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Biological invasions in international seaports: a case study of exotic rodents in Cotonou

Sylvestre Badou[1,2,3] · Karmadine Hima[4] · Clément Agbangla[3] · Philippe Gauthier[2] · Antoine A. Missihoun[3] · Gualbert Houéménou[1] · Anne Loiseau[2] · Carine Brouat[2] · Gauthier Dobigny[2,5]

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Abstract

Black rat (*Rattus rattus*), brown rat (*Rattus norvegicus*), and house mouse (*Mus musculus*) are known to be among the most common anthropophilic rodent species in cities worldwide. These species are responsible for the destruction of domestic and industrial materials, considerable damage to food stocks as well as zoonotic pathogens circulation and transmission to humans and animals. These invasive species have disseminated in all continents following human-mediated exchanges, especially maritime transports. In particular, seaports appear as privileged rats and mice's entry points into new regions, thus making them international regulations' priorities for rodent surveillance and management. Yet, studies on seaport rodents are rare; in particular, investigations on their genetic structure are almost inexistent, thus precluding science-guided interventions. In order to fill such a gap, our study focused on the population genetics of *R. rattus*, *R. norvegicus* and *M. musculus* in the Autonomous Port of Cotonou, Benin. Nine different sites were surveyed for three years. In total, 366 *R. rattus*, 188 *R. norvegicus* and 244 M. *musculus* were genotyped using 18 microsatellites, 16 microsatellites and 17 microsatellites, respectively. Our results show very well-structured genetic clusters in all three species as well as limited impacts of rodent control campaigns. Using comparisons with genotypes from other European, Asian and African countries, we suggest for the first time that settlement of newly introduced individuals may be a rare event. Implications in terms of management units and control and monitoring are discussed.

Keywords Invasive rodents · Population genetics · Movement · Urban · Rodent management

Introduction

Human activities contribute strongly to the displacement of species outside their original distribution area, thus leading to an increased number of biological invasions (Wilson et al. 2009; Blackburn et al. 2011; Gallardo and Aldridge 2013; Padayachee et al. 2017; Seebens et al. 2017). In particular, maritime trade plays a major role in the global spread of exotic plant and animal species around the world (Veale et al. 2021). Among them, the transport and involuntary introduction of commensal rodents and their associated ectoparasites and pathogens are particularly worrying (Aplin et al. 2011; Song et al. 2003, 2014; Bona 2020). The black rat *Rattus rattus*, the Norway rat *Rattus norvegicus* and the domestic mouse *Mus musculus* fall within the 100 most impactful invasive alien species (Lowe et al. 2000; www.iucnredlist.org), ranking within the top 15 rodent pest taxa in the world (Capizzi et al. 2014). These species have invaded all the continents except Antarctica (Long 2003).

✉ Karmadine Hima
karmadine@gmail.com

1 Ecole Polytechnique d'Abomey-Calavi, Laboratoire de Recherche en Biologie Appliquée, Unité de Recherche sur les Invasions Biologiques, Université d'Abomey-Calavi, Cotonou, Benin

2 CBGP, CIRAD, INRAE, IRD, Institut Agro Montpellier, Université de Montpellier, Montferrier-sur-Lez, France

3 Faculté des Sciences et Techniques (FAST), Laboratoire de Génétique Moléculaire et d'Analyse des Génomes, Université d'Abomey-Calavi, Cotonou, Benin

4 Faculté des Sciences et Techniques, Université Abdou Moumouni, BP 10662 Niamey, Niger

5 Institut Pasteur de Madagascar, Unité Peste, Antananarivo, Madagascar

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The intensification of trade has accelerated their spread to new territories with invasion modalities that remain largely uncontrolled (e.g., Dalecky et al. 2015; Berthier et al. 2016). Consequently, they have now reached a quasi-global distribution (St Clair 2011). All three species impact local biodiversity, leading to the decrease or extinction of endemic species (Wyatt et al. 2009; Harper and Bunbury 2015; Doherty et al. 2016). They cause damage to infrastructure and human activities (Garba et al. 2014b; Panti-May et al. 2017) and huge economic losses, essentially related to the destruction of food stocks (Dossou et al. 2020; Diagne et al. 2020a, b, 2021). They are also involved in the transport, maintenance, and transmission of many zoonotic agents (review in Meerburg et al. 2009; Colombe et al. 2019). Their tigh interaction with humans has made them privileged sources of infectious diseases, thus inducing the loss of hundreds thousands of lives annually (Colombe et al. 2019). In order to avoid rodent-mediated dissemination of zoonotic agents showing epidemic/pandemic potential, International Health Regulation (World Health Organization 2008) imposes signatory states to monitor and control invasive rodents at their entry points, especially within seaport areas. However, scientific data to guide rodent management actions in such habitats are very scarce.

Thanks to its international seaport in the city of Cotonou (officially "Autonomous Port of Cotonou", hereafter designed as to APC), the Republic of Benin is at the heart of intercontinental trade between West African coastal as well as hinterland countries and the rest of the world. As a consequence, the APC constitutes a particularly favourable site for exotic rodents introduction and subsequent spread towards landlocked countries such as Niger, Burkina-Faso, Mali and Chad. For instance, trade flows from Benin to Niger are thought to have facilitated the introduction of the black rat and the house mouse in large cities such as Niamey, which is more than 1,000 km away from the coast (Berthier et al. 2016; Hima et al. 2019). This latter species was probably brought in by ships, settled in the seaport and then transported to Niamey with the goods loaded on the trucks (Hima et al. 2019).

Rattus rattus, *Rattus norvegicus* and *Mus musculus* are abundant within the APC, representing more than 80% of the small mammals caught (Hima et al. 2019; Dossou et al. 2020; Badou et al. submitted). In the industrial storehouses, Norway rats and house mice damage an average of 3,450 tons of imported rice, for an estimated loss of 58 k€ per warehouse and per year (Dossou et al. 2020). They may also be responsible for the destruction of the electricity networks, including those of some very expensive unloading machines (APC, pers. comm.). Additionally, they may be involved in the introduction of allochthonous zoonotic pathogens, such as Seoul Orthohantavirus that are responsible for hemorrhagic fevers (Castel et al. 2021). However, whether introduction events are frequent or not remains unknown, thus greatly limiting our ability to evaluate future risks.

In order to deal with these sanitary, food security, and economic issues, APC authorities periodically hire service providers which organize anticoagulant-based rodent control campaigns within the seaport. However, a three-year long survey of invasive rodent abundance in the APC suggests that deratization is rather ineffective in the short-term, with similar population levels being observed within six months (Badou et al. submitted). Yet, the processes at work after rodent control operations that enable population recovery (i.e., endogenous reproduction *vs*. immigration) remain unknown, thus obscuring the best options for coping with rodent control through efficient, sustainable, and cost-effective methods.

By allowing indirect estimation of rodent origin and dispersal at the spatial and temporal scales that are relevant for surveillance and control, population genetics may help to address these issues. In this study, we describe the population genetic structures of *R. rattus*, *R. norvegicus* and *M. musculus* within the APC using species-specific sets of microsatellite markers, and we evaluate gene flows at a very fine spatial scale. Using longitudinal sampling, we investigate the effect of rodent control campaigns on the population genetic estimates from the three pest species. Finally, we rely on samples from foreign countries to mimic putative introduction events and examine whether our microsatellite panels allow us to identify newly disembarked individuals.

Material and methods

Study area and sample collection

Between 2017 and 2020, rodents were sampled each semester at 9 different sites of the Cotonou seaport using a standardized protocol (Garba et al. 2014a; Badou et al. submitted). Two sites were located within the artisanal fishing port outside the industrial seaport: APC1 (fresh fish stores) and APC2 (fresh fish market). Within the industrial seaport, trapping was carried out in restaurants and canteens for local workers (APC3), in the Beninese Society of Port Manutention (SOBEMAP) warehouses number 1 (APC4), 2 (APC5), 3 (APC6) and 4 (APC7), in the garage and mechanical workshops of SOBEMAP (APC8) as well as in the parking lot of SOBEMAP heavy (including off-duty) gears (APC9) (Fig. 1). Details on each trapping sites are provided in Supplementary material 1.

At each session and in each site, locally-made wire mesh traps (LxWxH 30 × 10x10cm) and manufactured Sherman traps (Sherman Inc, USA; 23.2 × 7.3x8.8 cm) were systematically used in conjunction so as to maximize the chances of capturing both small and large species (Garba et al. 2014a;

