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## REVIEW

**Range expansion of the invasive house mouse *Mus musculus domesticus* in Senegal, West Africa: a synthesis of trapping data over three decades, 1983-2014**

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## **ABSTRACT**

1. The worldwide intensification of human-associated exchanges favours the multiplication of biological invasions. Among mammals, rodent species, including the house mouse *Mus musculus*, are identified as major invaders with profound impacts on native biodiversity, human health and activities. Though contemporary rodent invasions are described on several islands, there are few data describing ongoing house mouse invasions in continental areas.

2. We first outline the known picture of the distribution of the house mouse in Africa. We then describe the ongoing range expansion of the house mouse in Senegal, in order to update its distribution area, assess the location of the invasion front, describe the spatio-temporal dynamics of the invasion at the country scale, and evaluate its impact on native small mammal communities.

3. We briefly review the worldwide status of the house mouse, with special focus on its situation in Africa. Focusing on Senegal, we then use historical records and a large body of spatio-temporal indoor trapping data obtained from small mammal communities over the last 30 years to analyse the invasion dynamics of the subspecies at the scale of the country.

4. The geographic range of the invasive house mouse is surprisingly poorly known in Africa. In Senegal, we document a large range expansion of the subspecies in human settlements over the whole country within the last 30 years. The invasion is still ongoing further east and south within the country, and has major consequences for small mammal communities and thus probably for risks associated with zoonotic diseases.

Keywords: Biological invasion, commensalism, community ecology, rodent, species richness

Running head: Range expansion of the house mouse in Senegal

## **INTRODUCTION**

The worldwide intensification of human-associated exchanges is making previous biogeographical barriers meaningless in terms of living organism dispersion, and favours the multiplication of invasion processes at various geographical scales (Searle 2008). As a result,

invasions are now of major concern in biological sciences. They are identified as having a significant impact on evolutionary processes (Mooney & Cleland 2001), represent a major threat to biodiversity (Clavero & García-Berthou 2005), and are also likely to entail new sanitary and human health problems (Pyšek & Richardson 2010). Among invasive species, rodents undoubtedly represent the vertebrate group that has most often accompanied humans in their history of global dispersal. Rodents have also had numerous opportunities to settle where they were introduced, and then to become invasive. Ecological, palaeoecological, and archaeological studies have documented the direct and indirect impacts of invasive rodents on native plants and animals, leading to in-depth environmental modifications in some cases, for instance on islands (see Drake & Hunt 2009 and references therein). In addition to their effects on biodiversity, invasive rodents have profound impacts on human activities (Stenseth et al. 2003) and on health (Meerburg et al. 2009). These combined effects prompted Lowe et al. (2000) to include three rodent species in their list of 100 of the world's worst invasive alien species. Two of them (the black rat *Rattus rattus* and the house mouse *Mus musculus*) were also ranked among the top three main rodent pest species by Capizzi et al. (2014). Like other invasive species, rodents become difficult to eradicate once they have been introduced (Genovesi 2005). Recent bioeconomic analyses support the conclusion that preventing future invasions is the most cost-effective form of management (Broennimann & Guisan 2008). Accordingly, monitoring the spatial progress of ongoing rodent invasions is a major prerequisite that should represent a priority step in strategies aimed at controlling the effects of invasive rodents on native biodiversity, human health and human activities.

Surprisingly, there are still few data describing ongoing house mouse invasions (Nathan et al. 2015). Recent spatio-temporal surveys of rodent communities have been conducted on some invaded islands (e.g. Russell et al. 2011, Jones et al. 2012) but, to our knowledge, such studies are very scarce in continental areas (e.g. Khlyap & Warshavsky 2010, Jung et al.

2012). In this paper, we briefly review the worldwide status of the subspecies *Mus musculus domesticus*, with special focus on its situation in Africa. We then describe the ongoing range expansion of the house mouse in Senegal, in order to update its distribution area, assess the location of the invasion front, describe the spatio-temporal dynamics of the invasion at the country scale and evaluate its impact on native communities. Our work is based on analyses of small mammal trapping data in commensal habitats recorded throughout Senegal since 1983. This dataset is probably one of the most comprehensive ever gathered on commensal rodent communities at a country scale. It enables us to draw a clear picture of the trends observed in the last 30 years during this specific biological invasion.

### **Scales of house mouse colonization: from worldwide to Senegal**

One of the most widely distributed mammals at the worldwide scale is the house mouse *M. m. domesticus* (Musser & Carleton 2005). Originating from the Middle East, this subspecies probably became commensal in arid areas at the very beginning of the Neolithic in the Near East, by exploiting the niche offered by humans practicing sedentary agriculture (Brothwell 1981, Auffray et al. 1990, Cucchi et al. 2005, 2012). It then expanded its geographic range through human trade and transport. The past invasion history of *M. m. domesticus* has received much attention in the literature. Archaeological records and molecular data suggest a range expansion over several millennia from the Levant towards the Mediterranean area, and during the first millennium BC to Western Europe (Cucchi et al. 2005, Gündüz et al. 2005, Rajabi-Maham et al. 2008, Bonhomme et al. 2011). Phylogeographical studies indicate more recent expansions (during the last few centuries) of *M. m. domesticus* towards remote areas of Africa, the Americas, Oceania (Searle et al. 2009, Bonhomme & Searle 2012, Gabriel et al.

2012) and other islands (Förster et al. 2009, Hardouin et al. 2010, Gray et al. 2014), through ships of European explorers and settlers.

