

Sharing space between native and invasive small mammals: Study of commensal communities in Senegal

Laurent Granjon¹, Emmanuelle Artige¹, Khalilou Bâ², Carine Brouat¹, Ambroise Dalecky³, Christophe Diagne¹, Mamoudou Diallo², Odile Fossati-Gaschignard¹, Philippe Gauthier¹, Mamadou Kane², Laëtitia Husse², Youssoupha Niang², Sylvain Piry¹, Nathalie Sarr², Aliou Sow², and Jean-Marc Duplantier¹

¹CBGP, IRD, CIRAD, INRAE, Institut Agro, Univ Montpellier,

²IRD

³Institut de recherche pour le developpement

June 30, 2023

Abstract

Urbanization processes are taking place at a very high rate, especially in Africa, these. At the same time, a number of small mammal species, be they native or invasive, take advantage of these human-induced habitat modifications. They represent commensal communities of organisms that cause a number of inconveniences to humans, including as potential reservoirs of zoonotic diseases. We studied via live trapping and habitat characterization such commensal small mammal communities in small villages to large cities of Senegal, to try understand how the species share this particular space. Seven major species were recorded, with exotic invasive house mice (*Mus musculus*) and black rats (*Rattus rattus*) dominating in numbers. The shrew *Crocidura oliveri* appeared as the main and more widespread native species, while native rodent species (*Mastomys natalensis*, *M. erythroleucus*, *Arvicanthis niloticus* and *Praomys daltoni*) were less abundant and/or more localized. Habitat preferences, compared between species in terms of room types and characteristics, showed differences between house mice, black rats and *M. natalensis* especially. Niche (habitat component) breadth and overlap were measured. Among invasive species, the house mouse showed a larger niche breadth than the black rat, and overall, all species displayed high overlap values. Co-occurrence patterns were studied at the locality and local scales. The latter show cases of aggregation (between the black rat and native species, for instance) and of segregation (as between the house mouse and the black rat in Tambacounda, or between the black rat and *M. natalensis* in Kédougou). While updating information on commensal small mammal distribution in Senegal, a country submitted to a dynamic process of invasion by the black rat and the house mouse, we bring original information on how species occupy and share the commensal space, and make predictions on the evolution of these communities in a period of ever-accelerating global changes.

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¹ CBGP, IRD, INRAE, CIRAD, Montpellier SupAgro, Univ Montpellier, Montpellier, France

² BIOPASS, CBGP-IRD, ISRA, UCAD, CIRAD, Campus de Bel-Air, Dakar, Senegal

³ IRD, Aix Marseille Univ, LPED, Marseille, France

* Corresponding author: Laurent Granjon, CBGP, 755 avenue du Campus Agropolis, Campus de Baillarguet CS 30016, 34988 Montferrier-sur-Lez cedex, France.

E-mail :laurent.granjon@ird.fr

Abstract

Urbanization processes are taking place at a very high rate, especially in Africa, these. At the same time, a number of small mammal species, be they native or invasive, take advantage of these human-induced habitat modifications. They represent commensal communities of organisms that cause a number of inconveniences to humans, including as potential reservoirs of zoonotic diseases. We studied via live trapping and habitat characterization such commensal small mammal communities in small villages to large cities of Senegal, to try understand how the species share this particular space. Seven major species were recorded, with exotic invasive house mice (*Mus musculus*) and black rats (*Rattus rattus*) dominating in numbers. The shrew *Crocidura olivieri* appeared as the main and more widespread native species, while native rodent species (*Mastomys natalensis*, *M. erythroleucus*, *Arvicanthis niloticus* and *Praomys daltoni*) were less abundant and/or more localized. Habitat preferences, compared between species in terms of room types and characteristics, showed differences between house mice, black rats and *M. natalensis* especially. Niche (habitat component) breadth and overlap were measured. Among invasive species, the house mouse showed a larger niche breadth than the black rat, and overall, all species displayed high overlap values. Co-occurrence patterns were studied at the locality and local scales. The latter show cases of aggregation (between the black rat and native species, for instance) and of segregation (as between the house mouse and the black rat in Tambacounda, or between the black rat and *M. natalensis* in Kédougou). While updating information on commensal small mammal distribution in Senegal, a country submitted to a dynamic process of invasion by the black rat and the house mouse, we bring original information on how species occupy and share the commensal space, and make predictions on the evolution of these communities in a period of ever-accelerating global changes.

Keywords: Community ecology; co-occurrence; rodents; shrews; West Africa

Cover letter

Dear Editor,

You will find hereafter our manuscript “Sharing of space between native and invasive small mammals: Study of a commensal community in Senegal” that presents and analyses data on the distribution of commensal small mammals obtained via intensive trapping operation and habitat description in a series of localities in Senegal. Our aims are i) to describe the community of small mammals living in contact with humans and evaluate the respective share that native and invasive species occupy with this community; ii) to better understand the factors that govern species distribution and co-occurrence using a series of analyses using habitat characteristics gathered at the moment of captures.

We believe that this study represents an original community ecology approach towards the understanding of patterns and processes at work in a group of organisms of particular concern regarding their interactions with humans.

We thank you in advance for your consideration and time on our manuscript

On behalf of all co-authors

Yours sincerely,

Laurent Granjon

Introduction

Urbanization in developing countries has for long been identified as a major process with multiple consequences at the global scale (Cohen, 2006; Henderson & Turner, 2020). This process comprises both the

emergence of megacities and the rapid growth of small and medium cities (Cohen, 2006; United Nations, Department of Economic and Social Affairs, Population Division 2018). As a result, urban areas are projected to house 60 per cent of people globally by 2030, with almost 90 per cent of this growth taking place in Asia and Africa (*un.org*). The corresponding rise of the “indoor biome” raises new eco-evolutionary questions regarding species, and species communities, associated with this expanding environment (Martin et al., 2015; Hulme-Beaman et al., 2016). Long composed mainly of native species, these communities (like others from more natural biomes) have been progressively colonized by introduced species benefitting from human-caused global changes (Vitousek et al., 1997).

