Black rat invasion of inland Sahel: insights from interviews and population genetics in south-western Niger

KARINE BERTHIER[1], MADOUGOU GARBA[2†], RAPHAEL LEBLOIS[3,4], MIGUEL NAVASCUÉS[3,4], CAROLINE TATARD[4], PHILIPPE GAUTHIER[5], SAMA GAGARÉ[6], SYLVAIN PIRY[4], CARINE BROUAT[5], AMBROISE DALECKY[7], ANNE LOISEAU[4] and GAUTHIER DOBIGNY[5*]

[1]*INRA, UR0407 Pathologie Végétale, F-84143, Montfavet, France*
[2]*Université Abdou Moumouni, Faculté des Sciences, BP10662, Niamey, Niger*
[3]*Institut de Biologie Computationnelle, Montpellier, France*
[4]*INRA, Centre de Biologie pour la Gestion des Populations (UMR IRD-INRA-Cirad-Montpellier SupAgro), Campus International de Baillarguet, CS30016, 34988 Montferrier-sur-Lez, France*
[5]*IRD, CBGP (UMR IRD-INRA-Cirad-SupAgro), Campus International de Baillarguet, CS30016, 34988, Montferrier-sur-Lez, France*
[6]*Centre Régional Agrhymet, BP11011, Niamey, Niger*
[7]*IRD, Laboratoire Population Environnement Développement (UMR AMU-IRD), Aix-Marseille Université, Centre Saint Charles, CS80249, 13331, Marseille Cedex 03, France*

Human population migrations, as well as long-distance trade activities, have been responsible for the spread of many invasive organisms. The black rat, *Rattus rattus*, has colonized most of the world following ship-mediated trade. Owing to its tight association with human infrastructures, this species has been able to survive in unfavourable environments, such as Sahelian Africa. In this work, we combined interview-based and population genetic surveys to investigate the processes underlying the ongoing invasion of south-western Niger by black rats, with special emphasis on the capital city, Niamey. Our trapping and interview data are quite congruent, and all together point towards a patchy, but rather widespread, current distribution of *R. rattus*. Genetic data strongly suggest that road network development for truck-based commercial flow from/to international harbours located in neighbouring countries (Benin, Togo, and Nigeria) facilitates the passive dispersal of black rats over a long distance through unfavourable landscapes. Another potentially, more ancient, invasion route may be associated with boat transport along the Niger River. Human-mediated dispersal thus probably allows the foundation of persisting populations within highly anthropized areas while population dynamics may be more unstable in remote areas and mostly depends on propagule pressure. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **119**, 748–765.

KEYWORDS: Africa – *Rattus rattus* – trade-mediated invasion – urban habitat.

*Corresponding author. E-mail: gauthier.dobigny@ird.fr
†Current address: Direction Générale de la Protection des Végétaux, BP323, Niamey, Niger
We dedicate this paper to our friends and colleagues Khalilou Bâ and Jean-Marc Duplantier who have recently retired after a lifetime of work on African rodents.

INTRODUCTION

Bioinvasions may have major environmental and socio-economic consequences, such as biodiversity loss (Courchamp, Berec & Gascoigne, 2008), negative impacts on food resources (e.g. Balirwa *et al.*, 2003; Morse & Hoddle, 2006), or spread and emergence of

pathogens (e.g. Azad *et al.*, 1997; Woolhouse, Haydon & Antia, 2005; Masuzawa *et al.*, 2006; Lin *et al.*, 2012). Invasion processes and patterns may be influenced by numerous interacting factors (e.g. Seastedt, 2009; Roura-Pascual *et al.*, 2011). A common and pivotal aspect of all bioinvasions is dispersal (Wilson *et al.*, 2009). Migration of humans, as well as long-distance trade activities, are responsible for the spread of many invasive organisms (Wilson *et al.*, 2009). Among them, rodents might be a serious threat for public health as they carry pathogens that can be transmitted, directly or indirectly, to humans (review in Meerburg, Singleton & Kijlstra, 2009). *Rattus rattus* (lineage I *sensu* Aplin *et al.*, 2011) is of major concern (Aplin, Chesser & ten Have, 2003) and is listed by the International Union for Conservation of Nature (UICN) as among the most preoccupying invasive taxa on earth (Global Invasive Species Database: http://www.issg.org/database, 2013). Although native to the Indian Peninsula (Niethammer, 1975), black rats have reached all continents (with the exception of Arctic and Antarctic landmasses), as well as many islands around the world (Musser & Carleton, 2005), helped by a tight association with humans and their infrastructures (Aplin *et al.*, 2003, 2011). Obviously, ship-mediated trade has played a major role in their dissemination worldwide, as shown by several phylogeographical and population-genetic studies (Tollenaere *et al.*, 2010; Aplin *et al.*, 2011; Kalémé *et al.*, 2011; Lack *et al.*, 2013; Brouat *et al.*, 2014; Colangelo *et al.*, 2015). The black rat is now settled in many areas, where, along with *Mus domesticus* and *Rattus norvegicus*, it has become one of the major components of commensal rodent assemblages following native species displacement, especially in deeply human-modified habitats (e.g. Audoin-Rouzeau & Vigne, 1994).

In essence, cities provide excellent habitats for opportunistic commensal species (Luniak, 2004). Moreover, because cities constitute important hubs for people and for goods exchange, they represent critical zones for the introduction and subsequent spread of alien organisms. This is the most probable reason why one may expect black rats to be mainly associated with villages and towns, at least in the first steps of the invasion process. Accordingly, black rats have invaded many parts of sub-Saharan Africa, where they are essentially recorded from commensal habitats (Rosevear, 1969; Granjon & Duplantier, 2009; Happold, 2013). *Rattus rattus* was recently found in south-western Niger (Dobigny *et al.*, 2011), where the capital, Niamey, is likely to act as a major hub facilitating the invasion process at a regional scale (Garba, 2012). A fine-scale survey of rodent species-assemblages within the city showed that black rats displayed a patchy distribution in households, industrial sites, coach stations, public buildings, and markets of the core city, while the native species, *Mastomys natalensis*, occupied most of the remaining urban environment (Garba *et al.*, 2014). South-western Niger is very likely to be under an ongoing process of black rat invasion. To provide a more precise assessment of the spatial distribution of *R. rattus* in this secluded country, we conducted rodent-trapping sessions and interviews of local inhabitants in Niamey as well as in several surrounding villages and cities. We also performed population genetics analyses to document the genetic structure and recent history of black rats in this poorly investigated part of Sahel. We paid special attention to the *R. rattus* population structure within Niamey, thus providing one of the first population genetic surveys ever conducted on urban black rats (see also Magombi *et al.*, 2016).

MATERIAL AND METHODS

SAMPLING AND INTERVIEWS

Between October 2009 and February 2011, a city-wide survey of urban rodents was conducted in Niamey. About 15 000 trap-nights were achieved in 52 different areas of the town (see details in Garba, 2012; Garba *et al.*, 2014). During this survey, 182 black rats were caught (Garba *et al.*, 2014), 113 of which were included in the present study. Rats were sampled from six sites within Niamey (Table 1 and Fig. 1): the municipal slaughter house (NGAM); a rice hulling industry (NKIR); the so-called 'Great' (NGRM) and 'Little' (NPEM) markets and surrounding households; two mud-constructed houses, as well as two store houses lying within the Ministry of Agriculture plant nursery along the Corniche Yantala (NCYA); and two mud-made households in the Corniche Gamkalleye district (NCGA, where 18 out of 19 rats were caught within the same house).

In addition, in June/July 2011 and November 2012, 3109 trap-nights, based on the same protocol as in Niamey, were performed in various localities of south-western Niger (Table 1 and Fig. 1A). These localities were selected according to their geographical position and their connection with other localities through the Niger River or the main commercial tarred roads (Fig. 1A and Table 1). The villages of Boumba (BOU) and Hamma Dendi (HAM) lie along the Niger River, 130 km and 50 km downstream from Niamey, respectively, with no large road connection to the capital. Dosso (DOS), located 145 km east from Niamey, is an important junction between two major roads (RN7 and RN1) used by trucks traveling from Benin, Togo, and Nigeria. Gaya (GAY) is

Table 1. Localities where samplings and interviews were conducted

Locality	Site	GPS Latitude	GPS Longitude	Position and connection	Historical record	NI	NNT	Captures Total	Captures Rat	Gentoyped rats
Niamey	NCGA	13.50222	2.11235	Within Niamey, along the riverside	Created at the end of the 19th century	0	326*	20	19	19
	NCYA	13.51231	2.09906	Within Niamey, along the riverside		0	1161*	88	26	15
	NGAM	13.48950	2.12275	Within Niamey, along the riverside		0	890*	77	77	32
	NGRM	13.51882	2.11500	Within Niamey, core city		0	305*	84	11	11
	NKIR	13.49489	2.10978	Within Niamey, along the riverside		0	1086*	24	23	24
	NPEM	13.51396	2.10997	Within Niamey, core city		0	374*	37	13	13
All within Niamey						0	4142	330	169	114
Boumba	BOU	12.405	2.840	Niger River, connected only by gravel roads	Probably founded much earlier than 1896	14	563	54	8	25**
Hamma Dendi	HAM			Niger River, no road	Founded in 1964	12	326	30	29	29
Dosso	DOS	13.039	3.195	RN1 to Niamey, eastern Niger, Nigeria as well as Guinean Gulf harbours (via RN7 and Gaya)	Mentioned from the late 16th century	0	427	36	31	31
Gaya	GAY	11.885	3.448	Niger River and RN7 connecting Niamey to Guinean Gulf harbours via Dosso	Mentioned from the late 17th century	2	304	40	32	32
Say	–	13.074	2.355	Niger River, RN27 to Niamey	Founded in the early 19th century, growing since 1825	16	338	27	0	–
Tillaberi	–	14.195	1.461	Niger River, and RN1 connecting Niamey and Northern Mali	Already founded in the early 19th century	29	609	23	0	–
Mossi Paga	–	12.750	1.638	RN6 connecting Niamey to Burkina Faso	?	4	15	2	0	–
Torodi	–	13.086	1.794	RN6 connecting Niamey to Burkina Faso	Mentioned from the 19th century	14	208	5	0	–

Table 1. *Continued*

Locality	Site	GPS Latitude	GPS Longitude	Historical record	Position and connection	NI	NNT	Captures Total	Captures Rat	Gentoyped rats
Makalondi	–	12.836	1.687	?	RN6 connecting Niamey to Burkina Faso	10	334	15	0	–
Outside Niamey	All outside Niamey					101	3124	232	92	117
All	All within and outside Niamey					101	7266	562	261	231

*See Garba et al, 2014 for details.

