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ORIGINAL ARTICLE

Tempo and mode in biological invasions: exotic rodents in the small mammal community of Bamako (Mali)

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Abstract

Small mammals are regular inhabitants of urban centres worldwide. The house mouse *Mus musculus* and rats of the genus *Rattus*, major invasive alien species, are increasingly present, particularly in West Africa where house mice and black rats (*Rattus rattus*) are frequently met in commensal small mammal communities. We studied the case of Bamako the capital of Mali, through intensive city-wide trapping, and found a strong dominance of invasive alien species over native ones, with house mouse representing more than half and the brown rat (*Rattus norvegicus*) nearly one quarter of the captures. Shrews (*Crocidura olivieri*) and multimammate rats (*Mastomys natalensis*) represented the main native species still found in the city. The spatial and ecological determinants of these species' distribution were analysed, showing segregation between species at different spatial scales. At the housing unit scale, *M. musculus* and *M. natalensis* appeared associated with inner parts of buildings, while *R. norvegicus* and *C. olivieri* occured at the interface between the indoor and outdoor environments. At the city scale, invasive species were more abundant in older quarters than in more recent peripheral ones. This was particularly true for the house mouse which probably colonized Bamako during the 21st century, while the brown and the black rats had done so a century before. This process of invasion of a native community of small mammals by cosmopolitan invasive species is discussed in a regional context, as are the potential consequences it may have in terms of public health and social well-being.

Keywords Invasive species · *Mus* · *Rattus* · Species interactions · Urbanization · West Africa

Introduction

Urban life is changing at an accelerating pace, reflecting the trend of increasing urbanization (i.e., human-driven modification of natural habitats) worldwide (Johnson and Munshi-South 2017). This is even more true in tropical areas, mainly in Asia and Africa, which account for nearly 90% of current global urbanization (UN Habitat 2019; Dobigny and Morand 2022). In these regions, the urban transition is often rapid and difficult to control, leading to significant and often irreversible changes that exert strong selective pressures on local biodiversity (Collins et al. 2021; Verrelli et al. 2022). Therefore, urbanization is likely to alter the eco-evolutionary dynamics of local biological communities, making urban socio-ecosystems and their surrounding peripheries particularly well-suited terrains for the development of new eco-evolutionary pathways and scenarios (Alberti et al. 2020). Among the substantial environmental changes induced by urban transformation, biological invasions (i.e., successful introduction, spread and impact of non-native species in new areas) stand out as particularly emblematic (Cadotte et al. 2017). Indeed, although the positive relationship between urbanization and biological invasions is not always systematic (Gippet et al. 2022), it is well established that *(i)* urban areas serve as major gateways for

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non-native species due to the concentration of human activities, and *(ii)* urban-modified conditions favour the survival, reproduction, and spread of these species (Santana Marques et al. 2020).

However, biological invasions remain largely understudied in urbanizing socio-ecosystems, particularly in the Global South where non-native species raise key questions about invasion patterns and processes, as well as management strategies that need to be implemented in these contexts (Gaertner et al. 2017; Collins et al. 2021; Nuñez et al. 2022). Yet, uncovering the patterns and pathways of introduction of non-native species in urban areas is essential to adequately estimate invasion rates and effectively anticipate the socio-ecological impacts of these species (Everett 2000; Novoa et al. 2020). In particular, a crucial challenge is to decipher the spatiotemporal dynamics and eco-evolutionary consequences of interactions between invasive and native species in the colonized areas, both at community and ecosystem scales (Mooney and Cleland 2001; Dubart et al. 2019). Addressing this question requires solid data on the distribution and ecological requirements of species within the communities and guilds into which invasive species enter, as well as detailed information on the sequence of their arrival and spread.

Rats of the genus *Rattus* (and in particular *R. norvegicus* the brown rat and *R. rattus* the black rat) and mice of the genus *Mus* (especially *Mus musculus* the house mouse) are unanimously recognized as being among the “worst” invasive alien species in the world (Lowe et al. 2000; Capizzi et al. 2014; IPBES 2023), from their Asian centres of origin (Aplin et al. 2011; Suzuki et al. 2013; Zeng et al. 2018). Their relatively small size, reproductive potential, the breadth of their ecological niche and their adaptation to commensalism (*sensu* Hulme-Beaman et al. 2016) make them particularly susceptible to being transported and spread by humans across the world. Although they can invade outdoor habitats within their invasion ranges, these species particularly thrive in urban environments, where they typically become the dominant part of small mammal communities. In the New World, this dominance is evident in various cities where small mammal communities have been studied, such as Rio Cuarto and Buenos Aires (Argentina: Castillo et al. 2003; Cavia et al. 2009) and Sao Paulo (Brasil: Masi et al. 2009) in South America, or Vancouver and New Orleans in North America (Himsworth et al. 2014; Peterson et al. 2020). However, their ecology in urban habitats remains poorly understood (see Feng and Himsworth 2014 for *Rattus*).

In West Africa, these three species show differential success according to syntheses at the continental scale, with the black rat being much more widespread than the house mouse, and the brown rat being even less common (Kaleme et al. 2011; Happold 2013; Wilson et al. 2017). Brought to the coasts by sailing ships for centuries, they first settled in coastal colonial trading posts before penetrating into the interior areas following the main transport routes for goods and people, whether rivers, railways or roads (Rosevear 1969). This scenario has been well documented in Senegal where the invasion pathways of the black rat (Duplantier et al. 1991; Konečný et al. 2013; Lucaccioni et al. 2016) and the house mouse (Dalecky et al. 2015; Lippens et al. 2017) are now well known. The resulting distribution pattern of commensal small mammals in Senegal currently shows an overwhelming dominance of these two non-native species over native ones throughout the country (Dalecky et al. 2015; Granjon et al. 2021, 2023), including in the capital city of Dakar (Stragier et al. 2022). The brown rat appears to be present only in Dakar, Saint-Louis, and scattered localities along the Senegal River (Stragier and Dalecky unpubl. data). In Benin, the black rat represents by far the main small mammal present in the economic capital of Cotonou (Houemenou et al. 2014; Hima et al. 2019), and remains dominant along the road linking Cotonou to Niamey in Niger (Hima et al. 2019). Only in the Port of Cotonou are the brown rat and the house mouse present at high levels of abundance (Badou et al. 2024). In Abidjan, the economic capital of Côte d’Ivoire, the black rat and the house mouse dominate the small mammal community in the large commune of Yopougon, with the native multimammate rat *Mastomys natalensis* remaining in appreciable numbers only in the most deprived quarters (Akpatou et al. 2018). The situation in landlocked countries of West Africa is less well known, except in Niger where a comprehensive programme on commensal small mammals was recently conducted. In the early 2010s, Garba et al. (2014) showed the dominance of native *M. natalensis* over invasive *R. rattus* and *M. musculus* in the capital Niamey. The latter species were then confined to certain quarters of the city centre. However, the black rat currently appears to be invading quarters of the city where it was absent a decade ago (Danzabarma et al. 2025).

Here, we aim to provide the first description of the small mammal community of Bamako, the capital of Mali, which is a landlocked country of West Africa, bordered by Burkina-Faso and Niger to the East, Senegal to the West and Côte d’Ivoire and Guinea to the South. During the colonial period of “French West Africa” (1895–1958), and even during the first decades following Mali’s independence, most imports to Bamako originated from France via Senegal. Economic liberalization since the 1990s and the complete urbanization of the Bamako district at the turn of the twenty-first century have been accompanied by the proliferation of subregional trade, with Senegal and Côte d’Ivoire playing a major role as contemporary suppliers of imported goods and materials to Mali, through their respective ports and rail and road transport networks.

As for their invasive alien rodent species, there are a few recent mentions of *Rattus* spp. and *Mus musculus* presence in this city (Meinig 2000; Granjon and Duplantier 2009; Bondaz 2020), suggesting that invasion processes are at work within this urban small mammal community. However, no study has investigated the link between the urban transition (past and present) and changes in the local small mammal community. In this context, our specific objectives were: i) to describe the composition and relative abundance of species (native and/or invasive) at the community scale; ii) to analyse how these species occupy and share space at the city scale; iii) to decipher the sequence and timing of the arrival and establishment of invasive species in the city during its growth.