Among other groups of living organisms, rodents comprise species that are especially prone to take advantage of the modification of habitats by human activities, being core species in an urbanization context (Capizzi et al., 2014; Rothenburger et al., 2017). Their impacts are diverse and multidimensional, including notably biodiversity loss (Doherty et al. 2016), threats to food security (Singleton et al., 2021), disease transmission (Han et al., 2015), economic burdens (Dossou et al., 2020; Diagne et al., 2023) and societal decay (Colombe et al., 2019). Some of these rodents are well-known as major invasive alien species (hereafter ‘invasive rodents’) worldwide (Lowe et al., 2000; Capizzi et al., 2014). This is the case of *Rattus rattus*, the black rat, and *Mus musculus*, the house mouse, which are both listed amongst “100 of the world’s worst invasive species” of the planet (Lowe et al., 2000). The ongoing expansion of those invasive rodents in several parts of the world (see for instance Dalecky et al., 2015; Zeng et al., 2018; Yu et al., 2022) leads to multispecific assemblages of small mammals (mainly rodents) that combine invasive and native species in a variety of ecological and evolutionary contexts. One of these contexts is represented by commensalism in anthropogenic environments, where the species concerned literally “live within houses”, in close proximity with humans (Hulme-Beaman et al., 2016). There, despite ever-increasing studies on the distribution (including invasion history of invasive small mammals), impacts and dynamics of individual species over space and time, the multispecific assemblages of these rodent-dominated communities has rarely been studied from a community ecology perspective.

Species sampling in anthropogenic habitats is often complicated because it involves going into people’s homes or industrial or commercial buildings. Moreover, even if rodent communities in such habitats are often depauperate, diversity is generally not taken into account because one focus on a (or a pair of) target species in relation with specific questions raised by it/them. This is the case in the review by Feng & Himsforth (2014) on *R. norvegicus* and *R. rattus*, in the studies focusing on the impact of urban characteristics on the genetic structure of rodent populations in different cities (*R. norvegicus* in American cities: Combs et al. 2018; *M. musculus* in Dakar (Senegal): Stragier et al. 2020), or in experiments on species cohabitation and interspecific competition involving *M. musculus* in SW Argentina (Castillo et al., 2003; Gomez et al., 2008). However, some studies have already considered more complete communities. For instance, Panti-May et al. (2012) measured data on abundance, population and habitat use parameters of *M. musculus* and *R. rattus* among their native counterparts in households of a rural area of Mexico as part of a study on zoonotic disease transmission. Masi et al. (2010) evaluated the respective importance of socioeconomic and environmental risk factors for urban rodent (including *R. rattus*, *R. norvegicus* and *M. musculus*) infestation in Sao Paulo, Brazil. Cavia et al. (2009) analyzed the relation between rodent community composition and diversity and the landscape structure in the city of Buenos Aires, showing a clear trend of habitat partitioning between invasive *R. rattus*, *R. norvegicus* and/or *M. musculus* (dominant in parklands, shantytowns or industrial-residential neighborhoods) and native species (dominant in a natural reserve but also present in parklands). In Africa, Olaseha et al. (1994) presented general considerations on the importance of housing and sanitation on the presence of rats (*R. rattus* and *R. norvegicus*) and mice (*M. musculus*) based on questionnaires completed by interviews in towns and villages of a rural area in southwestern Nigeria. Demby et al. (2001), followed by Fichet et al. (2005, 2009) provided information on small mammal distribution in urban as well as in rural areas of Guinea, in relation to Lassa virus distribution and prevalence. Taylor et al. (2008) gave a few elements of urban distribution of rodents in Durban (South Africa) in a small mammal community largely dominated by *R. norvegicus*. Monadjem et al. (2011) compared movement patterns and possible interactions of *Mastomys natalensis* (a native rodent species) and *R. rattus* in distant sites of Tanzania, Malawi and Namibia using telemetry and Rhodamine B marker. In the capital city of

Niger, Niamey, Garba et al. (2014) analysed the distribution of native and invasive rodents in a series of sites corresponding to habitation districts, cultivated gardens and industrial zones. They showed the dominance of the native *M. natalensis* over the invasive *R. rattus* and *M. musculus* and spatial segregation between them, that they interpreted as the result of an ongoing native-to-invasive species turn over. Hima et al. (2019) assembled an important dataset on commensal small mammal distribution in a series of localities along the Benin-Niger “corridor”, between Cotonou and Niamey. They showed the dominance of either invasive *R. rattus* in Cotonou (see also Houemenou et al., 2014) or native *M. natalensis* in Niamey, with segregation patterns between *Rattus* spp. and *M. natalensis*, and a very regular and important presence of *Crocidura* spp. (incl. *C. olivieri*), especially at lower latitudes. None of these studies has nonetheless addressed in detail the co-distribution and coexistence of a set of species (both native and invasive) belonging to a whole small mammal community in human-made environments, especially at a fine spatial scale. At best, they considered co-occurrence patterns at the scale of a country, a region or a whole city, but never at the level of the housing units or the buildings, where inter-individual (be they intra- or interspecific) interactions actually occur. Yet it is precisely at this fine scale that the ecological interactions take place which probably determine the trajectory of the communities in terms of their distribution in space and time.

Niche / resource partitioning represents a way to manage coexistence among competing species within habitats (Pianka, 1973; Chesson, 2000). Indeed, the complex and interactive effects of species niche overlap, niche breadth and environmental heterogeneity on species co-occurrence patterns have been highlighted repeatedly (see a synthesis in Bar Massada, 2015). In the particular case of commensal small-mammal communities, information on and analyses of species co-distribution and co-existence, habitat partitioning (if any), and interspecific interactions between species (including invasive ones) are lacking, being however of paramount importance to better understand: i) the way invasive species spread at the microhabitat scale; ii) the consequences of this spread on the distribution of native species at the microhabitat scale; iii) the actual associations between species likely to represent zoonotic disease reservoirs at the very contact with humans.

In Africa, both *R. rattus* and *M. musculus* colonized most countries via boats of European or Arab settlers, often centuries ago (Happold, 2013). Long confined to coastal areas and larger cities, they have been spreading continuously over inland areas thanks to the development of infrastructures and associated human exchanges (e.g. movements of goods and people) that accompanies the ongoing urbanization of rural areas. This is the case in Senegal (West Africa) where both *R. rattus* and *M. musculus* have experienced recent range expansion eastward from the western Atlantic coastal areas (Duplantier et al., 1991; Dalecky et al., 2015; Konečný et al., 2013). Being exclusively commensal in this country, they encounter native species that inhabit human settlements, leading to inevitable interactions which ultimately determine the patterns of cohabitation between them. To describe this coexistence and try understand the underlying interactions, we sampled communities of commensal small mammals from localities of various size within the southern half of Senegal (corresponding to the distribution range of *R. rattus* in the country) within a 3-year time period. The sites sampled were widely invaded by the black rat and/or the domestic mouse, which most of the time cohabited with a wide spectrum of native rodent and shrew species. We aim at providing novel insights from the following questions: i) which invasive and native species compose the small mammal community across the different localities targeted? ii) what are the preferred habitat types and ecological niches of each of these species? iii) do these species show particular interspecific associations (segregation or aggregation) globally and/or locally? To answer these questions, we investigated here the composition, geographic distribution, micro-habitat use, ecological niche breadth and overlap, and species co-occurrence within the target small mammal community at various spatial scales.