The geographic range of the house mouse in Africa has been recently synthesized by Happold (2013). While referring to *Mus musculus*, this synthesis most probably concerned *M. m. domesticus*, which is the only subspecies of house mouse present in continental Africa, except in Kenya and in South Africa where *Mus musculus castaneus* and *Mus musculus musculus*, respectively, also occur (Bonhomme et al. 2011, Bonhomme & Searle 2012, Monadjem et al. 2015). *M. m. domesticus* appears to be patchily distributed on the continent: large permanent populations exist in North Africa, Senegal, Namibia, South Africa and Zimbabwe, and there are sparse records from numerous coastal cities (Happold 2013). However, this distribution has to be treated with caution, as it is based on few documented data. *M. m. domesticus* might be much more widely present in Africa. For instance, in West Africa, *M. m. domesticus* has also been found in inland localities in Mauritania (Hopf et al. 1976, Granjon & Duplantier 2009), Nigeria (Hopf et al. 1976) and Niger (Dobigny et al. 2002, Granjon & Duplantier 2009, Garba et al. 2014). Furthermore, *M. m. domesticus* has not been recorded in the Democratic Republic of Congo (DRC) by Happold (2013), while Kaleme et al. (2011) studied a sample from Kinshasa, stating that “older records suggest its presence in the east (Misonne 1963)” and that “anecdotal reports also raise the possibility of the presence of the house mouse in the northeastern part of the DRC, specifically around Kisangani.” The species is not reported either from western Cameroon by Happold (2013), while Ihle et al. (2006) sampled a natural population in Kumba (Southwest Province). Similarly, no mention of the species in Sierra Leone and Guinea is made by Happold (2013), while Leslie and Davis (1939) captured it in Freetown (Sierra Leone), and both Fichet-Calvet et al. (2005) and Denys et al. (2009) showed it to be present in villages of the prefecture of Kindia (west of Guinea). Recent city surveys in northern Nigeria (Kano, M. Garba,

unpublished data) and eastern Gabon (Franceville, J. Mangombi, unpublished data) have also yielded house mouse specimens in areas where the species was not mentioned by Happold (2013). From these few examples, it is quite clear that the geographic range of the house mouse in Africa is probably widely underestimated.

The situation in Senegal may appear to be unusual, as historical information on the presence of the house mouse in the country appears to be fairly comprehensive. The house mouse may have reached sub-Saharan West Africa from the 15<sup>th</sup> century with Portuguese sailors (Rosevear 1969b). To our knowledge, archeological information is not available for this area. Preliminary molecular data did not contradict the classical view of an introduction of *M. m. domesticus* in Senegal by Western European settlers (Bonhomme et al. 2011), probably a few centuries ago. The first historical inventories of rodent fauna in West Africa date from the late 19<sup>th</sup> century. They report large and likely standing populations of house mice in colonial coastal cities without mention of specific localities (Temminck 1853, Rochebrunne 1883). In Senegal, historical inventories from the early 20<sup>th</sup> century indicated a distribution of the house mouse restricted specifically to Dakar, surrounding localities (Lafont 1915, Léger & Baurly 1923, Blazy 1924, Sorel & Armstrong 1929, Cazanove 1929, 1932) and other places located less than a few tens of km from the coast along the main road and railway connecting Dakar to Saint-Louis (Lefrou 1929). In the second half of the 20<sup>th</sup> century, house mice were found to be well established in the main coastal cities of the country (e.g. Dakar, Saint-Louis) and to dominate the rodent communities of villages in coastal areas north of the Gambia River. They were absent further south and inland (Duplantier et al. 1991, 1997). Recent inland occurrences of the species were in Richard-Toll city, on the edge of Senegal River delta, ca. 100 km from the coast (Böhme & Hutterer 1978). The last published update on house mouse distribution in Senegal included a number of localities further east in the



country, up to 350-400 km from the coast, mostly along the main west-east road that runs north of the Gambia (Granjon & Duplantier 2009).

## **MATERIAL AND METHODS**

### **Captures**

The dataset presented here results from a historical compilation of 700 indoor trapping sessions that have taken place during the last 30 years (March 1983 - February 2014) in ca. 376 localities throughout Senegal. It was extracted from the Sahelo-Soudanian Rodent Database (Granjon & Duplantier 2009) and complemented using our original field notes for the most ancient records (for information on the small mammal collection see <http://www1.montpellier.inra.fr/CBGP/?q=fr/content/petits-mammifères-0>). For this paper we only considered trapping sessions conducted indoors in human settlements (hamlets, villages or cities; hereafter referenced as localities, see Fig. 1A) because *M. m. domesticus* is strictly commensal (i.e. confined to human buildings) in West Africa (Rochebrunne 1883, Rosevear 1969a, Granjon & Duplantier 2009, Happold 2013).

In trapping sessions, small mammals including rodents and shrews were caught in live traps. Between 1983 and 1994, we mainly used single capture wire-mesh traps (Firobind 8 x 8 x 25 cm and Manufrance 9 x 10 x 26 cm), but we occasionally added Sherman folding box traps (8 x 9 x 23 cm) or multiple capture traps (Manufrance 38 x 13 x 13 cm, equipped with a gravity-closing door). Between 1998 and 2014, we typically used both locally made single capture wire-mesh live traps (8.5 x 8.5 x 26.5 cm) and Sherman folding box traps (8 x 9 x 23 cm). Traps were set inside buildings (dwelling houses, storehouses or shops) for trapping sessions of 1-5 consecutive days. A variable number of rooms were sampled (median ~ 20) in

each locality and trapping session; typically two traps (one wire-mesh and one Sherman) were set per room. Traps were checked and baited once a day with peanut butter, sometimes supplemented with other food items such as fresh onions.