Materials and methods

Study area

Bamako is located in the southwest of Mali. Occupied since prehistoric times, it only emerged as such between the 18th and 19th centuries. It had fewer than 1,000 inhabitants at the start of the French colonial period in 1883 (Philippe 2009), around 130,000 at the time of independence in 1960, nearly 2 million at the 2009 population census (Diarra 2015), and more than 4.2 million at the 2022 census. With a record annual growth rate for Africa of 5–6% since the 1990s, the population continues to increase steadily, within administrative/geographic limits which are themselves the subject of debate (Bertrand 2021). A prominent feature of Bamako is the Niger River which flows through the city from west to east. The focus here is on the "Bamako District" (as understood until 2022 at least), which comprises six communes. Four of them (communes I to IV, from east to west) are located on the left bank of Niger River. Communes II and III correspond to the city's initial development zone (during the colonial era). The larger communes V and VI, located on the right bank of the river, developed more recently, following the construction of bridges connecting the two banks (in 1960 and 1992, respectively, for the first two). Details on the administrative division of Bamako and its surrounding areas, as well as characteristics of Bamako's communes and quarters, are provided in Diarra (2015) and Bertrand (2021).

The trapping plan involved sampling of two quarters per commune in the four communes on the left bank of the river, and three quarters per commune on the right bank of the river, to account for the larger size and population of communes on the right bank (Bertrand 2021, Suppl. Information: Table S1). Quarters were selected to represent intra-communal diversity in terms of urbanization and socioeconomic characteristics, ensuring that they were not too close to each other to ensure good spatial coverage of the city. In sufficiently large quarters (i.e., most), two distinct sectors were sampled, separated by at least a few hundred metres. The sampled housing units were chosen randomly, spaced at least 50 m apart.

Trapping methodology

Trapping campaigns (six days each) took place between October 2021 and March 2023 (Suppl. Information: Table S2), each involving between four and six people. Elements of the trapping procedures followed here have been previously described by Dalecky et al. (2015), Diagne et al. (2021) and Granjon et al. (2021, 2023). Briefly, two types of live traps were used: locally manufactured wire mesh live traps (8.5 × 8.5 × 26.5 cm) and Sherman (H.B. Sherman Traps, Inc., Tallahassee, Florida, USA) folding box traps (8 × 9 × 23 cm), which have shown their complementarity for capturing different species (Granjon et al. 2021). The traps were set inside housing or working units (e.g., residential houses, warehouses, shops and workshops), potentially including courtyards and their ancillary areas (e.g., external staircases and verandas). At each site, the traps were set for between one and three consecutive nights in different rooms or parts of housing/working units (4.1 on average, and between one and six generally). Most of the time, two traps (one of each type) were placed in each room, generally on the floor and sometimes on furniture or even high up (above wall, roof frame …). We generally did not place traps in adjacent rooms to limit the potential attraction of baits from one room to another. Traps were checked and (re)baited once a day with peanut butter spread on a slice of fresh onion.

Data collection

Captured rodents were morphologically identified (according to the keys provided by Granjon and Duplantier 2009), euthanized, then weighed to the nearest 0.5 g, sexed and dissected within hours of capture. In a few cases, molecular data were generated to enable unambiguous species identification (following procedures described in Dobigny et al. 2011).

When installing the traps, each sampled room was georeferenced (GPS recording with an accuracy of ± 5 m). The rooms were classified into ten "room types," namely: bedrooms, corridors/staircases, garages/sheds, kitchens, living rooms, shops, stock rooms, verandas, workshops and yards. In the rooms, the presence/absence of food and the nature (materials) of the floor, walls and ceiling (see modalities in the legend of Suppl. Information: Fig S1) were noted. This information constitutes markers of the type of building (more or less modern/of more or less high standing) in which the small mammals studied live in contact with their human hosts.

Data analysis

Most analyses were done in R (R Core Team 2024). First, we assessed the quality of our sampling and the representativeness of the collected specimens compared to the actual sampled communities. Rarefaction curves were constructed for the entire dataset and specimen samples from each quarter, using the R package *iNEXT* (Hsieh et al. 2025), on the data presented in Suppl. Information: Table S2.

Second, trapping results (number of individuals captured) were related to trapping effort (expressed as number of trap-nights) for inter-species and/or inter-quarter comparisons. Pearson's Chi-squared tests were performed on contingency tables, which document the numbers of captures of:

i) the five main species in each of the two types of traps used, to assess the relative efficiency of the traps for the captured species;

ii) the five main species in three sets of quarters defined according to their urbanization period (according to the typology of Keita 2018; Suppl. Information: Table S1): "ancient and pre-independence" (including Niaréla in Commune II, Bamaco Coura and Ouolofobougou in Commune III); "post-independence to 1979" (including Fadjiguila in Commune I, Hippodrome in Commune II, Lafiabougou in Commune IV, Badalabougou, Bacodjicoroni and Sabalibougou in Commune V and Niamakoro in Commune VI); "recent" (including Sotuba in Commune I, Kalabanbougou in Commune IV, and Missabougou, and Sokorodji in Commune VI). An alternative scheme where Sokorodji is classified in the "post-independence to 1979" period and Bacodjicoroni in the "recent" one (following Diarra 2015; Bertrand 2021) was also tested;

iii) the four main species in the ten room types surveyed (see above) to assess the habitat preferences of the captured species (the numbers of *R. rattus* and *C. gambianus* were too low to be included).

Table 1 Niche breadth (on the diagonal) and niche overlap between species pairs

	Crocidura olivieri	*Mastomys natalensis*	*Mus musculus*	*Rattus norvegicus*	*Rattus rattus*
Crocidura olivieri	*4.6*	0.40	0.49	0.95	0.70
Mastomys natalensis		*5.0*	0.98	0.48	0.58
Mus musculus			*6.0*	0.59	0.72
Rattus norvegicus				*4.5*	0.86
Rattus rattus					*4.5*

Calculated from their frequencies of capture in the different "room types"

Then, the distribution of species in the different room types (considered as integrative descriptors of the microhabitat) was used to describe the "habitat" component of the species' ecological niche, via two indices (Pianka 1973): i) niche breadth quantified using Simpson's index of diversity $B = 1/\sum p_i^2$, where p_i is the proportion of the ith room type actually used by the species; ii) niche overlap between species pairs based upon Levins index $O_{ij} = \sum p_{ij} p_{ik} / \sqrt{(\sum p_{ij}^2 \sum p_{ik}^2)}$, where p_{ij} and p_{ik} are the proportions of the ith room type used by the jth and the kth species, respectively (Levins 1968).

Third, we focused on the most abundant exotic invasive species to test the hypothesis that these species would spread from the historic city centre (which generally serves as an invasion bridgehead) to more or less distant peripheries over time. To do so, we first defined a "hypothetical point of introduction" (HPI) of these invasive species based on the city's construction history as recounted and mapped by Philippe (2009): we placed it by hand between the historic colonial quarters of Ouolofobougou, BamakoCoura and Niarela, close to Bamako's railway station and main market (see first row of Table 1, and Fig. 1). Then, we plotted the percentages of invasive and native species relative to all captures in all quarters against the distance of the barycentre of these quarters relative to the location of the HPI. Quarter barycentres were calculated as the average longitude and latitude of all captures recorded in each quarter.

Fourth, we examined co-occurrence patterns by analysing presence–absence matrices with "null model" randomization tests of marginal row and column totals (Gotelli 2000; Gotelli and Ulrich 2010) using the *pairs* software (Ulrich 2008) at the quarter level. Aggregated/random/segregated pattern of species pairwise co-occurrence was inferred from the *p*-value associated with the Z-score for each pair of species, in each of the 14 quarters (using houses as sites). We used the "fixed row–fixed column" and "fixed row–equiprobable column" randomization algorithms to generate randomized matrices that served as null models as recommended by Gotelli (2000), and ran the models with 10,000 iterations.