Materials and Methods

Detailed trapping data are presented in Granjon et al. (2021) with, among others, information on the associated variables and capture results of each of the 13,283 trapnights that yielded the dataset analysed here.

Study area

Forty-nine localities were sampled between May 2012 and September 2015 throughout the southern half of Senegal (between 12.40° and 15.20°N, and 12° and 17.30°W). They are listed in Table 1 with their geographic coordinates (see also Fig. 1). In terms of human population, they range between a few hundreds to around 500,000 inhabitants (Rufisque) and accordingly, they were sampled during periods ranging between 2 and 21 days. They can be grouped in nine areas/locality as follows: North of the Gambia, the “*Petite Côte*” area along the Atlantic coast south of Dakar, and the “*Kaolack-Tambacounda*” axis along National Road (NR) 1; South of the Gambia along NR 6, “*Basse Casamance*” in the West and “*Haute Casamance*” in the East; from the main city of *Tambacounda*, lying at the crossroad of National Roads 1, 6 and 7, the “*Tambacounda-Kidira*” axis along NR1 to the Senegal-Mali border; South of this last axis, the relatively landlocked “*Boundou*” area, and along the Senegal-Mauritania border, the “*Bakel*”; in the extreme southeast, the “*Kédougou*” area. These areas are delimited in Fig. S1 with included localities (see also Table 1).

Sampling scheme and protocols

Elements of the trapping procedures followed here have already been partly described in Dalecky et al. (2015), Diagne et al. (2021), and Granjon et al. (2021). The live traps used were of two types: locally made 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). Traps were set inside housing or working units (e.g. dwelling houses, storehouses, shops, workshops) which potentially included inner yards and associated parts (e.g. exterior staircases, verandas). In each of these buildings, traps were set between one and three consecutive nights in different “rooms”. Most of the time, a trap of each type was placed in each room, on the floor, on furniture, or even high up (wall tops, frame...). When the traps were initially set up, each room sampled was georeferenced (geographic coordinates GPS-recorded with an accuracy of +/- 5m). The rooms were classified as belonging to eight “room types”, namely bedrooms, granaries, food shops, kitchens, non-food stores, outdoors, stock rooms and workshops. In the rooms, the presence or absence of food, and the nature (materials) of the floor, walls and ceiling (see modalities in Fig. 1 legend) was noted. This information represents markers of the type of habitat (traditional *vs.* modern) in which the small mammals studied live in contact with their human hosts. Traps were checked and then baited once a day with peanut butter spread on a slice of fresh onion.

Captured rodents were morphologically identified (following keys provided in Granjon and Duplantier 2009), euthanized by cervical dislocation as recommended by Mills et al. (1995), then weighed to the nearest 0.5g, sexed and dissected. When necessary, molecular data were generated to allow unambiguous species identification of rodents (following procedures described by Lecompte et al., 2005; Dobigny et al., 2011).

Data treatment

Using a multivariate approach, we explored and described our data using a three-step procedure, taking into account the type of variables (quantitative or qualitative) considered. As quantitative variables, we determined (i) species abundances (i.e. number of individuals trapped) by trap, room, locality and group of localities, and (ii) capture rates (i.e. number of individuals of a given species divided by trapping effort) for each locality. As qualitative variables, we considered the type of trap (wire mesh or Sherman) at the trap scale, and the presence of food, the type of room and nature of the floor (mostly concrete *vs.* clay, aka “banco”), walls (mostly concrete *vs.* clay), and ceiling (mostly concrete or corrugated iron *vs.* straw) at the room scale. Note that variables noted at the scale of the rooms were aggregated in percentages for each locality. We first performed i) a centred Principal Component Analysis (cPCA) on the localities x species table (using square roots of trapping success as data); ii) a fuzzy Correspondence Analysis (fCA), on the localities x room characteristics (using numbers of each modality for each variable); iii) a K+1 analysis coupling the previous two analyses (Bougéard et al., 2011; Bougéard & Dray, 2018), with the aim of describing the relationships between these two types of data (rooms treated through partial least squares (PLS) regressions and mammals described through a cPCA). The method is a multiblock PLS regression (mbpls) applied to the particular case of a single response dataset. Block of response variables are explained by a large number of explanatory variables which are divided into K meaningful blocks. All the variables – explanatory and dependent – are measured on the same localities. The main results are summarized using overall graphical displays. All data

were analysed using ade4 R package (Chessel et al., 2004; Dray et al., 2007; R Core Team 2022).

Then, a Pearson’s Chi-squared test was realised on the contingency table enumerating the numbers of captures of the seven main species of the small mammal community in the room types recorded, in order to evaluate whether room types may explain the local distribution of each species. The habitat component of the ecological niche of each species was further evaluated using its distribution in the different room types (considered as integrative descriptors of microhabitat) recorded. Following Pianka (1973), we used two indices to characterize each species niche and their overlap between species pairs:

Niche breadth quantified using Simpson’s index of diversity $B = 1 / \sum p_i^2$, where p_i is the proportion of the i^{th} room type actually used by the species.

Niche overlap based upon Levin’s (1968) index $O_{ij} = \sum p_{ij} p_{ik} / \sum (p_{ij}^2 + p_{ik}^2)$, where p_{ij} and p_{ik} are the proportions of the i^{th} room type used by the j^{th} and the k^{th} species, respectively

Finally, we examined co-occurrence patterns through the analyses of presence–absence matrices with “null model” randomization tests of marginal row and column totals (Gotelli, 2000; Gotelli & Ulrich, 2010) using *pairs* software (Ulrich, 2008). Aggregated / random / segregated pattern of co-occurrence of species pairs was inferred from the *p value* associated with the Z–score for each pair of species, either using the global dataset (from all 49 localities) or local datasets (per locality and per district in large cities). We used the “fixed row–fixed column” and “fixed row–equiprobable column” randomization algorithms to generate randomized matrices that serve as null models as advised by Gotelli (2000), and ran the models with 10,000 iterations.

Ethical statement

Permission to enter and work within villages was systematically obtained from the appropriate institutional, traditional and familial authorities. Trapping sessions were carried out in accordance with requirements of Senegalese and French legislations. Every protocol used here received prior explicit approval from the relevant institutional comitee (Centre de Biologie pour la Gestion des Populations (CBGP): *Agreement pour l’utilisation d’animaux a des fins scientifiques* E 34-169-001). All animal-related procedures were performed according to official ethical guidelines provided by the American Society of Mammalogists (Sikes & Gannon, 2011).

