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RESEARCH ARTICLE

Evidence of admixture between differentiated genetic pools at a regional scale in an invasive carnivore

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Abstract Invasive species represent a major threat to biodiversity, and the understanding of their population genetics is one of the most important goals in conservation biology. Recently, it has been proposed that methods using molecular tools could help define efficient eradication strategies and should be a preliminary step in the management process. The American mink was introduced in Europe for fur farming purposes in the 1920s, and, due to escapees, several feral populations have been mentioned in the last decades. In France, feral mink have been observed since the 1970s, and the largest population, located in Brittany, is considered to be still expanding. We investigated the genetic variability and population structure of 149 feral mink and 21 farmed mink from this area using six microsatellite loci. Our results showed three genetically distinct population units at the regional scale. A pattern of isolation by distance was observed for the whole sample. In our case we explain this pattern by recent admixture of the three genetic units. Our findings suggest that populations have recently met and started to homogenise.

Keywords American mink · Biological invasion · Clustering analysis · Isolation by distance · *Mustela vison* · Population structure

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Introduction

Biological invasions are recognised as a major threat to biodiversity and represent a significant component of human-caused environmental global change (Williamson 1996; Vitousek et al. 1997). As a result of international trade and transport, the number of introduced species increased, and consequently the number of potential invaders with devastating effects (Mack et al. 2000). The understanding of population biology and genetics of invasive species may provide valuable information to predict the efficiency of control methods and subsequent consequences of removal (Sakai et al. 2001), and is therefore one of the most important goals in conservation biology. For example, studies of genetic variation may help predict the potential for invasive populations to evolve in response to management practises (Sakai et al. 2001). In the same way, comparisons of the genetic composition of native and invasive populations could provide information about the process of invasion. Incorporating molecular techniques in the development of wildlife management strategies is a promising approach especially for invasive species control (lowering of the introduced population numbers) or eradication (Hampton et al. 2004; Abdelkrim et al. 2005; Cowled et al. 2006).

The American mink (*Mustela vison*) was introduced in Europe in the 1920s for the purpose of fur farming, and farmed mink come from at least three sub-species of wild mink (Dunstone 1993). Many mink escaped from farms, giving the opportunity for feral populations to become established. Several invasive populations have been mentioned throughout Europe for the last decades (see Bonesi and Palazon 2006). The impact of feral mink could be particularly detrimental for native birds like coots (*Fulica atra*) or moorhens (*Gallinula chloropus*) and voles

(*Arvicola terrestris*, *Microtus agrestis*) (Halliwell and Macdonald 1996; Macdonald and Harrington 2003; Banks et al. 2004). The American mink threaten European mink (*Mustela lutreola*) populations essentially by competing for resources, by interspecific aggressions and by introducing a fatal disease, the Aleutian mink disease parvovirus (Maran et al. 1998). Introgression is impossible because crossing between *M. vison* and *M. lutreola* lead to resorption of hybrid embryos (see Larivière 1999).

In France, the development of fur farms increased in the 1960s, and the first feral mink were observed in the 1970s (Phelipot 1974). According to Léger and Ruette (2005), three established populations can be found in the western part of the country (Fig. 1a). The largest population is located in Brittany, where most farms were concentrated (see Léger and Ruette 2005, and Fig. 1b). This feral population is thought to be still expanding despite the closing of nearly all farms in the 1980–1990s and despite local culling operations. In this area, the benefits of culling mink on a local scale are not proved, and efficient control strategies are still lacking. One way to improve the effectiveness of management programmes of a pest species is to study its population genetics (Hampton et al. 2004; Cowled et al. 2006). Indeed, establishing the best strategy to control invasive populations could be inferred from the understanding of the genetic population structure of the species and gene flow (e.g., Abdelkrim et al. 2005). Despite the growing literature considering the American mink as an invasive species, to our knowledge, there has been no attempt to study the genetic structure of feral mink populations in Europe, in a context of introduction.

In this work we assessed the genetic variability and investigated the delineation of genetic units in feral American mink from Brittany, western France, using six microsatellite loci. The study of genetic variation in this area is particularly interesting. In fact, one could expect a genetic structure between individuals among the different farms due to different introduction origins or different subsamples from the same origin and having experienced divergence by genetic drift. Admixture between different genetic pools could lead to an increase of genetic diversity and of adaptive potential (Ellstrand and Schierenbeck 2000; Kolbe et al. 2004). In the case of admixture between different origins, allelic diversities could be higher than in natural populations. Thus, as high genetic diversity could condition invasion success, assessing the genetic structure and the eventual degree of admixture in such a small geographical scale (ca. 30,000 km^2) is particularly relevant.