**17 extra specimens captured in 2007 (see text).

For each locality, the table provides: the abbreviation (site) and geographical position of the locality and its connection to other localities (position and connection); the presumed date/period of foundation of the localities when available; the number of persons interviewed (NI); the trapping effort [number of night-traps (NNT)]; the trapping success for all rodents species (Total) and for the black rat (Rat); and the number of black rat samples that were available for genetic analyses (Genotyped rats).

located along the Niger River, 300 km from Niamey at the border between Niger and Benin. However, it is also connected to the capital, via Dosso, through the RN7 then RN1 roads. This geographical position makes Gaya a major stop between the Guinean Gulf harbours (e.g. Accra in Ghana, Cotonou in Benin, and Lomé in Togo) and Niamey. In total, 100 black rats were trapped from these four localities, and 17 extra samples, collected in Boumba in 2007 (see Dobigny *et al.*, 2011), were added to this sampling. The genetic study was thus conducted on a data set of 230 samples (including 113 from Niamey) genotyped at 17 microsatellite loci (see below).

Interviews were conducted not only within the four localities where rats were trapped outside Niamey (i.e. Boumba, Dosso, Gaya, and Hamma Dendi) but also in localities where the trapping was unsuccessful and the black rat was not even observable (Table 1 and Fig. 1). This included the cities of Say and Tillabéri, located 40 km south and 115 km north of Niamey, respectively, as well as the village of Mossi Paga and the small towns of Torodi and Makalondi (see Table 1 and Fig. 1 for details). Say is connected to Niamey through a dead-end tarred road, while Tillabéri is connected to Niamey by the RN1 tarred road that leads to Ansongo and Gao in northern Mali. Mossi Paga, Torodi, and Makalondi are located 60–90 km west of Niamey along the only tarred road (RN6) that links Niamey and Ouagadougou in Burkina-Faso (the border post is at Makalondi). This road is also occasionally used by trucks to travel between the Guinean Gulf coast and Niamey.

Interviews consisted of open discussions (i.e. with a minimum of oriented questions) in local languages (essentially Hausa and Djerma) that aimed at assessing, first, whether inhabitants recognized the black rat, with no confusion with other rodent or shrew species, and, second, if 'yes' to the first point, whether they had already observed it locally, as well as whether they could remember when it was first observed. To do so, we relied on adult women and men who had freely agreed to answer our questions, either alone or in groups. Each time it was feasible, we tried to target persons more likely to provide expert knowledge (e.g. employees of the Agriculture Service who have a good awareness of pest rodents, workers in industrial food stores, farmers, sellers in markets, etc.). Finally, blind tests with live trapped rodents were performed in some instances, to eliminate possible confusion between black rats and other small mammals. Historical records were gathered either from the literature (Hama, 1967; Salifou, 2010) or from interviews of traditional chiefs. This allowed us to estimate the dates of foundation of the different towns and villages and, in some instances,
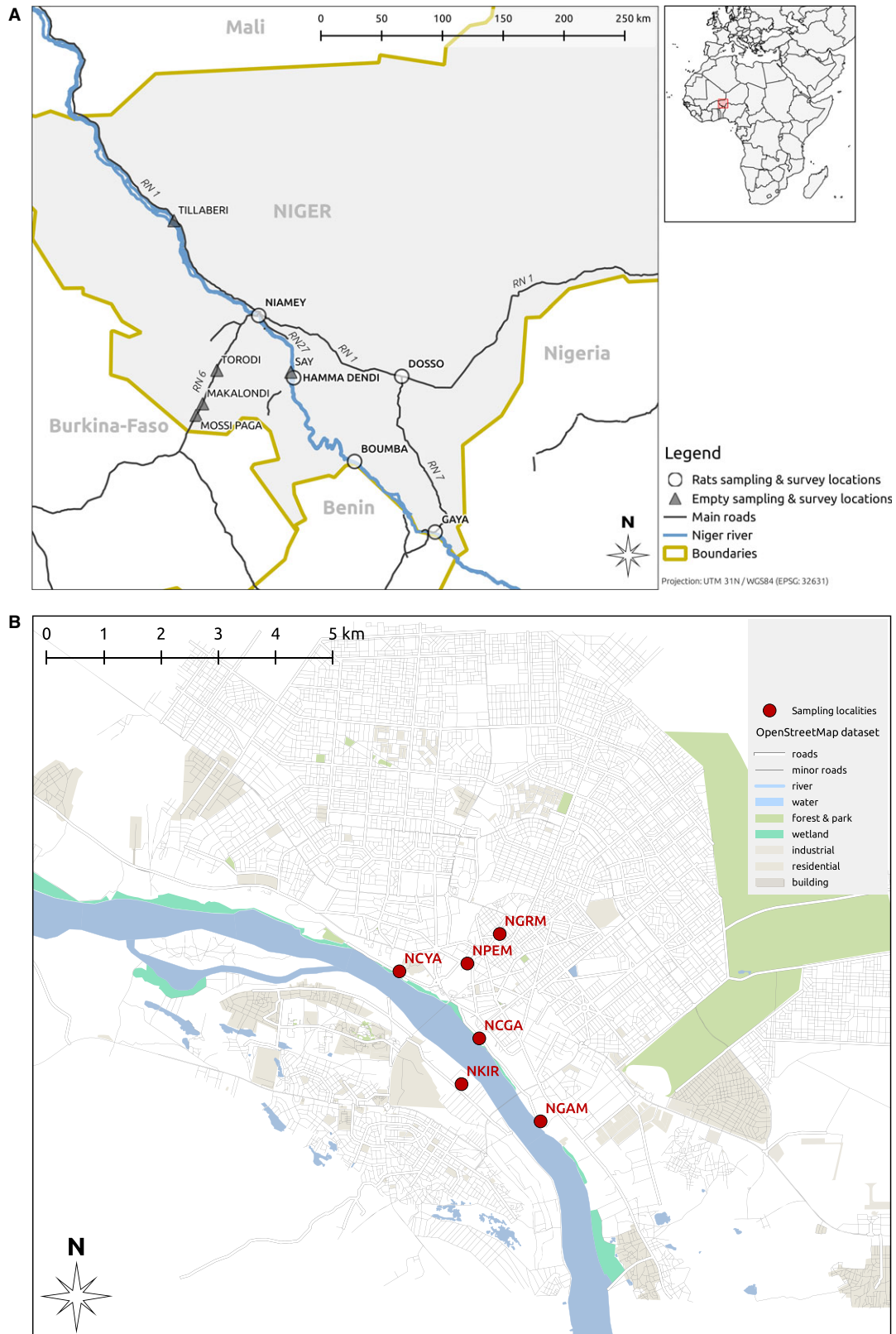
Figure 1. Localities where interviews and trapping were conducted at the scale of south-western Niger (A) and Niamey city (B). Circles and triangles mark sites where black rats have been successfully captured or not captured, respectively (see Table 1 for details).

the most recent reliable mention of the black rat (Table 1).

POPULATION GENETICS ANALYSES

DNA extraction and genotyping

Genomic DNA was extracted from spleen tissue samples using the Qiagen DNeasy Blood and Tissue Kit, and then used as a template for individual multiplex genotyping at 17 microsatellite loci, seven (D10R20, D11M5, D11R56, D16R81, D2M14, D5R83, and D7R13) of which were originally developed for *R. norvegicus* (Jacob *et al.*, 1995) and ten (Rr14, Rr17, Rr21, Rr22, Rr54, Rr67, Rr68, Rr93, Rr107, and Rr114) for *R. rattus* (Loiseau *et al.*, 2008). Polymerase chain reaction (PCR) amplifications were conducted in 10-μL reaction volumes containing Qiagen Multiplex PCR Master Mix (1X), 0.2 μM of each primer, and approximately 50 ng of genomic DNA, and were performed on a Mastercycler ep gradient S (Eppendorf) using a Multiplex PCR Kit (Qiagen). The first set of markers was amplified in two PCR amplifications using touchdown PCR conditions: 33 cycles of 95 °C for 15 min, 94 °C for 30 s, 67 °C for 90 s (temperature decreased by 2 °C at each cycle for seven cycles, then maintained at 53 °C for 25 cycles), 72 °C for 60 s, and a final elongation step for 30 min at 60 °C. The second set of markers was amplified in two PCR amplifications using regular PCR conditions: 95 °C for 15 min, 33 cycles of 94 °C for 30 s, 60 °C for 90 s, and 72 °C for 60 s, and a final elongation step at 60 °C for 30 min. The two PCR products of each set were pooled and diluted 40-fold, then 2 μL of the latter dilute PCR solution was mixed with 0.1 μL of GeneScan 500 LIZ and 15 μL of Hidi Formamide (Applied Biosystems). The samples were separated and detected on an ABI 3130 automated sequencer and analysed using GeneMapper v.3.7.