Results

Trapping results

The total trapping effort represented 13,283 trapnights, which led to the capture of 3,160 small mammals, including 2590 rodents, 569 shrews (g. *Crocidura*) and one hedgehog (*Atelerix albiventris* ; Table 1). Regarding the specific abundance, exotic species were dominant, with first of all *M. musculus* (N = 945 captures, 30% of the total captures), then *R. rattus* (N = 804, 25%). The native shrew *Crocidura olivieri* (N = 556, 18%), the two species of *Mastomys* (*M. natalensis* , N = 308, 10%; *M. erythroleucus* , N = 278, 9%), *Arvicanthis niloticus* (N = 141, 4%) and *Praomys daltoni* (N = 91, 3%) followed. The remaining individuals, determined as *Atelerix albiventris* , *Cricetomys gambianus* , *Crocidura* sp., *Gerbilliscus gambianus* , *Mastomys* sp., *Mus* (including the subgenus *Nannomys*) spp. and *Steatomys* sp. accounted for ca. 1.2% of the total captures (N = 37). Fig. 1 presents the relative frequencies of these species per locality. Regarding their geographic distribution, the species present in the largest number of localities were, respectively, *C. olivieri* (N = 39 localities) and *M. erythroleucus* (N = 33), followed by *R. rattus* (N = 29), *P. daltoni* (N = 24), *M. musculus* (N = 21) and *A. niloticus* (N = 18). At the same time, the exotic rodents *M. musculus* (N = 16 localities) and *R. rattus* (N = 14) were the species more often dominant numerically, far ahead of *C. olivieri* (N = 7) and *M. natalensis* (N = 6).

Community structuration

The corresponding data (limited to the seven most captured small mammal species) were subjected to cPCA at the scale of the 9 areas encompassing the 49 localities, the first axis of which (Fig. S2) showed distinct distribution trends for the exotic *M. musculus* and all other small mammals. *Mus musculus* appears to be

highly dominant overall on the coastal area North of the Gambia as well as on the Kaolack-Tambacounda axis, and present at high frequency in Tambacounda, in localities around Kidira (at the Senegal – Mali border) and in Haute-Casamance. Conversely, this species is absent from Basse-Casamance and south-Eastern Senegal, where the exotic *R. rattus* or native species mainly occur (Fig. 1). The second axis of the cPCA mostly showed a contrasted distribution of both exotic species and *C. olivieri*. The native *M. natalensis* which is largely dominant in the Kedougou region, and is limited in the west by the eastern limit of Niokolo-Koba National Park, and the locality of Bransan (ndeg7 in Fig. 1) to the north. The other native rodent species (*M. erythroleucus*, *P. daltoni*, *A. niloticus* in particular) are generally present in low frequency at all localities. However, we can note their particularly high proportions in villages of the Senegal river Valley north of Bakel (locality ndeg1 in Fig. 1). *Crocidura olivieri* is rarely absent from sampled localities (only 10/49), and regularly (co)dominant in catches around Tambacounda and on both sides of the Tambacounda-Kidira axis.

Habitat preferences

The distribution of all the captures of the seven main species of the community in the eight room types is given in Table 2. Small mammal species appear not to be randomly distributed in the room categories defined ($\chi^2 = 401.34$; 42df; $p = 3.62 \cdot 10^{-60}$). The distribution of *M. musculus* appears as the most divergent from random expectations, the species being clearly over-represented in kitchens (and to a lesser extent in stores) and under-represented in outdoors, granaries, and stock rooms. The distribution of the room types and their modalities (nature of floor, walls and ceiling) across the localities sampled did not show any particular trend, as evidenced by the results of fCA (Fig. S3). An overall opposition between more urbanized (Petite Cote, Tambacounda) vs . more rural (Boundou) areas appears however, associated with a dominance of distinct room type (workshops and non-food stores vs . granaries) or construction materials (concrete and metal vs . adobe and straw). From there, a k+1 analysis was performed between the cPCA of small mammals and the fCA of room types / modalities grouped by geographic areas. This K+1 C1-C2 factorial map illustrates graphically (Fig. 2) the relationships between species, geographic areas and room types and characteristics. The most visible associations are, on axis 1, between *M. musculus*, kitchens and concrete walls, mainly on the Petite Cote, the Kaolack-Tambacounda axis, and in Tambacounda (positive side of C1). On the opposite (negative) side of C1 are all the other small mammals, *M. natalensis* excepted, stock rooms and adobe walls (and to a lesser extent presence of large food stocks and straw ceiling), in Boundou, Basse Casamance and the Tambacounda – Kidira axis, to a lesser extent. C2 mainly contrasts *M. natalensis* associated with average levels of food and concrete floor in the area of Kedougou vs . *R. rattus* and *M. erythroleucus* related to non-food stores and outdoors, absence of stocks, concrete floor and ceiling, and metal sheet walls.

Niche breadth and overlap

Niche breadth and niche overlap values are presented in Table 3. They did not show any differences between exotic and native species. Niche breadth ranges between 2.9 for *Praomys daltoni* and 4.2 for *A. niloticus*. Niche breadth of the domestic mouse is higher than of the black rat (4 vs 3.2). Niche overlap values are generally high, ranging between 0.74 and 0.99. *Arvicanthis niloticus* shows the lower mean value (0.84) and *C. olivieri* the highest (0.95). Mean niche overlap values of *M. musculus* and *R. rattus* with other species are the same and are high (0.94), suggesting regular co-occurrence of these invasive species with native ones at the room scale (see hereunder).

Co-occurrence analyses

At the global level (i.e. with localities as sites), two significant patterns of aggregation were revealed, both implying *M. erythroleucus*: with *C. olivieri* ($Z = -2.20$, $p = 0.0274$ with “fixed row–fixed column” [ff] randomization; $Z = -2.32$, $p = 0.0202$ with “fixed row–equiprobable column” [fe] randomization), and with *P. daltoni* ($Z = -2.01$, $p = 0.0440$ with “fe” randomization). Conversely, five segregation patterns were found significant using at least one of the two randomization schemes. Four of them are suspected to be biased by overall differences in spatial distribution of the species involved, at the scale of southern Senegal: between *M. musculus* and *P. daltoni*, between *C. olivieri* and *M. natalensis*, between *R. rattus* and *M. natalensis*,

and even more conspicuously between *M. musculus* and *M. natalensis*, which distributions were completely disjoint at the time of sampling (see Fig. 1). The last one, implying *M. erythroleucus* and *M. musculus* ($Z = 3.35$, $p = 0.00078285$ with “ff” randomization, $Z = 2.84$, $p = 0.0044$ with “fe” randomization) is less prone of being influenced by distribution range differences.