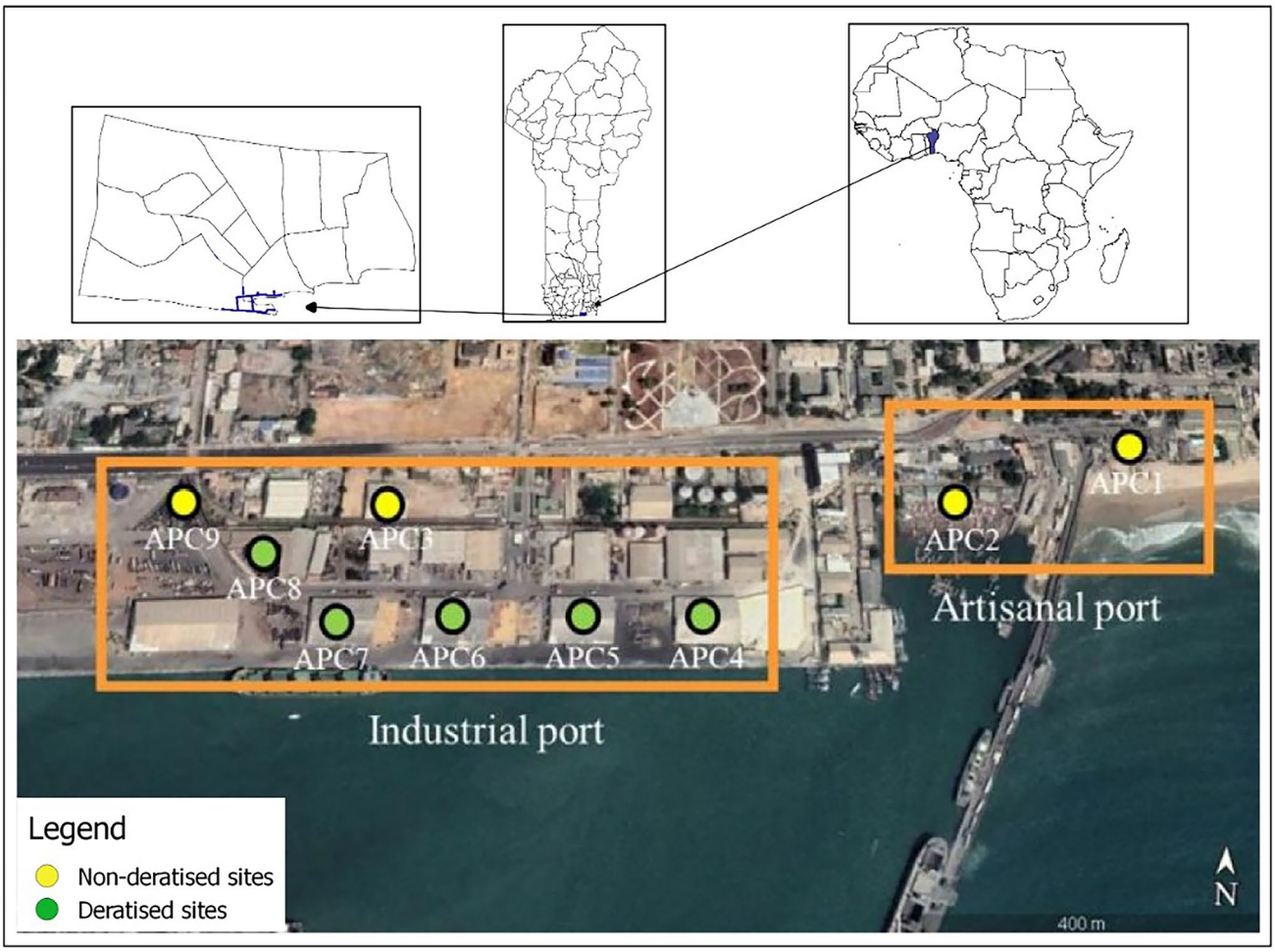

Fig. 1 Trapping sites in the Autonomous Port of Cotonou (APC) on Google Earth©. Deratised and non-deratised sites are indicated in green and yellow, respectively

Dalecky et al. 2015; Lucaccioni et al. 2016; Badou et al. submitted). A mixture of peanut butter and sardines in oil was used as bait. The traps were set for 3–4 consecutive nights and were collected each morning. Rodents captured were brought to the laboratory and treated within the same day. The exact GPS coordinates of each capture were systematically recorded. In total, six sampling sessions were conducted: session 1: September–October 2017; session 2: March–April 2018; session 3: September–October 2018; session 4: March–April 2019; session 5: September–October 2019; session 6: March–April 2020. Importantly, two anticoagulant-based rodent control campaigns were conducted in APC4 to 8 before our trapping sessions 3 and 4, respectively.

Ethical aspect and data sharing

This program was conducted within the framework of the research agreement between the Republic of Benin and the French National Institute for Sustainable Development (IRD) that was reapproved on the 6th April 2017, as well as the partnership agreement between IRD and the University of Abomey-Calavi (signed on the 30th September 2010 and renewed on the 3rd July 2019). All trapping sessions were authorized by the APC administrative authorities and no trap was set without the explicit oral consent of port staff or artisanal seaport site owners/operators.

Rodents were captured and brought alive to the lab where they were treated in a respectful manner in accordance with the guidelines of the American Society of Mammalogists (Sikes and Gannon 2011), sedated, and then sacrificed by cervical dislocation as recommended by Mills et al. (1995). Access to and benefit-sharing of genetic resources produced during the course of the present study was authorized by the Benin national authorities following the Nagoya international protocol (permit 608/DGEFC/DCPRN/PF-APA/SA). Samples and associated data were deposited in the Small

Mammal Collection at the IRD/CBGP (https://doi.org/10.15454/WWNUPO) as well as at URIB/LARBA/EPAC.

Laboratory analyses

Genomic DNA was extracted from ethanol-preserved tissues (kidney, spleen or liver for animals captured alive, and hind toes for individuals that were found dead inside the traps) with the Qiagen DNeasy Blood and Tissues kit as recommended by the supplier. The amplification was carried out in multiplex with three species-specific microsatellite panels. For *R. rattus*, we used a panel of eighteen microsatellite loci of which eight (D10Rat20, D11Mgh5, D11Rat56, D16Rat81, D2Mgh14, D5Rat83, D7Rat13 and D18Rat75) were originally developed for *R. norvegicus* (Jacob et al. 1995) while ten (Rr14, Rr17, Rr21, Rr22, Rr54, Rr67, Rr68, Rr93, Rr107 and Rr114) were *R. rattus*-specific (Loiseau et al. 2008). For *R. norvegicus*, we used a panel of sixteen microsatellite loci (D1VKORC1-C, D1VKORC1-A, D3Rat159, D4Rat59, D5Rat43, D8Rat162, D10Rat105, D11Rat11, D12Rat49, D13Rat21, D14Rat110, D15Rat64, D18Rat116, D19Rat62, D20Mit4, D2Rat97) (Desvars-Larrive et al. 2017). For *M. musculus*, we used a panel of seventeen microsatellite loci (D1Mit291, D2Mit456, D3Mit246, D4Mit17, D4Mit241, D6Mit373, D7Mit176, D8Mit13, D9Mit51, D10Mit186, D11Mit236, D14Mit66, D16Mit8, D17Mit101, D18Mit8, D19Mit30 and D5Mit30) (available from the MMDBJ database: http://www.shigen.nig.ac.jp/mouse/mmdbj/top.jsp; Lippens et al. 2017). Polymerase Chain Reactions (PCR) and genotyping were conducted according to previously described procedures for *R. rattus* (Berthier et al. 2016), *M. musculus* (Lippens et al. 2017) and *R. norvegicus* (Desvars-Larrive et al. 2017). Genotyping was performed with an ABI 3500xl sequencer (Applied Biosystems) with 2 µl of diluted PCR product to which a 15 µl mix of formamide and the GS 500 LIZ size marker (ABI 3100 model) were added. Microsatellite profiles were read independently by two persons using GeneMapper v.4.0. In the case of ambiguous reading at a given microsatellite, the individual was genotyped de novo and re-read for that particular locus.

Spatial patterns of population genetic structure

Analyses were performed for each species separately. They were done first on sessions pooled for each site. Unless specified, only samples from sites with at least 11 individuals for a given species were used. Deviation from Hardy–Weinberg equilibrium (HWE) for each site and each locus as well as linkage disequilibrium (LD) between each pair of loci at each site were tested using GENEPOP v.4.6 (Rousset 2008). Corrections for multiple tests were performed using the false discovery rate (FDR) approach (Benjamini and Hochberg 1995) implemented in the Bioconductor qvalue R package (Storey 2002).

FreeNa (Chapuis and Estoup 2007) was used to estimate the presence of null alleles in each dataset in order to test whether they may explain heterozygote deficiencies (see below).

The allelic richness (a_r) was calculated at each site using the rarefaction procedure in FSTAT v2.9.4 (Goudet 2003). The observed (H_O) and expected (H_E) heterozygosities were estimated using GeneClass2 (Piry et al. 2004) and the F_{IS} (Weir and Cockerham 1984) using Genepop.

Genetic differentiation between sites was estimated by pairwise F_{ST} estimates (Weir and Cockerham 1984) using FSTAT. A 95% confidence interval (CI) for mean F_{ST} was generated by bootstrap resampling (10,000 permutations) across loci.

Under a model of isolation by distance (IBD), genetic distance between individuals is expected to increase with geographical distance (Rousset 1997). IBD was estimated using the regression method based on the expected linear relationship between genetic and geographic distances (Rousset 1997, 2000) in GENEPOP. Mantel tests (10,000 permutations) were performed using the pairwise genetic differentiation estimator $\hat{e}$ (Watts et al. 2007) calculated between all pairs of individuals genotyped and the logarithm of their Euclidean geographical distances. The minimum distance between sites (d = 100 m) was used as a threshold to exclude pairs of individuals from the same site.

Population genetic structure was then explored using the clustering approach implemented in STRUCTURE V.2.3.4 (Pritchard et al. 2000) using all individuals genotyped in order to determine the number of homogeneous genetic clusters (K) present in each species-specific dataset. The analyses were performed with a model including admixture and correlated allele frequencies, for K ranging from 1 to 10. Each run included a burn-in phase of 200,000 iterations followed by 600,000 iterations. We performed 10 independent analyses for each K value. The number of genetic groups was inferred by the delta-K method applied to the log probabilities of data (Evanno et al. 2005). For *R. rattus*, fifteen individuals from four districts (Agla, N = 4; Ladji, N = 4, Saint Jean, N = 5 and Zongo, N = 2) of the city of Cotonou were also included in our analyses (Dossou et al. 2022).

Population genetic structure was also investigated through Discriminant Principal Component Analysis (DAPC) which can handle the absence of HW equilibrium (Jombart et al. 2010). Analyses were conducted using all individuals under the R software using the *adegenet* and *devtools* packages, for $K = 1$ to 10. The most likely number of genetic groups (K) was determined using the Bayesian Information Criterion (BIC; Lebarbier and Mary-Huard 2006), and the a priori criterion of a delta-BIC less than six (Kass and Raftery 1995).

Changes in population genetic structure through time

Genotype data for each species were then separated into three temporal datasets, regrouping sessions "before" (sessions 1 and 2), "during" (sessions 3 and 4) and "after" rodent control campaigns (sessions 5 and 6), respectively. Using STRUCTURE, we investigated whether genetic clustering in "before" and "after" datasets was similar to that observed in the whole dataset for each species. We then used NeEstimator v2 (Do et al. 2014) to estimate effective population size (N_E) for each site or group of sites corresponding to a genetic cluster in the industrial seaport before, during (when sufficient sampling) and after control campaigns. These analyses were conducted in both deratised and non-deratised sites, using the linkage disequilibrium (LD) method with a threshold minimum allele frequency of 0.02 (i.e. *Pcrit* parameter) (Waples and Do 2008). Sites or groups of sites with less than 10 genotyped individuals were excluded from the analyses. Signals for bottleneck effects were looked for using the Stepwise Mutation Model (SMM) on BOTTLENECK V1.2 (Piry et al. 1999) in each species-specific dataset.