Genetic diversity

Genotypic linkage disequilibrium for each pair of loci, and deviation from Hardy–Weinberg equilibrium (HWE) within each sampling site, were tested using GENEPOP v.4.3 (Rousset, 2008). We used the false discovery rate (FDR) approach to account for multiple testing (Benjamini & Hochberg, 1995). Deviation from HWE was quantified by computing F_{IS} (average inbreeding coefficient of individuals relative to population) according to Weir & Cockerham (1984). Genetic variability was estimated over all loci by calculating unbiased expected (H_e; Nei, 1978) and observed (H_o) heterozygosities and allelic richness (A_r) corrected for a sample size of 11 diploid individuals (i.e. the smaller number of individuals genotyped for a locus in our samples) (El Mousadik & Petit, 1996). Two-sided permutation tests implemented in FSTAT v. 2.9.3 (Goudet, 1995, 2001) were used to compare the mean levels of within-site genetic diversity (H_e, H_o and A_r), and structure (F_{IS}) observed within Niamey (six sites) and outside Niamey (four sites).

Kinship

Commensal black rats are well known for their highly structured social organization, thus leading to the existence of spatially well-delimited groups (Ewer, 1971). Consequently, as for other rodent species, the social and territorial behaviour of black rats can impact spatial patterns of genetic variation (Dobson, 1998, 2007). To assess whether individuals from the same locality could represent kin groups, we used the software SPAGEDI v.1.4 (Hardy & Vekemans, 2002) to compute the kinship coefficient of Loiselle *et al.* (1995) for all pairs of individuals belonging to that locality. Kinship was estimated using the full data set (all sampling localities within and outside Niamey) as a reference for allelic frequencies. For Niamey, we first considered all pooled sites as a single locality and, second, we considered each site independently.

Spatial structure

Tests for genetic differentiation and computation of F_{ST} (fixation index) estimates (Weir & Cockerham, 1984) between sampling sites were performed using GENEPOP (Rousset, 2008). Isolation by distance was tested using the Mantel test (10 000 permutations) to assess the correlation between genetic [$F_{ST}/(1-F_{ST})$] and log-transformed between-sites geographical distances. Two-sided permutation tests were implemented in FSTAT (Goudet, 2001) to compare the mean level of differentiation (F_{ST}) observed between sites located within Niamey and between sites located outside Niamey. To evaluate the role of the Niger River and the roads in black rat dispersal, we compared F_{ST} values between each site sampled within Niamey and (1) Dosso and Gaya, located along main road axes, and (2) Boumba and Hamma Dendi located along the Niger River away from main road axes.

Black rat population structure was further investigated using Discriminant Analysis of Principal Components (DAPC; Jombart, Devillard & Balloux, 2010) implemented in the *adegenet* R package (Jombart, 2008). As a discriminant analysis, DAPC requires information on the number and composition of the potential genetic groups. When such information is not available, the optimal number of clusters in the data set can be determined using k-means clustering, as implemented in *adegenet*. We used this approach with the maximal number of clusters fixed to 20. The best clustering solution was determined based on Bayesian Information Criterion (BIC) decrease. The lowest BIC value is usually informative on the number of clusters

(K) that best describe the data (i.e. optimal K) (Jombart *et al.*, 2010). As the current spatial genetic structure of black rats is likely to result from different processes acting at different spatial and timescales (e.g. initial founder effects, genetic drift, social organization, natural and human-mediated dispersal along roads and rivers, and environmental variations), we not only determined the optimal number of clusters describing the data, but we also assessed clustering solutions with lower K values that made sense geographically (see Meirmans, 2015). For all DAPC analyses, a stratified cross-validation procedure was used to determine the optimal number of principal components (PCs) to be retained in the discriminant analysis. For each number of PCs tested, we ran 1000 repetitions, and the DAPC was performed on a training set including 90% of observations from each group. The results were used to predict the group of the remaining 10% of observations. We used the average prediction success per group and retained the number of PCs associated with the lowest Mean Squared Error (Jombart *et al.*, 2010).

Demographic history

An Approximate Bayesian Computation (ABC) (Beaumont, Zhang & Balding, 2002) approach was used to examine historical population size changes at each sampling site and to visualize them in skyline plots (Ho & Shapiro, 2011). We implemented a single population model consisting of several demographic periods with constant effective population sizes. The command-line version of DIYABC v. 2.0 (Cornuet *et al.*, 2014) was used to simulate microsatellite data sets with sample sizes equal to our study populations and evolving according to demographic scenarios in a coalescent framework characterized by demographic and mutational parameters sampled from prior distributions. A log uniform distribution (10^{-3}, 10^4) was used as prior for the parameter θ ($\theta = 2N_e\mu$) (i.e. the population scaled mutation rate). The number of population size changes was taken from a Poisson distribution with parameter $\lambda = \log(2)$ (NB: nine changes were used when values higher than nine were drawn). The age of the events (measured in mutational units, $\tau = t\mu$) was taken randomly from a uniform distribution in the interval from 0 to 6. Microsatellite mutations were simulated using a generalized stepwise mutation model with parameter pGSM = 0.5. Summary statistics (mean number of alleles, mean gene diversity, mean allele size variance, and mean M index across loci; Garza & Williamson, 2001) were computed from a total of one million simulated data sets. The 0.1% simulations with summary statistics closest to those observed in each population sample were retained in order to estimate posterior probabilities distribution of the

parameters (Beaumont *et al.*, 2002). Skyline plots were built using posterior distributions of θ (median and 95% highest density probabilities) at 100 time points (regularly distributed in the explored time period), following the approach described in Burgarella *et al.* (2012) using R v. 3.2.0 (R Core Team, 2015) and the *abc* package (Csilléry & Blum, 2012).

Demographic history was also explored using MIGRAINE v.0.4.1 (http://kimura.univ-montp2.fr/~rousset/Migraine.htm) and a model with a past variation in population size (Leblois *et al.*, 2014). This model consists of a single, isolated panmictic population that undergoes a continuous exponential change in population size starting at time T generations in the past and going on until the moment of sampling (i.e. present). MIGRAINE uses the class of importance sampling algorithms developed by De Ioro & Griffiths (2004a,b), De Ioro *et al.* (2005), and extended in Leblois *et al.* (2014). We used microsatellite loci with repetitions of two base-pair motifs that varied in length as a result of the addition or deletion of one or several complete motifs ($N = 14$: D10R20, D11R56, D16R81, D2M14, D5R83, D7R13, RR107, RR14, RR17, RR21, RR22, RR54, RR67, and RR68) to test for past changes in population sizes and to estimate: (1) current and ancestral scaled population sizes ($\theta = 4N\mu$ and $\theta_{anc} = 4N_{anc}\mu$, where N and N_{anc} are the current and ancestral diploid population sizes, respectively, and μ is the mutation rate per generation of the whole locus); and (2) D, the starting time of demographic change, scaled by population size (i.e. $D = T/2N$). To characterize the strength of the demographic events, we used the extra parameter $N_{ratio} = N_{act}/N_{anc}$, which is < 1 in the case of a past contraction and > 1 in the case of an expansion. Significant change in population size was determined when 1 lies outside the 95% confidence intervals (95% CIs) of the N_{ratio} parameter (Leblois *et al.*, 2014). The MIGRAINE software was used on each of the ten sampled populations separately to infer local past changes in population size. A benefit of using MIGRAINE over MSVAR (Beaumont, 1999; Storz & Beaumont, 2002), which carries out similar analyses, is that it allows departure from the strict Stepwise Mutation Model (SMM) by using a generalized stepwise mutation model (GSM). All MIGRAINE analyses in this study used 20 000 trees, 2400 points and three to four iterations (see the MIGRAINE manual for details about these settings).

RESULTS

TRAPPING AND INTERVIEWS

The number of black rats captured from each sampling site within and outside Niamey is presented in

Tables 1 and 2. No *R. rattus* were trapped or even observed in Tillabéri, Say, Mossi Paga, Makalondi, and Torodi (Fig. 1). Images of various rat-invaded sites are provided in the Supporting Information (Fig. S1).

As expected, in all localities where black rats were trapped, all interviews confirmed that the species was well known and well discriminated from other widely distributed rodent species, namely *Arvicanthis niloticus* and *Mastomys* spp., through specific features like 'its long tail' and 'its ability to climb' on roofs or trees. This was the case in Gaya (two interviews), Boumba (14 interviews), Dosso (18 interviews), and Hamma Dendi (12 interviews).

In localities where no black rat was captured, interviews also provided important information. In Say, 16 persons out of the 21 interviewed seemed to confound *R. rattus* and *A. niloticus*. The remaining five persons appeared to make a clear distinction between *Arvicanthis*, *Mastomys* spp. and *R. rattus*, to which they give three different local names in Djerma language: 'kali tchan', 'foura tchan', and 'kowaya', respectively. One person even claimed that she saw black rats in Say around 2007–2008, but not afterwards. In Tillabéri, the term 'kowaya' was never quoted by any of the 29 persons interviewed. Among them, 11 clearly stated that they really did not know the black rat (never seen, never heard about it, did not know it existed); including an employee of the Agriculture Ministry, who was working and living in the city

between 2003 and 2011 and is supposed to be well trained in pest rodent biology. Among the 18 remaining inhabitants of Tillabéri who were interviewed, 16 clearly confounded *R. rattus* and other small mammals (e.g. *A. niloticus* and, in some instances, shrews), while two others made more ambiguous declarations regarding the presence of black rats in the town. Along the only tarred road towards Burkina-Faso, where 28 interviews were performed, nobody seemed to be aware of the existence of *R. rattus*, with the notable exceptions of nine persons who had seen and/ or had heard about the species – that they call 'kowaya' – from Say or Gaya, but that they never encountered it in Makalondi, Torodi, or Mossi Paga.