Permission to enter and work within villages was obtained from the appropriate institutional, traditional and familial authorities. Animals were treated in a humane manner, in accordance with relevant requirements of Senegalese legislation and following Sikes et al. (2011). Small mammals were euthanized by cervical dislocation once trapped, as recommended by Mills et al. (1995), and were then weighed, measured, and dissected for research purposes beyond the scope of this paper (e.g. tissue sampling for screening of pathogens, rodent phylogeography and population genetics).

### **Species identification**

Small mammal species nomenclature follows Wilson & Reeder (2005). Most of the rodents and shrews trapped could be identified to the species or genus level based on morphological, ecological and biogeographical knowledge of this region (Granjon & Duplantier 2009, Happold & Happold 2013). When necessary, molecular or chromosomal data were obtained to allow unambiguous species identification of rodents (following procedures described by Granjon & Dobigny 2003, Lecompte et al. 2005, Dobigny et al. 2011). For house mice, 51 males from 38 localities throughout Senegal between 2011 and 2013 (1-3 mice per locality) were identified with the aid of molecular genetics at the subspecies level using the nuclear genetic marker *Zfy2*, following Prager et al. (1998).

### **Distribution maps**

We first drew geographical maps to illustrate the geographic range of *M. m. domesticus* throughout Senegal, and the rough evolution of the range between 1983 and 2014. We used grid cells of 33 x 33 km. For each cell for a given period of time, we combined all available data corresponding to several sampling sessions and localities. We estimated the proportions of trapped individuals made up of invasive rodents (*M. m. domesticus* and *Rattus* spp. – *Rattus rattus* and a few individuals of *Rattus norvegicus* caught in only two sessions), native rodents and shrews. Maps showing these proportions were created for three sampling periods, corresponding to different time ranges with rather similar sampling efforts and numbers of captures (1983-1994: 324 trapping sessions, >17000 trap-nights and 3573 captures; 1998-2010: 249 trapping sessions, ≥17800 trap-nights and 3515 captures 1998-2010; 2011-2014: 127 trapping sessions, 19300 trap-nights and 4132 captures). For specific localities, we calculated the shortest distance to the coast (which was lower than the distance by road or path from a coastal city and the focal locality). In addition, we investigated the distribution of *M. m. domesticus* at smaller spatial scales, focusing on the proportions of trapped individuals that were invasive rodents, native rodents and shrews per locality in recent surveys at the regional scale of the medium valley of River Senegal, and per building at the scale of a recently colonised locality (Dodel).

### **Spatio-temporal dynamics of the house mouse invasion**

For the whole country of Senegal, we analysed spatio-temporal variation in the proportion of the total number of individual small mammals trapped within a session that were identified as *M. m. domesticus* [ $p(Mus)$ ]. We only used data from sessions in which 10 or more individual

small mammals were captured. The relationships between  $p(Mus)$  and longitude, latitude and date of sampling were assessed using a multiple logistic regression with the likelihood-ratio method implemented in SAS v.9.4 (Anonymous 2002). From the logistic regression we inferred the amount of change of the proportion of *M. m. domesticus* relative to the proportion of other small mammal species [i.e. the odds ratios of  $p(Mus)$ ] in local communities associated with each predictor variable.

To assess the temporal dynamics of the *M. m. domesticus* invasion at the local scale, we used data from localities where trapping sessions had been performed both before and after a first capture of *M. m. domesticus* between 1983 and 2014, and in which more than 10 individual small mammals had been captured per trapping session. We considered that these localities had recently been invaded by *M. m. domesticus*. The relationship between  $p(Mus)$  and the time elapsed between the session in which the first house mouse had been caught and the previous session with no house mouse capture was assessed using a logistic regression analysis with the likelihood-ratio method implemented in SAS. We used the results of the logistic regression to extrapolate the time required for *M. m. domesticus* (1) to reach numerical dominance over the set of other small mammal species [i.e. estimated  $p(Mus) \geq 0.50$ ] and (2) to approach exclusion of these species [i.e. estimated  $p(Mus) \geq 0.90$ ].

### **Impact on native communities**

We aimed to evaluate the changes caused by the invasion of *M. m. domesticus* on the community structure of small mammals. We first analysed the spatio-temporal variation of small mammal species richness with regard to  $p(Mus)$ . We expected the presence of invasive species to reduce species richness at local scales (Gotelli & Arnett 2000). For each trapping