At the locality level (i.e. with “houses” as sites within the 49 localities and districts of Kedougou and Tambacounda, see details in Table S1), a total of 586 species pair associations were tested. Only 39 (27 with “fe” + 12 with “ff” randomization schemes, respectively) of them (10.75%) proved to show a significant pattern of segregation or aggregation, 33 (22 + 11) of which concerned the seven most abundant species. They are detailed in Table 4. *Mus musculus* and *R. rattus* were involved in most of the segregation cases (13 / 15). In the large cities (where more than 50 sites were considered in co-occurrence analyses), a significant segregation was observed between *M. musculus* and *R. rattus* in Tambacounda as well as in two of its districts, and between *M. natalensis* and both *R. rattus* and *C. olivieri* in Kedougou (where *M. musculus* is absent). Conversely, *M. musculus* was never involved in aggregative patterns, to the opposite of *R. rattus* which was regularly found more often than expected to co-occur with *C. olivieri* and *M. erythroleucus* (for instance in Kedougou and Rufisque). Native species of small mammals also show aggregative patterns in a number of other localities.

Discussion

Commensal small mammal community composition and distribution

A previous analysis of commensal small mammal communities at the scale of Senegal has been presented by Dalecky et al. (2015). While it was primarily focused on the house mouse distribution, this work depicted data gathered between 1983 and early 2014 on the expansion of both exotic *M. musculus* and *R. rattus* vs. all native species taken as a whole. The present study extends the effort of Dalecky et al. (2015) both temporally (to September 2015) and spatially by adding large localities such as Tambacounda and Rufisque, and new areas such as the one north of Kidira at the Senegal-Mauritania eastern border. Using data from 49 localities in the southern half of the country (i.e. covering the Senegalese distribution of *R. rattus*), it also details the patterns of occurrence / co-occurrence of all the small mammal species encountered.

Commensal species can be classified precisely following Hulme-Beaman et al. (2016) who provided a series of definitions concerning the type of relationship that species can have with anthropogenic environments. According to this terminology, we have here a mixture of ‘obligate commensals’ represented by the exotic invasive species *M. musculus* and *R. rattus* that can only survive in the study area because of their ability to occupy houses, and of ‘occasional commensals’ that occur both within houses and in outdoor habitats (all the native species). Among the latter, *M. natalensis* tends however to be an obligate commensal in Senegal (Duplantier & Granjon, 1988), even if the species is known to occur outdoors elsewhere in Africa (Leirs, 2013).

In the sample gathered here, exotic invasive species outnumbered native ones from nearly all points of view. Indeed, *M. musculus* and *R. rattus* represented more than 55% of all the small mammals captured (1749 / 3160). They were also found dominant in the largest number of localities (16 and 14, respectively), even though they are not present in the majority of them. These data testify for the success of these invasive species in Senegal, where the trend toward a rapid west-to-east expansion (i.e. from coastal areas where they were first introduced, to inland) has been spectacular over the last decades (see Fig. 1 in Dalecky et al., 2015). In other words, once these species colonize a new place, they can rapidly become dominant over native ones. This seems to be especially the case for *M. musculus* which is dominant in the majority of the localities where it is present (16 / 21). This potential to rapidly invade a small mammal community and extirpate the native species previously present has been documented in a number of localities of northern Senegal over the last two decades (Dalecky et al., 2015; Diagne et al., 2020, 2021). It even seems that this recent expansion of *M. musculus* has come at the expense of *R. rattus*, as suggested by the comparison of the data presented in Duplantier et al. (1991) and ours. One may bet that this situation of dominance of invasive species over native ones in commensal small mammal communities is going to become the rule

in a number of regions / countries all over Africa. As an example, *R. rattus* appears as often dominant in Benin’s localities in the survey of Hima et al. (2019) along a Benin-Niger axis. In Guinea, *M. musculus* was only found in the coastal region by Demby et al. (2001), and especially in the city of Kindia where its abundance decreased from the centre to the periphery. Later, Fichet-Calvet et al. (2005) found *R. rattus* as the dominant commensal species in smaller villages of the coastal region. Interestingly, nearly 30 years ago, the study by Olaseha et al. (1994) suggested that *Rattus* spp and *M. musculus* were already the main commensal species in the urban and rural areas they studied in south-western Nigeria. This may also be the trend in the New World where, even in rural areas, invasive rodents already constitute the bulk of small mammals found within houses. For instance, 74% of the rodents caught in various urban habitats of the city of Rio Cuarto, province of Cordoba, Argentina (Castillo et al., 2003) were of (mainly) *M. musculus* and *Rattus* spp.; similarly, 92% of the captures indoors and in the yards surrounding the houses were of *M. musculus* and *R. rattus* in a rural area of Yucatan State, Mexico (Panti-May et al., 2012).

The only native rodent species that stays dominant wherever present is *M. natalensis*. However, it has to be underlined that this species, restricted to the southeastern part of Senegal (Duplantier & Granjon, 1988), is only co-occurring with an exotic invasive species (here *R. rattus*) in one locality, namely Kedougou, this locality constituting the invasion front of the species in this part of the country. There, *M. natalensis* has apparently resisted to the arrival of *R. rattus*, that occurred at the end of the 1990’s (Ba, 2002), since its dominance in this city has continued until this period (unpubl. data). This situation also occurs in villages of Upper Guinea where *M. natalensis* was found as the main commensal species (Fichet-Calvet et al., 2009), as well as in a number of localities of Niger, including the majority of its capital city (Niamey) districts (Garba et al., 2014; Hima et al., 2019).

In our dataset, the other native rodent species which stay dominant in only a small number of localities are *M. erythroleucus* and *P. daltoni* in the extreme East of the study area, where *M. musculus* is apparently progressing and is expected to replace them in a near future. As found by Hima et al. (2019) at lower latitudes, the native small mammal species which finally stays as the most regularly present, and often co-dominant with invasive rodents is the shrew *C. olivieri*. This species proves here that it can behave as a true commensal species even if rarely presented as such (Churchfield & Hutterer, 2013).