Finally, interesting pieces of information about the timing of the black rat invasion were provided by several inhabitants of Boumba (14 interviews) as well as by the village head of Hamma Dendi. This latter village was founded *ex nihilo* in 1964, and *R. rattus*, also called 'kowaya' there, is supposed to have immediately colonized traditional houses (*c.* 1964–1965) where it is currently the only commensal species observed. In Boumba, the black rat was said to be already present during the responding person's youth (i.e. in the early 1970s).

POPULATION GENETICS

Genetic diversity

Of the 1264 exact tests performed for linkage disequilibrium, only 33 (< 5%) were still significant after FDR correction for multiple testing (Benjamini & Hochberg, 1995). Significant values involved different pairs of loci and occurred in different sampling sites. After FDR correction, most sites (five within Niamey and three outside Niamey) showed significant heterozygote deficiencies: the latter were associated with F_{IS} values ranging from 0.004 to 0.151 (within Niamey) and from 0.102 to 0.181 (outside Niamey) (Table 2). There was no significant difference in within-site F_{IS} values between the sites sampled within and outside Niamey (two-sided permutation test *P*-value = 0.601). Genetic diversity estimates (A_r, H_o, and H_e), averaged over loci within each site, are summarized in Table 2. Only A_r, which ranged from 2.65 to 4.62, was, on average, significantly lower within the sites sampled inside Niamey than within the sites sampled outside Niamey (3.42 vs. 4.35, respectively; two-sided permutation test *P*-value = 0.018).

Kinship

Distribution of Loiselle's kinship coefficients within sampling sites (Fig. 2) showed that individuals sampled within Niamey were locally more closely related than those sampled outside the capital city. For

Table 2. Sample size (N) and allelic richness (A_r) computed for 11 individuals, observed (H_o) and expected (H_e) heterozygosities, and intrapopulation fixation index (F_{IS}), estimated for all sampling sites outside and within Niamey

Sampling site	N	A_r	H_o	H_e	HW_p	F_{IS}
Outside Niamey						
Boumba	25	4.03	0.474	0.527	**< 0.0001**	0.102
Dosso	31	4.56	0.547	0.615	**< 0.0001**	0.111
Hamma Dendi	29	4.17	0.617	0.602	0.1302	−0.024
Gaya	32	4.62	0.493	0.601	**< 0.0001**	0.181
Within Niamey						
NCGA	19	2.65	0.424	0.447	**< 0.0001**	0.053
NCYA	15	3.98	0.541	0.600	**0.0148**	0.102
NGAM	32	3.71	0.537	0.576	**0.0097**	0.069
NGRM	11	3.65	0.487	0.569	**0.0014**	0.151
NKIR	23	3.18	0.431	0.433	**0.0021**	0.004
NPEM	13	3.37	0.502	0.529	0.3160	0.052
All inside Niamey	113	4.91	0.488	0.669	**< 0.0001**	0.272

Significant *p*-values associated with the rejection of Hardy–Weinberg equilibrium (HW_p) are indicated in bold.

three sites (NCGA, NKIR, and NPEM) the median of the kinship coefficient distribution was equal or greater than what can be expected for half-siblings (i.e. 0.25) (Loiselle *et al.*, 1995). When Niamey was considered as a single sampling site, the median value dropped to 0.008. Outside Niamey, Boumba and Hamma Dendi showed the highest median values of kinship coefficients (0.202 and 0.164, respectively). The other localities (Dosso and Gaya) did not show strong within-site relatedness.

Spatial structure

All sampling sites were highly differentiated ($P < 0.0001$) with F_{ST} estimates ranging from 0.17 to 0.36 (mean = 0.23 ± 0.07; Table 3). There was no significant pattern of isolation-by-distance (IBD; increase of genetic differentiation with geographical distance), regardless of whether we considered all sampling sites ($P = 0.446$), within-Niamey sites only ($P = 0.777$), or outside-Niamey sites only ($P = 0.915$). Although they were less distant from one another,
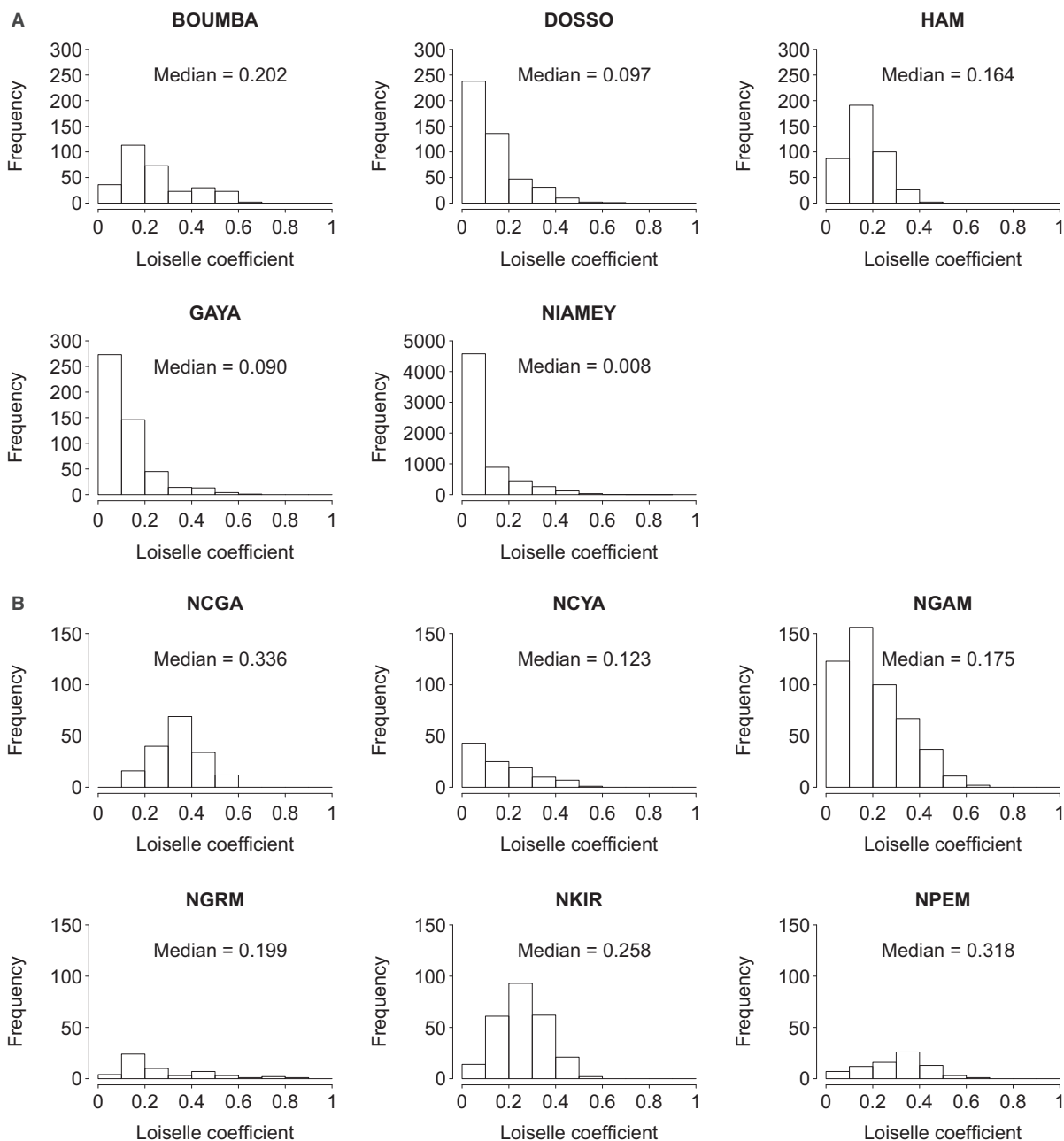

Figure 2. Distribution of Loiselle kinship coefficients computed between pairs of individuals.

Table 3. Overall loci F_{ST} values between sampling sites

	BOU	DOS	HAM	GAY	NCGA	NCYA	NGAM	NGRM	NKIR
DOS	0.1959	–							
GAY	0.1695	0.1735	–						
HAM	0.1643	0.1115	0.1225	–					
NCGA	0.3070	0.2519	0.2537	0.2563	–				
NCYA	0.2400	0.1339	0.1886	0.1712	0.2225	–			
NGAM	0.2813	0.1801	0.2308	0.1865	0.3007	0.1432	–		
NGRM	0.3033	0.1903	0.2535	0.2082	0.3199	0.1845	0.1837	–	
NKIR	0.2733	0.2021	0.2231	0.1708	0.3590	0.2580	0.2786	0.3504	–
NPEM	0.3273	0.1958	0.2803	0.2488	0.3043	0.1562	0.1628	0.1169	0.3633

there was a clear trend for higher genetic differentiation between sites sampled within Niamey than between sites sampled outside Niamey (mean $F_{ST} = 0.256$ vs. 0.154, respectively; two-sided permutation test, P-value = 0.077). Figure 3 shows that there was also a clear trend for lower genetic differentiation between within-Niamey and outside-Niamey sites when they are connected by road (i.e. Dosso and Gaya) rather than by river only (i.e. Boumba and Hamma Dendi).