session in which at least 10 individual small mammals had been captured, small mammal species richness was estimated using the rarefaction method implemented in EcoSim v.7.72 (Gotelli & Entsminger 2006). The relationship between species richness and  $p(Mus)$ , controlling for the potential effects of latitude, longitude, and date of sampling, was assessed using backward multiple regression analysis implemented in SAS. Both linear and quadratic terms for centred values of every predictor variable were used to allow for non-linear responses, for instance between species richness and geography, as expected based on earlier analyses (Bâ 2002). The comparison of species richness estimates between trapping periods was done using a Mann-Whitney non-parametric test. We then compared the patterns of co-occurrence of commensal small mammal species in the absence and presence of *M. m. domesticus*. We expected the presence of invasive species to alter the co-occurrence patterns of native species (Gotelli & Arnett 2000). We only used trapping sessions in which at least 10 individual small mammals had been captured. The data were organized as matrices of occurrence of capture events in which each row referred to a species and each column to a trapping session. We first focused on sessions in which only native species were captured. We then analysed sessions in which *M. m. domesticus* was captured. We compared observed and expected patterns under the null hypothesis of random assembly (Gotelli 2000). To do so, we used the standardized C-score (SCS; Stone & Roberts 1990) as a quantitative index of co-occurrence, with significant negative and positive SCS indicating aggregation and segregation, respectively. We compared the observed SCS to values obtained from 10000 iterations using null models with random matrices constrained for row and column totals to match the original matrix (“fixed-fixed” algorithm). We estimated pairwise co-occurrence scores using Pairs 1.1 (Ulrich 2008) and applied the confidence limit criterion (Gotelli & Ulrich 2010) to determine whether a particular pair of species was statistically aggregated, segregated, or randomly associated. Results are presented for four native taxa (*Mastomys*

*erythroleucus*, *Arvicanthis* spp., *Praomys daltoni*, *Crocidura* spp.) that were frequently trapped (in  $\geq 25\%$  of the trapping sessions for each taxon) and that share a part of their geographic range with *M. m. domesticus* in Senegal to make the comparison meaningful.

## RESULTS

Genetic analyses confirmed that the 51 house mice examined belonged to the subspecies *M. m. domesticus*, as was expected on the basis of previous research (12 house mice from two localities of Senegal were molecularly identified as *M. m. domesticus*: Bonhomme et al. 2011). We thus considered that *M. m. domesticus* was the only subspecies that occurred in Senegal, at least for the period covered in this study.

### Distribution maps

Small mammals were detected in 95% of the 700 indoor trapping sessions. Trapping yielded a total of 11220 captured individuals, including three exotic species: *M. m. domesticus* (2684 individuals), *Rattus rattus* (2245) and *Rattus norvegicus* (3), and 14 native taxa: *Mastomys erythroleucus* (2285 individuals), *Mastomys natalensis* (2074), *Crocidura* spp. (786), *Arvicanthis* spp. (705; *Arvicanthis niloticus* in central and northern Senegal, *Arvicanthis ansorgei* in southern Senegal), *Praomys daltoni* (352), *Mastomys huberti* (29), *Taterillus* spp. (17; *Taterillus gracilis* and *Taterillus pygargus* in sympatry), *Cricetomys gambianus* (16), *Atelerix albiventris* (7), *Heliosciurus gambianus* (5), *Mus* (*Nannomys*) spp. (4), *Gerbillus* cf. *nigeriae* (4), *Gerbilliscus gambianus* (2) and *Steatomys* spp. (2).

The distribution of *M. m. domesticus* in Senegal was spatially and temporally heterogeneous over the 30 years surveyed (Fig. 1). During 1983-1994 (324 trapping sessions, >17000 trap-nights and 3573 captures), *M. m. domesticus* was mostly restricted to localities close to coastal areas (Fig. 1B). Indeed, all but one *M. m. domesticus* record (99.1%, n = 106 sessions with captures of house mice) and individual (99.8%, n = 555 house mouse individuals) were concentrated less than 120 km from the coast. Importantly, at the end of this time period, a first non-ambiguous capture of *M. m. domesticus* was reported at a large distance from the coast (ca. 350 km in 1994 in Djinkore Kountou Diombo near Tambacounda). In coastal areas of the northern half of the country, *M. m. domesticus* was the most abundantly captured species in most of the localities sampled. *M. m. domesticus* was not detected in coastal Casamance, south of the Gambia River, where *Rattus rattus* was the most frequently trapped rodent species. House mice were also absent from most inland localities where the typical community of indoor trapped small mammals was numerically dominated by very few species, or even consisted of a single species. *Mastomys erythroleucus* and *Arvicanthis niloticus* dominated in northern Senegal, *Mastomys natalensis* in south-eastern Senegal, and *Rattus rattus* was occasionally supplemented by a set of native rodents (*Mastomys erythroleucus*, *Praomys daltoni*, *Arvicanthis* spp.) and shrews (mostly *Crocidura* spp.) elsewhere (e.g. lower to upper Casamance, villages along the road Tambacounda-Kidira). *Rattus rattus* and *Mastomys natalensis* were found to live in sympatry in a unique locality: the city of Kédougou, south-eastern Senegal (see Fig. 1A).

During 1998-2010 (249 trapping sessions, ≥17800 trap-nights and 3515 captures), *M. m. domesticus* expanded inland (Fig. 1C). In addition to in the coastal areas reported above, the house mouse was repeatedly captured at large distances from the coast in several parts of the country: along the Upper Senegal River (ca. 420 km from the coast in 1998 in Dembankané near Bakel; ca. 500 km from the coast in 2007 in Diboli near Kidira at the border with Mali, a

village where the species was not detected in 1983 / 1985 / 2005); in the central Ferlo arid area (ca. 190 km from the coast in 2000 in Barkédji); and in south-central Senegal (e.g. ca. 200 km from the coast in 2006 in Darou Wolof, Koumpentoum Department, west of Tambacounda, a village where the species was not detected in 1989). During this period *M. m. domesticus* thus appeared to be present in a few isolated inland populations surrounded by villages that were still occupied by native species only.