Detection of potentially newly introduced individuals

For each species, individuals from three other countries (one individual/country) were genotyped and added to the APC dataset. For *Rattus rattus*, additional individuals were from Dakar (Senegal), Franceville (Gabon) and Niamey (Niger). The fifteen individuals from Cotonou core city were also included in the analyses. For *Rattus norvegicus*, the additional individuals were from Lyon (France), Bamako (Mali) and Ratchaburi (Thailand). For *Mus musculus*, extra individuals were from Dakar (Senegal), Lyon (France) and Niamey (Niger). Factorial correspondence analyses were performed using Genetix v 4.05 (Belkhir et al. 1996–2004) in order to evaluate if the additional individuals could be clearly identified as different from those trapped within the APC.

Results

Rodent trapping success

Across the six sampling sessions, a total of 803 rodents (367 *Rattus rattus*, 189 *Rattus norvegicus* and 247 *Mus musculus*) were captured in the nine APC sites out of a total of 6,569 trap nights (Table 1 and Fig. 1). *Rattus rattus* was mostly trapped in the artisanal seaport (sites APC1 and APC2) and, to a lesser extent, in the industrial seaport (especially in APC3, then in APC8 and APC9, and more marginally in other sites; Table 1). *Rattus norvegicus* and *M. musculus* were seldom in the artisanal seaport (APC1 and 2) as well as in some sites of the industrial seaport (APC 3 and 9). However, these two species were largely dominant in SOBEMAP warehouses (APC4, APC5, APC6 and APC7) and garage (ACP8; Table 1). Trap success was lower in sessions 3 and 4 (8.43% and 5.78%), which were both concomitant to two rodent control campaigns (Table 1). Detailed analyses of spatio-temporal variations of species-specific abundances as well as of species assemblages are available in Badou et al. (submitted).

Population genetic structure

A total of 366 *R. rattus*, 188 *R. norvegicus* and 244 M. *musculus* were successfully genotyped. Considering only sites with at least 11 individuals for a given species, our datasets included 353 individuals from six sites (APC1, APC2, APC3, APC6, APC8 and APC9) in *R. rattus*, 179 individuals from five sites (APC4, APC5, APC6, APC7 and APC8) in *R. norvegicus* and 244 individuals from five sites (APC4, APC5, APC6, APC7 and APC8) in *M. musculus*.

For *R. norvegicus*, linkage disequilibrium was significant for 9 out of the 600 tests performed (1.5%), and 5 of the significant values implicated the allele pair D1VKORC1-C and D1VKORC1-A, which were thus considered as linked. After having removed D1VKORC1-C locus, only 3 out of the 525 pairs of loci remained significantly linked (0.57%). The remaining loci were thus considered to be genetically independent, and were kept for subsequent analyses. For *R. rattus* and *M. musculus*, 21.13% (194 of 918) and 22.5% (153/680) of the LD tests were found significant (q-value < 0.05), respectively. Significant values concerned nearly all pairs of loci and all sites in both species. All loci were thus kept for subsequent analyses in these two species.

All loci were found at HW equilibrium for *R. rattus*, except D18R75. For *R. norvegicus*, all loci were found at HW equilibrium except D8Rat162. For *M. musculus,* seven loci (D2Mit456, D3Mit456, D4Mit241, D5Mit30, D6Mit373, D7Mit176 and D18Mit8) were not at HW equilibrium, exhibiting F_{IS} values ranging (between -0.09 and 0.56). Mean null allele frequencies estimated with FreeNA for loci that were not at HW equilibrium in the three species were sufficiently low not to affect significantly estimates of genetic diversity and differentiation (Chapuis and Estoup 2007; Chapuis et al. 2008), except for D5Mit30 in *M. musculus* (mean null allele frequency = 0.24; $F_{IS} = 0.56$), which was then excluded from the microsatellite panel.

Genetic analyses were thus conducted using eighteen microsatellites for *R. rattus*, fifteen microsatellites for *R. norvegicus* and sixteen microsatellites for *M. musculus*.

Genetic diversity estimates varied among sites for the three rodent species (Table 2). In *R. rattus*, mean values were

Table 1 Sampling of invasive rodents in nine sites of the Autonomous Port of Cotonou (APC) over six quaterly monitoring sessions. For each site and session, raw number of captures as well as an estimate of the trapping success (Ts = 100 *Nm / NTN, Nm being the total number of small mammals captured and NTN the total number of trap-nights) are provided. R. ra: *Rattus rattus*, R. no: *Rattus norvegicus*, M. mu: *Mus musculus*

Sites	APC1 (6.351°N, 2.434°E)							APC2 (6.351°N, 2.432°E)							APC3 (6.350°N, 2.426°E)						
sessions	S1	S2	S3	S4	S5	S6	**Total**	S1	S2	S3	S4	S5	S6	**Total**	S1	S2	S3	S4	S5	S6	**Total**
Ts	13.6	6.7	14.8	9.8	13.9	13.6	**11.9**	10.4	7.7	9.5	14.8	18.1	26.1	**14.1**	2.7	15.3	28.4	18.9	31.4	9.7	**17.6**
R. ra	16	14	27	21	30	27	**135**	8	8	8	12	17	19	**72**	1	10	20	11	16	6	**64**
R. no	0	0	1	0	0	0	**1**	0	0	0	0	0	0	**0**	1	0	1	0	6	1	**9**
M. mu	0	0	0	0	0	0	**0**	0	0	0	0	0	0	**0**	0	1	0	0	0	0	**1**
Total	**16**	**14**	**28**	**21**	**30**	**27**	**136**	**8**	**8**	**8**	**12**	**17**	**19**	**72**	**2**	**11**	**21**	**11**	**22**	**7**	**74**
Sites	APC4 (6.349°N, 2.429°E)							APC5 (6.349°N, 2.428°E)							APC6 (6.349°N, 2.427°E)						
sessions	S1	S2	S3	S4	S5	S6	**Total**	S1	S2	S3	S4	S5	S6	**Total**	S1	S2	S3	S4	S5	S6	**Total**
Ts	5.9	14.1	3.4	4.9	8.5	13.9	**8.4**	20.9	13.5	4.9	4.2	5.7	36.5	**13.6**	17.2	17.7	10.6	6.9	36.1	35.5	**19.1**
R. ra	0	0	0	0	3	2	**5**	0	0	0	0	1	3	**4**	0	0	0	2	4	5	**11**
R. no	5	5	2	7	10	9	**38**	4	9	2	4	4	20	**43**	8	17	6	5	10	9	**55**
M. mu	3	10	1	0	0	5	**19**	23	7	3	2	3	15	**53**	13	10	5	5	25	19	**77**
Total	**8**	**15**	**3**	**7**	**13**	**16**	**62**	**27**	**16**	**5**	**6**	**8**	**38**	**100**	**21**	**27**	**11**	**12**	**39**	**33**	**143**
Sites	APC7 (6.349°N, 2.426°E)							APC8 (6.349°N, 2.425°E)							APC9 (6.350°N, 2.423°E)						
sessions	S1	S2	S3	S4	S5	S6	**Total**	S1	S2	S3	S4	S5	S6	**Total**	S1	S2	S3	S4	S5	S6	**Total**
Ts	15.8	16.5	3.9	3.3	19.2	23.5	**12.5**	13.4	11.8	1.1	0.9	14.2	15.6	**8.1**	7.3	26.9	4.2	3.5	9.8	2.5	**8.24**
R. ra	0	0	0	0	1	3	**4**	7	15	0	0	12	4	**38**	3	17	3	4	5	2	**34**
R. no	3	10	2	3	5	5	**28**	1	0	1	1	5	7	**15**	0	0	0	0	0	0	**0**
M.mu	13	12	2	1	16	16	**60**	9	3	1	2	10	10	**35**	1	1	0	0	0	0	**2**
Total	**19**	**23**	**4**	**5**	**23**	**24**	**92**	**17**	**18**	**2**	**3**	**27**	**21**	**88**	**4**	**18**	**3**	**4**	**5**	**2**	**36**

Table 2 Polymorphism descriptors at 18 microsatellites loci for *Rattus rattus*, 15 microsatellites for *Rattus norvegicus* and 16 microsatellites for *Mus musculus*. The number of individuals analysed per population (*N*), Loiselle coefficient (ρ), the allelic richness (a_r), expected heterozygosities (H_E) and the inbreeding coefficient (*Fis*) were reported

Sites	APC1	APC2	APC3	APC4	APC5	APC6	APC7	APC8	APC9	Mean
Rattus rattus										
N	135	72	64	5	4	11	4	38	34	367
ρ	0.07	0.14	0.06	-	-	0.007	-	0.06	0.06	-
a_r	3.78	4.2	4.95	-	-	5.33	-	4.86	4.56	4.62
H_e	0.50	0.58	0.64	-	-	0.64	-	0.64	0.60	0.60
F_{IS}	0.07	0.07	0.03	-	-	0.04	-	0.01	0.08	0.05
Rattus norvegicus										
N	1	0	9	38	43	55	28	15	0	189
ρ	-	-	-	0.09	0.02	0.02	0.04	0.03	-	-
a_r	-	-	-	3.92	4.26	3.98	4.15	3.8	-	4.02
H_e	-	-	-	0.57	0.61	0.56	0.59	0.58	-	0.58
F_{IS}	-	-	-	0.07	0.03	0.06	-0.06	0.09	-	0.04
Mus musculus										
N	0	0	1	19	53	77	60	35	2	247
ρ	-	-	-	0.06	0.08	0.03	0.03	0.1	-	-
a_r	-	-	-	4.25	4.72	5.50	5.43	4.85	-	4.95
H_e	-	-	-	0.60	0.59	0.68	0.70	0.62	-	0.64
F_{IS}	-	-	-	0.01	-0.002	0.06	0.05	0.09	-	0.04

of 4.62 ± 1.6 for allelic richness, of 0.60 ± 0.2 for expected heterozygosity and of 0.05 ± 0.02 for F_{IS}. In *R. norvegicus*, mean values of genetic diversity estimates were quite similar to those of the former species, being of 4.02 ± 1.1 for allelic richness, of 0.58 ± 0.16 for expected heterozygosity, and of 0.04 ± 0.01 for F_{IS}. In *M. musculus*, mean values were of 4.95 ± 1.2 for allelic richness, of 0.64 ± 0.14 for expected heterozygosity, and of 0.04 ± 0.02 for F_{IS}.