The decrease in BIC values associated with the k-means clustering solutions for K, ranging from 1 to 20, suggested an optimal number of 10 clusters (Supporting Information, Fig. S2A). Based on the cross-validation procedure, 20 PCs (69% of variance) and nine discriminant functions were retained to run the DAPC (Supporting Information, Fig. S2B). The mean of the posterior membership probabilities was 0.995 ± 0.04 and the clusters mainly identified the ten sites sampled (Fig. 4). Among the 230 individuals analysed, 19 (8.3%) were better assigned to another locality than their sampling locality, with a posterior membership probability of ≥ 0.98 (Table 4). Among them, six animals trapped outside Niamey (four from Gaya and two from Dosso) were assigned to sampling sites located within Niamey.

The analysis of clustering solutions with suboptimal K values (<10) suggested a hierarchical structure. For $K = 2$ and $K = 3$, there was a clear separation between individuals from Niamey and those from outside the city, with the exception of NKIR, which clustered with localities outside Niamey and NCGA, which formed an independent group (Supporting Information, Fig. S3). For $K = 4$, the analysis separated the sites located along the Niger River outside Niamey (Boumba and Hamma Dendi) and the sites located along the road (Dosso and Gaya; Fig. 4). Within Niamey, NKIR grouped with Dosso and Gaya, while NCGA still constituted a highly homogeneous, well-differentiated cluster (Fig. 4).
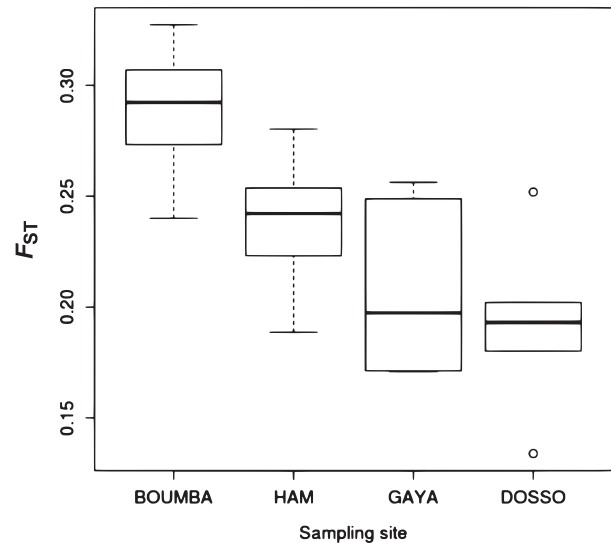

Figure 3. Boxplot of overall loci F_{ST} values computed between each sampling site within Niamey and the external sites connected to Niamey only by the Niger River (Boumba and Ham) or by a road axis (Gaya and Dosso – the former being also connected to Niamey by the river). Circles indicate outliers.

Demographic history
Two methods [i.e. ABC Skyline Plot (ABCSP) and MIGRAINE] were used to reconstruct past demographic history of the different black rat populations from Niamey and south-western Niger. Both approaches were highly congruent in showing past population size contractions (Fig. 5; Table 5) in all but one population (NKIR), which showed rather constant size through time in the Bayesian Skyline Plot analysis (Fig. 5) and non-significant weak demographic contraction using MIGRAINE (Table 5). Inference of population sizes and time of the contraction (i.e. $\log_{10}\theta$, θ_{anc}, and D) were associated with very large standard deviations in all instances (Table 5; Fig. 5), thus making reasonable inferences on the age and strength of potential past bottlenecks unrealistic.

DISCUSSION

BLACK RAT DISTRIBUTION IN SOUTH-WESTERN NIGER

Studies based on interviews are highly complementary to field and laboratory investigations and can provide helpful insights on invasion patterns and processes of emblematic animals. Popular knowledge can add support to the recorded absence of a remarkable species, which is always highly difficult to demonstrate through sampling only. Here, we used interviews, together with a population genetic approach, to draw a general picture of the black rat invasion process in a poorly documented region of Central Sahel.

Black rats have colonized most of the world, following human trade and transport (Aplin *et al.*, 2003, 2011). Africa is no exception, but the process is still in progress with some regions apparently still rat-free (Happold, 2013; J. M. Duplantier, unpubl. data). Being known as an arboreal species of southern Indian origin (Ewer, 1971; Niethammer, 1975; Armitage, 1994; see lineage I in Aplin *et al.*, 2011), *R. rattus* is very unlikely to be able to survive outdoors in Sahel, where it has only been recorded as strictly commensal (Granjon & Duplantier, 2009). The study of its distribution and invasion routes within the region thus requires a focus on human infrastructures.

Our trapping and interviews data are quite congruent and all together point towards a patchy, but rather widespread, current distribution of *R. rattus* in south-western Niger. The species was found to be well established in many towns and villages of the Middle Valley of the Niger River (e.g. Niamey, Gaya, and Boumba), even small and isolated ones (e.g. Hamma Dendi). We were unable to date the first occurrence of black rats in this area, which may potentially trace back between the early stages of colonization of the Guinean Gulf coasts (*c.* 15th century). The species has unambiguously been present in the area since the 1960s, as confirmed by the accounts collected in Boumba and Hamma Dendi, as well as from some anecdotal captures that were performed in the 1990s and 2000s in small villages lying along the river between Niamey and Hamma Dendi (B. Sidiki, pers. comm.). It may even have been present in south-western Niger more than a century ago, as suggested by one museum collection specimen (see below). The black rat was also well established in Dosso and Gaya. Our survey also confidently showed that some small towns and villages (e.g. Makalondi, Torodi, and Mossi Paga) were still rat-free and that some medium-size cities could also be rat-free or, at least, only poorly or non-continuously invaded (e.g. Tillabéri and Say).
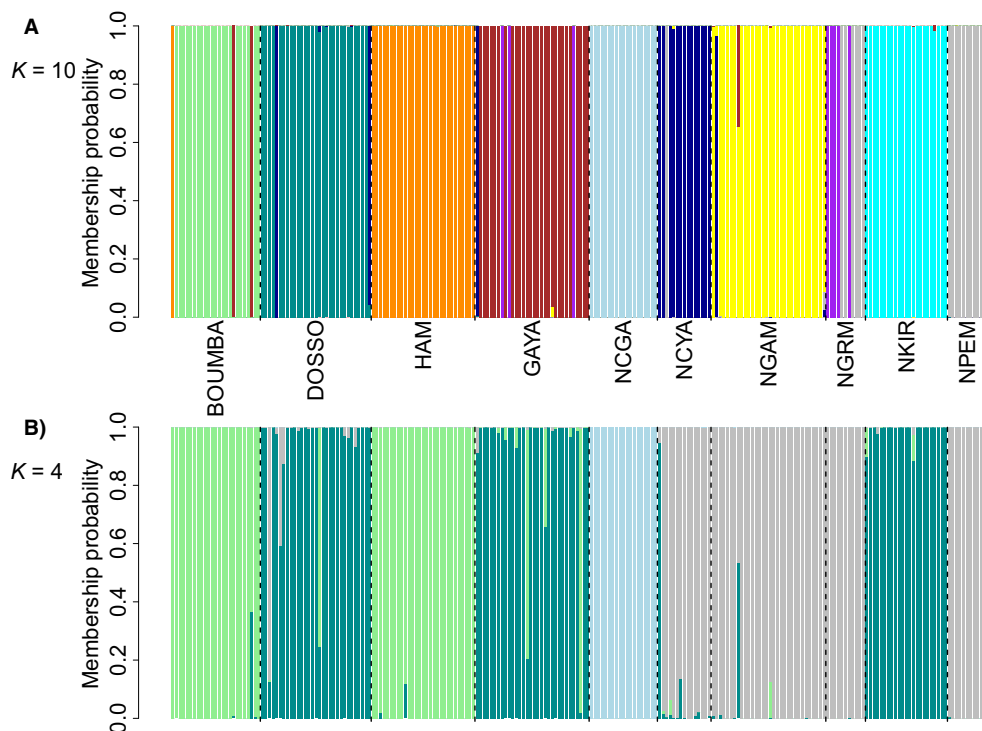

Figure 4. DAPC plot for the optimal number of cluster for $K = 10$ (A) and for $K = 4$ (B). Each bar represents an individual that is coloured according to its probability of belonging to a given cluster.