The period 2011-2014 (127 trapping sessions, 19300 trap-nights and 4132 captures) gave a clear picture of the current status of *M. m. domesticus* in Senegal (Fig. 1D). The species was captured in most parts of the country, except in lower Casamance, south-eastern Senegal and isolated localities in the central Ferlo. It occurred in 2013 in localities where it had not been detected before, despite previous trapping sessions, such as villages along the asphalted road in the medium part of the valley of River Senegal (Dodel and Diomandou-Diéry, not detected in 1990 and in 1990 / 2007 / 2008 / 2009 / 2010 / 2011 respectively, ca. 230 km from the coast), cities along the road axis between Tambacounda and Kidira (e.g. Kidira, not detected in 1998 / 1999 / 2007, ca. 500 km from the coast; Kothiari, not detected in 1984, ca. 350 km from the coast), major villages and cities along the main road axis between Tambacounda and Upper Casamance (Gouloumbou and Vélingara, not detected in 1994 and in 1984 / 1988 respectively, ca. 300 km from the coast).

Grid representation illustrates the inland progress of *M. m. domesticus* over the country during the last 30 years (Fig. 1). However this does not provide detailed patterns of house mouse distribution at smaller scales. Representations of captures of house mice realized at the regional and local scales revealed that recently invaded localities were still surrounded by non-invaded ones at the time of sampling (e.g. the medium valley of the River Senegal; see Fig. 2A). They also indicated that in recently colonised localities where *M. m. domesticus* and



native species still coexist, house mice were mostly trapped along the paved road and near markets and shops (Fig. 2B).

### **Spatio-temporal dynamics of the house mouse invasion**

We used 357 trapping sessions to analyse the spatio-temporal dynamics of the house mouse invasion at the country scale. We found that the proportion of house mice,  $p(Mus)$ , varied significantly with longitude, latitude and time (likelihood ratio:  $\chi^2_{(3)} = 396.21$ ,  $P < 0.001$ ; Table 1). The odds ratio of  $p(Mus)$  increased westward by a factor of 2.25 (95% CI = [1.92; 2.67]) every one degree of longitude (ca. 108 km), northward by a factor of 2.27 (95% CI = [1.93; 2.68]) every one degree of latitude (ca. 111 km), and by a factor of 1.09 (95% CI = [1.06; 1.12]) every year. The significant decrease in  $p(Mus)$  from north to south remained significant when trapping sessions conducted in localities south of latitude 13.59°N (the southern limit of the historical edge of the house mouse range during the second half of the 20<sup>th</sup> century: Duplantier et al. 1991, 1997) were excluded (results not shown).

We used seven localities to analyse the temporal dynamics of the house mouse invasion at a local scale. In one case, we needed to group trapping sessions that occurred within a period of two months to reach the threshold of 10 individuals captured. We found that in recently invaded localities,  $p(Mus)$  was positively correlated with the time elapsed between the last session in which no *M. m. domesticus* were trapped and the first one in which house mice were captured (estimate  $\pm$  SE =  $0.052 \pm 0.022$ ,  $\chi^2_{(1)} = 5.7$ ,  $P = 0.017$ ; model likelihood ratio:  $\chi^2_{(1)} = 6.26$ ,  $P = 0.012$ ). Every year the odds ratio of  $p(Mus)$  increased by a factor of 1.05 (95% CI = [1.01; 1.10]) at this local scale. Based on these results, the predicted estimate of  $p(Mus)$  was 0.50 (95% CI = [0.35; 0.65]) 33 years after the first detection of the house

mouse. Similarly, the predicted estimate of  $p(Mus)$  was 0.90 (95% CI = [0.46; 0.99]) 76 years after its first detection.

### **Impact on native communities**

Local species richness of commensal small mammals ranged between 1 and 5 species for 10 sampled individuals, with a mean  $\pm$  SE of  $2.03 \pm 0.05$  species per trapping session and locality. Although only slightly variable, the estimated species richness of small mammals decreased significantly with  $p(Mus)$ , as predicted. It also varied quadratically with latitude and to a lesser extent increased with time ( $F_{4,352} = 70.45$ , adjusted  $R^2 = 0.438$ ,  $P < 0.001$ ; Table 2). The significant quadratic term for latitude indicates a mid-latitude peak of species richness located in central Senegal around  $14^\circ\text{N}$ , north of the Gambia. The temporal effect suggests that species richness estimated among the captured small mammal individuals increased during the study period. Indeed, species richness estimated over the 1998-2014 period (mean  $\pm$  SE =  $2.12 \pm 0.06$ ,  $n = 231$  sessions) was slightly but significantly higher than the richness estimated over the 1983-1994 period (mean  $\pm$  SE =  $1.86 \pm 0.08$ ,  $n = 126$  sessions; Mann-Whitney test,  $P = 0.011$ ). The seven localities that were used for estimating the dynamics of the invasion at the local scale had highly heterogeneous species richness levels (mean  $\pm$  SE =  $2.18 \pm 0.24$ , range = 1.42–3.47) in trapping sessions occurring before the first detection of *M. m. domesticus*.

In the absence of *M. m. domesticus*, four pairs of native species were significantly aggregated, and the other two were randomly associated (Table 3a). By contrast, when *M. m. domesticus* was captured, only one pair of native species was found to be significantly

aggregated (*Mastomys erythroleucus* and *Praomys daltoni*), while the other five were randomly associated (Table 3b).