In this study we tested the occurrence of different genetic units and putative admixture. The occurrence of population bottlenecks, a classical feature of introduced populations, was inferred from observed genetic variability. Occurrence of isolation by distance (IBD) was tested in Brittany using an individual-based method (Rousset 2000). In such a small spatial scale, no relationship should have been observed between genetic differentiation and geographical distance because extensive gene flows are expected as observed by Stevens et al. (2005) in native populations. However, invasive populations are not in migration-drift equilibrium, and IBD could be identified because of their recent history, but it should decrease if homogenising gene flow occurs (e.g., Herborg et al. 2007). The insights of those results for the understanding of the population genetics of the American mink are discussed, as well as their consequences for biological conservation.

Methods

DNA extraction, amplification, and genotyping

From April 2004 to October 2006, 149 mink carcasses were collected from trappers from Brittany, and 133 of them were geographically located (Fig. 1). The study area approximately covered 27,200 km^2. In addition, 21 farmed

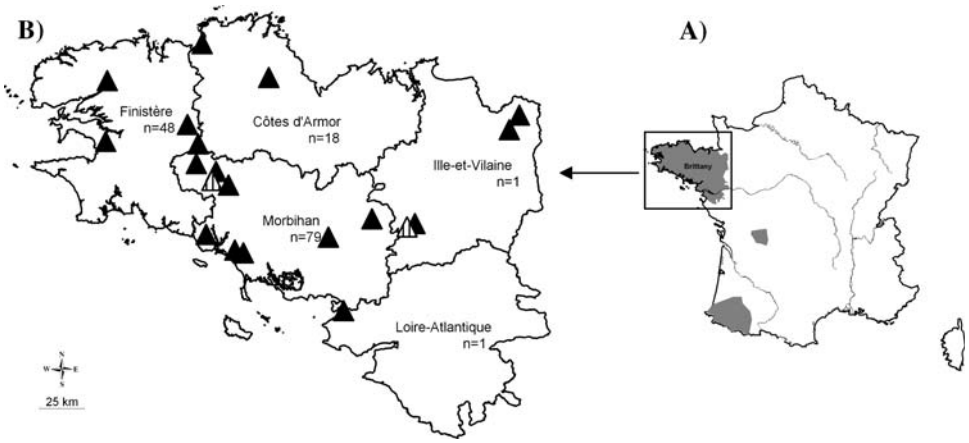

Fig. 1 **a** Distribution of feral mink (*Mustela vison*) populations in France (the *shaded zones* correspond to the distribution area of the species according to Léger and Ruette 2005). **b** Geographic distribution of mink farms in Brittany (the *black triangles* represent old farms closed in the 1980–1990s, and the *hatched ones* represent the two farms in activity). In each area, the number of feral mink samples (*n*) is mentioned

mink were analysed because they belonged to the most recently established farm in the area. Muscle samples were taken from the carcasses, and DNA was extracted by using Chelex® 5%. In a first step, ten pairs of microsatellite primers, containing up to seven alleles, were selected from Fleming et al. (1999) and Vincent et al. (2003). Six loci were polymorphic (Mvi1321, Mvi1322, Mvi1302, Mvi1341, Mvi1273, Mvi1272 meant up to seven alleles per locus) and were scored on the total samples.

Amplifications were carried out in 15-µl volumes, including ~50 ng of DNA template, 0.2 mM of dNTPs, 2 mM $MgCl_2$, 1× Taq buffer, 0.13 pM of the forward primer + 0.2 pM IRDye 700 or IRDye 800, 0.26 pM of the unlabelled reverse primer, and 0.60 units of *Taq* DNA polymerase (Eurobio).

PCR was performed as follows: first denaturation at 94 °C for 4 min, then 94 °C for 30 s, 45 s at annealing temperature (varying according the microsatellite), 72 °C for 1 min for 10 cycles, then 94 °C for 30 s, 51 °C for 45 s (IRDye), and 72 °C for 1 min for 30 cycles, followed by a final extension at 72 °C for 10 min.