Table 4. Posterior membership probability (P_{post}) of individuals assigned to a site (Assigned) other than their sampling site (Site) following DAPC analysis

Individual	Site	Assigned	P_{pos}
GAY006A	Gaya	Niamey-NCYA	0.99
GAY016A	Gaya	Niamey-NGRM	1.00
GAY018A	Gaya	Niamey-NGRM	1.00
GAY039A	Gaya	Niamey-NGRM	0.99
BOU001A	Boumba	Hamma Dendi	0.99
BOU063A	Boumba	Gaya	0.99
BOU087A	Boumba	Gaya	0.99
DOS005A	Dosso	Niamey-NCYA	0.99
DOS028A	Dosso	Niamey-NCYA	0.96
CYA003A	Niamey-NCYA	Niamey-NPEM	0.99
GAM016A	Niamey-NGAM	Niamey-NCYA	0.99
GAM017A	Niamey-NGAM	Niamey-NPEM	0.98
GAM053A	Niamey-NGAM	Niamey-NPEM	0.99
GRM034A	Niamey-NGRM	Niamey-NPEM	0.99
GRM035A	Niamey-NGRM	Niamey-NPEM	0.99
GRM233A	Niamey-NGRM	Niamey-NPEM	0.99
GRM236A	Niamey-NGRM	Niamey-NPEM	0.99
GRM238A	Niamey-NGRM	Niamey-NPEM	0.99
GRM239A	Niamey-NGRM	Niamey-NPEM	0.99

GENETIC STRUCTURE

Genetic differentiation was very high (F_{ST} values ranging from 0.11 to 0.36; mean 0.23), even between close sampling sites within Niamey (Table 3). This range of differentiation was much higher than that observed for *R. rattus* at the scale of the Madagascar Island (F_{ST} ranging from 0.01 to 0.21, mean = 0.07; Brouat *et al.*, 2014) or at the scale of Franceville city, Gabon (F_{ST} = 0.01–0.05, mean = 0.03; Magombi *et al.*, 2016). Yet, it is congruent with those found between localities colonized by black rats in the southern part of Senegal (i.e. F_{ST} ranging from 0.07 to 0.51, mean = 0.25; Konecny *et al.*, 2013). These variations in the current level of genetic structure of black rat populations may be the result of differences in introduction times and spatial modality of propagation. Colonization of Madagascar has been shown to be the result of one major event of introduction in the 10th century and ancient expansion (Brouat *et al.*, 2014). In contrast, multiple introductions from different European ports may be at the origin of *R. rattus* populations in Senegal, the species having then spread inland following various human trade routes: rivers, railways, and, much more recently, tarred roads (Konecny *et al.*, 2013). Under such an invasion scenario, populations establishing in villages and cities are prone to founder effects (Konecny *et al.*, 2013). Similarly, our ABCSP and MIGRAINE approaches detected signs of past demographic

bottlenecks in Niger for all but one sampling sites (NKIR). These results suggest that the colonization of a new locality by rats, or even of an urban block within a city like Niamey, constitute a founder event that will give rise to patchy structured deme rather than large continuous populations.

The black rat is a social species that establishes and defends its territory (Ewer, 1971); demes may thus exhibit strong local structure (Dobson, 2007). Understanding of F_{IS} and relatedness values is then not straightforward: genetic patterns will depend on interactions between demographic and behavioural processes on the one hand, and on the spatial scale at which each site has been sampled on the other. For instance, in NCGA, which displayed low F_{IS} (0.053) and high relatedness (0.336) values, 18 out of 19 individuals were trapped inside the same house, and thus probably belonged to the same family group. In other cases, such as NGRM where three shops were sampled, high relatedness values (0.199) were associated with high F_{IS} values (0.151). This pattern is likely to have resulted from recent admixture (Wahlund effect), as suggested by the result of the DAPC for $K = 10$, which assigned individuals from this site into two different clusters (Fig. 4). Other situations, such as in Gaya where the sampling encompassed several, sometimes distantly spaced, sites, led to low relatedness (0.09), together with high F_{IS} (0.181), because a few individuals from several distinct colonies were probably sampled. Behind these different effects, the intra- as well as the inter-deme genetic structure also depends strongly on colonization processes underlying the current invasion processes (e.g. origins and number of founders) (Wade & McCauley, 1988; Pannell & Charlesworth, 1999). Kin structure and inbreeding among colonizers can reduce effective population size. Such a process, together with a founder effect, are expected to induce strong genetic drift and may lead to rapid and strong differentiation between demes (Whitlock & McCauley, 1990; Ingvarsson, 1998), as observed in our study. At a local scale, this can reduce genetic diversity when only one colony is present (or sampled), as suggested by our sampling from NCGA, which exhibited the lowest levels of A_r and H_o (Table 2). Genetic diversity can, however, remain quite high if different colonies that carry different alleles originating from diverse sources are present and sampled.

HUMAN-MEDIATED DISPERSAL: THE ROLE OF FLUVIAL AND ROAD NETWORKS

The high level of genetic differentiation observed in our study could not be explained by IBD because no IBD was detected whatever spatial scale was considered (i.e. within Niamey only or all sampling sites
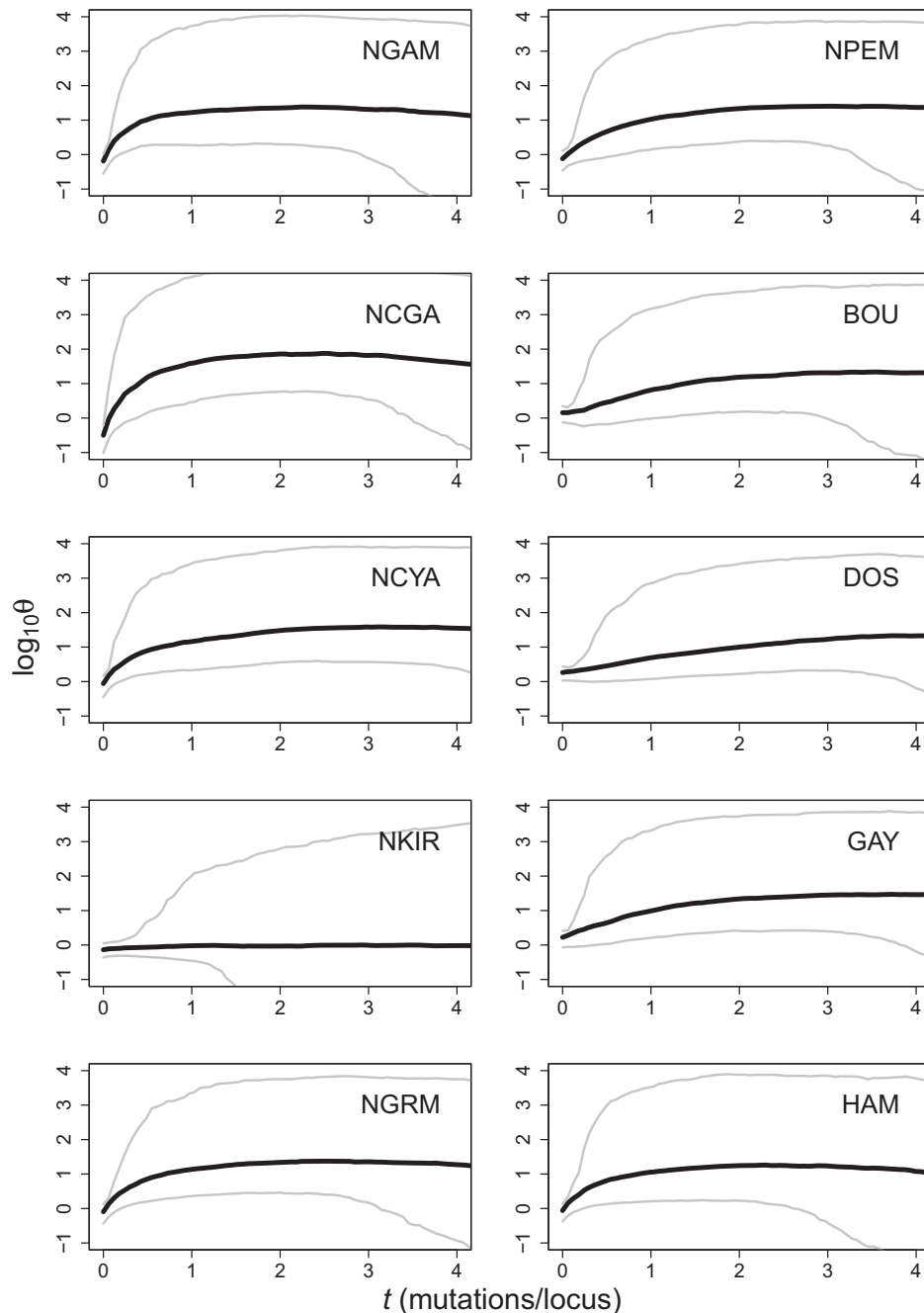
Figure 5. Bayesian Skyline Plots showing Approximate Bayesian Computation (ABC) -based simulations of past demographic changes for each population. Black and grey lines correspond to the median and 95% highest density probabilities of the population size (θ), respectively.

together). This suggests that the natural dispersal abilities of black rats are not sufficient to explain the current pattern of genetic structure, even between sites that are geographically close (i.e. within Niamey). The lack of correlation between genetic and geographical distances can be expected when passive dispersal occurs (e.g. Holland & Cowie, 2007;

Fountain *et al.*, 2014). Such a process occurring along trade routes in Niger is supported by the genetic structure resulting from the DAPC at $K = 3$ and $K = 4$, and by the comparison of F_{ST} values between sampling sites that are, or are not, well connected by road. In this analysis, the locality sampled along the Niger River (Boumba and Hamma Dendi)

Table 5. Past demographic inferences using MIGRAINE

Population	pGSM	θ	D	θ_{anc}	N_{ratio}	Past demography
NGAM	0.39 (0.17–0.65)	0.47 (10^{-4} to 1.0)	0.87 (0.095 to 3.4)	9.3 (1.5–61)	0.05 (5.10^{-5} to 0.37)	Significant contraction
NCGA	0.45 (0.098–0.75)	0.29 (0.019 to 0.51)	6.3 (0.21 to 8.7)	950 (1.1–Inf)	0.0003 (3.10^{-7} to 0.37)	Significant contraction
NCYA	0.59 (0.31–0.74)	0.99 (0 to 1.5)	3.8 (0.035 to 8.1)	120 (1.1–395)	0.0086 (0.001 to 0.44)	Significant contraction
NKIR	0.64 (0.53–0.75)	0.0039 (0 to 356)	0.12 (0 to 40)	0.091 (0.24–9.9)	0.0043 (10^{-6} to 440)	Non-significant contraction
NGRM	0.44 (0.39–0.73)	0.46 (0 to 1.0)	1.5 (0 to 3.5)	11 (0.99–510)	0.041 (10^{-6} to 0.70)	Significant contraction
NPEM	0.44 (0.01–0.65)	0.74 (0.26 to 1.0)	4.7 (1.1 to 7.5)	230 (32–2500)	0.0032 (0.00033 to 0.16)	Significant contraction
DOS	0.46 (0.27–0.57)	1.5 (1.0 to 2.0)	4.4 (0.7 to 8.5)	240 (5.9–1400)	0.0062 (0.0012 to 0.24)	Significant contraction
GAY	0.64 (0.5–0.73)	1.3 (10^{-6} to 39)	3.8 (10^{-5} to 35)	79 (2.8–250)	0.016 (0.00054 to 0.62)	Significant contraction
HAM	0.55 (0.28–0.68)	0.96 (0.48 to 1.4)	4.8 (0.29 to 8.6)	290 (2.2–Inf)	0.0033 (0.00077–0.37)	Significant contraction
BOU	0.58 (0.44–0.69)	0.94 (10^{-6} to 1.9)	1.4 (10^{-5} to 117)	69 (1.0–474)	0.137 (0.0021 to 0.28)	Significant contraction