## DISCUSSION

Small mammals were caught in the majority of trapping sessions and localities. Capture efficiency may vary according to rodent species and trap type, and a large number of traps per session as well as the concomitant use of different types of trap is known to reduce strongly the likelihood of a species being present but not being captured (Garba et al. 2014). Thus, we cannot formally exclude that the use of different trapping methods between the periods 1983-1994 and 1998-2014 could have partly contributed to the significant temporal variation in the proportion of house mice we observed. However, the range expansion of *M. m. domesticus* was also observed between the periods 1998-2010 and 2011-2014, for which data were acquired using the same standardized trapping method. Our trapping data thus seem suitable for our examination of the geographic range of the house mouse and its variation in space and time.

### **Following the inland invasion of *M. m. domesticus***

Our results support the hypothesis that the range of *M. m. domesticus* has changed during the period surveyed, and suggest that process of expansion has not reached equilibrium yet. Distribution maps and statistical tests converge to show an expansion of *M. m. domesticus* in Senegal over the 30 years surveyed, from coastal to inland areas. Quantitative estimates of range expansion rates through space and time suggest that the proportion of *M. m. domesticus*

relative to the proportion of the other small mammal species increased by about 9% every year and by about 11.5% every ten km westward and northward. This pattern of inland expansion shows strong similarities with recent spatio-temporal changes in road infrastructures, in transport networks, and in the distribution of weekly rural markets (Ninot 2003). Indeed, the current distribution of *M. m. domesticus* covers much of north and central Senegal, with the exception of areas less regularly connected by human traffic and commercial transportation. In the central Ferlo, for instance, the house mouse was only recorded in highly connected cities and villages along the paved part of the main road axis. It was not captured in villages located along the inland part of the road which was asphalted toward the Mauritanian boarder only after 2011. We predict a further ongoing invasion of *M. m. domesticus* along this road, which could be verified by future surveys of rodent communities in this area.

*M. m. domesticus* was historically absent further south, in Casamance and south-eastern Senegal (Kédougou district, Fig. 1A) (Duplantier et al. 1991, 1997). We show that the subspecies has not yet expanded towards these regions, except very recently in Upper Casamance. The significant decrease of  $p(Mus)$  from north to south suggests a clinal variation of the proportion of *M. m. domesticus* within the geographic range of the species. Climatic effects, interspecific interactions and historical contingencies may have contributed to this pattern. For instance, Sahelian arid climatic conditions in North Senegal may be more favourable for the house mouse than southern Sudanian climatic conditions. In contrast, these may be more favourable for the invasive *Rattus rattus*, well established in southern Senegal where it may also represent a strong competitor that could limit the expansion of the house mouse (Duplantier et al. 1991). The clinal variation in the house mouse's distribution may also relate to historical factors such as the initial introduction or introductions that probably occurred in the north of Senegal, via the historical harbour and former capital of colonial

French West Africa Saint-Louis, or via the subsequent development of the city of Dakar. If this hypothesis could be corroborated by genetic analyses, it would contribute to explain the pattern of north/south expansion.

In areas recently invaded by *M. m. domesticus*, distribution maps show a mosaic of invaded and non-invaded localities (e.g., Fig. 2A), in contrast with the homogeneous layer of localities invaded long ago observed along the coast. This mosaic pattern, rather than a frontal wave separating invaded and non-invaded homogeneous areas, is typical of biological invasions of human-dispersed species (e.g. Bossenbroek et al. 2001, Florance et al. 2011). In recently invaded areas of Senegal, the localities colonized first are in the cities and villages with weekly rural markets (e.g., Podor, Thillé-Boubacar, Dodel, Aéré Lao, Mboumba, Galoya in the medium valley of the Senegal River; see Fig. 2B). These inland localities are well-connected with the major coastal cities (Dakar, Saint-Louis), where *M. m. domesticus* has a long history of presence, through trade. At a very local scale within recently invaded localities, a heterogeneous distribution of small mammals is also observed and corroborates this scenario: *M. m. domesticus* captures are most often distributed along main roads or near markets, whereas native small mammals are captured both in the same buildings as house mice (thus in syntopy, at least temporarily) and in areas not invaded yet (thus in allotopy with the house mouse), usually at the periphery of the locality. Hence, these first invaded localities may be viewed as “invasion hubs” and act as bridgeheads towards geographically close, but less accessible, villages. This scenario has previously been demonstrated for other biological invasions (e.g. Hastings et al. 2005, Lombaert et al. 2010, and references therein), and formal testing of the theory for the invasive house mouse may be beneficial.

### **Consequences of the house mouse invasion for native communities of small mammals**

During the Iron Age, an increase in trade and human migrations resulted in the invasion, by the house mouse, of the whole of Western Europe in a short time span, and the mouse became numerically dominant in the commensal small mammal fauna (Cucchi et al. 2005). In Senegal, our results show that in only a few decades *M. m. domesticus* has invaded a large part of the country where it now dominates small mammal communities. Rapid spatial expansion combined with a severe decline in native mammals may be typical of recent invasions, due to the massive intensification of human-associated exchanges. Indeed, similar dynamics and impacts have already been observed for the house mouse in villages of western Guinea, following the increase in human population movements and traffic with nearby Sierra Leone during the 1991-2002 civil war (Fichet-Calvet et al. 2005), for rodent species on islands (Wyatt et al. 2008, Harris 2009), and more generally for recent invasions of other mammals (e.g. Waithman et al. 1999, Carden et al. 2011, McDevitt et al. 2014, and references therein).