In all three species, genotypic differentiation was significant between sampled sites ($P < 0.0002$). In *R. rattus*, mean **F_{ST} value was of 0.06 (95% CI = [0.098; 0.133])**. Pairwise F_{ST} estimates ranged from 0.02 (between APC8 and APC9 in the industrial seaport) to 0.16 (between APC1 and APC2 in the artisanal seaport) (Table 3A). Considering only the industrial seaport (which is the area where both other rodent species were found), mean F_{ST} value was of 0.02 (95% CI = [0.018; 0.04]). In *R. norvegicus*, **mean F_{ST} value was of 0.06 (95% CI = [0.055; 0.074])**. Pairwise F_{ST} estimates ranged from 0.02 (between APC6 and APC7) to 0.11 (between APC4 and APC7; between APC4 and APC8) (Table 3B). In *M. musculus*, **mean F_{ST} value was of 0.09 (95% CI = [0.075; 0.1])**. Pairwise F_{ST} estimates ranged from 0.04 (APC6 and APC7) to 0.13 (APC5 and APC8) (Table 3C).

Spatial patterns

Mantel tests performed between individuals revealed significant IBD in *R. rattus* (slope = 0.039, intercept = -0.250, $P < 0.0001$); IBD remained significant when considering only individuals from the industrial seaport (slope = 0.011, intercept = -0.06, $P < 0.0001$). Significant IBD were also detected in *R. norvegicus* (slope = 0.027, intercept = -0.159, $P < 0.0001$) and in *M. musculus* (slope = 0.033, intercept = -0.192, $P < 0.0001$).

In *R. rattus*, STRUCTURE clearly identified three genetic groups (Fig. 2A): the highest delta-*K* value was for $K = 3$ (delta-$K = 1{,}405.69$), and was considerably higher than for $K = 4$ (delta-$K = 16.96$). In the DAPC analysis, two genetic groups were identified: the highest delta-BIC value was 33.21 for $K = 2$. However, the genetic groups observed at $K = 3$ were very similar to those obtained with STRUCTURE, with APC1 and APC2 being distinct genetic groups, while a third group included the individuals from the industrial seaport (APC3-9). When STRUCTURE is performed with the individuals from the core city of Cotonou, they also identified three genetic groups, with individuals from the city clustering with those from the industrial seaport.

In *R. norvegicus*, STRUCTURE clearly identified two genetic groups (Fig. 2B): the highest delta-*K* was for $K = 2$ (delta-$K = 681.08$), and was considerably higher than for $K = 3$ (delta-$K = 31.29$). The DAPC highest delta-BIC value (9.06) was obtained for $K = 2$, and patterns were very similar to those obtained with STRUCTURE: a first cluster gathered the individuals from the APC3, APC6, APC7 and APC8 sites, while the individuals from APC4 were assigned to a second cluster. The individuals from APC5 had a variable mixed inferred ancestry.

In *M. musculus*, STRUCTURE clearly identified three genetic groups (Fig. 2C): the highest delta-*K* value was for $K = 3$ (delta-$K = 236.93$), and was considerably higher than for $K = 4$ (delta-$K = 168.85$). In the DAPC analysis,

Table 3 Pairwise F_{ST} values among sampled sites calculated for all loci in each species, using 18 microsatellites for *Rattus rattus* (A), 15 microsatellites for *Rattus norvegicus* (B), and 16 microsatellites for *Mus musculus* (C)

A) Sites	APC1	APC2	APC3	APC4	APC5	APC6	APC7	APC8
APC2	0.16							
APC3	0.13	0.13						
APC4	-	-	-					
APC5	-	-	-	-				
APC6	0.09	0.09	0.02	-	-			
APC7	-	-	-	-	-	-		
APC8	0.13	0.12	0.03	-	-	0.01	-	
APC9	0.13	0.12	0.04	-	-	0.02	-	0.02
B) Sites	APC1	APC2	APC3	APC4	APC5	APC6	APC7	APC8
APC2	-							
APC3	-	-						
APC4	-	-	-					
APC5	-	-	-	0.06				
APC6	-	-	-	0.10	0.04			
APC7	-	-	-	0.11	0.05	0.02		
APC8	-	-	-	0.11	0.06	0.05	0.05	
APC9	-	-	-	-	-	-	-	-
C) Sites	APC1	APC2	APC3	APC4	APC5	APC6	APC7	APC8
APC2	-							
APC3	-	-						
APC4	-	-	-					
APC5	-	-	-	0.09				
APC6	-	-	-	0.09	0.09			
APC7	-	-	-	0.08	0.10	0.04		
APC8	-	-	-	0.11	0.13	0.10	0.08	
APC9	-	-	-	-	-	-	-	-

the highest delta-BIC value (12.01) was obtained for $K=2$, while the delta-BIC value for $K=3$ was 8.68. However, patterns for $K=3$ were very similar to those obtained with STRUCTURE, thus pointing towards three genetic clusters: individuals from APC4 and APC5 were mainly assigned to a first genetic pool; individuals from APC6 and APC7 formed a second group; and individuals from APC8 constituted a third group on their own.

Changes through time

Effective population sizes (N_E) were estimated for sites or groups of sites before, during and after rodent control campaigns in the industrial seaport for all three species, as well as for sites of the artisanal seaport at the same period of time for *R. rattus*.

In *R. rattus*, N_E increased strongly from 11.3 (sessions 1 and 2, before control) to 34.2 (session 5 and 6, after control) in the group formed by APC4-8 sites where deratization occurred. Only two individuals were captured in these sites during sessions 3 and 4 which fell during control operations. N_E values increased slightly in the same period for sites that were non-deratized (APC1: from 11.6 to 19.5, and ACP2: from 5.8 to 12.7).

Effective population size also rapidly increased after deratting campaigns in some genetic clusters for both *R. norvegicus* and *M. musculus*. Indeed, in the *R. norvegicus* genetic cluster from APC4-5 sites, N_E increased from 19.5 (sessions 1 and 2) to 35.1 (sessions 5 and 6). In the same manner, in the *M. musculus* genetic cluster from APC6-7, effective population size increased from 21.2 (sessions 1 and 2) to 35.6 (sessions 5 and 6). In contrast, N_E remained globally stable in APC6-8 (43.5 to 43) in *R. norvegicus* and in APC4-5 (8.8 to 7.4) in *M. musculus*. However, in APC8 N_E has decreased from 24.7 to 8.6.

Significant signals for bottleneck effects were detected in nearly all sites for *R. rattus* ($p<0.01$), except in APC2 ($p=0.06$). In *R. norvegicus* a significant signal was found in only one site (APC6: $p=0.02$). In *M. musculus*, significant signals were found in APC5 ($p=0.03$), APC6

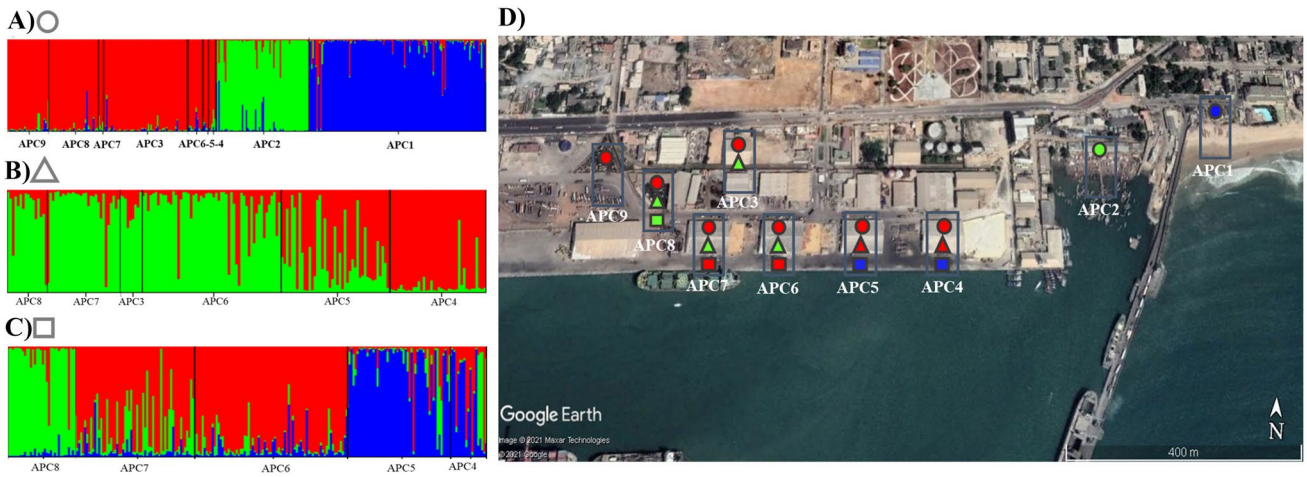

Fig. 2 Spatial genetic structure in the Autonomous Port of Cotonou using STRUCTURE. **A** Results for *R. rattus* for $K=3$; **B** *R. norvegicus* for $K=2$; **C** *M. musculus* for $K=3$. Each vertical line represents an individual and barplots indicate individual ancestry estimates. **D** Report on the APC map of species-specific genetic clusters retrieved by STRUCTURE analyses. Rounds, triangles, and squares represent *R. rattus*, *R. norvegicus,* and *M. musculus*, respectively. Colors on the STRUCTURE diagram (**A**, **B** and **C**) and on the map (**D**) are identical and correspond to the different genetic clusters obtained in each species

($p=0.007$) and APC8 ($p=0.02$), but not in other sites (APC4 and APC7).