Allele size was determined with a LI-COR Global IR^2 DNA Analyser, using fluorescent forward primers at IRDye 700 and IRDye 800. To avoid artefacts caused by poor amplification, two individuals for whom amplifications failed at more than two loci were excluded from the analyses.

Data analyses

The observed and expected heterozygosity and deviations from Hardy-Weinberg equilibrium for each locus and globally were computed with GENETIX (version 4.05.2, Belkhir et al. 1996–2004) and GENEPOP (version 3.4, Raymond and Rousset 1995) ($n = 149$). The F_{IS} and F_{ST} parameters were estimated following Weir and Cockerham (1984). Significance of F_{IS} estimates ($\hat{f}$) was tested using the permutation by population procedure with GENETIX (10,000 permutations). We tested genotypic linkage disequilibrium for each pair of loci with GENEPOP. Allelic richness per locus (R_S), which allows comparisons when sample size varies, was calculated using the software FSTAT (Goudet 2002).

Inferences regarding the genetic structure of the feral mink population were made using two independent clustering methods based on Bayesian models. These analyses were carried out for the 133 geographically located individuals. We first used STRUCTURE 2.2 (Pritchard et al. 2000; Falush et al. 2003). The model assumes K population units characterised by a set of allele frequencies at each locus. The likelihood of K is estimated from the allele frequencies. The highest likelihood value indicates the most likely number of populations in the sample. Results were based on runs of 100,000 iterations, following a burn-in period of 20,000 iterations. We performed a series of ten independent runs for each value of K from 1 to 9. The estimated log probability of data $Pr(X|K)$ can be used as an indication of the most likely number of groups (Pritchard et al. 2000). However, according to Evanno et al. (2005), $Pr(X|K)$ usually plateaus or increases slightly after the 'right' K is reached. Thus, following Evanno et al. (2005) ΔK was calculated.

Sampling scheme could affect STRUCTURE results and lead to erroneous conclusions on landscape genetics results (Schwartz and McKelvey 2008). Then, independently, we used GENELAND 2.0.1 (Guillot et al. 2005), which integrates the spatial coordinates of the samples, and may therefore provide a better definition of spatial genetic units. We allowed the number of populations to vary from 1 to 9 and inferred the most probable K with 100,000 MCMC iterations. We then ran 100,000 MCMC with K fixed to this number. Delta coordinates (error for spatial coordinates) was set at zero because each individual was accurately georeferenced.

We then performed the same standard population genetic analyses (as on the whole sample above) on the three populations units ($n = 25$, $n = 31$, and $n = 19$) inferred by STRUCTURE 2.2 and GENELAND 2.0.1. Evidence of recent bottleneck events was investigated using BOTTLENECK 1.2 (Cornuet and Luikart 1996), which compares the gene diversity observed (H_E) with the one expected from the number of alleles per locus when population size remains constant and for a given mutation model. We used the TPM (two-phased model of mutation, 70% SMM), which is more realistic for analysing microsatellite data (Cornuet and Luikart 1996). Significance was assessed by the Wilcoxon sign rank test. We test for microsatellite null alleles using the software developed by Van Oosterhout et al. (2006).

We then used an individual-based admixture analysis in BAPS 5.0 (Corander et al. 2003, 2004), which estimates the optimal posterior mode of the proportion of an individual's multilocus genotype, which is represented by each population. Comparison of the likelihood of the modal solution with the likelihood if the individual was forced to have pure ancestry gives the posterior probability that an individual does not show evidence of recent immigrant ancestry. This analysis was carried out for 121 individuals corresponding to individuals from the genetic units inferred by STRUCTURE 2.2 and GENELAND 2.0.1 and to individuals located in the areas between these units, thereafter designed as "contact areas". BAPS was used to estimate in these contact areas the proportion of individual's multilocus genotype, which is represented by two or three of the genetic units inferred by STRUCTURE and GENELAND. The option "last population consists of individuals who do not contribute to allele frequencies of any cluster" was

selected. In our case the allele frequencies of each cluster were determined by each genetic unit. The "last population" was constituted by individuals from contact areas in order to estimate, in these areas, the proportion of individuals with a mixed origin from two or three genetic units. To test the robustness of these analyses, we performed ten independent iterations. The critical α for admixture was set to 0.05.

