGCACTC R: GGCAGGATAGGATGTGAGCT	125–128	55	Fleming et al. 1999
Mvis072	F: CTGCAAAGCTTAGGAATGGAGA R: CCACTATGGAGTTTCAGCA	291–297	52	
Mvi111	F: GTGGGCATAGAATTTAGAGG R: TTATCAAAGACAATGTGCGAG	86–106	55	Lecis et al. 2008, Zalewski et al. 2010
Mvi219	F: GGGTGCGGCTCTCACTGC R: GGAGTATTGTCCTCACCTGC	162–176	51	Lecis et al. 2008, Zalewski et al. 2010
Mvis027	F: CCACAATAAGTTTCACTAACAC R: TGGAGGGAGGAACATAAG	190–192	51	O'Connell et al. 1996
Mvis192	F: TGAGCGGGACAGAACTGG R: GGAAAGCTCCAAGACCCC	128–144	62	Brusgaard et al. 1998

Table 1. Characterisation of six microsatellites in *N. vison*

Ta – PCR annealing temperature, F – forward primer, R – reverse primer.

Taq DNA polymerase (Thermo Fisher Scientific, Lithuania), and 50 ng of template DNA.

The PCR conditions were as follows: an initial denaturation at 95°C for 1 min; 30 cycles of denaturation at 94°C for 20 s, annealing at 51–62°C for 20 s, and extension at 74°C for 20 s; followed by a final extension at 72°C for 20 min.

Amplified DNA fragments were separated by electrophoresis on a vertical 8% polyacrylamide gel. Capillary electrophoresis was performed for accurate genotyping of fluorescently labelled PCR products on a SeqStudio™ Genetic Analyzer (Thermo Fisher Scientific, Vacaville, CA, USA) using the GeneScan™ 500 LIZ™ size standard. DNA fragment sizes were automatically called by the GeneMapper software, version 4.0 (Thermo Fisher Scientific 2010) and manually checked.

Data analysis

Genetic diversity within each subpopulation was assessed by calculating the observed number of alleles (N_a), effective number of alleles (N_e), observed heterozygosity (H_o), and expected heterozygosity (H_e). Population structure and genetic differentiation among subpopulations were examined using mean F_{ST} values, Nei's standard genetic distances (Nei 1978), analysis of molecular variance (AMOVA) and Principal Coordinates Analysis (PCA) using the GenAlEx software package, version 5.5 (Peakall and Smouse 2012). The possible presence of null alleles was estimated using the Microchecker software package, version 2.2.3 (Oosterhout et al. 2004), and null allele frequencies were estimated using the Brookfield 1 estimator (Brookfield 1996). A Bayesian Markov Chain Monte Carlo (MCMC) approach was used to estimate population structure using the STRUCTURE software package, version 2.3.4 (Pritchard et al. 2000). For each *K* value (range 1−10), ten independent runs were performed, each consisting of an 800,000-iteration burn-in phase followed by 200,000 MCMC repetitions. The optimal number of genetic clusters (*K*) was identified using the Structure Harvester web-based program, version 0.6.93 (Earl and von Holdt 2012) based on the Δ*K* method, which evaluates the rate of change in the log-likelihood between successive values of *K* (Evanno et al. 2005).

Results

In total, 62 American mink individuals from three Lithuanian subpopulations (Zarasai, Alytus, and Šilutė) were successfully genotyped at six microsatellite loci, yielding a total of 29 alleles. Analysis using Microchecker software revealed no evidence of null alleles in any of the six microsatellite loci examined ($r > 0.2$). The absence of null alleles in our dataset increases confidence in the accuracy of genotyping results. It ensures that null allele effects did not bias the calculated genetic diversity parameters. The number of alleles (N_a) per locus ranged from two (Mvi57) to six (Mvi54 and Mvis586). Despite its low diversity, Mvi57 amplified reliably in all samples and was therefore included in the analysis. The effective number of alleles (N_e) varied from 1.748 in Mvi57 (Alytus) to 5.500 in Mvi54 (Šilutė). Observed heterozygosity (H_o) values ranged from 0.136 (Mvis075, Zarasai) to 0.828 (Mvis072, Alytus), while expected heterozygosity (H_e) ranged from 0.428 (Mvi57, Alytus) to 0.818 (Mvi54, Šilutė). The mean H_o was the highest in Šilutė (0.712), followed by Alytus (0.649) and Zarasai (0.333). The mean H_e was highest in Šilutė (0.730) and lowest in Alytus (0.640). Polymorphic information content (PIC) values ranged from 0.298 (Mvi54, Šilutė) to 0.500 (Mvi57 in all subpopulations). The mean PIC was the highest in Alytus (0.441), followed by Zarasai (0.438) and Šilutė (0.371). Loci with higher PIC values (> 0.4), such as Mvi57 and Mvi232, were considered highly informative, while those with lower values indicated reduced marker informativeness in specific populations (Table 2).