The species richness estimated in this study is rather low compared to similar estimates derived from outdoor small mammal communities in Senegal (Bâ 2002, Granjon & Duplantier 2009, Bâ et al. 2013). Numerical dominance by very few species is, however, typical of commensal communities (e.g. Fichet-Calvet et al. 2010, Shochat et al. 2010, Weissbrod et al. 2014). We found that species richness varies with latitude with a peak at around 14°N. This non-linear spatial variation of species diversity was also observed for trapping sessions in which only native commensal mammals were captured (results not shown). A similar pattern was previously detected in studies of outdoor rodent communities in Senegal (Bâ 2002), suggesting that it is probably independent of the house mouse invasion. It may rather result from local mixtures of different fauna at the transition between the Sahelian and Sudanian climatic and biogeographical zones at these latitudes. Species richness increased during the study: estimates were slightly higher during the 1998-2014 period (in

which two complementary models of trap were used) than during the 1983-1994 period (in which single-capture wire-mesh traps were mainly used). The use of different trapping methods between these two periods may partly contribute to the significant temporal variation in the estimated small mammal species richness. Indeed, inspection of trapping results shows that one of the most notable differences between these periods is the proportion of shrews that were captured: 1.6% of 2872 captured individuals for 1983-1994 versus 9.5% of 7057 captured individuals for 1998-2014, almost a six-fold increase with the systematic use of Sherman traps in addition to wire-mesh live traps.

Species richness decreases with an increasing proportion of *M. m. domesticus*, thus small mammal communities invaded by house mice have lower species richness than non-invaded ones. This low species richness seems to be a consequence rather than a cause of the invasion processes. Indeed, the localities that were used for estimating the temporal dynamics of the invasion at the local scale had highly heterogeneous species richness levels in trapping sessions occurring before the first detection of *M. m. domesticus*. Furthermore, no difference in species richness was detected between these estimates and those based on seven nearby paired localities sampled in the same periods of time and not invaded by *M. m. domesticus* (results not shown). The analysis of co-occurrence patterns of commensal small mammal species provides additional information allowing us to understand the potential consequences of *M. m. domesticus* invasion on native communities. Our data suggest that the communities of native commensal small mammals were initially structured so that most species were aggregated, possibly around shared resources that are considered abundant and temporally more stable in human buildings than in outdoor environments (Pocock et al. 2004). The introduction of *M. m. domesticus* in such assemblages may destabilise this community structure, allowing it ultimately to converge towards a random assembly pattern. This shift from structured to random community assemblages may represent a widespread consequence

of invasions, as it was already observed in plant, arthropod and amphibian invasions (Gotelli & Arnett 2000, Sanders et al. 2003, Reshi et al. 2008, Santoro et al. 2012, Richter-Boix et al. 2013). The shift may be explained by competition resulting in lowered species richness in localities invaded by house mice, which can translate into fewer opportunities for native species to co-occur. Furthermore, the heterogeneous distribution of the house mouse within recently colonised villages may affect interspecific interactions. For instance, native mammal individuals living in allotopy with regards to house mice do not face the same risks of interspecific competition and of host shifts of pathogens than those living in syntopy with invasive mice. These changes in co-occurrence patterns, interspecific interactions and species richness may therefore have important epidemiological consequences (Keesing et al. 2006, Bradley & Altizer 2007, Telfer & Bown 2012). Small mammals play a significant role as reservoirs of zoonotic diseases, so changes in small mammal communities following biological invasions could affect the distribution and transmission of zoonotic agents in the wild and in human populations (e.g. Gardner-Santana et al. 2009, Harris 2009, Marsot et al. 2013). Further surveys of rodent-borne zoonotic agents are therefore required to assess the potential increase in health risks mediated by the house mouse invasion in Senegal.

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**Table 1.** Spatio-temporal variation, over the whole country of Senegal, in the proportion of small mammals trapped within a session consisting of *Mus musculus domesticus* [ $p(Mus)$ ]. Maximum likelihood estimates for the relationship between  $p(Mus)$  and longitude, latitude and sampling date were assessed using multiple logistic regression analysis. SE = standard error.

Parameter	Estimate±SE	Wald $\chi^2_{(1)}$	<i>P</i>
Intercept	-34.216±2.578	176.22	< 0.001
Longitude	-0.812±0.085	92.08	< 0.001
Latitude	0.818±0.083	96.39	< 0.001
Sampling date	0.085±0.013	45.79	< 0.001

**Table 2.** Small mammal species richness estimated using the rarefaction method based on a subsample of 10 individuals, as explained by the proportion of small mammals trapped within a session consisting of *Mus musculus domesticus* [ $p(Mus)$ ], latitude, longitude and sampling date. Multiple regression statistics with linear and quadratic terms for centred values of predictor variables were used to allow for non-linear responses;  $b_{yi}$ : partial regression coefficient,  $b_{yi}'$ : standard partial regression coefficient.

Effect	$b_{yi} \pm SE$	$b_{yi}'$	$t$	$P$
Intercept	3.114 $\pm$ 0.083	--	37.41	< 0.001
$[p(Mus)]^2$	-5.438 $\pm$ 0.552	-1.115	-9.85	< 0.001
$p(Mus)$	2.069 $\pm$ 0.275	0.836	7.53	< 0.001
(Latitude) <sup>2</sup>	-0.169 $\pm$ 0.023	-0.315	-7.21	< 0.001
Sampling date	0.018 $\pm$ 0.004	0.206	4.95	< 0.001

1 **Table 3.** Effect of *Mus musculus domesticus* on the community structure of native small mammals. Four commensal native taxa were considered:  
 2 *Mastomys erythroleucus*, *Arvicanthis* spp., *Praomys daltoni*, *Crocidura* spp. The standardized C-score (SCS) measured the extent to which  
 3 pairwise species co-occur: significant negative SCS indicates aggregation, whereas SCS that does not deviate significantly from the null  
 4 distribution suggests random associations. Significant *P*-values are in bold. We considered two types of communities: (a) those for which only  
 5 native species had been captured (n = 131 sessions), (b) those in which *M. m. domesticus* was captured (n = 123 sessions).