To test the occurrence of isolation by distance, genetic distances between individuals ($\hat{a}$, Rousset 2000) were computed with the programme SPAGeDI (version 1.2., Hardy and Vekemans 2002) ($n = 133$, all georeferenced individuals). Regression between $\hat{a}$ and the ln of Euclidean distances between individuals (according to a two-dimensions stepping stone model) was tested using 1,000 permutations.

Results

Six microsatellites were used to genotype 147 feral mink and 21 farmed mink. All loci were polymorphic, showing an average of 8.5 alleles per locus in feral mink (minimum = 7, maximum = 12 alleles) and 6.3 alleles per locus in farmed mink (minimum = 5, maximum = 8 alleles). Average values of observed and expected heterozygosity were, respectively, $H_o = 0.74$ and $H_e = 0.67$ for feral mink and $H_o = 0.62$ and $H_e = 0.76$ for farmed mink (Table 1). Global F_{IS} estimates were 0.1004 for feral mink and 0.1913 for farmed mink, and heterozygote deficiency was highly significant for the two populations (feral: $P < 0.0001$, farmed: $P = 0.0004$). Significant linkage disequilibrium was found for all except one pair of loci in the feral population (according to $P < 0.05$) and for one association in farmed mink (Mvi1321 and Mvi1273, $P < 0.001$). The F_{ST} estimate between feral and farmed mink populations was highly significant ($\hat{\theta} = 0.07$, $P < 0.001$). Allelic richness was equivalent in the feral ($R_S = 5.78$) and farmed samples ($R_S = 5.77$ for a sample of 11 individuals).

The Bayesian clustering procedure implemented in Structure 2.2 (Pritchard et al. 2000; Falush et al. 2003) allowed observing genetic structure with no prior information. This method detected the maximum likelihood for a model of three genetically distinct populations ($\ln L = -2292.4$). For $K > 3$, the clustering process failed to calculate a homogeneous posterior probability of the data between each iteration (Fig. 2a). The best clustering was

Table 1 Summary of basic population genetic analyses for the whole sample of feral mink, the three inferred populations with Structure 2.2 and Geneland 2.1.0, and the farmed mink

	Whole sample				W population				SW population			
n	147				25				31			
Locus	H_o	H_e	$\hat{f}$	*P* values	H_o	H_e	$\hat{f}$	*P* values	H_o	H_e	$\hat{f}$	*P* values
1321	0.6529	0.6552	0.038	0.8959	0.4400	0.5633	0.222	0.2799	0.5328	0.7400	−0.075	0.8917
1322	0.6897	0.8046	0.143	**0.0000**	0.7083	0.8112	0.129	0.2990	0.6000	0.6124	−0.020	0.6548
1341	0.7172	0.7734	0.073	0.0653	0.8333	0.7296	−0.146	0.6893	0.6800	0.7076	0.043	**0.0344**
1302	0.6718	0.7753	0.134	**0.0000**	0.6364	0.5381	−0.188	0.8676	0.8750	0.7421	−0.246	0.4098
1273	0.5797	0.6871	0.157	**0.0001**	0.7727	0.6850	−0.132	**0.0000**	0.3043	0.4561	0.224	0.5063
1272	0.7305	0.7703	0.052	**0.0046**	0.6957	0.6135	−0.137	0.4040	0.6522	0.6812	0.029	0.7088
All loci	0.6698	0.7443	0.100	**0.0000**	0.6811	0.6568	−0.038	**0.0000**	0.6158	0.6220	−0.024	0.4744

	SE population				Farmed mink			
n	19				21			
Locus	H_o	H_e	$\hat{f}$	*P* values	H_o	H_e	$\hat{f}$	*P* values
1321	0.8500	0.7667	−0.114	0.2788	0.8095	0.8630	0.063	0.4646
1322	0.6000	0.8293	0.285	**0.0058**	0.4286	0.6806	0.376	**0.0066**
1341	0.5000	0.5391	0.043	0.5622	0.8571	0.7700	−0.116	0.5685
1302	0.5000	0.7041	0.299	0.0597	0.3500	0.7449	0.537	**0.0000**
1273	0.4000	0.4310	0.098	0.5258	0.4545	0.6840	0.346	0.243
1272	0.8000	0.6671	−0.156	0.5341	0.8125	0.8206	0.010	0.2639
All loci	0.6083	0.6562	0.081	**0.0355**	0.6187	0.7605	0.191	**0.0000**