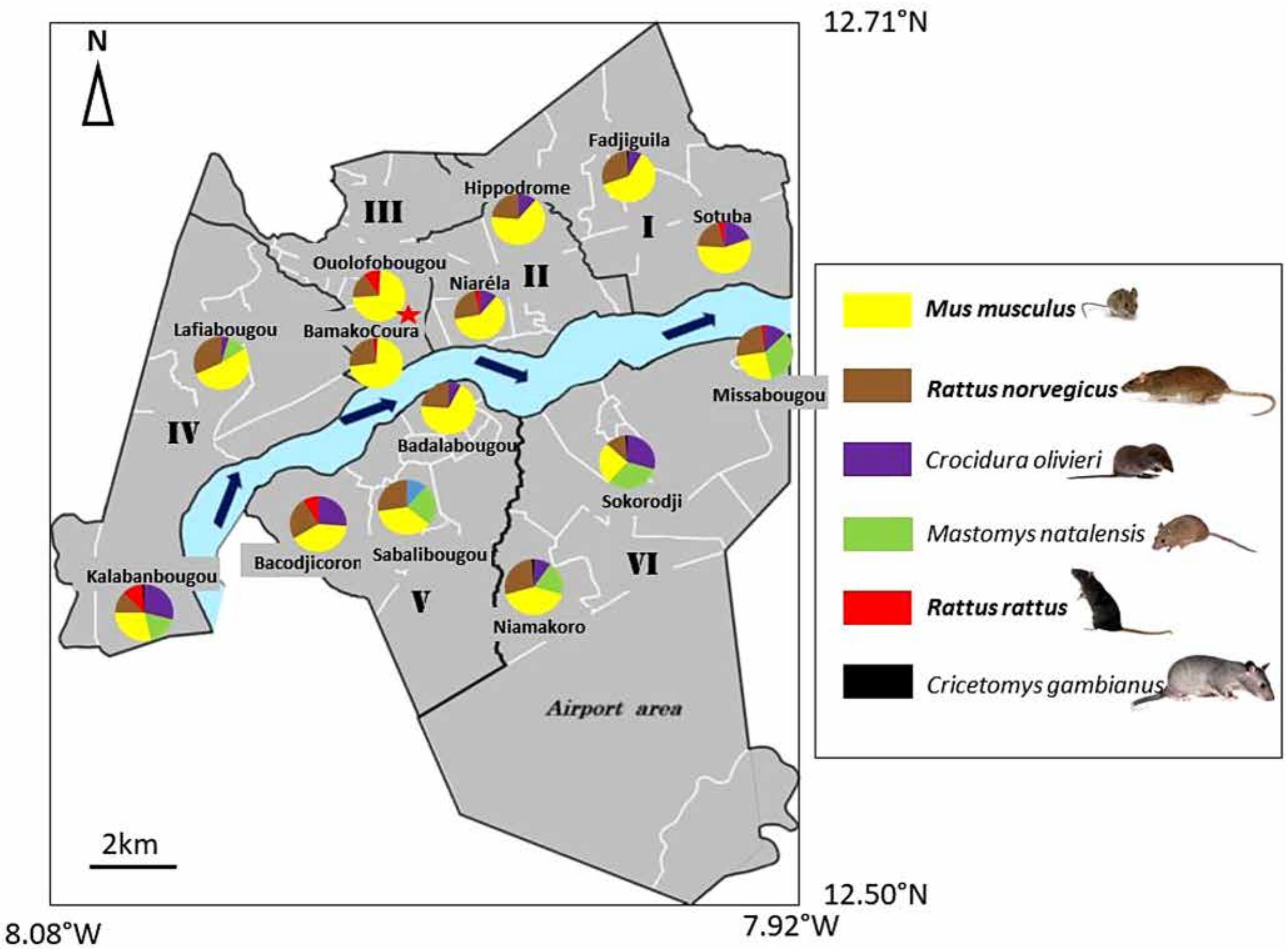

Fig. 1 Distribution of commensal small mammal captures in 14 quarters of Bamako district. Numbers of houses and rooms sampled per quarter are given in Table S2. Invasive exotic species in bold in the legend. I to VI refer to commune numbers, and the red star to the "hypothetical point of introduction" of exotic invasive species in the historic city centre

Finally, Generalized Linear Mixed Models (GLMMs) were used to assess the influence of environmental variables on the distribution of each captured species within the small mammal community, using the R package *lme4* (Bates et al. 2015). To ensure adequate statistical power, analyses focused on the four most abundant species. Given the observed interspecific segregation in the small mammal community (as detailed in the Results), each species was analysed separately. For each model, the number of individuals captured per sampled room was used as a response variable, assuming a Poisson distribution with a log link function. Residual diagnostics (see below) showed no sign of overdispersion or distributional issues, so alternative distributions (e.g., quasi-Poisson or negative binomial) were not necessary. The sampling house was considered as a random effect to account for potential non-independence of small mammals captured within the same trapping sites. A model selection procedure (Burnham and Anderson 2013) was performed using the 'dredged" function in the R package *MuMIn* (Barton and Barton 2019). We used the Akaike information criterion with correction for finite sample sizes (AICc) as a quantitative indicator for comparing all models generated (Howard-Spink et al. 2024). The following predictors were included in each model:

(i) 'quarter' to represent socio-environmental parameters at the local scale [14 modalities, see Fig. 1 for details];
(ii) 'urbanization period', with three modalities: *pre-independence*, *post-independence*, and *recent*, following Keita (2018) as a proxy of the city's history (undergoing ongoing urban transition) as well as of the potential spread of invasive species (whose abundance generally increases with age and/or the level of urban transition);
(iii) 'room type' [10 modalities, see list above]
(iv) 'food stock' [two modalities: *presence* or *absence* of food in the room]
(v) 'habitat type': we considered the quantitative data derived from the axis 1 of a multiple correspondence

analysis (MCA) applied to the information recorded during trapping sessions on building materials [*floor*, *walls*, and *ceiling*]; this axis appeared to represent a habitat gradient from outdoor to indoor areas in the domestic space (Suppl. Information: Fig. S5).

Models with all possible combinations of these predictors were generated, and those with a ΔAICc < 2 relative to the model with the lowest AICc were selected as final candidate models. The most parsimonious of these models (i.e., the model with the fewest predictors and the highest variance explained) was selected. We assessed multicollinearity among fixed effects using variance inflation factors (VIFs), and all values were below conventional thresholds (VIF < 3), indicating that multicollinearity was not of concern. The assumptions of each final model were evaluated graphically using residual diagnostics, including quantile-quantile plots of residuals versus predicted values, as implemented in the R package *DHARMa* (Hartig 2020). To assess the significance of the explanatory variables, deletion testing and log-likelihood ratio (LRT) tests were performed. When significant multimodal predictors were identified, post-hoc comparisons were carried out using pairwise Wilcoxon rank sum tests (PWT), applying a 95% family-wise confidence level.

Results

Trapping results and sampling representativeness

The overall trapping effort over the 14 targeted quarters represented 8149 trap-nights (4060 with wire-mesh traps, and 4089 with Sherman traps). A total of 1446 individuals belonging to six small mammal species were captured. The overall capture success for small mammals was 17.7%, but rose to 22% when the 1611 traps found “closed and empty” (i.e. having been triggered independently of a capture) were not included in the trapping effort. Wire-mesh traps were found more often closed and empty than Sherman traps (938 out of 4060 vs 673 out of 4089, i.e. 23.1% vs 16.5%, respectively; Pearson’s Chi-squared test$_{1df}$ = 37.7; $p < 0.001$).

House mice accounted for more than half of the captures with 742 individuals (51.3%), followed by brown rats (337 individuals; 23.4%), the native shrew *Crocidura olivieri* (181 individuals; 12.6%) and the multimammate rat *Mastomys natalensis* (140 individuals; 9.7%). Black rats (42 individuals; 2.9%) and Gambian pouched rats (*Cricetomys gambianus*; four individuals; 0.3%) completed the list of small mammals captured (Suppl. Information: Table S2). Non-target species included four unidentified toads, 20 lizards, and seven geckos (probably *Agama agama* and *Tarentola parvicarinata*, respectively).

The rarefaction curves tended to reach an asymptote, characteristics of well-sampled assemblages, at both the quarter and city-wide scales (Fig. 2). This was observed regardless of trapping effort (405 trap-nights in Ouolofobougou vs 773 in Bacodjicoroni). Based on this result, no additional species is expected in the strictly domestic habitat of the city.