Habitat preferences and niche breadth/overlap

Habitat represents one of the main niche dimension, which has often been considered in community ecology studies (Morris, 1996). Nevertheless, most studies conducted to date concerned communities in outdoor environments, where habitats may differ according to several factors like vegetation, soil, elevation, among others. Here, room type and rooms characteristics were chosen as easy-to-describe proxies of habitat / microhabitat structure that may be relevant for commensal small mammals. Indeed, the variables recorded here enable us to distinguish between categories of domestic spaces, in terms of “privacy” (from bedrooms to outdoor spaces or shops), type of activities hosted, hiding places and food resources present. Also, the nature of construction materials used for rooms can help to distinguish between traditional (use of clay for floor and walls, and of straw for ceiling) and more modern buildings (use of concrete for floor and walls, and of corrugated iron for ceiling), the latter being expected in villages that are more integrated in commercial networks and directly connected to large cities, thus more prone to the introduction of exotic rodents (Diagne et al. 2016, but see Lucaccioni et al. 2016).

Our analyses present *M. musculus* as more abundant in some room types (kitchens and stores), especially when built with non-traditional construction materials (cement and iron, particularly), similarly to *M. natalensis* in its area of occurrence. These habitat types contrast with those where *A. niloticus* is found more often than expected (granaries and outdoors), which is coherent with the ecology of the latter species, more abundant in grassy habitats and grain fields in outdoor environments (Granjon et al., 2013). *Arvicanthis niloticus* also shows both the larger niche breadth and the lower mean overlap with other species. These characteristics may represent attributes of the “occasional commensal” category of Hulme-Beaman et al. (2016), of which *A. niloticus* is probably the most extreme representative. Interestingly, *P. daltoni*, which is regularly found indoors in West Africa (Bryja et al., 2010), has the smallest niche breadth – being often

under-represented in the room types sampled, and nearly only over-represented in bedrooms, mainly in the extreme East of the country. This species may suffer from the arrival of exotic invasive species, and be pushed back into the innermost rooms of the houses until it is excluded. The only non-rodent species, i.e. the shrew *C. olivieri* appears as very catholic in its habitat preference, being found in all room types in numbers close to those expected from their proportions in the overall sample. This also translates in a relatively high value of niche breadth, and also high niche overlap values with all rodent species. The wide range of habitats occupied and adaptability of this species have already been underlined (Churchfield & Hutterer, 2003). The habitat niche overlap with rodent species here observed probably relates to the fact that this shrew does not belong to the same ecological guild (*sensu* Simberloff & Dayan, 1991) and as such, is probably not submitted to competitive interactions with them likely to constrain its ecological distribution. Here, another type of interaction may rather be at work between shrews and rodents, namely a predator-prey relation: a preliminary metabarcoding study of the gut and faeces content of *C. olivieri* individuals provides support for such a hypothesis, that would imply active predation, possibly mostly on neonates or non-active unweaned juveniles, directed primarily against *M. musculus* (Galan et al. 2023). *Rattus rattus*, which was very abundant in stock rooms where it probably causes important damages to food stuff (see Dossou et al., 2020 for an example in Cotonou, Benin), presents an average value of niche breadth compared to other species, and high overlap values with other species. Using telemetry in a rural area around Berega in Tanzania, Monadjem et al. (2011) found that within the houses or buildings they live in, black rats (also called roof rats) were located in the roof (37% of fixes), in the bedroom (35%), kitchen (14%) and in walls and windows (14%). Even if some *R. rattus* were caught in traps set on top of furniture items or wall tops, we were not able to quantify the three-dimensional activity of the species known to be at home in the upper parts of dwellings (Granjon & Duplantier, 2009; Monadjem et al., 2011). This vertical component of its spatial niche may however participate to the ecological distribution of the species and help its coexistence with the other ones. Its tolerance for quite traditional and rural conditions also makes it a good candidate for long-term persistence in relatively marginal areas, even in the absence of intense and regular road traffic (Lucaccioni et al. 2016)

As precised by Colwell & Futuyama (1971), such raw measures of actual niche breadth and overlap cannot *per se* give conclusive answers on the potential competition between coexisting species from a community. However, they can help formulate hypotheses to be tested via experimental procedures. In between, co-occurrence analyses may also help go further in the understanding of actual interspecific relationships at various spatial scales.

Co-occurrence patterns

Co-occurrence analyses at large geographic scales give information on patterns issued from historical processes, often shaped by life history traits of the species involved (see Davis et al. 2018 for an example on Carnivores). Concerning West African commensal rodents, the only significant interspecific segregation pattern found by Hima et al. (2019) among the four dominant species (*M. natalensis*, *R. rattus*, *Crocidura* spp., and *R. norvegicus*) along the Cotonou (Benin) – Niamey (Niger) corridor was between *R. norvegicus* and *M. natalensis*. Conversely, the two *Rattus* species and the pair *R. norvegicus* / *Crocidura* spp. showed significant aggregation at this spatial scale (i.e. they were found more often than expected by chance in the same localities). The authors did not propose any explanation of these trends, that may typically result from a mixture of historic and stochastic processes on the one hand, and behavioural ones on the other hand, especially when the co-occurrence event do correspond to real co-existence / syntopy at the microhabitat scale. In Senegal, Dalecky et al. (2015) showed that aggregative patterns between native species of rodents seem to be disrupted by the presence of *Mus musculus* in commensal assemblages. At the scale of the city of Niamey and using different methodological approaches, Garba et al. (2014) found strong segregation patterns between native *M. natalensis* and both invasive *R. rattus* and *M. musculus*, whereas the latter two species showed either random or slightly aggregated (depending on the set of districts considered) co-occurrence patterns. Invasive rats and mice were found associated with urban areas characterized by intense commercial and exchange activities (markets, coach stations and stores) that lies in the heart of town. In these habitats, they probably replaced native *M. natalensis* which has been formerly present, leading to the

native / invasive segregation patterns observed.

Here, we were able to tackle the species co-occurrence questions at two different scales, thanks to our standardized sampling protocol. At the global scale, aggregation cases were only observed between native species, that probably share the commensal space for long. Both cases involved *M. erythroleucus*, with a relatively closely-related rodent species (*P. daltoni*) on the one hand, and with the shrew (*C. olivieri*) on the other hand. Interestingly, these three species can be considered as the most prone to live as commensals of humans among native ones, to the exception of *M. natalensis*, which may partly explain their regular associations in the localities sampled. Most of the segregation patterns observed cannot be discussed as they are likely biased by distribution differences between the species concerned. Conversely, the segregation observed between the invasive *M. musculus* and the native *M. erythroleucus*, well supported using both randomization schemes, is especially interesting as it echoes the situation observed in northern Senegal where the house mouse is progressively, and apparently rapidly, replacing native rodents (and especially *M. erythroleucus*; Dalecky et al., 2015; Diagne et al., 2021). The processes underlying this invasion success are not yet fully understood, but they may include parasitological (Diagne et al., 2016, 2020, 2021) and/or immunological (Diagne et al., 2017) aspects. The speed of this replacement, which was estimated to cover a few dozens of years in Dalecky et al. (2015), is here highlighted by the segregation pattern observed, which tends to indicate that once the house mouse has colonized a new locality, *M. erythroleucus* rapidly declines in abundance, until it disappears. New samplings in sites where *M. erythroleucus* was still present in this 2013-2015 time window, especially along the Tambacounda – Kidira axis and along the Mauritania – Senegal border, would confirm this trend if it showed that the house mouse had become the dominant, or even the unique, rodent species present.