H_o and H_e, observed and expected heterozygosity, $\hat{f}$ estimates of F_{IS} values, *P* values for the 'exact Hardy–Weinberg test' from GENEPOP
Significant *P* values are shown in bold type

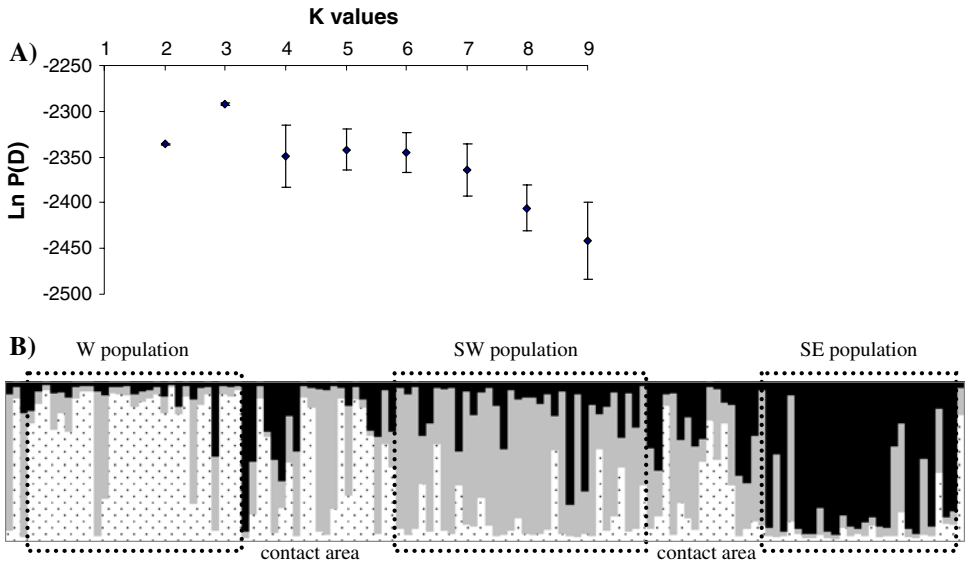

Fig. 2 **a** Results of the Bayesian clustering analysis performed with STRUCTURE 2.2: plot of the estimated logarithms of data [LnP(D)] against the number of populations tested (*K*). *Bars* show standard deviation. **b** Estimated population structure inferred from the whole feral mink samples for $K = 3$. Individuals are ranked according to their geographic location along the x-axis. Each individual is represented by a *thin vertical line*, which is partitioned into *K* coloured segments representing the individual's estimated membership fraction in *K* clusters. *Dotted lines* indicate the three groups of individuals determined by their geographic origin and because most of the individuals are genetically assigned to one main cluster ($q > 0.7$). These groups are regarded as W, SW and SE populations. In those populations, individuals not assigned to the main cluster were considered as migrants (or represented assignment uncertainty, possibly arising from homoplasy, rather than real migrants) and were excluded from the genetic analyses concerning W, SW and SE populations

observed for $K = 3$, and, within each group, individuals were mainly assigned to one cluster according to $q > 0.7$ (cluster 1: $n = 25$, cluster 2: $n = 31$, cluster 3: $n = 19$, Fig. 2b). We arbitrarily used a q value of 0.7 because we chose to accept approximately 1/3 of introgression between our populations (with $q > 0.8$ our results were very slightly affected and our interpretations were the same). Geographically, the three inferred clusters corresponded to distinct units (Fig. 3). The *K* estimator (Evanno et al. 2005) failed to discriminate between $K = 2$ and $K = 3$. The same geographic units corresponding to the genetic clusters were independently observed with GENELAND 2.0.1 (Fig. 4). These three geographical units were considered as points of establishment and invasion of feral populations from mink farms. Between each geographical unit, no concordance was observed between geographic location and genetic assignation (Figs. 2b, 3): these areas were defined as "contact areas".