Detecting potential new migrants

In *Rattus rattus*, individuals sampled in APC were grouped with those sampled in the cities of Cotonou and Niamey, while this cluster was clearly distinct from both Franceville (Gabon) and Dakar (Senegal) individuals (Fig. 3a). In *R. norvegicus*, individuals sampled in APC formed a well-defined group from which the three individuals from Mali, France, and Thailand were very distinctly separated (Fig. 3b). In the same manner, *M. musculus* individuals from APC formed a group that was also clearly differentiated from mice from France, Dakar and Niamey, although the two individuals from Niamey did not group together (Fig. 3c).

Discussion

Human movements and migrations have played a leading role in the global spread of domestic rodents (Roberts 1991; Kovács 2012; Puckett et al. 2020). In particular, commercial exchanges (imports and/or exports) through maritime trade largely contribute to the long-distance transport and introduction of invasive rodent species in seaports around the world (Veale et al. 2021), from which they colonise entire continents. Among these species, *R. rattus*, *R. norvegicus* and *M. musculus* are currently spreading in Africa (Konečný et al. 2013; Dalecky et al. 2015; Berthier et al. 2016; Hima et al. 2019). Here, we investigated and compared for the first time the population genetic structures of these three species that coexist in an international seaport.

Rodent sampling in 9 different sites of the port first indicated spatial segregation of the species: *R. rattus* was found in much higher numbers in the artisanal seaport, where the two other species did not occur, or occur only on very rare occasions. *Rattus norvegicus* and *M. musculus* co-occurred in the industrial seaport and dominated largely the trapping results in the warehouses located along the unloading docks (APC4-7). The spatial segregation observed between these three species in APC could be due to habitat preferences, interspecific competition and/or historical factors that are beyond the scope of the present paper, but discussed in Badou et al. (submitted).

Population genetic studies using microsatellite markers of commensal rodents in urban contexts were often conducted at larger spatial scales than that considered in our study. For instance, the rare studies conducted on *R. rattus* all focused on West African cities with sampling covering several different districts (Niamey, Niger: Berthier et al. 2016; Franceville, Gabon: Mangombi et al. 2016; Cotonou, Benin: Badou et al. 2021). Urban *R. norvegicus* genetics was investigated in a few cities in North and South America (i.e., Baltimore, USA: Gardner-Santana et al. 2009; Salvador, Brazil: Kajdacsi et al. 2013; New York City, USA: Combs et al. 2018a; Salvador, Brazil; New Orleans, USA; Vancouver, Canada; and New York City, USA: Combs et al. 2018b). The only study on urban *M. musculus* we are aware of was conducted in Dakar, Senegal (Stragier et al. 2022), and again was conducted at the scale of the city. To our knowledge, the only genetic study available on rodent populations from a seaport area and its surroundings was conducted in Paranagua, Brazil on 71 *R.*

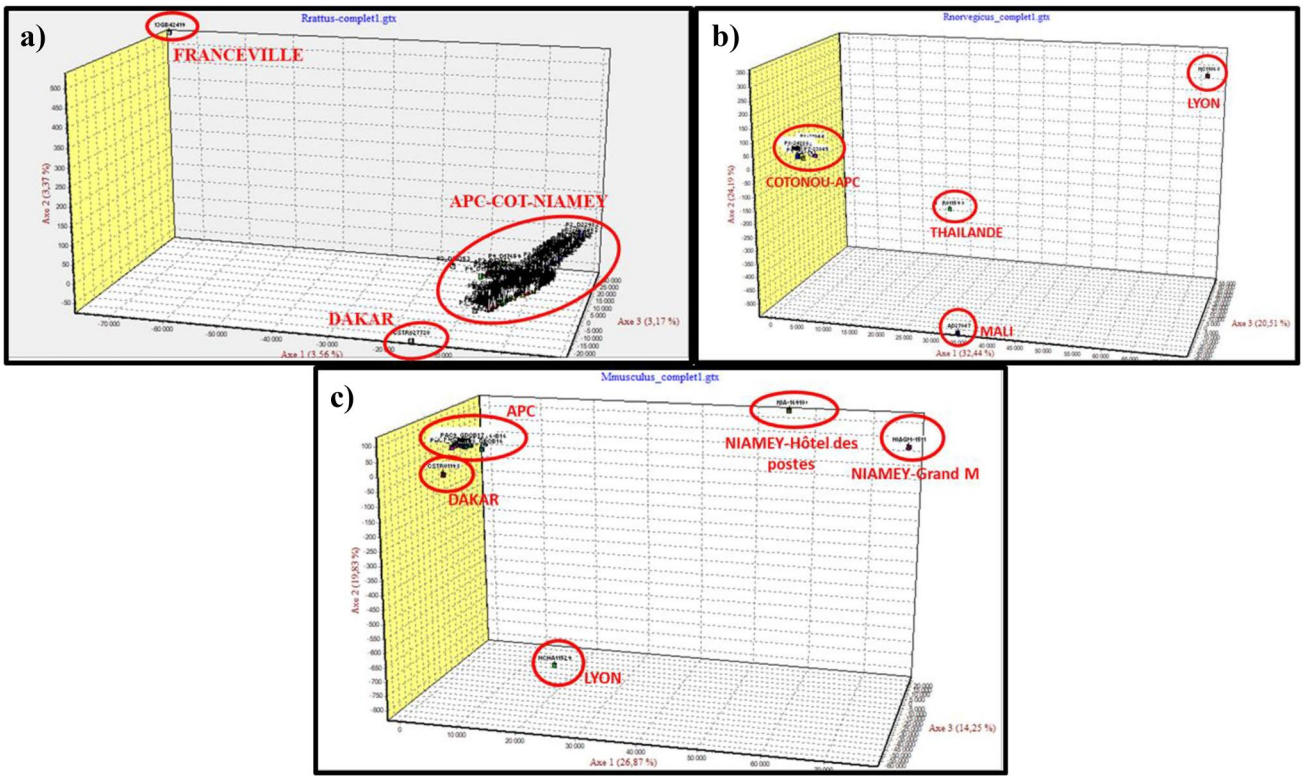

Fig. 3 FCA analyses conducted on microsatellite data for **a** *R. rattus* from the APC and the cities of Cotonou, Franceville (Gabon), Dakar (Senegal) and Niamey (Niger); **b** *R. norvegicus* from APC and the city of Cotonou, Lyon (France), Mali, and Thailand; and **c** *M. musculus* from APC, Dakar, Lyon and Niamey. Only the three first FCA axes are provided here

norvegicus using 11 microsatellite loci (Gatto-Almeida et al. 2022). Differences in spatial scales and genetic markers used in all these studies make meaningful comparisons difficult. However, it is noteworthy that genetic diversity estimates observed for all three species within the APC were of the same order of magnitude as those obtained in other studies. This suggests similar introduction histories throughout the world (Gardner-Santana et al. 2009; Desvars-Larrive et al. 2019; Gatto-Almeida et al. 2022).

Our results suggest that new introductions of rodents are rare in the APC. Indeed, no outlier individual was detected by the FCA analysis in rodents sampled within the APC during our 3 year-long monitoring study. Also, allele numbers and allelic richness in *R. rattus* from Cotonou ($a_r = 4.41$; Badou et al. 2021) and in the APC ($a_r = 4.62$; this study) are quite similar, whereas one would expect these estimates to be higher in the seaport if individuals had been regularly (and, especially, recently) disembarked off moored ships and then persisted within the local black rat population. We were surprised by such patterns since the absence of signal reflecting new introduction events suggest that rats and mice do not descend frequently from the boats. Yet, considering the quasi-global distribution of these three species in the world, it is unlikely that this does not occur on a rather frequent basis. Moreover, we observed that anti-rat discs along mooring cables, though mandatory by IHR, were poorly and/or badly used by ships docking at APC: out of 13 vessels and 119 cables inspected, only 79 discs (69%) were indeed installed, many of which being badly installed; in total, no ship was perfectly protected with all the cables with well-laid discs (personal observations). Finally, the recent detection of Seoul virus in *R. norvegicus* captured in the APC in 2018 (Castel et al. 2021) suggested that the introduction of some migrant rats sometimes occurs. Those individuals could however have just transmitted their pathogens before dying, being unable to establish themselves and reproduce with resident rodents. Indeed, the non-detection of new introductions in genetic data may be explained by the presence of small mammal communities already on-site, which could render the settlement of newly immigrating individuals or species difficult. This hypothesis is supported by eco-ethological studies on commensal rodents, showing that introduced individuals may be rapidly identified as intruders by the residents, and subsequently rejected (e.g., in *R. rattus*: Ewer 1971; Granjon and Cheylan 1989; Barnett 1958; in *R. norvegicus* and *M. musculus* Berdoy and Drickamer 2007). If this is indeed the case, it is important to note that deratisation campaigns leading to the

temporarily extirpation of the local rodent populations may open the gate to the successful settlement of newly introduced rodents (and associated pathogens). Although data are lacking to conclude definitely, it may be an additional argument in favour of a rigorous prevention strategy against rodent introduction through ships, rather than rodent control only.

Within APC, population genetic analyses showed very marked spatial patterns for the three species. This of course has important consequences in terms of rodent control since the genetic clusters observed should serve as a basis to guide deratization campaigns through the adequate definition of eradication units (Richardson et al. 2019). In *R. norvegicus* and *M. musculus*, two and three genetic clusters were observed within the industrial seaport, respectively. In *R. rattus*, two different groups were observed within the artisanal seaport, but only one within the industrial seaport. This pattern for the last species strongly contrasts with that observed using the same microsatellite markers at the whole Cotonou city scale, where only two genetic clusters associated with lower mean F_{ST} (0.107) were detected in black rats (Badou et al. 2021).