On the y axis, species diversity is expressed as the number of species

As for the trappability of the different species in these two types of traps, it clearly appeared that the different species were not captured in the same proportions in the wire-mesh and Sherman traps: the house mouse was nearly eight times more often caught in the Sherman traps than in wire-mesh traps, while the brown rat and the black rat were four and five times more often captured in the wire-mesh traps than in the Sherman traps, respectively. *Crocidura olivieri* and *M. natalensis* were captured twice as often in Sherman traps than in wire-mesh traps. (Suppl. Information: Table S2; Pearson’s Chi-squared test$_{4df}$ = 524.7; $p < 0.001$ for the five more abundant small mammal species, i.e. excluding *C. gambianus*).

Spatial distribution, habitat correlates and species co-occurrence

The house mouse, brown rat and shrew *C. olivieri* were captured in all quarters of Bamako, while the black rat and *M. natalensis* were found in only half of them. Interestingly, the house mouse accounted for more than half of the catches in seven of the eight sampled quarters on the left bank of the Niger River, while it accounted for less than half in five of the six quarters on the right bank. The exceptions were Kalabanbougou, an peripheral quarter southeast of commune IV on the left bank (which had the most balanced community in terms of species diversity), on the one hand, and Badalabougou, the oldest inhabited quarter on the right bank, on the other. Conversely, *M. natalensis* occured in significant numbers mostly in quarters of the right bank, with the exception of Kalabanbougou (Fig. 1 and Suppl. Information: Table S2).

Considered within the frame of the historical typology of Bamako’s quarters (Keita 2018), these distribution trends clearly showed a non-random pattern (Pearson’s Chi-squared test = 209.9, $p < 0.001$), with a sharp decrease of relative abundance of the house mouse between older quarters where the species nearly reaches 70% of total captures and more recent ones where it represents only a third. At the same time, the proportions of native *M. natalensis* and *C. olivieri* increased along the same gradient (from 0% and 4%

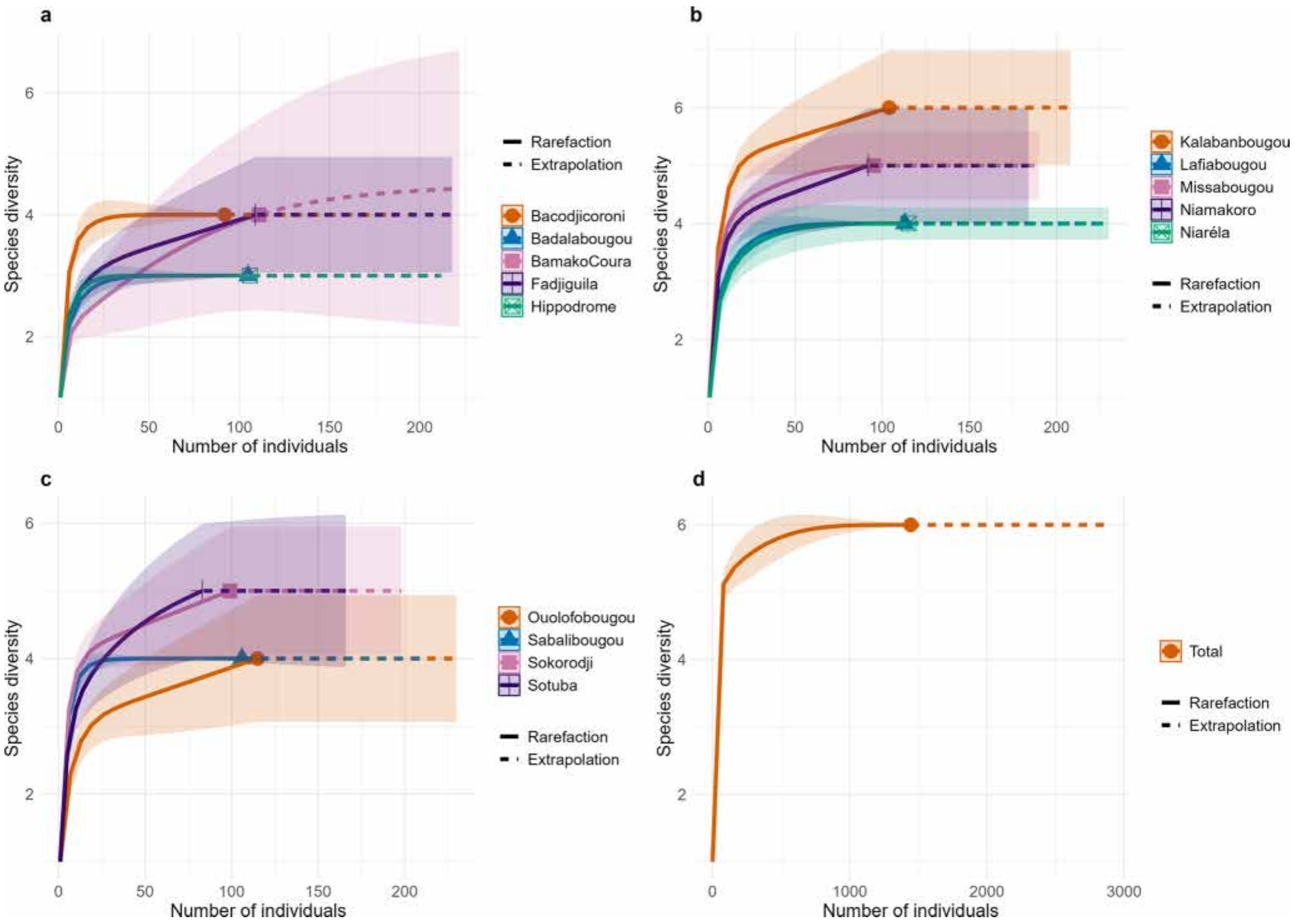

Fig. 2 Sample size-based rarefaction and extrapolation sampling curves, using iNEXT software: (**a**), (**b**) and (**c**) for the 14 quarters sampled for their small mammal communities; (**d**) for Bamako as a whole using the entire dataset

to more than 20% for each, respectively). The relative share of the two *Rattus* species showed less variability and no trend related to quarter age (Fig. 3). The same trends were observed with the alternative scheme where Sokorodji and Bacodjicoroni are classified in different urbanization timing periods (see Materials and Methods).

At the quarter scale, the same pattern was illustrated by i) the significantly negative and positive correlations between the relative frequency of the house mouse and *M. natalensis*, respectively (Figs. 4a and 4b), and the distance of the barycentre of the corresponding quarters to HPI of invasive species in the historic city centre of Bamako (Pearson's correlation, $p = 0.002$ and $p = 0.034$); ii) the absence of significant correlation in the case of the brown rat ($p = 0.603$; Fig. 4c).

The house mouse showed the highest niche breadth value calculated from capture frequencies in the different room types recorded ($B = 6$ vs 4.5–5 for the other species). It also displayed the highest value of niche overlap, with *M. natalensis* ($O_{ij} = 0.98$), closely followed by the pair *R. norvegicus*/*C. olivieri* ($O_{ij} = 0.95$). These two pairs of species showed the lowest values of overlap with each other ($0.48 < O_{ij} < 0.59$), meaning that each of them tended to be preferentially caught in a distinct set of rooms (Table 1).

At the scale of each quarter, co-occurrence analyses mainly revealed significant cases of segregation (16 in total) between species pairs, meaning that species were captured less than expected in the same house. This was obtained mainly using the "fixed rows – equiprobable columns" randomization scheme, particularly suited to our data, which can be considered as "standardized samples collected in areas of [rather] homogenous habitat" (SIM2 scheme in Gotelli 2000). Interestingly, these cases of segregation mainly involved the house mouse, with all other species except the black rat. The brown rat and *M. natalensis* also appeared segregated in three quarters. None of these segregation cases occurred in the three "ancient" quarters (*sensu* Keita 2018), which all showed random co-occurrence between species. Indeed, the few aggregative patterns observed (all using the "fixed rows – fixed columns" randomization scheme) were also found in relatively recent quarters (Table 2).