For each cluster inferred by STRUCTURE 2.2, we selected the individuals assigned to this cluster according to $q > 0.7$ and to geographic contiguity, and ran the standard population genetic analyses (Table 1). Estimates of F_{IS} were $\hat{f} = -0.038$, $\hat{f} = -0.024$, and $\hat{f} = 0.081$ in the western, southwestern, and southeastern populations, respectively (Table 1). There was significant Hardy-Weinberg disequilibrium for W and SE populations ($P < 0.001$ and

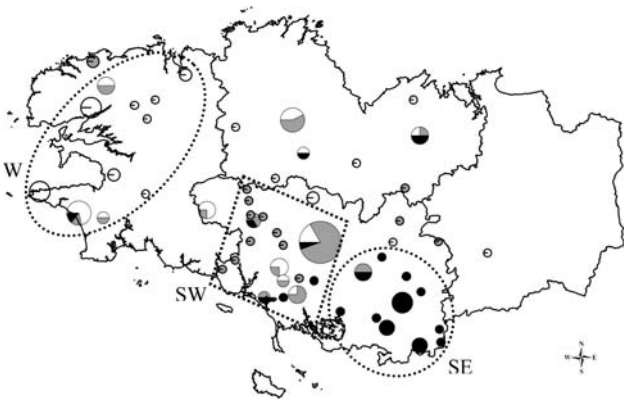

Fig. 3 Geographic distribution of feral mink samples [BD CARTHAGE®© IGN-MATE (2005)]. Circles correspond to results of the clustering analysis performed with STRUCTURE 2.2: *white circles* correspond to individuals assigned to W population, *grey circles* to individuals assigned to SW population, and *black circles* to individuals assigned to SE population (according to $q > 0.70$). The *size of the circle* depends of the number of individuals analysed. *Dotted lines* roughly indicate the W, SW and SE populations defined using STRUCTURE 2.2. Contact areas are presumed outside these lines

$P = 0.036$, respectively). The test for microsatellite null alleles showed null alleles for only two loci, Mvi1322 and Mvi1321. Locus Mvi1322 showed 3–10% of null alleles for the three populations, and locus Mvi1321 showed 10% of null alleles for the W population. All other loci and

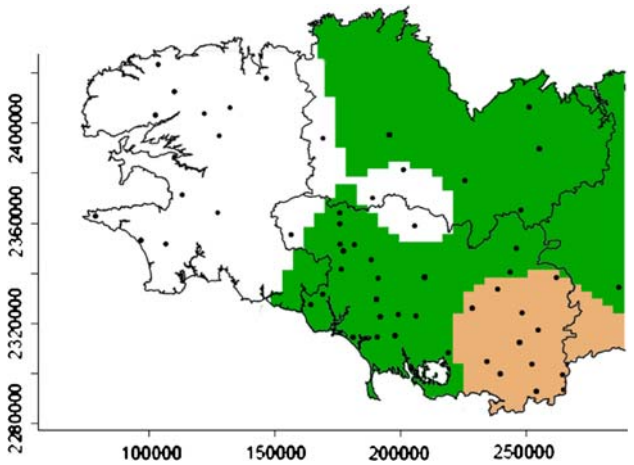

Fig. 4 GENELAND assignment of individuals for $K = 3$ and 100,000 MCMC iterations. Plots correspond to the geographical location of feral mink individuals (one plot could represent several individuals from the same origin) [BD CARTHAGE®© IGN-MATE (2005)]. Each *colour* represents a distinct genetic unit

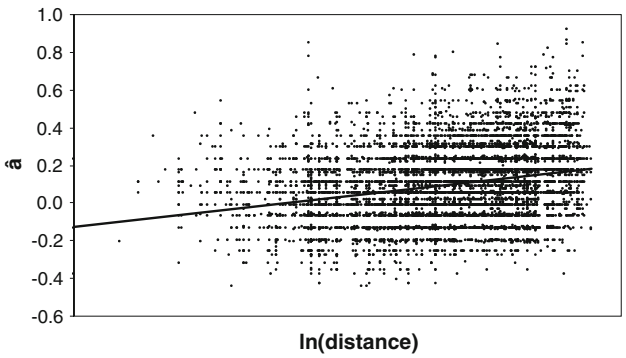

Fig. 5 Genetic differentiation in feral American mink. Pairwise genetic differentiation between individuals ($\hat{a}$) are plotted against logarithm of distance (in metres)

populations showed less than 1% of null alleles. When removing locus Mvi1322 showing 10% of null alleles for the SE population, Hardy–Weinberg disequilibrium for this population became no significant. Significant linkage disequilibrium was only observed between loci Mvi1273 and Mvi1272 in the W population ($P < 0.05$). The three populations showed lower allelic richness than the farmed mink population ($R_S = 4.52$, $R_S = 3.73$, and $R_S = 4.73$, respectively, vs. $R_S = 5.77$, for a sample of 11 individuals).