Genetic structure may reflect genetic isolation by distance, which is significant in all species. Indeed, invasive pests that occupy a broad range of urban conditions (primarily constrained by access to water, food/rubbish and nesting/burrowing sites) might be expected to exhibit spatial genetic patterns driven only by isolation by distance, thus reflecting spatial limitation of dispersal (Combs et al. 2018b). As such, the gradual pattern of differentiation observed between both sides of the industrial seaport in *R. norvegicus* (Fig. 2B) could suggest IBD at the scale of the port. IBD may also result from social behaviour of rodent species. Indeed, *R. norvegicus* (Combs et al. 2018a, b; Gardner-Santana et al. 2009) and *M. musculus* (Lippens et al. 2017) are known for strong social structure and very limited active dispersal. In *M. musculus* in particular, home ranges of a few tens of metres in commensal habitats (Pocock et al. 2005), and effective dispersal of only few hundred meters (Lippens et al. 2017) may explain the high F_{ST} values observed in this species (within the industrial seaport: mean $F_{ST}=0.09$ for *M. musculus*; 0.06 for *R. norvegicus*; 0.02 for *R. rattus*). High genetic structure levels such as those observed within the APC in *R. rattus* ($F_{ST}>0.16$) and *M. musculus* ($F_{ST}>0.13$) between genetic groups, may also be explained by other factors. Indeed, they may reflect the presence of physical barriers to individual dispersal. Such barriers within the urban landscape have already been evidenced for Norway rats, such as major waterways in Baltimore (Gardner-Santana et al. 2009), Salvador (Kajdacsi et al. 2013) and New Orleans (Combs et al. 2018b), roadways in Salvador and Vancouver, or resource deserts in New York City (Combs et al. 2018b). Within the APC, however, we could not identify obvious physical barriers that could explain the observed marked genetic partitions. Finally, genetic structure may result from variations in effective population size, i.e. demographic barrier (Piry et al. 2004; Berthier et al. 2016; Richardson et al. 2017; Stragier et al. 2019). Such a demographic process may be especially relevant for commensal rodents whose natural dispersal distances (i.e. not human-mediated) are generally short ranged (< 1 km) and mainly prompted by the lack of feeding and harborage sites (Byers et al. 2019; Pocock et al. 2005). Control measures could also be another factor generating important gaps in densities and thus genetic discontinuities, such as for instance between the deratised industrial port (which may have been recolonized from the city) and the non-deratised artisanal port in *R. rattus*.

Some genetic signatures may suggest an effect of control measures on population structures. For instance, high LD values and significant tests for bottleneck signals were observed in both *R. rattus* and *M. musculus*. Increased linkage disequilibrium can indeed reflect bottleneck events (Slatkin 2008). However, similar results (i.e., LD disequilibrium and significant tests for bottleneck) were also observed for *R. rattus* in the non-deratized APC1 site, thus suggesting that other processes are at work. Also, high LD values may reflect the recent mixing of individuals from several subpopulations that have different allele frequencies (Slatkin 2008), which may also result from rodent control events. Rodent reinfestation after control operations may occur either by reproduction of non-poisoned or poison-resistant individuals, or by immigration of new individuals from neighbouring sites (Richardson et al. 2019).

Whatever the invasive rodent species considered here, our FCA analyses demonstrated that microsatellite markers makes it possible to detect recently introduced, hence expectedly genetically distant individuals. Indeed, for all three species, all individuals collected within the Autonomous Port of Cotonou over the three years of our study appeared much more similar to each other than to "allochthonous" ones. The only exception was APC and some Niamey black rat, which cluster together; but this supports the hypothesis that Niamey black rat originated from Benin seaport (Hima et al. 2019). These results thus highlight the interest of our panel of microsatellite loci as a valuable tool to trace back the geographic origin of house mice potentially introduced at APC. This should be useful to help seaport authorities to survey new rodent introductions in their facilities, thus allowing them to operationalize the IHR in terms of surveillance of maritime trade-associated rodent reservoirs introduction at entry points (World Health Organization, 2006). In the particular case of APC, this seems particularly realistic because of the recent implementation of a lab following an academic / seaport partnership initiative, and essentially dedicated to invasive terrestrial and marine species monitoring and management within Cotonou seaport ("Portuary Platform

for Environmental Surveillance"; see https://view.genial.ly/6059bb3f64e78f0d9cb32a7f).

With the high increasing rate of invasions (Pimentel et al. 2005; Seebens et al. 2017), there is a serious need for the development of methods for invasive species control (Brockerhoff et al. 2010; Glen et al. 2013; Thresher et al. 2014). Our trapping data suggested that populations of all three species rapidly recovered in terms of number of individuals (i.e., six and twelve months after control). In *R. rattus*, population genetic analyses integrating fifteen individuals from the core city showed that they grouped within the same genetic cluster than those from the industrial seaport. This pattern confirms the limited effect of the control measures deployed in the industrial seaport, at least on black rats which, otherwise, should result in higher genetic differentiation of the local populations (Gatto-Almeida et al. 2022). This adds to our previous results here above that poisoning campaigns alone (and as they stand) are insufficient to reach long-term decrease of invasive rodent abundances within the seaport area, and that accompanying measures are required. The latter could consist of environmental modifications towards less rodent-favoring habitats (e.g., rearrangement and physical protection of food stocks inside warehouses, rat-proofing of buildings, fueling of cracks and holes, setup of rat-proof grids along sewer networks, favoring of cats within the seaport, etc.). This would also reduce the dependency on toxicons such as anticoagulant rodenticides that may be dangerous for non-target species as well as to humans (Salas et al. 2000; Hendges et al. 2019; Kasiotis et al. 2021), and favor resistance evolution among target rodents (Hodroge et al. 2011; Buckle 2013). Such more suitable and long-term adapted measures have already been suggested in other settings (e.g., sewer networks: Channon et al. 2006; United States: Witmer and Shiels 2017; Brazilian slum: Hacker et al. 2016; Richardson et al. 2019). Unfortunately, we are not aware of such environmentally-based rodent management strategies in seaport habitats while their implementation in this type of close areas sounds quite feasible. Our study highlights the importance of monitoring of what descends from the ships to detect the eventual introduction of new invasive species (i.e. *R. tanezumi*; Bastos et al. 2011; Kosoy et al. 2015; Ringani et al. 2022) and the pathogens they could host. On the other hand, to monitor those that are carried on trucks to avoid propagations beyond the APC or even in the hinterland countries.

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Data availability All datasets used for this study are entirely deposited in the Small Mammal Collection at the IRD/CBGP (https://doi.org/10.15454/WWNUPO) as well as at URIB/LARBA/EPAC. The datasets are available upon request.

Declarations

Ethical approval Rodents handling followed the procedures recommended by the guidelines of the American Society of Mammalogists (Sikes and Gannon 2011) and Mills et al. (1995).

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflicts of interests The authors have no conflict of interest to declare.

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References

Aplin KP, Suzuki H, Chinen AA, Chesser RT, Ten Have J, Donnellan SC, Catzeflis F (2011) Multiple geographic origins of commensalism and complex dispersal history of black rats. PloS One 6:e26357. https://doi.org/10.1371/journal.pone.0026357

Badou S, Gauthier P, Houéménou G, Loiseau A, Dossou J, Etougbétché J, Houéménou H, Agbangla C, Brouat C, Dobigny G (2021) Population genetic structure of blacks rats in an urban environment: a case study in Cotonou, Benin. Hystrix Ital J Mammal. ISSN 1825–5272. https://doi.org/10.4404/hystrix-00417-2021

Barnett SA (1958) An analysis of social behaviour in wild rats. In: Proceedings of the Zoological Society of London, vol 130, no 1. Blackwell Publishing Ltd., Oxford, UK, pp 107–152. https://doi.org/10.1111/j.1096-3642.1958.tb00565.x

Bastos AD, Nair D, Taylor PJ, Brettschneider H, Kirsten F, Mostert E, Chimimba CT (2011) Genetic monitoring detects an overlooked cryptic species and reveals the diversity and distribution of three invasive Rattus congeners in South Africa. BMC Genet 12:26. https://doi.org/10.1186/1471-2156-12

Belkhir K, Borsa P, Chikhi L, Raufaste N, Bonhomme F (1996-2004) GENETIX 4.05, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions,