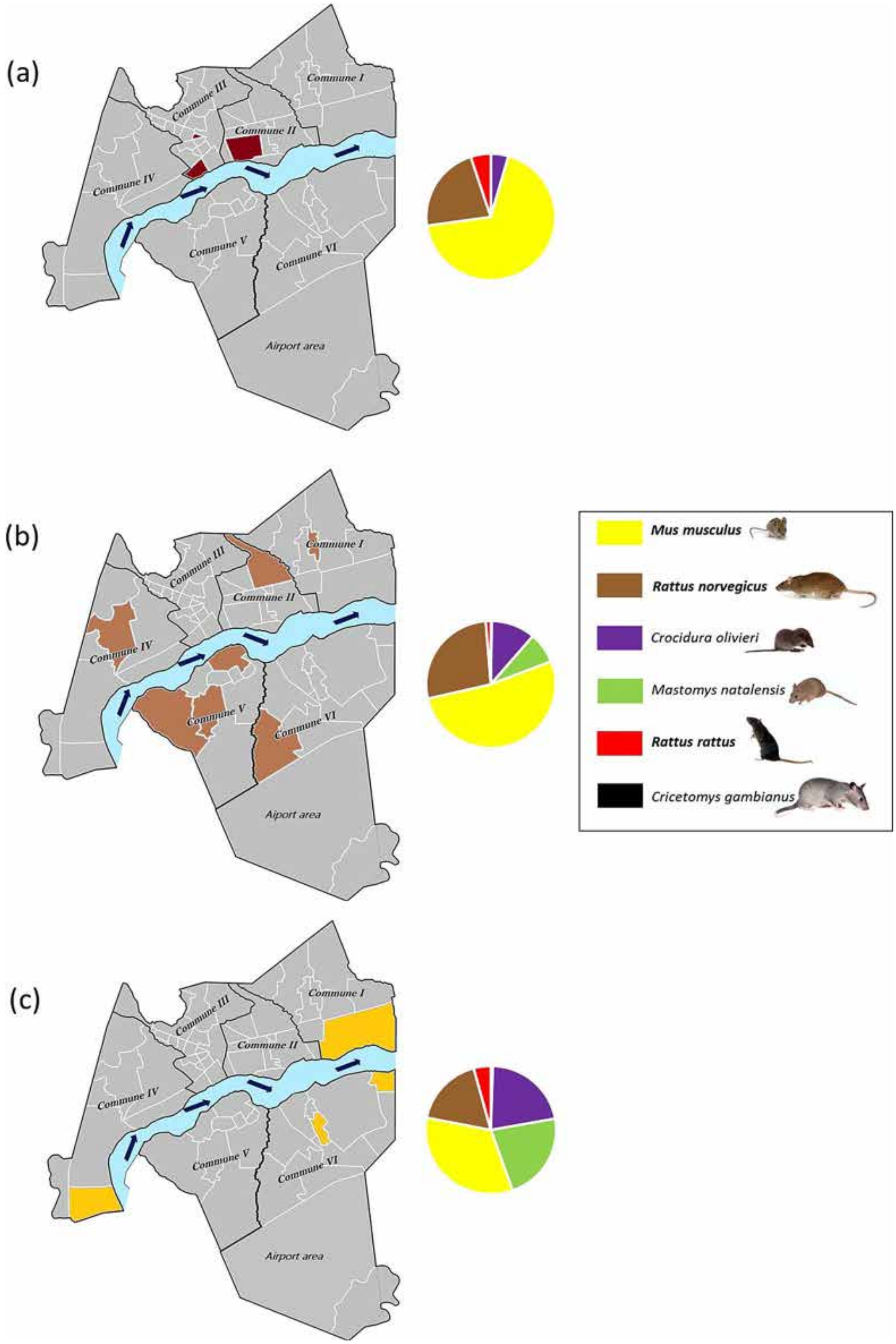

Fig. 3 Relative frequencies of the commensal small mammals in age-classified quarters of Bamako: (**a**) ancient, (**b**) independence-to-1979, and (**c**) recent quarters

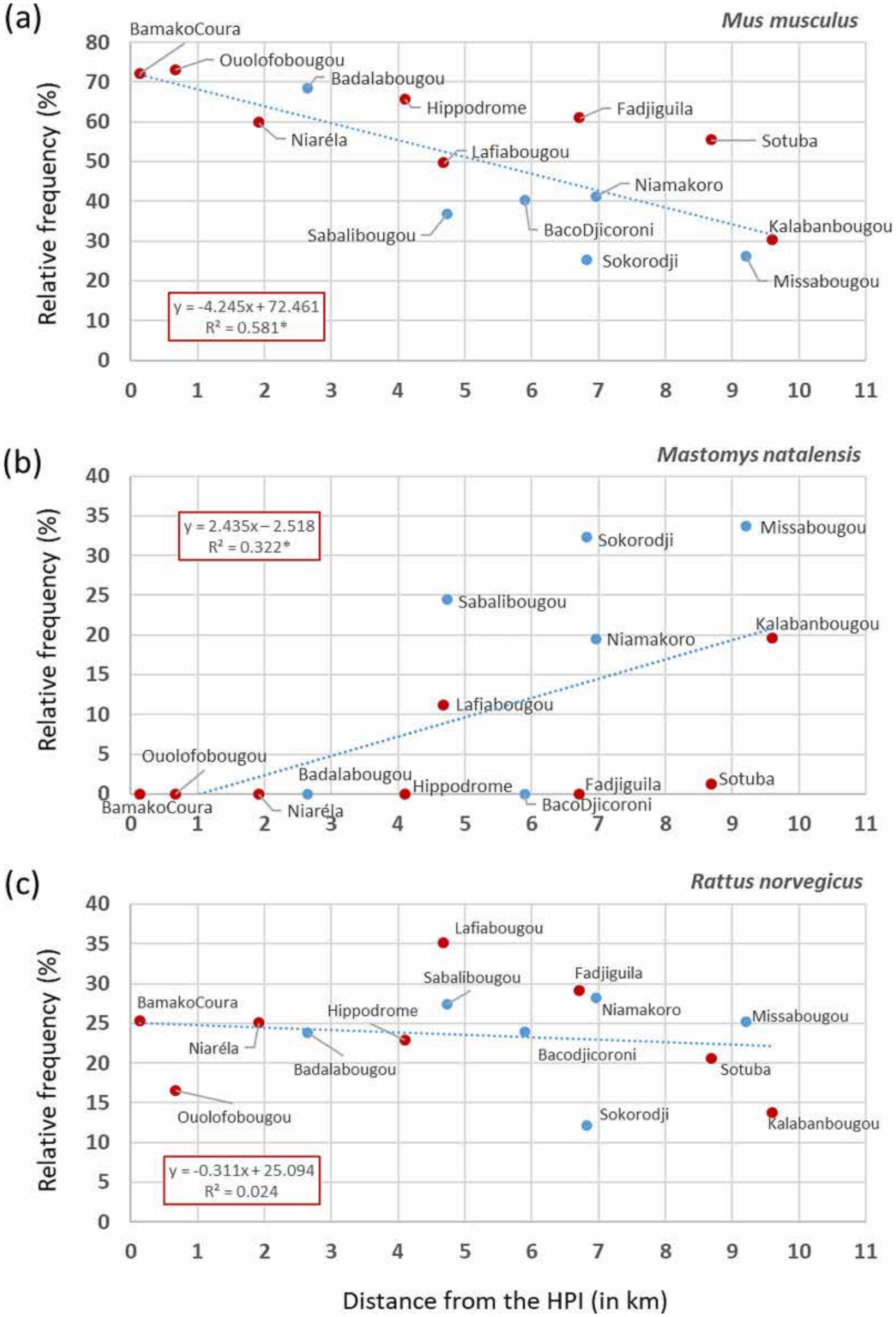

Fig. 4 Relative frequencies of *Mus musculus* (**a**), *mastomys natalensis* (**b**) and *Rattus norvegicus* (**c**) vs. distance from the HPI in the city quarters. HPI = hypothetical point of introduction of invasive species in Bamako; red and blue dots: quarters of the left and right bank of Niger River, respectively. Regression equations and coefficients of determination of the regression lines withing the red rectangles (* indicates statistically significant correlations)

Table 2 Co-occurrence patterns between species pairs in the 14 quarters sampled in Bamako