Table 2. American mink subpopulation microsatellite loci characteristics in Lithuania: sample size (N), observed number of alleles (N_a), effective number of alleles (N_e), Shannon index (I), observed heterozygosity (H_o) and expected heterozygosity (H_e), and polymorphism information content (PIC)

Pop	Locus	N	N_a	N_e	I	H_o	H_e	PIC
Zarasai	Mvi232	22	5,000	2,978	1,259	0,318	0,664	0.446
	Mvi54		6,000	3,385	1,439	0,318	0,705	0.416
	Mvi57		2,000	1,984	0,689	0,364	0,496	0.500
	Mvis072		5,000	2,602	1,156	0,318	0,616	0.473
	Mvis075		5,000	3,281	1,341	0,136	0,695	0.424
	Mvis586		6,000	4,137	1,586	0,545	0,758	0.367
	Mean		4,833	3,061	1,245	0,333	0.656	0,438
Alytus	Mvi232	29	5,000	2,935	1,254	0,586	0,659	0.449
	Mvi54		5,000	2,920	1,296	0,655	0,658	0.450
	Mvi57		2,000	1,748	0,619	0,621	0,428	0.490
	Mvis072		5,000	3,721	1,439	0,828	0,731	0.393
	Mvis075		5,000	3,318	1,342	0,621	0,699	0.421
	Mvis586		5,000	3,004	1,250	0,586	0,667	0.444
	Mean		4,500	2,941	1,200	0,649	0,640	0,441
Šilutė	Mvi232	11	5,000	3,967	1,477	0,818	0,748	0.377
	Mvi54		6,000	5,500	1,745	0,727	0,818	0.298
	Mvi57		2,000	1,984	0,689	0,727	0,496	0.500
	Mvis072		4,000	3,723	1,345	0,727	0,731	0.393
	Mvis075		5,000	4,566	1,556	0,727	0,781	0.342
	Mvis586		6,000	5,149	1,709	0,545	0,806	0.313
	Mean		4,667	4,148	1,420	0,712	0,730	0,371

Molecular analysis of variance (AMOVA) revealed that the inter-subpopulation variability of *N. vison* was 27%, and the intra-subpopulation variability was 73%. Pairwise F_{ST} values among subpopulations ranged from 0.045 to 0.195, indicating low to high levels of genetic differentiation among the sampled sites. The lowest pairwise F_{ST} value (0.045) was observed between the Zarasai and Šilutė subpopulations, while the highest value (0.195) was between the Zarasai and Alytus subpopulations (Table 3).

Principal Coordinates Analysis (PCA) (Figure 2) revealed partial clustering of individuals according to their subpopulation. Several individuals from the Šilutė subpopulation overlapped with those from the Alytus and Zarasai subpopulations, suggesting shared genetic components or recent gene flow. Additionally, a slight dispersion of individuals within the Alytus and Šilutė groups indicates the presence of intra-population genetic variability.

Bayesian clustering was applied to infer the genetic structure of American mink populations in Lithuania and to evaluate its correspondence with geographic sampling regions. According to the Δ*K* method proposed by Evanno et al. (2005), the most likely number of genetic clusters was $K = 2$ (Figure 3B), as indicated by the highest Δ*K* value. However, visual inspection of bar plots for $K = 4$ (Figure 3D) revealed more detailed genetic subdivision, suggesting the presence of four distinct genetic components within the sampled individuals. The pie charts in Figure 1 illustrate the proportion of genetic clusters identified by STRUCTURE analysis at $K = 2$ for each subpopulation, with red corresponding to Cluster 1 (predominating in Zarasai and Šilutė) and green to Cluster 2 (more common in Alytus. These proportions indicate the relative genetic contribution of each cluster within the subpopulations.