CNRS UMR 5000, Université de Montpellier II, Montpellier (France). http://www.genetix.univ-montp2.fr/genetix/genetix.htm
Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J Roy Stat Soc Ser B (Methodol) 57(1):289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x
Berdoy M, Drickamer LC (2007) Comparative social organization and life history of Rattus and Mus. Rodent Soc Ecol Evol Perspect 380–392
Berthier K, Garba M, Leblois R, Navascués M, Tatard C, Gauthier P, Dobigny G (2016) Black rat invasion of inland Sahel: insights from interviews and population genetics in south-western Niger. Biol J Lin Soc 119(4):748–765. https://doi.org/10.1111/bij.12836
Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26(7):333–339. https://doi.org/10.1016/j.tree.2011.03.023
Bona F (2020) Earliest evidence of *Mus musculus* ssp. In Western Europe during the Late Neolithic (Tosina, Mantova, Northern Italy): new insights on the house mice migratory waves. Hystrix 31(2):1–6. https://doi.org/10.4404/hystrix-00335-2020
Brockerhoff EG, Liebhold AM, Richardson B, Suckling DM (2010) Eradication of invasive forest insects: concepts, methods, costs and benefits. N Z J For Sci 40(suppl.):S117–S135
Buckle A (2013) Anticoagulant resistance in the United Kingdom and a new guideline for the management of resistant infestations of Norway rats (*Rattus norvegicus* Berk.). Pest Manag Sci 69(3):334–341. https://doi.org/10.1002/ps.3309
Byers KA, Lee MJ, Patrick DM, Himsworth CG (2019) Rats about town: a systematic review of rat movement in urban ecosystems. Front Ecol Evol 7:13. https://doi.org/10.3389/fevo.2019.00013
Capizzi D, Bertolino S, Mortelliti A (2014) Rating the rat: global patterns and research priorities in impacts and management of rodent pests. Mammals Rev 44:148–162. https://doi.org/10.1111/mam.12019
Castel G, Kant R, Badou S, Etougbétché J, Dossou HJ, Gauthier P, Dobigny G (2021) Genetic characterization of Seoul virus in the seaport of Cotonou. Benin Emer Infect Dis 27(10):2704–2706. https://doi.org/10.3201/eid2710.210268
Channon D, Channon E, Roberts T, Haines R (2006) Hotspots: are some areas of sewer network prone to re-infestation by rats (R*attus norvegicus)* year after year? Epidemiol Infect 134(1):41–48. https://doi.org/10.1017/S0950268805004607
Chapuis MP, Estoup A (2007) Microsatellite null alleles and estimation of population differentiation. Mol Biol Evol 24:621–631. https://doi.org/10.1093/molbev/msl191
Chapuis MP, Lecoq M, Michalakis Y, Loiseau A, Sword GA, Piry S, Estoup A (2008) Do outbreaks affect genetic population structure? A worldwide survey in *Locusta migratoria*, a pest plagued by microsatellite null alleles. Mol Ecol 17(16):3640–3653. https://doi.org/10.1111/j.1365-294X.2008.03869.x
Combs M, Puckett EE, Richardson J, Mims D, Munshi-South J (2018a) Spatial population genomics of the brown rat (*Rattus norvegicus*) in New York City. Mol Ecol 27(1):83–98. https://doi.org/10.1111/mec.14437
Combs M, Byers KA, Ghersi BM, Blum MJ, Caccone A, Costa F, Munshi-South J (2018b) Urban rat races: spatial population genomics of brown rats (Rattus norvegicus) compared across multiple cities. Proc R Soc B Biol Sci 285:20180245. https://doi.org/10.1098/rspb.2018.0245
Colombe S, Jancloes M, Rivière AE, Bertherat E (2019) Weekly Epidemiological Record, 2019, vol. 94, 17 [full issue]. Wkly Epidemiol Rec Relevé Épidémiol Hebd 94(17):197–212, 26 April 2019, 94th Year / 26 Avril 2019, 94e Année. http://www.who.int/wer
Dalecky A, Bâ K, Piry S, Lippens C, Diagne CA, Kane M, Sow A, Diallo M, Niang Y, Konecny A, Sarr N, Artige E, Charbonnel N, Granjon L, Duplantier JM, Brouat C (2015) Range expansion of the invasive house mouse Mus musculus domesticus in Senegal, West Africa: a synthesis of trapping data over three decades, 1983–2014. Mammal Rev 45(3):176–190. https://doi.org/10.1111/mam.12043
Desvars-Larrive A, Pascal M, Gasqui P, Cosson JF, Benoit E, Lattard V, Vourc'h G (2017) Population genetics, community of parasites, and resistance to rodenticides in an urban brown rat (*Rattus norvegicus*) population. PloS One 12(9):e0184015. https://doi.org/10.1371/journal.pone.0184015
Desvars-Larrive A, Hammed A, Hodroge A, Berny P, Benoît E, Lattard V, Cosson JF (2019) Population genetics and genotyping as tools for planning rat management programmes. J Pest Sci 92(2):691–705. https://doi.org/10.1007/s10340-018-1043-4
Diagne C, Catford JA, Essl F, Nuñez MA, Courchamp F (2020a) What are the economic costs of biological invasions? A complex topic requiring international and interdisciplinary expertise. NeoBiota 63:25. https://doi.org/10.3897/neobiota.63.55260
Diagne C, Leroy B, Gozlan RE, Vaissière AC, Assailly C, Nuninger L, Courchamp F (2020b) InvaCost, a public database of the economic costs of biological invasions worldwide. Scientific Data 7(1):1–12. https://doi.org/10.1038/s41597-020-00586-z
Diagne C, Leroy B, Vaissière AC, Gozlan RE, Roiz D, Jarić I, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. Nature 592(7855):571–576. https://doi.org/10.1038/s41586-021-03405-6
Do C, Waples RS, Peel D, Macbeth GM, Tillett BJ, Ovenden JR (2014) NeEstimator v2: re-implementation of software for the estimation of contemporary effective population size (Ne) from genetic data. Mol Ecol Resour 14:209–214. https://doi.org/10.1111/1755-0998.12157
Doherty TS, Glen AS, Nimmo DG, Ritchie EG, Dickman CR (2016) Invasive predators and global biodiversity loss. Proc Natl Acad Sci 113(40):11261–11265. https://doi.org/10.1073/pnas.1602480113
Dossou HJ, Adjovi N, Houéménou G, Bagan T, Mensah GA, Dobigny G (2020) Invasive rodents and damages to food stocks: a study in the Autonomous Harbor of Cotonou, Benin. Biotechnol Agron Soc Environ 24(1):28–36. https://doi.org/10.25518/1780-4507.18326
Dossou HJ, Le Guyader M, Gauthier P, Badou S, Etougbétché J, Houemenou G, Djelouadji Z, Dobigny G (2022) Fine-scale prevalence and genetic diversity of urban small mammal-borne pathogenic Leptospira in Africa: A spatiotemporal survey within Cotonou. Zoonoses and Public Health, Benin. https://doi.org/10.1111/zph.12953
Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol Ecol 14(8):2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x
Ewer RF (1971) The biology and behaviour of a free-living population of black rats (*Rattus rattus)*. Anim Behav Monogr 4(3):127–174
Gallardo B, Aldridge DC (2013) The 'dirty dozen': socio-economic factors amplify the invasion potential of 12 high-risk aquatic invasive species in Great Britain and Ireland. J Appl Ecol 50:757–766. https://doi.org/10.1111/1365-2664.12079
Gardner-Santana LC, Norris DE, Fornadel CM, Hinson ER, Klein SL, Glass GE (2009) Commensal ecology, urban landscapes, and their influence on the genetic characteristics of city-dwelling Norway rats (R*attus norvegicus)*. Mol Ecol 18(13):2766–2778. https://doi.org/10.1111/j.1365-294X.2009.04232.x
Garba M, Dalecky A, Kadaoure I, Kane M, Hima K, Veran S, Dobigny G (2014a) Spatial segregation between invasive and native commensal rodents in an urban environment: a case study in Niamey, Niger. PLoS One 9(11):e110666. https://doi.org/10.1111/1365-2664.12079
Garba M, Kane M, Gagare S, Kadaoure I, Sidikou R, Rossi JP (2014b) Dobigny G (2014b) Local perception of rodent-associated problems in Sahelian urban areas: a survey in

Niamey, Niger. Urban Ecosyst 17:573–584. https://doi.org/10.1007/s11252-013-0336-x

Gatto-Almeida F, de Araújo SA, Degrandi TM, Tiepolo LM, Pichlmueller F, Hass I (2022) Assessment of dispersal and population structure of Norway rats (Rattus norvegicus) in a seaport setting. Urban Ecosyst 25(2):535–544. https://doi.org/10.1007/s11252-021-01171-x

Glen AS, Atkinson R, Campbell KJ, Hagen E, Holmes ND, Keitt BS, Torres H (2013) Eradicating multiple invasive species on inhabited islands: the next big step in island restoration? Biol Invasions 15(12):2589–2603. https://doi.org/10.1007/s10530-013-0495-y

Goudet J (2003) FSTAT (version 2.9. 4), a program (for Windows 95 and above) to estimate and test population genetics parameters. Dept Ecol Evol, Lausanne University, Switzerland, p 53

Granjon L, Cheylan G (1989) Le sort de rats noirs (Rattus rattus) introduits sur une île, révélé par radio-tracking. CR Acad Sci Paris 309:571–575

Hacker KP, Minter A, Begon M, Diggle P, Serrano S, Reis MG, Costa F (2016) A comparative assessment of track plates to quantify fine scale variations in the relative abundance of Norway rats in urban slums. Urban Ecosyst 19(2):561–575. https://doi.org/10.1007/s11252-015-0519-8

Harper GA, Bunbury N (2015) Invasive rats on tropical islands: their population biology and impacts on native species. Glob Ecol Conserv 3:607–627. https://doi.org/10.1016/j.gecco.2015.02.010

Hima K, Houéménou G, Badou S, Garba M, Dossou HJ, Etougbétché J, Dobigny G (2019) Native and invasive small mammals in urban habitats along the commercial axis connecting Benin and Niger, West Africa. Diversity 11:238. https://doi.org/10.3390/d11120238

Hendges C, Schiller ADP, Manfrin J, Macedo EK Jr, Gonçalves AC Jr, Stangarlin JR (2019) Human intoxication by agrochemicals in the region of South Brazil between 1999 and 2014. J Environ Sci Health B 54(4):219–225. https://doi.org/10.1080/03601234.2018.1550300

Hodroge A, Longin-Sauvageon C, Fourel I, Benoit E, Lattard V (2011) Biochemical characterization of spontaneous mutants of rat VKORC1 involved in the resistance to antivitamin K anticoagulants. Arch Biochem Biophys 515(1–2):14–20. https://doi.org/10.1016/j.abb.2011.08.010

Jacob HJ, Brown DM, Bunker RK, Daly MJ, Dzau VJ, Goodman A, Koike G, Kren V, Kurtz T, Lernmark A, Levan G, Mao YP, Pettersson A, Pravenec M, Simon JS, Szpirer C, Szpirer J, Trolliet MR, Winer ES, Lander ES (1995) A genetic linkage map of the laboratory rat, *Rattus Norvegicus*. Nat Genet 9(1):63–69. https://doi.org/10.1038/ng0195-63

Jombart T, Devillard S, Balloux F (2010) Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genet 11:94. https://doi.org/10.1186/1471-2156-11-94

Kajdacsi B, Costa F, Hyseni C, Porter F, Brown J, Rodrigues G, Caccone A (2013) Urban population genetics of slum-dwelling rats (*Rattus norvegicus*) in Salvador, Brazil. Mol Ecol 22(20):5056–5070. https://doi.org/10.1111/mec.12455

Kasiotis KM, Baira E, Manea-Karga E, Nikolopoulou D, Ganas K, Machera K (2021) Investigating a human pesticide intoxication incident: The importance of robust analytical approaches. Open Chem 19(1):107–118. https://doi.org/10.1515/chem-2021-0193

Kass RE, Raftery AE (1995) Bayes factors. J Am Stat Assoc 90(430):773–795. https://doi.org/10.1080/01621459.1995.10476572

Konečný A, Estoup A, Duplantier JM, Bryja J, Bâ K, Galan M, Tatard C, Cosson JF (2013) Invasion genetics of the introduced black rat (*Rattus rattus*) in Senegal, West Africa. Mol Ecol 22(2):286–300. https://doi.org/10.1111/mec.12112

Kosoy M, Khlyap L, Cosson JF, Morand S (2015) Aboriginal and invasive rats of genus Rattus as hosts of infectious agents. Vector-Borne Zoonotic Dis 15(1):3–12. https://doi.org/10.1089/vbz.2014.1629

Kovács Z (2012) Dispersal history of an invasive rodent in Hungary–subfossil finds of *Rattus rattus*. Acta Zool Acad Sci Hungaricae 58(4):379–394

Lebarbier É, Mary-Huard T (2006) Une introduction au critère BIC: fondements théoriques et interprétation. Journal de la SFdS 147(1):39–57. http://www.numdam.org/item/JSFS_2006__147_1_39_0/

Lippens C, Estoup A, Hima MK, Loiseau A, Tatard C, Dalecky A, Brouat C (2017) Genetic structure and invasion history of the house mouse (Mus musculus domesticus) in Senegal, West Africa : a legacy of colonial and contemporary times. Heredity 119(2):64–75. https://doi.org/10.1038/hdy.2017.18

Loiseau A, Rahelinirina S, Rahalison L, Konečný A, Duplantier JM, Brouat C (2008) Isolation and characterization of microsatellites in *Rattus rattus*. Mol Ecol Resour 8(4):916–918. https://doi.org/10.1111/j.1755-0998.2008.02115.x

Long JL (2003) Introduced mammals of the world: their history, distribution, and influence. CSIRO Publishing

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the World's Worst Invasive Alien Species A selection from the Global Invasive Species Database. Published by The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), 12pp. First published as special lift-out in Aliens 12, December 2000. Updated and reprinted version: November 2004.