Pairwise F_{ST} estimates between population units were all highly significant ($P < 0.001$) (Table 2). The highest estimate values $\hat{\theta} = 0.177$ and $\hat{\theta} = 0.163$ were observed between W and SE populations, and between SW and SE populations, respectively. Pairwise F_{ST} estimates between feral and farmed populations were also significant, and the highest value, $\hat{\theta} = 0.14$, was observed with the W population.

The Wilcoxon rank test performed with BOTTLENECK was significant for the SW population ($P = 0.03$), but were not significant for W, SE, and farmed populations ($P = 0.156$, 0.687, and 0.438, respectively). Hence, there is no conclusive evidence of a past bottleneck event in these populations.

As expected, in the contact areas BAPS 5.0 allowed detecting individuals with mixed origins from the genetic clusters inferred by STRUCTURE 2.2 and GENELAND 2.0.1. The same results were obtained between the ten iterations for all but one individual (significantly admixed or not). In the contact areas, depending on iterations, 32–35% of individuals were significantly admixed ($P < 0.05$).

A pattern of isolation by distance was observed among individuals for the whole sample (Fig. 5). Maximum geographical distance was ca. 200 km between western and eastern individuals and ca.100 km between northern and southern samples. The slope b of the regression of genetic vs. logarithm of geographic distances was estimated to be 0.073 ($P < 0.001$). Within groups, genetic distances were not significantly correlated with geographical distances (W population, $P = 0.250$; SW population, $P = 0.385$, and SE population, $P = 0.327$).

Table 2 Pairwise F_{ST} estimates ($\hat{\theta}$) of feral mink populations from three localities (western, southwestern, and southeastern populations) and farmed mink

Locality	W	SW	SE	Farmed
W				
SW	0.102*			
SE	0.163*	0.177*		
Farmed	0.142*	0.103*	0.103*	

* Indicates significant values according to $\alpha = 0.05$

Discussion

Population structure and admixture

Significant deviation from Hardy–Weinberg equilibrium, as well as linkage disequilibrium, observed in the whole sample of feral mink may be due to the Wahlund effect. A deficit of heterozygosity is expected when distinct gene pools are sampled together (Hartl and Clark 1997). The fact that feral mink may be structured in subpopulations at lower geographical scale is confirmed when looking for genetic partitions using Bayesian methods. The results generated independently by STRUCTURE 2.2 and GENELAND 2.0.1 suggested three genetic units at the regional scale, located in the western, southwestern, and southeastern parts of the area (Figs. 3, 4). As expected by the clustering procedure implemented in STRUCTURE, a reduction of loci

displaying a deviation from Hardy-Weinberg expectation was observed in each of the three groups. The inferred population units showed significant differentiations as indicated by estimates of pairwise F_{ST} values. In the three distinct geographical units, individuals were mainly assigned to a single cluster ($q > 0.7$). These three zones match the distribution of the largest mink farms in Brittany and are considered as point of establishment and invasion of feral populations. The northern region is essentially constituted by individuals either assigned to the W or to the SW population. This pattern might suggest colonisation events that are congruent with the lesser occurrence of farms in this area (i.e., farms could act as source populations). Our results allowed detecting areas called contact areas (geographically located between the three distinct genetics units) where individuals were either assigned to one cluster ($q > 0.7$) without geographical consistency or were not predominantly assigned to a unique cluster. This pattern could be explained by recent migration from the three points of invasion and by the proportion of individuals with mixed origins (due to mating between migrants). In these contact areas, BAPS results showed that 32–35% of individuals were significantly admixed. The linkage disequilibrium observed between two loci in only one population (W population) could be due to a higher level of admixture in this area. Indeed admixture should bolster linkage disequilibrium, and different areas in the study area should have different levels of admixture (see, for example, Forbes and Allendorf 1991).

Hypothetical scenario of introduction and invasion

Significant genetic structure in American mink populations was observed at the regional scale. Two non-exclusive hypotheses can explain this pattern. Firstly, in farms, animals can have been introduced from different source populations. Multiple introductions, by producing sometimes more genetic diversity in introduced populations than in source ones, could explain the success of invasive species (e.g., Kolbe et al. 2004; Genton et al. 2005). The scenario of multiple sources of introduction of mink in Brittany may be supported by the large number of mink farms in the area, especially where genetic clusters were observed (Finistère and Morbihan). Farmed mink come from at least three sub-species of wild American mink (Dunstone 1993). Moreover, mink brought to Europe are likely to come from distinct source populations and trade within farms (between regions and/or countries) is expected (Belliveau et al. 1999). The hypothesis of multiple sources of introduction could also explain why we failed to detect recent bottlenecks.