Table 3. Estimates of pairwise F_{ST} (below diagonal) and Nei's genetic distance (above diagonal) between *N. vison* subpopulations

Zarasai subpopulation	Šilutė subpopulation	Alytus subpopulation	-
-	0.180	0.523	Zarasai subpopulation
0.045	-	0.245	Šilutė subpopulation
0.195	0.140	-	Alytus subpopulation

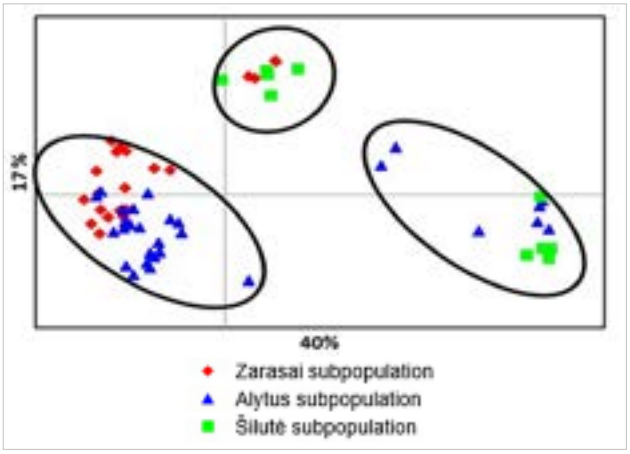

Figure 2. Principal Coordinates Analysis (PCA) based on genetic distances between American mink samples

Principal Coordinates Analysis (PCA) of American mink (*N. vison*) subpopulations sampled in Lithuania between 2018 and 2020. The analysis was conducted using GenAlEx v6.5 (Peakall and Smouse 2012) with six microsatellite loci. The percentages on the axes represent the proportion of total genetic variation explained by each coordinate (PCoA axis 1 = 40%, axis 2 = 17%).

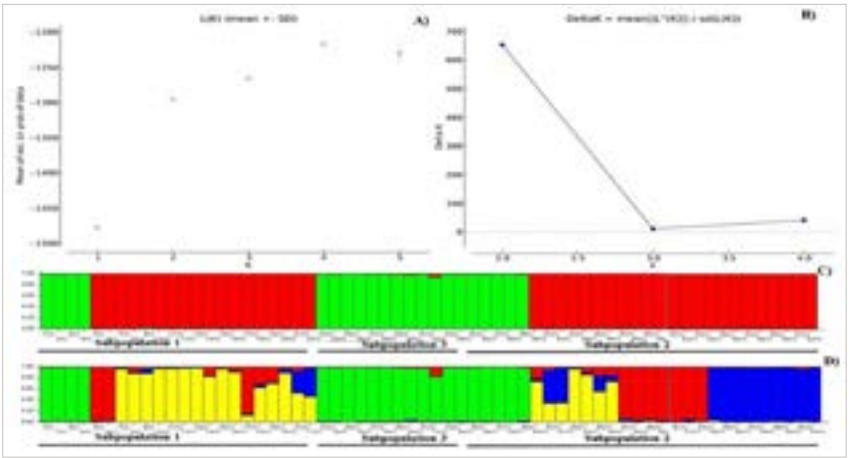

Figure 3. (A) Mean estimated log probability of the data [LnP(D)] ± SD for each *K* value, as calculated by STRUCTURE. (B) Delta *K* (Δ*K*) (Earl and von Holdt 2012) values used to determine the most likely number of clusters based on the method of Evanno et al. (2005). (C) Population structure of *N. vison* individuals from three sampling sites (subpopulation 1 – Zarasai, subpopulation 2 – Alytus, subpopulation 3 – Šilutė), inferred using STRUCTURE v2.3.4 over *K* = 1–10. (D) Bayesian STRUCTURE bar plot for *K* = 4

Each vertical bar represents an individual; colours indicate the proportion of each individual's genome assigned to one of the four inferred genetic clusters.

Discussion

In the present study, we collected genetic data to analyse three subpopulations of *N. vison*, which originated from different introductory sources. The Zarasai subpopulation exhibited the lowest heterozygosity. Its observed heterozygosity ($H_o = 0.333$) occurred significantly lower than expected ($H_e = 0.656$), indicating a pronounced heterozygote deficiency. The founder effect can explain this pattern, as historical sources evidence that in 1953, American mink was introduced to the Zarasai district from Tatarstan (Prūsaitė et al. 1988, Balčiauskas 1996). The introduction likely involved a small number of founders, which would reduce genetic variation. Subsequent isolation of this subpopulation, combined with possible inbreeding, may have further contributed to the loss of genetic diversity. Such reduced variability is a common feature of populations established from a few individuals, particularly when there is limited gene flow with neighbouring populations. The Alytus subpopulation exhibited balanced heterozygosity values ($H_o = 0.649$; $H_e = 0.640$). This may reflect a more stable population established through early and limited introduction events. Historical sources indicate that American mink naturally colonised the Lower Nemunas River region from Kaliningrad after World War II (Prūsaitė et al. 1988, Balčiauskas 1996), possibly including escapees from fur farms or migrants from Poland, which could have enhanced genetic stability in Alytus.

The highest genetic diversity was observed in the Šilutė subpopulation, which likely reflects gene flow from multiple sources, including Alytus, Kaliningrad, and Poland. Such diversity may have been further enhanced by hybridisation between genetically distinct individuals, a phenomenon observed in other invasive species introductions (Moody and Les 2007, Wolfe et al. 2007).