Lucaccioni H, Granjon L, Dalecky A, Fossati O, Le Fur J, Duplantier JM, Handschumacher P (2016) From human geography to biological invasions: the black rat distribution in the changing southeastern of Senegal. PloS One 11(9):e0163547. https://doi.org/10.1371/journal.pone.0163547

Mangombi JB, Brouat C, Loiseau A, Banga O, Leroy EM, Bourgarel M, Duplantier JM (2016) Urban population genetics of the invasive black rats in Franceville, Gabon. J Zool 299(3):183–190. https://doi.org/10.1111/jzo.12334

Meerburg BG, Singleton GR, Kijlstra A (2009) Rodent-borne diseases and their risks for public health. Crit Rev Microbiol 35(3):221–270. https://doi.org/10.1080/10408410902989837

Mills JN, Yates TL, Childs JE, Parmenter RR, Ksiazek TG, Rollin PE, Peters CJ (1995) Guidelines for working with rodents potentially infected with hantavirus. J Mammal 76(3):716–722. https://doi.org/10.2307/1382742

Padayachee AL, Irlich UM, Faulkner KT, Gaertner M, Procheş S, Wilson JR, Rouget M (2017) How do invasive species travel to and through urban environments ? Biol Invasions 19(12):3557–3570. https://doi.org/10.1007/s10530-017-1596-9

Panti-May JA, Sodá-Tamayo L, Gamboa-Tec N, Cetina-Franco R, Cigarroa-Toledo N, Machaín-Williams C, Hernández-Betancourt SF (2017) Perceptions of rodent-associated problems: an experience in urban and rural areas of Yucatan, Mexico. Urban Ecosyst 20(5):983–988. https://doi.org/10.1007/s11252-017-0651-8

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52(3):273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002

Piry S, Luikart G, Cornuet JM (1999) BOTTLENECK : a program for detecting recent effective population size reductions from allele data frequencies. J Hered 90:502–503

Piry S, Alapetite A, Cornuet JM, Paetkau D, Baudouin L, Estoup A (2004) GENECLASS2: a software for genetic assignment and first-generation migrant detection. J Hered 95(6):536–539. https://doi.org/10.1093/jhered/esh074

Pocock MJ, Hauffe HC, Searle JB (2005) Dispersal in house mice. Biol J Lin Soc 84(3):565–583. https://doi.org/10.1111/j.1095-8312.2005.00455.x

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155(2):945–959. https://doi.org/10.1093/genetics/155.2.945

Puckett EE, Orton D, Munshi-South J (2020) Commensal rats and humans: integrating rodent phylogeography and zooarchaeology to highlight connections between human societies. BioEssays 42(5):1900160. https://doi.org/10.1002/bies.201900160

Richardson JL, Burak MK, Hernandez C, Shirvell JM, Mariani C, Carvalho-Pereira TSA, Pertile AC, Panty-May JA, Pedra GG, Serrano S, Taylor J, Carvalho M, Rodrigues G, Costa F, Childs JE, Ko AI, Caccone A (2017) Using fine-scale spatial genetics of Norway rats to improve control efforts and reduce leptospirosis risk in urban slum environments. Evol Appl 10(4):323–337. https://doi.org/10.1111/eva.12449

Richardson JL, Silveira G, Soto-Medrano I, Arietta AZ, Mariani C, Pertile AC, Pereira TC, Childs JE, Ko AI, Costa F, Caccone A (2019) Significant genetic impacts accompany an urban rat control campaign in Salvador, Brazil. Front Ecol Evol 7:115. https://doi.org/10.3389/fevo.2019.00115

Ringani GV, Julius RS, Chimimba CT, Pirk CWW, Zengeya TA (2022) Predicting the potential distribution of a previously undetected cryptic invasive synanthropic Asian house rat (*Rattus tanezumi*) in South Africa. J Urban Ecol 8(1):juac005. https://doi.org/10.1093/jue/juac005

Roberts M (1991) Origin, Dispersal Routes, and Geographic Distribution of *Rattus exulans*, with Special Reference to New Zealand!. Pac Sci 45(2):123–130. By University of Hawaii Press. All rights reserved. https://doi.org/10.1007/978-1-349-11386-6_9

Rousset F (1997) Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. Genetics 145(4):1219–1228. https://doi.org/10.1093/genetics/145.4.1219

Rousset F (2000) Genetic differentiation between individuals. J Evol Biol 13:58–62

Rousset F (2008) Genepop'007: a complete re-implementation of the genepop software for Windows and Linux. Mol Ecol Resour 8(1):103–106. https://doi.org/10.1111/j.1471-8286.2007.01931.x

Salas BV, Duran EG, Wiener MS (2000) Impact of pesticides use on human health in Mexico: a review. Rev Environ Health 15(4):399–412. https://doi.org/10.1515/REVEH.2000.15.4.399

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Essl F (2017) No saturation in the accumulation of alien species worldwide. Nat Commun 8:14435. https://doi.org/10.1038/ncomms14435

Sikes RS, Gannon WL (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J Mammal 92(1):235–253. https://doi.org/10.1644/10-MAMM-F-355.1

Slatkin M (2008) Linkage disequilibrium—understanding the evolutionary past and mapping the medical future. Nat Rev Genet 9(6):477–485. https://doi.org/10.1038/nrg2361

Song M, Wang B, Liu J, Gratz N (2003) Insect vectors and rodents arriving in China aboard international transport. J Travel Med 10(4):241–244. https://doi.org/10.2310/7060.2003.40603

Song Y, Lan Z, Kohn MH (2014) Mitochondrial DNA phylogeography of the Norway rat. PLoS One 9:e88425. https://doi.org/10.1371/journal.pone.0088425

St Clair JJ (2011) The impacts of invasive rodents on island invertebrates. Biol Cons 144(1):68–81. https://doi.org/10.1016/j.biocon.2010.10.006

Storey JD (2002) A direct approach to false discovery rates. J R Stat Soc Ser B 64:479–498. https://doi.org/10.1111/1467-9868.00346

Stragier C, Piry S, Loiseau A, Kane M, Sow A, Niang Y, Diallo M, Ndiaye A, Gauthier P, Borderon M, Granjon L, Brouat C, Berthier K (2019) Impact of historical and current features of the cityscape on the genetic structure of the house mouse (*Mus musculus domesticus*) in Dakar (Senegal, West Africa). bioRxiv 557066

Stragier C, Piry S, Loiseau A, Kane M, Sow A, Niang Y, Diallo M, Ndiaye A, Gauthier P, Borderon M, Granjon L, Brouat C, Berthier K (2022) Interplay between historical and current features of the cityscape in shaping the genetic structure of the house mouse (*Mus musculus domesticus*) in Dakar (Senegal, West Africa). Peer Community J 2:e11. https://doi.org/10.24072/pcjournal.85

Thresher RE, Hayes K, Bax NJ, Teem J, Benfey TJ, Gould F (2014) Genetic control of invasive fish: technological options and its role in integrated pest management. Biol Invasions 16(6):1201–1216. https://doi.org/10.1007/s10530-013-0477-0

Veale AJ, King CM, Johnson W, Shepherd L (2021) Commensal Rodents in 19th Century Australasia: Diversity, Invasion Routes and the China Connection. https://doi.org/10.21203/rs.3.rs-339763/v1

Waples RS, Do CHI (2008) LDNE: a program for estimating effective population size from data on linkage disequilibrium. Mol Ecol Resour 8(4):753–756. https://doi.org/10.1111/j.1755-0998.2007.02061.x

Watts PC, Rousset F, Saccheri IJ, Leblois R, Kemp SJ, Thompson DJ (2007) Compatible genetic and ecological estimates of dispersal rates in insect (Coenagrion mercuriale: Odonata: Zygoptera) populations: analysis of 'neighbourhood size'using a more precise estimator. Mol Ecol 16(4):737–751. https://doi.org/10.1111/j.1365-294X.2006.03184.x

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 1358–1370. https://doi.org/10.2307/2408641

Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. Trends Ecol Evol 24(3):136–144. https://doi.org/10.1016/j.tree.2008.10.007

Witmer GW, Shiels AB (2017) Ecology, impacts, and management of invasive rodents in the United States. In Ecology and Management of Terrestrial Vertebrate Invasive Species in the United States (pp. 193–220). CRC Press

World Health Organization (2006) International health regulations (2005). World Health Organization

Wyatt KB, Campos PF, Gilbert MTP, Kolokotronis SO, Hynes WH, DeSalle R, Daszak P, MacPhee RDE, Greenwood AD (2009) Historical mammal extinction on Christmas Island (Indian Ocean) correlates with introduced infectious disease. PLoS One 4(1). https://doi.org/10.1371/annotation/9fbe9687-682e-4010-97e4-139b33343d34