At the local scale, various patterns were observed between the commensal species in southern Senegal. The segregation observed in Tambacounda as well as in some of its districts between the invasive *R. rattus* and *M. musculus* was among the most significant. This trend toward a mutually exclusive distribution in separate housing or working plots may be the result of direct or indirect interactions between these two species. Such interactions have been documented in outdoor habitats of Pacific islands as in the Galapagos or in New-Zealand (Harper & Cabrera; 2010, Bridgman et al., 2018). In these cases, a negative impact of *R. rattus* on *M. musculus* was suspected, based more on indirect (risk effect) than direct / exploitation competition (possibly including predation by *R. rattus* on *M. musculus*). The processes at work in complex commensal environments such as those found in large cities may be different, and the outcome of the interactions may not systematically benefit to the larger species (here the black rat). Instead, the house mouse may well be favoured in urbanized environments such as those that are developing in sub-Saharan Africa, as exemplified by the situation observed in Dakar (Stragier et al., 2020) and in most of the cities from the western part of Senegal North of the Gambia, i.e. the area which has benefitted from the groundnut trade for its early and accelerated development since the 1960s' (Lombard et al., 2020). In such habitats, the small size of the house mouse could represent a real advantage to i) better hide from predators (including humans), ii) more easily slip in well-protected buildings and rooms and iii) subsist on less abundant food resources. From there, competition with larger rodent species (including native ones) may not represent a hindrance to the house mouse range expansion, contrary to what has been hypothesized from results obtained on experimental vs control grids in a 150,000 inhabitant city of central Argentina (Gomez et al., 2008). The continuous development of urbanization according to modern standards along the West-to-East major communication axes (mainly roads) should therefore lead to the continued invasion of the country by *M. musculus*, a trend that could be confirmed in the future by re-sampling localities where the species is either absent or sharing the space with *R. rattus*.

Other major cases of segregation at the local scale involve *M. natalensis* in Kedougou, with both *C. olivieri* and *R. rattus* (only with one randomization scheme, however). Here also, interactions probably occur regularly between these species that appear abundant in this city, which may have led to some kind of mutual exclusion at the scale of the housing or working units sampled. Competition between *M. natalensis* and *R. rattus* is regularly proposed to be at work, or to have occurred in situations where they were confronted: in Eastern RDC villages, it turned to the advantage of the black rat who replaced *M. natalensis* in a

number of villages during the first half of the 20th century (Misonne, 1959). In Tanzania and Swaziland, the fact that *M. natalensis* rarely entered houses was associated to the dissuasive presence of *R. rattus* (or *R. tanezumi*) in this habitat, a hypothesis which was strengthened by the regular observation of *M. natalensis* in commensal habitat in Namibia where no *Rattus* species occurs (Monadjem et al., 2011). Trying to find out which process may underlie this potential exclusion of *M. natalensis* by *R. rattus* in commensal habitats, Cuypers et al. (2017) failed to demonstrate an avoidance behaviour mediated by scent markings. Additional works are necessary to understand the processes at work, but the relative stability of the ratio *R. rattus* / *M. natalensis* in Kedougou since the arrival of the former species in this city more than 25 years ago (Ba, 2000) advocate for good competitive skills of *M. natalensis* in this context. This is all the more apparent as, immediately around the distribution area of *M. natalensis* in southern Senegal, the black rat is very well installed and often dominant (Duplantier et al., 1997; Dalecky et al., 2015; Lucaccioni et al., 2016; this study).

At the same time, it has to be noticed that *R. rattus* and *C. olivieri*, in Kedougou as in other localities (namely Rufisque and Dielyani), show a clear aggregative pattern suggesting that they apparently co-habit quite easily in the commensal space. The fact that the black rat partly forages and lives in upper parts of buildings when the shrew exclusively lives at ground level may explain such cohabitation. These two species were also the most regularly involved in aggregative associations with native rodent species, and especially with *M. erythroleucus*. This may testify for an ancient cohabitation history between these species (more ancient than with *M. musculus*, in particular), and / or be linked with less overall niche overlap between them. The latter is not apparent when looking only at the microhabitat dimension, but may involve dietary, space use or other niche components.

Conclusions

We here present a “snapshot” picture of the community structure of commensal small mammals captured in southern Senegal. This area corresponds to the current distribution area of *R. rattus*, a major invasive species well-established for more than one century in this part of Senegal (Konečný et al., 2013). Most of this area has apparently been colonized more recently by *M. musculus*, another major invasive rodent species with a rapid and ongoing invasion dynamics (Dalecky et al., 2015; Lippens et al., 2017). The contact between these invasive species and the native ones may therefore date from various periods according to the time of arrival / installation of *R. rattus* and *M. musculus*. This probably results in communities that cannot be considered at equilibrium in a number of cases, which in turn makes it difficult to envisage stabilized assembly rules in these species assemblages (see also Hima et al., 2019).

Nevertheless, the results obtained here, associated with others presented recently on each of these two invasive species in Senegal (e.g. in Lucaccioni et al., 2016; Stragier et al., 2020; Diagne et al., 2021) help to better understand their ecological characteristics and requirements, and to make some hypotheses on the evolution of the communities they constitute with their native counterparts in commensal contexts. Indeed, the invasive black rat and house mouse do not seem to have very specific habitat requirements, and they share similar niche breadth with native species in this respect. They also show important overlap in terms of room types they occupy, which should lead to frequent interactions. Other components of the ecological niche of these species should be considered, which may be more informative on the outcome of co-occurrence patterns and interspecific interactions. In these communities where the spatial range dynamics of the invasive species is rather well-known, a better knowledge of both niche characteristics and the nature of interactions between the species concerned will enable us to better understand co-occurrence patterns, and even to make some predictions on the temporal evolution of these patterns at different spatial scales (Bar-Masada et al., 2015). At the local scale, fine-grained co-existence mechanisms would worth be studied in large cities showing both habitat complexity and a reasonable diversity of interacting species (such as Kédougou or Tambacounda). In addition to continuous spatio-temporal surveys over the studies areas to capture the changing dynamics within these small mammal communities, further multidisciplinary research efforts should be devoted to (i) unravel the multifactorial mechanisms underlying the (potential) changes observed in the community structure over time, (ii) depict the consequences of these modifications at ecological (e.g. species

extirpation), social (e.g. threats to stored food) and/or health (e.g. emergence of rodent-borne zoonoses) levels, and (iii) move – by concerted efforts with local stakeholders and decision makers – from fundamental empirical results to sustainable and efficient management actions against the detrimental effects of some of these small mammals.