6 (a) Among the non-invaded communities

Species 1	Number of occurrences	Species 2	Number of occurrences	Number of joint occurrences	SCS	<i>P</i>
<i>M. erythroleucus</i>	91	<i>Arvicanthis</i> spp.	53	42	-2.68	<b>0.007</b>
<i>M. erythroleucus</i>	91	<i>P. daltoni</i>	35	28	-2.06	<b>0.039</b>
<i>M. erythroleucus</i>	91	<i>Crocidura</i> spp.	22	15	-0.25	0.799
<i>Arvicanthis</i> spp.	53	<i>P. daltoni</i>	35	18	-1.62	0.104
<i>Arvicanthis</i> spp.	53	<i>Crocidura</i> spp.	22	15	-2.71	<b>0.007</b>
<i>P. daltoni</i>	35	<i>Crocidura</i> spp.	22	10	-2.01	<b>0.044</b>

7

8 (b) Among the communities invaded by *M. m. domesticus*

Species 1	Number of occurrences	Species 2	Number of occurrences	Number of joint occurrences	SCS	<i>P</i>
<i>M. erythroleucus</i>	53	<i>Arvicanthis</i> spp.	43	30	-1.13	0.260
<i>M. erythroleucus</i>	53	<i>P. daltoni</i>	23	21	-2.43	<b>0.015</b>
<i>M. erythroleucus</i>	53	<i>Crocidura</i> spp.	48	29	0.52	0.605
<i>Arvicanthis</i> spp.	43	<i>P. daltoni</i>	23	16	-1.04	0.299
<i>Arvicanthis</i> spp.	43	<i>Crocidura</i> spp.	48	25	0.23	0.818
<i>P. daltoni</i>	23	<i>Crocidura</i> spp.	48	19	-1.94	0.052

9

10       **Fig. 1.** Geographical maps of sampled localities (A) and of the distribution of *Mus*  
11 *musculus domesticus* captures throughout Senegal, West Africa, in three sampling periods:  
12 1983-1994 (B), 1998-2010 (C) and 2011-2014 (D). In A, geographical areas cited in the text  
13 are indicated: Senegal and Gambia Rivers, central Ferlo (CF), Casamance (CA). Localities  
14 cited in the text are also indicated: Dakar (DK), Saint-Louis (SL), Richard-Toll (RT), Dodel  
15 (DL), Bakel (BK), Kidira (KD), Tambacounda (TB), Kédougou (KE). In B, C, and D, pie  
16 charts indicate the proportions of trapped individual small mammals that were identified as *M.*  
17 *m. domesticus* (red/dark grey), native rodents and shrews (green/medium grey) and *Rattus*  
18 spp. (yellow/light grey). The size of the pie charts is proportional to the total number of small  
19 mammal individuals trapped in a 33 x 33 km grid cell for a given period of time, and is  
20 expressed on a natural logarithmic scale. Arrows indicate first notable captures of *M. m.*  
21 *domesticus* for the following localities, as discussed in the text: Djinkore Kountou Diombo  
22 (DKD) in B; Barkédji (BK), Dembankané (DN), Diboli (DB), Darou Wolof (DR) in C; Dodel  
23 (DL), Diomandou-Diéry (DD), Kidira (KD), Kothiari (KT), Gouloumbou (GL), Vélingara  
24 (VL) in D.

25



26 **Fig. 2.** Distribution of invasive *Mus musculus domesticus* (in red/dark grey), native small  
27 mammals (in green/medium grey) and invasive *Rattus* spp. (a single *Rattus norvegicus*  
28 individual in Podor, in yellow/light grey) (A) in the medium valley of River Senegal in 2011-  
29 2014 at a regional scale, and (B) in 2012 and 2013 at a locality scale (Dodel, a recently  
30 invaded village). In A, the size of each pie chart is proportional to the total number of small  
31 mammal individuals trapped in a locality, and is expressed on a natural logarithmic scale.  
32 Localities are as follows: 1: Thillé-Boubacar, 2: Thillé-Boubacar / Kadiogne-réfugiés, 3:  
33 Croisement Boubé, 4: Thiewlé, 5: Niandane, 6: Podor, 7: Taredji, 8: Ndioum, 9: Diomandou  
34 Diéry, 10: Diomandou Walo, 11: Dodel, 12: Aere Lao, 13: Doumnga Lao, 14: Golléré, 15:  
35 Diammi Gallo, 16: Mboumba, 17: Lougué, 18: Saré Maoundé, 19: Galoya, 20: Agnam  
36 Thiodaye, 21: Boki Diawé, 22: Thiambé, 23: Matam, 24: Dendoudi, 25: Lambago. In B,  
37 crosses refer to all sampled houses, and the size of each symbol (red squares for *M. musculus*  
38 *domesticus* and green circles for native small mammals) is proportional to the number of  
39 small mammal individuals trapped in a room, expressed on an untransformed scale. Source of  
40 the satellite image: © 2015 CNES / Astrium, © 2015 Google Earth Pro (imagery date: July  
41 2013).