The following are indicated for each sampling site: the pGSM model parameter (pGSM), the current (θ) and ancestral (θ_{anc}) diploid population sizes, the time at which the demographic change starts (D; scaled by population size) and the strength of the demographic event (N_{ratio}).

clusters together, while Dosso and Gaya, both located on the road axis, cluster with the sampling site NKIR, which is situated on the right bank of the river inside Niamey (Fig. 4) but where rice-carrying trucks often stop and start. The results of the DAPC for $K = 10$ (Fig. 4 and Table 4) also support some level of genetic connectivity between Boumba, Gaya, and Hamma Dendi (all along the river), as well as between Dosso and Niamey (connected only by the road) and between Gaya and Niamey (connected by both the river and the road).

Roads are rather rare in Niger, and none was asphalted before the 1970s (Salifou, 2010). This has most probably greatly limited road exchanges, and hence opportunities for black rats to reach Niamey and other inland cities in trucks, except in the very last decades. Today, road trade with Benin, Togo, and Nigeria represents a major commercial activity in Niger. Road-based importations from Nigeria ranged between 3.8 and 10.5% during the 2005–2011, 7-years long period (but no particular trend, i.e. increase or decrease), and that the road-based importations from Benin/Togo ranged between 60.6 and 81% during the same period. For road-based exportations, it ranged between 34.4 to 70.4% to Nigeria, and between 2.6 to 12.4% to Benin/Togo (CNUT, 2013). In other words, around two-thirds of road exportations from, and three-quarters of road importations into, Niger concern the roads linking Niamey and Benin, Togo, and Nigeria, namely the RN1 that enters Niamey from Dosso (Fig. 1). This could explain the clear trend for a lower level of genetic differentiation between the sites within Niamey and these external sites located along this road (i.e. Dosso and Gaya; Fig. 3). As no black rat was caught, observed, or mentioned along the main road linking Niamey and Burkina-Faso (on the east, RN6; Fig. 1) or Mali (on the north, RN1 through Tillabéri; Fig. 1), we speculate that truck traffic, south of Niamey, between Niger, Benin, and Nigeria, represents the most probable network contributing to this black rat front of invasion.

In addition, as suggested by our results, passive dispersal through the fluvial network may have also occurred, and may still occur. Several dozen meters-long pirogues that carry people and various goods (e.g. squashes, grains, small-size livestock, etc.) navigate between Nigeria and Mali, regularly stopping in fluvial ports such as Gaya, Boumba, Hamma Dendi, or Niamey. These boats may possibly transport rodents, thus potentially serving as invasion vectors along the Niger River. More locally, small pirogues connect the small villages isolated along the riverbed. Local inhabitants testified that black rats had invaded several of these

remote fishermen settlements (M. Garba, unpubl. data), thus suggesting that local fluvial traffic may contribute significantly to the short-scale dissemination of black rats along the Niger River. As long-term human settlements, including trading posts in the Middle Valley of the Niger River, have existed since at least the 15th century, thus unambiguously predating the French colonization in southwestern Niger (Hama, 1967), such an invasion process may have started several centuries ago. Consequently, in the current state of our knowledge, we are unable to date it. Interviews indicate that it started at least 50 years ago. Furthermore, a museum specimen [MNHN-ZM-MO 1895–2067 (National Museum of Natural History, Paris, France), initially referred to as *Mus alexandrines*, which is now a synonym of *Rattus rattus*] was collected in Niger in the 1890s by Captain Toutée who was in charge of the first French exploration of the Niger River in 1894 and 1895 (Salifou, 2010). This strongly suggests that the presence of the black rat in the Middle valley of the Niger River predates the French colonization.

ACKNOWLEDGEMENTS

REFERENCES

Aplin KP, Chesser T, ten Have J. 2003. Evolutionary biology of the genus *Rattus*: profile of an archetypical rodent pest. In: Singleton GR, Krebs CJ, Spratt DM, eds. *Rats, mice and people: rodent biology and management.* Australian Centre for International Agricultural Research: Canberra, 487–498.

Aplin KP, Suzuki H, Chinen AA, Chesser RT, ten Have J, Donnellan SC, Austin J, Frost A, Gonzalez JP, Herbreteau V, Catzeflis F, Soubrier J, Fang YP, Robins J, Matisoo-Smith E, Bastos ADS, Maryanto I, Sinaga MH, Denys C, Van Den Bussche RA, Conroy C, Rowe K, Cooper A. 2011. Multiple geographic origins of commensalism and complex dispersal history of black rats. *PLoS ONE* **6:** e26357.

Armitage PL. 1994. Unwelcome companions: ancient rats reviewed. *Antiquity* **68:** 231–241.

Audoin-Rouzeau F, Vigne JD. 1994. La colonisation de l'Europe par le rat noir (*Rattus rattus*). *Revue de Paléontologie* **13:** 125–145.

Azad AF, Radulovic S, Higgins JA, Noden BH, Troyer JM. 1997. Flea-borne rickettsioses: ecologic considerations. *Emerging Infectious Diseases* **3:**319–327.

Balirwa JS, Chapman CA, Chapman LJ, Cowx IG, Geheb K, Kaufman L, Lowe-McConnell RH, Seehausen O, Wanink JH, Welcomme RL, Witte F. 2003. Biodiversity and fishery sustainability in the Lake Victoria basin: an unexpected marriage? *BioScience* **53:** 703–715.

Beaumont MA. 1999. Detecting population expansion and decline using microsatellites. *Genetics* **153:** 2013–2029.

Beaumont MA, Zhang W, Balding DJ. 2002. Approximate Bayesian computation in population genetics. *Genetics* **162:** 2025–2035.

Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B* **57:** 289–300.

Brouat C, Tollenaere C, Estoup A, Loiseau A, Sommer S, Soanandrasana R, Rahalison L, Rajerison M, Piry S, Goodman SM, Duplantier J-M. 2014. Invasion genetics of a human commensal rodent: the black rat *Rattus rattus* in Madagascar. *Molecular Ecology* **23:** 4153–4167.

Burgarella C, Navascués M, Zabal-Aguirre M, Berganzo E, Riba M, Mayol M, Vendramin GG, González-Martínez SC. 2012. Recent population decline and selection shape diversity of taxon-related genes. *Molecular Ecology* **21:** 3006–3021.

CNUT. 2013. *Conseil nigérien des utilisateurs des transports publics, direction de l'observatoire des transports.* Rapport de synthèse, Niamey, Niger.

Colangelo P, Abiadh A, Aloise G, Amori G, Capizzi D, Vasa E, Annesi F, Castiglia R. 2015. Mitochondrial phylogeography of the black rat supports a single invasion of the western Mediterranean basin. *Biological Invasions* **17:** 1859–1868.

Cornuet J-M, Pudlo P, Veyssier J, Dehne-Garcia A, Gautier M, Leblois R, Marin J-M, Estoup A. 2014. DIYABC v2.0: a software to make approximate Bayesian computation inferences about population history using single nucleotide polymorphism. *DNA sequence and microsatellite data. Bioinformatics* **30:** 1187–1189.

Courchamp F, Berec L, Gascoigne J. 2008. *Allee effect in ecology and conservation*. Oxford: University Press, Oxford.

Csilléry KOF, Blum MGB. 2012. abc: an R package for approximate Bayesian computation (ABC). *Methods in Ecology and Evolution* **3:** 475–479.

De Ioro M, Griffiths RC. 2004a. Importance of sampling on coalescent histories, I. *Advances in Applied Probability* **36:** 417–433.

De Ioro M, Griffiths RC. 2004b. Importance of sampling on coalescent histories, II: subdivided population models. *Advances in Applied Probability* **36:** 434–454.

De Ioro M, Griffiths RC, Leblois R, Rousset F. 2005. Stepwise mutation likelihood computation by sequential importance sampling in subdivided population models. *Theoretical Population Biology* **68:** 41–53.

Dobigny G, Poirier P, Hima K, Cabaret O, Gauthier P, Tatard C, Costa JM, Bretagne S. 2011. Molecular survey of rodent-borne *Trypanosoma* in Niger with special emphasis on *T. lewisi* imported by invasive black rats. *Acta Tropica* **117:** 183–188.

Dobson FS. 1998. Social structure and gene dynamics in Mammals. *Journal of Mammalogy* **79:** 667–670.

Dobson FS. 2007. Gene dynamics and social behavior. In: Wolff JO, Sherman PW, eds. *Rodent societies*. Chicago: University of Chicago Press, 163–172.

El Mousadik A, Petit R. 1996. High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic to Morocco. *Theoretical and Applied Genetics* **92:** 832–839.