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Figure legends

Figure 1. Relative frequencies of the small mammals caught in each of the 49 localities sampled. 1: Bakel, 2: Badi Nieriko, 3: Bala, 4: Bantako, 5: Birkelane, 6: Boutougoufara, 7: Bransan, 8: Dembankane, 9: Diakene-Wolof, 10: Dianke Makha, 11: Diattacounda, 12: Diawara, 13: Dide Gassama, 14: Dieylany, 15: Doulouyabe, 16: Fadiouth, 17: Gandiaye, 18: Goudiry, 19: Gouloumbou, 20: Goumbayel, 21: Ida Seco, 22: Joal, 23: Kedougou, 24: Kidira, 25: Kothiary, 26: Koukane, 27: Koussan, 28: Mako, 29: Marsassoum, 30: Mereto, 31: Ndiobene, 32: Niahene, 33: Panal, 34: Rufisque, 35: Sabodala, 36: Segou, 37: Seme, 38: Sil, 39: Sinthian Koundara, 40: Sinthiou Doube, 41: Sinthiou Maleme, 42: Soutouta, 43: Tambacounda, 44: Talibadji, 45: Tobor, 46: Tuabou, 47: Velingara, 48: Yafera, 49: Youppe Hamady (see Table 1 for geographic coordinates and home area of each locality)

Country map retrieved from GADM 3.6 (<https://gadm.org/index.html>) and roads from OpenStreetMap (<http://download.geofabrik.de/africa/senegal-and-gambia-latest-free.shp.zip>). NR1, NR6 and NR7: National Roads 1, 6 and 7.

Figure 2. k+1 analysis of the room characteristics and the rodent communities. A : C1-C2 factorial map of the rodents. B : Eigenvalues graph of the k+1 analysis. C : C1-C2 Factorial map of the localities grouped by areas. D to H : C1-C2 factorial maps of the room characteristics - *D* : Room type (br: bedrooms, gr: granaries, kt: kitchens, mw: workshops, nf: non-food stores, od: outdoors, sh: foodshops, sr: stock rooms); *E* : Stock (0: no stock, 2: some stock present, 3: large stock present); *F* : Floor (ad: adobe, co: concrete, df: dirt floor); *G* : Walls (co: concrete, ms: metal sheet, mw: mud wall, st: straw or without); *H* : Ceiling (co: concrete, ms: metal sheet, st: straw, adobe or without).

Data Accessibility Statement

The data set on which this paper is based is publicly available on the IRD data repository *DataSuds* (<https://doi.org/10.23708/PQTQDA>) as a living and updating resource. The static version of this data set

is also stored as a Supporting Information Data File in Granjon et al. (2021). *Ecology*, 102(10), e03470. <https://doi.org/10.1002/ecy.3470> (as Commensal_small_mammals_southern_Senegal_2012_2015.csv).

Competing Interests Statement

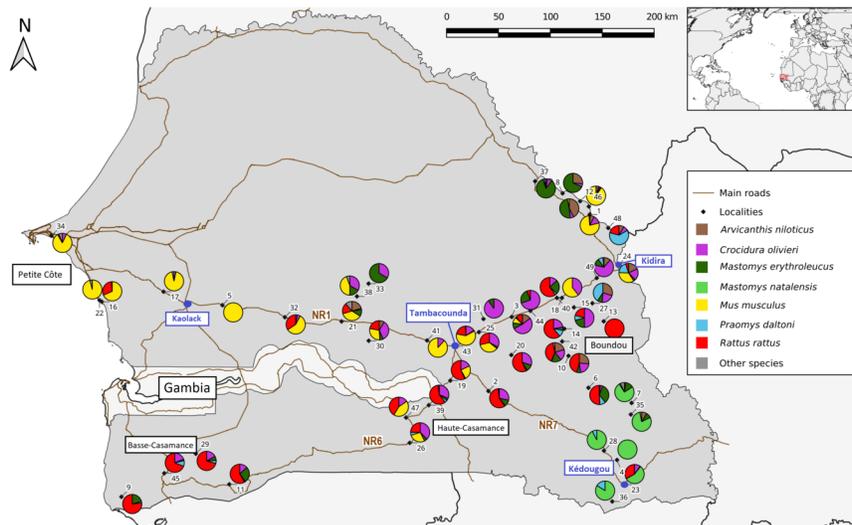
The authors declare that they have no competing interest regarding this article

Author Contributions

Laurent Granjon: Conceptualization (equal); investigation (equal); formal analysis (equal); supervision (equal); writing – original draft (lead); writing - review and editing (equal). Emanuelle Artige: Data curation (equal). Khalilou Bâ: Investigation (equal). Carine Brouat: Funding acquisition (equal); supervision (equal); writing – review and editing (equal). Ambroise Dalecky: Investigation (equal). Christophe Diagne: Investigation (equal); writing – review and editing (equal). Mamoudou Diallo: Investigation (equal). Odile Fossati-Gaschnard: Formal analysis (equal); Philippe Gauthier: Investigation (equal). Mamadou Kane: Investigation (equal), Laëtitia Husse: Investigation (equal). Youssoupha Niang: Investigation (equal). Sylvain Piry: Data curation (equal). Nathalie Sarr: Data curation (equal). Aliou Sow: Investigation (equal). Jean-Marc Duplantier: Conceptualization (equal); investigation (equal); supervision (equal); writing – review and editing (equal); funding acquisition (equal).

Acknowledgements,

We are particularly indebted to all the people in Senegal who welcomed us into their homes for small mammal trapping. We also thank all those who have helped us locally to make these surveys possible, from village chiefs to local contractors. Fundings came from the CHANCIRA (Contract "ANR-11-CEPL-010"), and ENEMI (Contract "ANR-11-JSV7-0006" projects. Additional fundings and logistical support came from Research Unit CBGP ("Centre de Biologie pour la Gestion des Populations").



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