The origin and composition of introduced populations play a decisive role in shaping genetic diversity after introduction. According to Dlugosch and Parker (2008), genetic differences observed in introduced populations may reflect variation among distinct source populations and the effects of genetic drift, rather than adaptive evolution. In this context, the founder effect, resulting from the introduction of small and isolated populations, can significantly shape the genetic structure of invasive species (Zeisset and Beebee 2003, Rollins et al. 2009, Zalewski et al. 2010). This was likely the case in Alytus, where low diversity may have resulted from such processes (Masel 2011). Our results are consistent with previous studies, showing that genetic diversity and structure in invasive American mink reflect founder effects and multiple introductions. Similar patterns have been reported in Poland (Zalewski et al. 2010) and Spain (Lecis et al. 2008), where mixing of source populations has shaped the subpopulation structure. The reduced genetic diversity in Alytus, together with evidence of admixture between Zarasai and Šilutė, is consistent with previously reported patterns. For aquatic and semi-aquatic species, rivers and their adjoining riparian zones are considered key habitats and dispersal corridors (Malanson 1993, Virgós 2001). Despite occasional immigration from neighbouring areas, barriers such as river basins (e.g. Nemunas and Dauguva) restrict gene flow and reduce the likelihood of detecting transient individuals in genetic samples (Zuberogoitia et al. 2013). Principal Coordinates Analysis (PCA) confirmed genetic differentiation between subpopulations, with the greatest divergence observed between Alytus and Zarasai. Isolation by landscape features has contributed to the observed genetic structuring (Frankham et al. 2002). In Lithuania, American mink is broadly distributed across the landscape, but its occurrence is not entirely continuous. Populations are primarily associated with river basins, lakes and wetlands, providing suitable habitats. At the same time, intervening areas of intensive agriculture and urban development may create partial gaps in their distribution. Such spatial heterogeneity likely contributes to the observed genetic differentiation between subpopulations (Prūsaitė et al. 1988, Mickevičius and Baranauskas 1992, Balčiauskas 1996).

The PCA also revealed that some individual minks from the Šilutė subpopulation overlapped with individuals from both the Alytus and Zarasai subpopulations, suggesting shared ancestry or recent gene flow. This supports the idea that some subpopulations in Lithuania originated from a mixture of sources and retained genetic connections across geographic regions, despite the separation of river basins.

In this study, STRUCTURE analysis revealed clear evidence of population structuring among *N. vison* individuals sampled across Lithuania. The highest ΔK value was observed at $K = 2$, indicating the presence of two main genetic clusters. However, the results for $K = 4$ displayed more detailed genetic subdivision and higher resolution of individual assignments, suggesting a complex admixture pattern likely shaped by multiple introduction sources and subsequent gene flow. Similar STRUCTURE-based analyses in other European countries have demonstrated comparable patterns. Zalewski et al. (2010) found that American mink populations in Poland exhibited high genetic structuring, shaped by multiple introduction events and local adaptation. Lecis et al. (2008) also reported significant differentiation among Spanish mink populations, especially where physical barriers limited gene flow. This pattern suggests gene flow among populations and supports the hypothesis of multiple introduction events involving genetically diverse source populations. The PCA confirmed the STRUCTURE results, showing a distinct spatial arrangement of the clusters largely corresponding to the three subpopulations. The Alytus individuals formed a clearly distinct group, while the Zarasai and Šilutė subpopulations were more closely related, with partial overlap indicating some mixing (Figure 2).

Studies in other European countries have similarly demonstrated how the history of introduction shapes genetic structure. High genetic diversity in Denmark and Poland is attributed to introductions from multiple sources (Brusgaard et al. 1998, Zalewski et al. 2010). In contrast, strong differentiation in Spain and Italy indicates independent introduction events (Lecis et al. 2008, Cirera et al. 2013). French studies show the emergence of new genetic clusters over time, reflecting ongoing colonisation and adaptation processes (Van Leeuwen et al. 2024). These findings highlight that the source, timing, and frequency of introductions are central to understanding the success and spread of *N. vison*.

Conclusions

Our results indicate that multiple introductions and interline crossings have shaped the genetic structure of American mink in Lithuania. These factors likely enhanced genetic variability, which in turn may have increased individual fitness, population viability, and the species' invasive potential. Future studies are necessary to explore how these genetic dynamics influence ecological performance and long-term invasion success.

Acknowledgements

This research is financed by the Research Council of Lithuania through grant No. LEK-14/2012. We appreciate contributions from all the hunters involved in obtaining N. vison tissue samples.

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