	Invasive species			Native species	
	Mus musculus	*Rattus norvegicus*	*Rattus rattus*	*Mastomys natalensis*	*Crocidura olivieri*
Mus musculus	-	Bacodjicoroni (post) Fadjiguila (post) Hippodrome (post) Lafiabougou (post) Missabougou (rec)		Kalabanbougou (rec) Niamakoro (post) Sabalibougou (post) Sokorodji (rec)	Bacodjocoroni (post) Hippodrome (post) Sokorodji (rec)
Rattus norvegicus		-		Missabougou* (rec) Niamakoro (post) Sabalibougou (post)	
Rattus rattus	Bacodjicoroni (post) Missabougou (rec)		-		
Mastomys natalensis				-	Sabalibougou (post)
Crocidura olivieri		Sabalibougou (post)			-

Segregation above diagonal, aggregation below diagonal; all segregation cases with f-e randomization; all aggregation cases and *R. norvegicus*/*M. natalensis* segregation in Missabougou* with f-f randomization (“pre” = pre-independance, “post” = post-independance, “rec” = recent)

Table 3 Distribution of the four main commensal small mammal species within the ten room types defined

	Crocidura olivieri	*Mastomys natalensis*	*Mus musculus*	*Rattus norvegicus*
Bedrooms	**8 (37)**	51 *(29)*	212 *(152)*	**15 (69)**
Living rooms	3 *(13)*	16 *(11)*	84 *(56)*	**2 (25)**
Stock rooms	19 *(35)*	25 *(28)*	160 *(146)*	72 *(67)*
Verandas	0 *(10)*	10 *(8)*	51 *(42)*	18 *(19)*
Kitchens	28 *(19)*	10 *(15)*	63 *(81)*	51 *(37)*
Garages/sheds	**16 (5)**	0 *(4)*	13 *(20)*	9 *(9)*
Corridors/stairs	**31 (15)**	7 *(12)*	44 *(63)*	36 *(29)*
Yards	**66 (33)**	9 *(26)*	**58 (136)**	**124 (62)**
Workshops	3 *(2)*	1 *(2)*	13 *(10)*	1 *(4)*
Shops	3 *(8)*	11 *(6)*	41 *(34)*	9 *(15)*

Rooms organized according to an indoor-outdoor gradient of housing units (from bedrooms to yards; workshops and shops are independent working units). Between brackets, expected numbers under the hypothesis of independence of the two variables (in bold the major contributions to Chi^2 in terms of deficit and excess of observed captures relative to expected ones)

Table 4 Summary of the most parsimonious generalized linear mixed models (GLMMs – Poisson distribution with a log link function) finally selected

Response variable	Dataset considered	Δ AICc	Predictors selected	LRT	*P*-**value**
Abundance (i.e. number of rodents captured within a single room)	*M. musculus*	0.01	habitat type	84.74	< 0.001
			quarter	143.27	< 0.001
	R. norvegicus	0	food stock	5.16	0.023
			habitat type	8.94	0.003
			room type	76.72	< 0.001
			urbanization period	21.21	< 0.001
	M. natalensis	0	habitat type	31.76	< 0.001
	C. olivieri	0.49	habitat type	13.73	< 0.001
			quarter	41.99	< 0.001
			room type	45.83	< 0.001

The sampling house was considered as a random factor. AICc: Akaike’s information criterion corrected for finite sample size. Δ: difference between the model selected and the model with the lowest AICc. LRT: Likelihood-ratio test

At an even finer scale, the overall habitat preferences of the four more abundant small mammal species in terms of the parts of the housing and working units they occupied deviated significantly from a random pattern (Table 3; Pearson’s Chi-squared test$_{27\text{df}} = 414.8$; $p < 0.001$). The house mouse and *M. natalensis* showed similar distributions with an excess of captures in bedrooms (and to a lesser extent living rooms), i.e., the innermost parts of houses, and a deficit of captures in yards that represent the outdoor habitats of the housing units. The brown rat and the shrew *C. olivieri* showed the exact opposite pattern, being much more often than expected captured in yards (and for *C. olivieri* also in garages and corridors/stairs representing other partially outdoor habitats), and rarely in bedrooms and living rooms.

Main predictors of rodent abundance

The GLMM revealed that the most important variables explaining the abundance of captured rodent species at the room scale were *(i)* ‘habitat type’ for all species; *(ii)* ‘quarter’ for *M. musculus* and *C. olivieri*; *(iii)* ‘room type’ for *R. norvegicus* and *C. olivieri*; and *(iv)* ‘food stock’ and ‘urbanization period’ for *R. norvegicus* only (see Table 4 for a detailed and quantitative description of the most parsimonious models selected for each species). Overall, our analyses confirmed the general spatial segregation trends highlighted above at the house scale. Indeed, *M. musculus* and *M. natalensis* were mainly captured in indoor habitats, while *R. norvegicus* and *C. olivieri* were mainly captured in outdoor habitats, especially in yards. This spatial pattern likely helps explain the positive association found between *R. norvegicus* abundance and locations without food stock. Finally, *R.*

norvegicus was less abundant in recent quarters compared to ancient and post-independence ones (note that this latter relationship disappears when the alternative classification of quarters in terms of urbanization period is chosen).

Discussion

Methodological considerations

The differential trappability between species in the two types of traps used was consistent with what was observed in Senegal for the house mouse, the shrew *C. olivieri* and the multimammate rat *M. natalensis* (mainly captured in Sherman traps), as well as the black rat (mainly captured in wire-mesh traps; Granjon et al. 2021). This new set of results tends to confirm the complementarity of the two trap types used to sample commensal small mammal communities in West Africa, as illustrated by rarefaction curves, and already discussed in Granjon et al. (2021, 2023).

Overall, the trapping success rates recorded in Bamako were lower than those found in Granjon et al. (2021) in communities of commensal small mammal sampled according to exactly the same protocols in villages and towns of southern Senegal (22% and 17.7% vs. 28.4% and 24.1% when "closed and empty" traps are taken into account or not, respectively). These differences are likely linked to i) the higher percentage of traps found "closed and empty" in Bamako (where this percentage reached almost 20% while it was barely above 15% in Southern Senegal, Granjon et al. 2021, ii) the higher degree of trap disturbance in this very densely populated city, and iii) the interactions between these two causes. As in Senegal, wire-mesh traps were found more often closed and empty than Sherman traps.

A diverse, yet segregated small mammal community

Six species were captured during this survey. Trapping results clearly show that Bamako is heavily invaded by exotic rodents, which represent 77.5% of the whole small mammal community. With more than half of the captured specimens, the house mouse appears to be the dominant species, just as in Dakar where its share is even higher (more than 80% according to C. Stragier and coll. unpubl. data). The brown rat ranks second in trapping records with less than a quarter of captures. This relatively high frequency is quite unusual in large contemporary West African cities. Published data indicate only moderate numbers of this species in the seaport of Cotonou (Benin; Badou et al. 2024), where it represents barely 10% of captures in the city itself (Hima et al. 2019). Similarly, it is rarely captured in Dakar (C. Stragier and coll. unpubl. data) and in Abidjan (Akpatou et al. 2018), and is not reported in Niamey (Garba et al. 2014), nor in any of the Senegalese cities studied in Dalecky et al. (2015) or Granjon et al. (2023). Elsewhere in Africa, it was found to be particularly abundant in Durban (South Africa), accounting for over 90% of catches (Taylor et al. 2008). In Bamako, the open wastewater evacuation network that converges towards the Niger River likely creates highly favourable conditions for the brown rat as anticipated by Rosevear (1969), observed in situ by Meinig (2000), and analysed by Guo et al. (2023) from an ecological perspective. The suitability of this species for this habitat type is also reflected in one of the common names of the brown rat, namely the sewer rat. Related to this ecological characteristic, brown rats were predominantly found in the outdoor parts of domestic habitats (especially yards), alongside *C. olivieri* shrews. In contrast, house mice and *M. natalensis* multimammate rats appeared to prefer the interior rooms of houses. The respective microhabitat preferences of these two pairs of species explain the habitat overlap values found within and between them. They echo the observation of Taylor et al. (2008) in Durban, where brown rats occupy squatter shacks rather than modern brick houses, the latter being preferentially frequented by house mice.