Ewer RF. 1971. The biology and behavior of a free-living population of black rats (*Rattus rattus*). *Animal Behaviour Monographs* **4:** 127–171.

Fountain T, Duvaux L, Horsburgh G, Reinhardt K, Butlin RK. 2014. Human-facilitated metapopulation dynamics in an emerging pest species, *Cimex lectularius*. *Molecular Ecology* **23:** 1071–1084.

Garba M. 2012. Rongeurs urbains et invasion biologique au Niger : écologie des communautés et génétique des populations. Unpubl. PhD Thesis, Université Abdou Moumouni, Niamey, Niger.

Garba M, Dalecky A, Kadaouré I, Kane M, Hima K, Véran S, Gagaré S, Gauthier P, Tatard C, Rossi JP, Dobigny G. 2014. Spatial segregation between invasive and native commensal rodents in an urban environment: a case study in Niamey, Niger. *PLoS ONE* **9:** e110666.

Garza JC, Williamson EG. 2001. Detection of reduction in population size using data from microsatellite loci. *Molecular Ecology* **10:** 305–318.

Goudet J. 1995. Fstat (version 1.2): a computer program to calculate F-statistics. *Journal of Heredity* **86:** 485–486.

Goudet J. 2001. Fstat, a program to estimate and test gene diversities and fixation indices (version 2.9.3). Available at http://www.unil.ch/izea/softwares/fstat.html.

Granjon L, Duplantier JM. 2009. *Les rongeurs de l'Afrique sahélo-soudanienne*. France: Publications Scientifiques IRD MNHN.

Hama B. 1967. *Histoire traditionnelle d'un peule, les Zarma-Songhay*. Présence Africaine, Paris.

Happold DCD. 2013. *Mammals of Africa, volume III: rodents, hares and rabbits*. Bloomsbury Publishing, London.

Hardy OJ, Vekemans X. 2002. SPAGeDI: a versatile computer program to analyze spatial genetic structure at the individual or population levels. *Molecular Ecology Notes* **2:** 618–620.

Ho SY, Shapiro B. 2011. Skyline-plot methods for estimating demographic history from nucleotide sequences. *Molecular Ecology Resources* **11:** 423–434.

Holland BS, Cowie RH. 2007. A geographic mosaic of passive dispersal: population structure in the endemic Hawaiian amber snail *Succinea caduca* (Mighels, 1845). *Molecular Ecology* **16:** 2422–2435.

Ingvarsson PK. 1998. Kin-structured colonization in *Phalacrus substriatus*. *Heredity* **80:** 456–463.

Jacob HJ, Brown DM, Bunker RK, Daly MJ, Dzau VJ, Goodman A, Koike G, Kren V, Kurtz T, Lernmark A, Levan G, Mao YP, Tetterson A, Pravenec M, Simon JS, Szpirer C, Szpirer J, Troliiet MR, Winer ES, Lander ES. 1995. A genetic linkage map of the laboratory rat, *Rattus norvegicus*. *Nature Genetics* **9:** 63–69.

Jombart T. 2008. Adgenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics* **24:** 1403–1405.

Jombart T, Devillard S, Balloux F. 2010. Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genetics* **11:** 1471–2156.

Kalémé PK, Bates JM, Belesi HK, Bowie RCK, Gambalemoke M, Kerbis-Peterhans J, Michaux J, Mwanga JM, Ndara BR, Taylor PJ, van Vuuren BJ. 2011. Origin and putative colonization routes for invasive rodent taxa in the Democratic Republic of Congo. *African Zoology* **46:** 133–145.

Konecny 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. *Molecular Ecology* **22:** 286–300.

Lack JB, Hamilton MJ, Braun JK, Mares MA, Van Den Busche RA. 2013. Comparative phylogeography of invasive *Rattus rattus* and *Rattus norvegicus* in the US reveals distinct colonization histories and dispersal. *Biological Invasions* **15:** 1067–1087.

Leblois R, Pudlo P, Néron J, Bertaux F, Reddy Beeravolu C, Vitalis R, Rousset F. 2014. Maximum-likelihood inference of population size contractions from microsatellite data. *Molecular Biology and Evolution* **31:** 2805–2823.

Lin XD, Guo WP, Wang W, Zou Y, Hao ZY, Zhou DJ, Dong X, Qu YG, Li MH, Tian HF, Wen JF, Plyusnin A, Xu J, Zhang YZ. 2012. Migration of the Norway rats

resulted in the worldwide distribution of Seoul hantavirus today. *Journal of Virology* **86:** 972–981.

Loiseau A, Rahelinirina S, Rahalison L, Konecny A, Duplantier JM, Brouat C. 2008. Isolation and characterization of microsatellites in *Rattus rattus*. *Molecular Ecology Resources* **8:** 915–918.

Loiselle BA, Sork VL, Nason J, Graham C. 1995. Spatial genetic structure of a tropical understory shrub, *Psychotria officinalis* (Rubiaceae). *American Journal of Botanic* **82:** 1420–1425.

Luniak M. 2004. Synurbanization: adaptation of animal wildlife to urban development. In: Shaw WW, Harris LK, VanDruff L eds. *Fourth international urban wildlife symposium*. Tucson, AZ: University of Arizona, 50–55.

Magombi 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. *Journal of Zoology* **299:** 183–190.

Masuzawa T, Okamoto Y, Une Y, Takeuchi T, Tsukagoshi K, Koizumi N, Kawabata H, Ohta S, Yoshikawa Y. 2006. Leptospirosis in squirrels imported from United States to Japan. *Emerging Infectious Diseases* **12:** 1153–1155.

Meerburg B, Singleton GR, Kijlstra H. 2009. Rodentborne diseases and their risks for public health. *Critical Reviews of Microbiology* **35:** 221–270.

Meirmans PG. 2015. Seven common mistakes in population genetics and how to avoid them. *Molecular Ecology* **24:** 3223–3231.

Morse JG, Hoddle MS. 2006. Invasion biology of thrips. *Annual Review of Entomology* **51:** 67–89.

Musser GG, Carleton MD. 2005. Superfamily Muroidea. In: Wilson DE, Carleton MD, eds. *Mammal species of the World: a taxonomic and geographic reference*. Baltimore: John Hopkins University Press, 894–1531.

Nei M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* **89:** 583–590.

Niethammer J. 1975. Zur Taxonomien und Ausbreitungsgeschichte der Hausratte *Rattus rattus*. *Zoologischer Anzeiger* **194:** 405–415.

Pannell JR, Charlesworth B. 1999. Neutral genetic diversity in a metapopulation with recurrent local extinction and recolonization. *Evolution* **53:** 664–676.

R Core Team. 2015. The R project for statistical computing. Available at: https://www.r-project.org/.

Rosevear DR. 1969. *The rodents of West Africa*. London, UK: Trustees of the British Museum (Natural History).

Roura-Pascual N, Hui C, Ikeda T, Leday G, Richardson DM, Carpintero S, Espadaler X, Gomez C, Guénard B, Hartley S, Krushelnycky P, Lester PJ, McGeoch MA, Menke SB, Pedersen JS, Pitt JPW, Reyes J, sander NJ, Suarez AV, Touyama Y, Ward D, Ward PS, Worner SP. 2011. Relative roles of climatic suitability and anthropogenic influence in determining the pattern of spread in a global invader. *Proceedings of the National Academy of Sciences USA* **108:** 220–225.

Rousset F. 2008. GENEPOP'007: a complete re-implementation of the GENEPOP software for Windows and Linux. *Molecular Ecology Resources* **8:** 103–106.

Salifou A. 2010. *Histoire du Niger : époque précoloniale et colonial*. Paris: Nathan.

Seastedt T. 2009. Traits of plan invaders. *Nature* **459:** 783–784.

Storz JF, Beaumont MA. 2002. Testing for genetic evidence of population expansion and contraction: an empirical analysis of microsatellite DNA variation using a hierarchical Bayesian model. *Evolution* **56:** 154–166.

Tollenaere C, Brouat C, Duplantier JM, rahalison L, Rahelinirina S, Pascal M, Moné H, Mouahid G, Leirs H, Cosson JF. 2010. Phylogeography of the introduced species *Rattus rattus* in the Western Indian Ocean with special emphasis on the colonization history of Madagascar. *Journal of Biogeography* **37:** 398–410.

Wade MJ, McCauley DE. 1988. Extinction and recolonization: their effects on the genetic differentiation of local-populations. *Evolution* **42:** 995–1005.

Weir BS, Cockerham CC. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* **38:** 1358–1370.

Whitlock MC, McCauley DE. 1990. Some population genetic consequences of colony formation and extinction – genetic correlations within founding groups. *Evolution* **44:** 1717–1724.

Wilson JUR, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM. 2009. Something in the way you move: dispersal pathways affect invasion success. *Ecology and Evolution* **24:** 136–144.

Woolhouse MEJ, Haydon DT, Antia R. 2005. Emerging pathogens: the epidemiology and evolution of species jumps. *Trends in Ecology and Evolution* **5:** 238–244.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Figure S1. Images of various rat-invaded sites that were sampled for the present study: (A) households on the Corniche Gamkalleye (NCGA); (B) the municipal slaughter house (NGAM); (C) shops along the RN7 in Dosso (DOS); (D) the isolated village of Hamma Dendi along the Niger River (HAM).

Figure S2. Variation in (A) the Bayesian Information criterion for an increasing number of clusters K from 1 to 20 used in K-means clustering, and (B) the proportion of successful predictions according to the number of PCs tested in the cross-validation (1000 repetitions).

Figure S3. DAPC plot from the analyses based on $K = 2$ and $K = 3$. Each bar represents an individual colored according to its probability to belong to a given cluster.