Secondly, genetic drift within farms could also explain the genetic structure observed. Indeed, genetic drift is likely to have led to a reduction in genetic variability as well as the few founder animals and an accumulation of inbreeding. These two hypotheses, multiple sources of introduction and genetic drift within farms, could both lead to a strong genetic differentiation between farms, and therefore in feral populations from separate farm origins. In our sample, we could not determine which of these scenarios have prevailed in Brittany. In this area, genetic diversity (according to H_e and R_S values) was equivalent between the feral population and the farmed mink samples. Allelic richness and gene diversity observed in our farmed sample suggest that potential high diversity was introduced in Europe. However, further investigations are needed with comparisons with native North American populations.

Towards a subpopulation homogenisation?

Landscape features can act as ‘moderator of gene flow’ and lead to the differentiation of genetic units (e.g., Coulon et al. 2006). In our study area, there is no obvious landscape feature that could explain the observed population partition. Mink are semi-aquatic mammals, using a wide array of aquatic habitats (Dunstone 1993). In Brittany, the extensive hydrographical system ($\sim$15,000 km of watercourses) is likely to have enhanced the establishment of escaped mink. Since the first observations of feral mink in the 1970s, a rapid demographic expansion has been observed (Léger and Ruette 2005). A previous study investigating population structure of wild mink at a microgeographic scale (until 50 km) in Northern America showed high levels of gene flow and predicted that mink might move quite frequently between streams (Stevens et al. 2005). In our study, the distance inside and between the observed clusters is not so important considering long-distance dispersal movements already mentioned in feral radiotracked mink (Gerell 1970). According to these results, the absence of IBD within each population in Brittany is not so surprising. For the whole sample, the correlation between genetic and geographic distances observed could not be confounded with what could be expected in populations at migration/drift equilibrium (i.e., IBD sensu Slatkin 1993). Based on the recent invasion history of mink in Western France (less than 30 generations), populations could not have reached this equilibrium. The correlation between genetic and geographic distances rather reflects a nonequilibrium situation: the occurrence of recent admixture between differentiated gene pools (e.g., Herborg et al. 2007). If the observed IBD pattern was resulting from a stepwise colonisation process, we should not detect (with STRUCTURE and GENELAND) any centre of invasion considering our spatial random sampling trying to maximise a geographical collection within the study area. The detection of admixed individuals in the contact areas

suggests that the three distinct populations could have recently met and populations start to homogenise. Over time, genetic differentiation should decrease because high levels of gene flow are expected in mink (Stevens et al. 2005).

Implications for conservation

Recently, genetic monitoring has been suggested to improve long-term eradication campaigns in an insular system (Abdelkrim et al. 2005). Indeed, delimiting eradication units could help draw efficient eradication strategies, taking into account dispersal and gene flow. In Western France, the eradication of the American mink populations seems to be quite unrealistic considering the rapid expansion of feral individuals and high reproductive rates in the area (A. Bifolchi, unpublished data). In addition, vacant territories resulting from local culling operations could rapidly be recolonized during juvenile dispersal (Frank and Woodroffe 2001). Sparing even a few individuals could lead to a high failure probability of an eradication project (Abdelkrim et al. 2007).

However, even if eradication seems to be unrealistic, our results could be useful to define control strategies (i.e., lowering of the introduced population numbers) and to manage efficient culling operations. Our results showed that mink from different origins were introduced in the wild. The admixture of these different genetic units could increase the genetic diversity of the species, and this is particularly disturbing in the case of an invasive species. Concentrating trapping efforts in the inferred contact areas could disrupt gene flow between populations. Such actions could help to prevent a genetic homogenisation at the regional scale. Indeed, admixture between different genetic pools could lead to an increase of adaptive potential (Ellstrand and Schierenbeck 2000; Kolbe et al. 2004; Lavergne and Molofsky 2007) and might substantially limit the chance to control invasive mink populations in Western France. Our results constitute then a fundamental work to improve the understanding of the biology of this invasive species, and it will be interesting to increase our results by a comparative study between native and invasive populations.

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