In addition, the large *Cricetomys gambianus* was occasionally captured but its true abundance was undoubtedly underestimated due to trap characteristics relative to its size. It could also be present more regularly in outdoor habitats of the city (such as urban market gardening areas or urban parks, not sampled here), along with other opportunistic species like *Mastomys erythroleucus*, *Arvicanthis niloticus*, *Taterillus gracilis* or *Praomys daltoni*, as observed in Niamey (Garba et al. 2014) or Dakar (Galan et al. 2023).

Overlaid with the specific microhabitat preferences presented above within the domestic space, co-occurrence patterns at the quarter scale illustrate how species share housing and working/commercial premises across the city. Segregation cases dominate between the four most abundant species, meaning that the pairs of species concerned were less than expected found in the same houses. To explain why no cases of segregation between species pairs occurred in the three "ancient" quarters (*sensu* Keita 2018) one must consider the strong dominance of the house mouse in these areas, where the brown rat is the only other species present in significant numbers. There, the random pattern of co-occurrence of these two species suggests they have reached an equilibrium in their distribution. This balance has probably not yet been reached in more recent quarters, which were probably invaded by the house mouse relatively recently (see below), and where the observed segregation could correspond to habitat partitioning due to ongoing interspecific interactions, particularly between native and invasive species or between invasive species. Indeed, many of these cases involved invasive species, namely the brown rat and the house mouse. Similar examples of local interspecific segregation involving the house mouse have been observed in major cities in south-eastern Senegal, namely between the house mouse and the black rat in Kédougou and Tambacounda (where the brown rat is absent; Granjon et al. 2023). A negative association between *R. rattus* and *M. musculus* was also observed in New Orleans by Peterson et al. (2020). It is difficult to determine whether this pattern reflects direct or indirect interactions, but competition between the brown rat and *M. natalensis* is possible, as was hypothesized between the latter species and the black rat in DR Congo, Tanzania and Eswatini (Misonne 1959; Monadjem et al. 2011). Parasite-mediated interactions could also contribute to such segregation patterns, as cross-species transmission of ecto- or endoparasites can alter host fitness and influence spatial overlap, particularly in the case of biological invasions (Dunn and Hatcher 2015; Daly et al. 2023). Predator-prey relations may also be at work in this community, for example between the brown rat and the house mouse, as proposed in Galapagos and New-Zealand by Harper and Cabrera (2010) and Bridgman et al. (2013, 2018) between the black rat and the house mouse, or in Senegal by Galan et al. (2023) between *C. olivieri* and the house mouse. The cases of segregation observed in Bamako between the house mouse and the native *M. natalensis* may also be the result of competitive interactions, as shown between *M. musculus* and native species in some areas of Rio Cuarto, Argentina, by Gomez et al. (2008). These authors concluded that such interactions could explain the coexistence between native rodents and the house mouse at the city scale, through habitat partitioning between native species dominant in vacant areas (i.e., those without buildings and dwellings) and house mice, abundant in built-up areas (or small vacant lots adjacent to them). Similarly, the co-occurrence segregation patterns between invasive and native species reported by Cavia et al. (2009) in Buenos Aires and Garba et al. (2014) in Niamey are largely due to habitat partitioning of the species within the urban landscape, more than to the age or urbanization level of the quarters. In the strictly commensal context here considered in Bamako, the situation rather resembles a transitional one, where *M. natalensis* gradually decreases in abundance due to the expansion of the house mouse in the city, as illustrated by the opposing patterns of relative abundance of these two species along the quarter age gradient. Ultimately, this progression of the house mouse could be particularly detrimental to multimammate rats, with which it shares more similar indoor microhabitats (in terms of rooms occupied) than with the shrew *C. olivieri*. However, these possible mechanisms - whether involving parasites, direct interference, or competition for resources - remain speculative in our case, as they would require specific data and explicit tests to be confirmed.

Towards a chronicle of the shift from native-to invasive-dominated commensal community

The information gathered here enables us to outline a scenario in which both rat species, and in particular the brown rat, have long been present in Bamako and are well distributed throughout the city, while the house mouse has only recently arrived and is still expanding. The earliest records of these species in Mali (presumably in Bamako) date back to the early 20th century, when all three species would have been present in the city. At that time, the black rat ("*Mus alexandrinus*" or "*Epimys rattus alexandrinus*") was considered the most widespread and the brown rat ("*Epimys norvegicus*") rather rare. Interestingly, the multimammate rat ("*Mus coucha*", probably corresponding to *Mastomys natalensis*) was quoted as "never seen" (Curasson 1932). This relatively imprecise information was not taken up by Rosevear (1969), who considered both the house mouse and the brown rat as restricted to coastal towns and ports of West Africa, and the black rat potentially present in more inland localities, either in forested areas or along waterways where they benefitted from river traffic. Later, Meinig (2000) based on two short surveys between the end of 1993 and the beginning of 1995, emphasized the abundance of brown rats in Bamako, along the Niger River as well as in other parts of the city. He also reported that "although intensively surveyed, no murid other than *R. norvegicus* could be detected". At that time, the shrew *Crocidura olivieri* was the only other small mammal species said to be present together with the brown rat in Bamako (Meinig 2000). However, it is reasonable to assume that the black rat and *M. natalensis* were present in Bamako at the turn of the 21st century, since specimens of these two species from Bamako or its immediate surroundings are represented in the CBGP-hosted small mammal database (http://BPM-CBGP.science), dated from 2003 and 1999, respectively.

Meinig's (2000) observations contrast with the data presented here, particularly concerning the house mouse, which definitely stands as a major species in present-day Bamako. It remains to be determined whether this dominance results from recent colonization followed by explosive spread and population increase, or from a recent increase in the density of a population present for some time but not very abundant and/or very localized. The first hypothesis, however, seems very likely, and would correspond to the story constructed by Bondaz (2020) from testimonies collected in Bamako in recent years. According to these accounts, small, fast mice of a previously unknown species (called *ɲinɛfitini*, i.e., "little mouse" in the Bambara language), arrived in Mali in the early 2010s, either in containers from China, India or Dubai, or from Senegal by the Dakar-Bamako railway. This species (unanimously nicknamed "Messi" by the inhabitants of Bamako, in reference to the famous footballer) would most likely corresponds to the house mouse *Mus musculus*, contrary to the hypothesis put forward by Bondaz (2020) who would have confused the house mouse with *M. natalensis*. A specimen of *Mus musculus* collected in October 2015 by A. Dalecky and S. Ag Atteynine in Bamako (Badialan quarter, close to the historic city centre) and preserved in the CBGP small mammal collection (https://doi.org/10.15454/WWNUPO) appears to be the oldest captured representative of this species. This recent invasion would have followed the more ancient one of a larger kind of rodent, named "*Senegal ɲinɛni*" (i.e., "Senegal mice") by the residents of Bamako, who generally consider that it originates from Dakar. The latter clearly refer to one or both of the *Rattus* species that people (logically) tend to confuse. This/these species would have been responsible for the decrease in abundance of the native rodent species, named *sokonoɲinɛ* or *soɲinɛ* (the "mouse from the rooms or from the house"), which most likely corresponds to *M. natalensis* (and not *Mus musculus* as in Bondaz 2020).

As for the brown rat, its abundance in Bamako is apparently exceptional for a landlocked country such as Mali. Indeed, it is only in coastal and/or port cities in Africa that this species has been reported as dominant among the commensal small mammals present: This was the case in the 1950s in Douala (Cameroon; Voelkel 1966 in Rosevear 1969), or more recently in 2004–2005 in Durban (South Africa; Taylor et al. 2008). Elsewhere in West Africa, it was generally found much less abundant than the black rat, as in Freetown (Sierra Leone) or Lagos (Nigeria) in the 1930s (in Rosevear 1969), or in Dakar (Senegal) where it represented less than 10% of the nearly 250,000 captures recorded in 1929 by the city's hygiene services (Cazanove 1932). At the same time, black rats represented more than 25% of the small mammals captured, and it is reasonable to think that this population reservoir could have served as a source for the colonization of Bamako by these two species from this time. It is all the more plausible that at this time, rail traffic between Dakar and Bamako was very intense in order to supply Bamako, then in full development, with construction materials and consumer goods (Lombard 2006; Philippe 2009). In fact, the oldest inhabitants of Bamako encountered during our trapping sessions often mention the very ancient presence of the "*Senegal ɲinɛni*" (i.e., the *Rattus* representatives) in Bamako, which is consistent with the scenario described above. The respective share of the two *Rattus* species may have varied over time, with *R. norvegicus* eventually taking over from *R. rattus* while the latter was dominant in the period following the two species arrival in Bamako. In support of this hypothesis, one may evoke the apparent higher propensity of the black rat to be transported by various means of transport (as illustrated by their current worldwide distribution pattern), the progressive development in the city of the wastewater network, which appears more favourable to the brown rat than to the black rat (Guo et al. 2023), and possible competitive interactions between them to the advantage of *R. norvegicus* (Feng and Himsworth 2014). Taylor et al. (2008) in Durban, based on historical and recent trapping data, also reported a similar trend of decrease of black rat abundance over time.

Conversely, "mice" represented only 1.2% of the catches in the Dakar hygiene service list in 1929 (Cazanove 1932). These could correspond, at least in part, to the house mouse, but they could also include young specimens of *Mastomys*. Such a low value, however, suggests that house mice were not very abundant at this time in Dakar. More recently, probably during the second half of the 20th century, the house mouse became the superdominant species in Dakar (Stragier et al. 2022), as in all localities in western Senegal (Dalecky et al. 2015). This may have created the conditions for a transport of individuals from Senegal to Mali, and in particular to Bamako. A more recent process than that of rats, the invasion of the house mouse could have started either by trains or by trucks and other vehicles traveling by road. Indeed, railway traffic between Senegal and Mali gradually declined from the beginning of the 21st century until 2018 when it finally ceased completely. At the same time, road traffic has increased dramatically, especially since the late 1990s and the gradual completion the Kidira (on the Senegal border) – Kayes – Bamako paved road, achieved in 2008 (Lombard 2022). Another possible (and not exclusive) origin of the Bamako house mouse population could also be Côte d'Ivoire, with which road trade has also increased in recent decades, although with strong interannual variations linked to political instability in that country (Lombard and Ninot 2013). Trade between Mali and other West African countries besides Senegal could also have brought specimens of house mice and black or brown rats to Bamako, making the populations of these species a mixture of samples of diverse origins. Such a hypothesis could be tested using genetic methods (as in Kaleme et al. 2011), as information on the genetic pools of some of the species concerned are already available in the West African region (e.g., in Benin, Badou et al. 2023; in Senegal; Konečný et al. 2013; Lippens et al. 2017; Stragier et al. 2022).

Perspectives for public health and social well-being

Rodents, the most abundant order of mammals, dominate the small mammal community in Bamako and represent a key taxonomic group in terms of the various impacts they may have in the context of urbanization. Beyond their massive socio-economic impacts (e.g., food losses and infrastructural damage (Capizzi et al. 2014) and eco-evolutionary consequences on local biodiversity (Mooney and Cleland 2001), they are known reservoirs for a wide array of zoonotic pathogens (reviewed in Meerburg et al. 2009), with 400 million human infections each year involving rodent-associated pathogens (Colombe et al. 2019). Some of these diseases have historically triggered major epidemics and pandemics in humans (e.g., plague), with the potential to transition into human-to-human transmission. Although urban-adapted rodent species constitute only a small fraction of global rodent diversity, they have been shown to share significantly more pathogens and parasites with humans than to their non-urban counterparts (Gibb et al. 2020). Furthermore, rodents undoubtedly carry as yet unknown pathogens that may cause new emerging diseases, highlighting their major role in public health (Han et al. 2015). In Bamako, rodents warrant particular vigilance in this regard.

In a context where uncontrolled urban expansion can intensify human-rodent interactions (Dobigny and Morand 2022), protecting public health from rodent-borne infectious diseases is paramount for ensuring sustainable urban trajectories. This is particularly important in socio-ecosystems experiencing ongoing invasions. The expansion of the house mouse is especially relevant for discussing local zoonotic risks and highlighting the complexity of the context-dependent processes at work during the transition from a native to an invasive rodent community (Young et al. 2017; Chalkowski et al. 2018). Indeed, the ongoing spread of *M. musculus* in Bamako could be perceived as “beneficial” if it results in a “dilution” effect of local pathogens that only circulate in native rodent reservoirs, as these native rodents are displaced during the expansion of the house mouse. Alternatively, *M. musculus* could introduce new pathogens into recently colonized ecosystems, serve as a competent host for local agents, and amplify their circulation, including among humans. The long-term presence of the brown and the black rats is also a concern, as these species are known to harbour a particularly wide variety of pathogens (Kosoy et al. 2015). Therefore, predicting the evolution of zoonotic risks remains complex in this context. From this perspective, we advocate for continued research efforts to provide knowledge on the zoonotic hazards borne and, more inclusively, on the various damages caused by small mammals in Bamako. Screening of zoonotic pathogens has begun based on the samples collected during this survey, and information on relatively high prevalence of two major pathogens, namely *Seoul orthohantavirus* and *Leptospira* bacteria, in *Rattus* specimens from Bamako, has recently been published (Garona et al. 2025). It will also be important to determine which socio-ecological factors may influence exposure to these risks during the urban transition. Beyond expanding the spatial scale considered, by including the city peripheries, this will also involve sampling urban habitat types other than that represented by domestic/residential housing. Indeed, sampling in places such as markets, waste dumps, parks and market garden areas will likely alter the overall composition of the small mammal community, but will also contribute to a better understanding of the parasite/pathogen dynamics between the species present. Ultimately, this information will be instrumental for considering, motivating, and prioritizing sustainable control and prevention measures, such as those based on ‘Ecologically-based Rodent Management’ (Dalecky et al. 2024).

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Author contributions Conceptualisation: Laurent Granjon, Solimane Ag Atteynine, Monique Bertrand; Data curation: Laurent Granjon, Christophe Diagne, Solimane Ag Atteynine; Formal analyses: Christophe Diagne, Laurent Granjon; Investigation: Solimane Ag Atteynine, Alida Dembélé, Fotigui Coulibaly, Laurent Granjon; Methodology: Laurent Granjon, Solimane Ag Atteynine, Monique Bertrand, Christophe Diagne; Software: Christophe Diagne; Supervision: Laurent Granjon, Solimane Ag Atteynine; Writing – original draft: Laurent Granjon; Writing – review & editing: Laurent Granjon, Solimane Ag Atteynine, Monique Bertrand, Christophe Diagne

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Data availability //http://doi.org/10.23708/UBPRJ5. Data reuse is granted under CC-BY license.

Declarations

Ethics statement *The project “Petits mammifères de Bamako: inventaire, déterminants de la distribution, parasites hébergés”*, in which this study is part was approved by the ethics committee of the National Institute of Public Health of Mali (decision n°18/2021/CE-INSP). It also received prior informed consent, in accordance with the provisions of the Nagoya protocol signed by Mali, from the National Director of Water and Forests of Mali (letter 0976/MEADD-DNEF of November 25, 2021). As part of the requirements of the ethics committee, all heads of families (or their representatives) where trapping was carried out were informed of the project and signed an agreement consenting to participate. The town halls of each of the six communes of Bamako, through the mayor or one of his deputies, have also approved the project, and informed the heads of the districts concerned by the trapping operations. The latter disseminated information on the upcoming trapping campaign via different means (mosque, WhatsApp group, town crier, etc.). He also selected a local citizen responsible for accompanying and guiding the sampling team in the quarter during the trapping campaigns. Every protocol used here received prior explicit approval from the relevant institutional committee *(Centre de Biologie pour la Gestion des Populations (CBGP): Agrément pour l'utilisation d'animaux à des fins scientifiques E34-169–001)*. All animal-related procedures were performed according to official ethical guidelines provided by the American Society of Mammalogists (Sikes and Gannon 2011). Euthanasia of less than 200 g specimens was performed via cervical dislocation, with previous parenteral injection of a derivative of pentobarbital in larger individuals (*Cricetomys gambianus* especially), as recommended by AVMA (American Veterinary Medical Association 2020).

Conflict of interest The authors have no conflict of interest of any kind to declare

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