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Parasites and invasions: changes in gastrointestinal helminth assemblages in invasive and native rodents in Senegal.

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Abstract

Understanding why some exotic species become widespread and abundant in their colonized range is a fundamental issue that still needs to be addressed. Among many hypotheses, newly established host populations may benefit from a "parasite release" through impoverishment of their original parasite communities or reduced infection levels. Moreover, the fitness of competing native hosts may be affected by the acquisition of exotic taxa from invaders ("parasite spill-over") and/or by an increased transmission risk of native parasites due to their amplification by invaders ("parasite spill-back"). We focused on gastrointestinal helminth (GIH) communities to determine whether these predictions could explain the ongoing invasion success of the commensal house mouse (*Mus musculus domesticus*) and black rat (*Rattus rattus*), as well as the associated drop of native *Mastomys* species, in Senegal. A decrease of overall prevalence and individual species richness of GIH were observed along the invasion gradients as well as lower specific prevalence/abundance (*Aspiculuris tetraptera* in *M. m. domesticus*, *Hymenolepis diminuta* in *R. rattus*) on the invasion front. Conversely, we did not find any strong evidence of GIH spill-over or spill-back in invasion fronts, where native and invasive rodents co-occurred. For both invasive species, our results were consistent with the predictions of the parasite release hypothesis. Further experimental research is needed to determine whether and how the loss of GIH and reduced infection levels along invasion routes may result in any advantageous effects on invader fitness and competitive advantage.

Keywords: Biological invasions; enemy release; spill-back; spill-over; gastrointestinal helminths; *Mus musculus domesticus*; *Rattus rattus*; parasite community structure.

1. Introduction

Parasites *sensu lato* are likely to have a strong influence on their host population ecology, evolution and dynamics by exerting strong selection pressures on host life-history traits (Phillips *et al.* 2010). Over the last decade, parasitism has been considered as a key factor underlying expansion success of some invading organisms, especially in animal invasions (Prenter *et al.* 2004). Three major and not mutually exclusive mechanisms have been emphasized. The most evocative is the enemy release hypothesis, hereafter referred as the parasite release (PR) hypothesis, which states that invasive species may benefit in their introduced range from the escape of their natural parasites (Colautti *et al.* 2004). The loss or reduced infection levels of parasite(s) may enhance host fitness and performances in the new environment compared to the original range, then facilitating its settlement and spread. The spill-over (SO) hypothesis states that exotic hosts may introduce some of their coevolved parasites, these latter having negative impacts on native hosts of the introduction area (Taraschewski 2006). Finally, the spill-back (SB) hypothesis states that invaders may be competent hosts for local parasites, leading to increased density and transmission of infective stages in environment at the expense of native hosts (Kelly *et al.* 2009). Despite a burgeoning interest on parasitism-related invasion processes in the scientific literature, several gaps were recently highlighted (Heger & Jeschke 2014). First, studies focusing on natural populations still seldom rely on the identification of invasion pathways, although it has been recognized as a critical step to design reliable sampling strategies and robust comparative analyses in invasion research (Muirhead *et al.* 2008). Also, most studies were mainly based on simple systems involving two host species (i.e. one native and one invasive) and one parasite species (Johnson *et al.* 2008), although the complexity of the factors involved would often require a detailed understanding of the interactions at the scale of host and parasite communities (Telfer *et al.* 2010). As a corollary, native parasites have often been considered as unimportant in the

invasion context. This issue was highlighted by Kelly *et al.* (2009) who pointed out a lack of parasite faunal surveys of native hosts prior to the arrival of invaders. Missing information on native communities leads to miss the opportunities to distinguish SO or SB processes. Thus, the ambiguous status of shared parasites (i.e., native or exotic) probably led to erroneous conclusions in many previous works (Lymbery *et al.* 2014)

In the present study, we propose to investigate parasitism-invasion success relationships by considering native and invasive host and parasite communities along two invasion gradients. We focused on the ongoing invasions of two major invasive species, the black rat (*Rattus rattus*) and the house mouse (*Mus musculus domesticus*) in Senegal (West Africa). Originating from Asia, *R. rattus* and *M. m. domesticus* made use of human migrations to expand their distribution range worldwide (Aplin *et al.* 2011; Bonhomme *et al.* 2011). Several studies have documented dramatic parasite-mediated impacts of these invasive rodents on insular indigenous faunas (e.g., Wyatt *et al.* 2008; Harris 2009), suggesting that they may be suitable biological models to study the relationships between parasitism and invasion success. In Senegal, both taxa are exclusively commensal, with distribution areas covering now much of North and Central Senegal for *M. m. domesticus* and much of Senegal South of Gambia River for *R. rattus* (Figure 1). Historical records (see references in Konecny *et al.* 2013; Dalecky *et al.* 2015) and molecular analyses (Konecny *et al.* 2013; Lippens *et al.* in revision) showed that these rodents were first brought to Senegalese coasts by European explorers and settlers, and remained in coastal villages and towns until the beginning of the 20th century. Both taxa have spread further inland during the last century, thanks to the improvement of human activities and transport infrastructures, resulting in the extirpation of native rodents (mostly *Mastomys* species) from commensal habitats beyond their invasion front (Dalecky *et al.* 2015).

Here, we used gastrointestinal helminths (GIH) communities in commensal rodents to test some predictions relating animal invasion success and parasitism. Besides of their known regulatory effects on rodent fitness (Deter *et al.* 2007) and population dynamics (Vandegrift & Hudson 2009), GIH were found to be highly diversified and prevalent in rodent populations in Senegal (Brouat *et al.* 2007). A loss or reduction of parasites by invasive rodents along their invasion route was expected under the PR hypothesis, and/or an increase of parasitism in native rodents when they co-occurred with invasive ones under the SO or SB hypotheses. Using an integrative framework combining systematics and community ecology, we focused on a comparison of GIH communities between natural populations of native and invasive rodents found in localities of long-established invasion, recently invaded and non-invaded localities distributed along well-described invasion routes in Senegal. The focus on Senegalese populations of invasive rodents was assumed, as parasitological signatures from their putative European sources have most probably disappeared during the last centuries. The consideration of non-invaded localities in the comparative design allowed having an overview of GIH communities infecting native rodent hosts before the arrival of the invaders.

2. Materials and methods

2.1. Ethical statement

Trapping campaigns within private properties was systematically realized with prior explicit agreement from relevant institutional (CBGP: 34 169 003) and local authorities. All animal-related procedures were carried out following official ethical guidelines (Sikes, Gannon & Amer Soc 2011).

2.2.Rodent sampling

We used data from historical inventories and ecological surveys (Dalecky *et al.* 2015) as well as recent molecular analyses (Konecny *et al.* 2013; Lippens *et al.* in revision) to define three categories of localities describing the invasion status: (i) localities of long-established

invasion on the west coast, where invasive rodents have settled since centuries and are highly dominant or even the single commensal species present; (ii) recently invaded localities (i.e. invasion front), where invasive rodents have settled for less than 30 years and occur in sympatry with native rodent species; and (iii) non-invaded localities, where invasive rodents have never been recorded. For each category of invasion status, three to six localities were sampled and fieldwork was conducted inside human dwellings along an invasion route for each invasive species (Fig. 1). It was performed in March-April 2013 for *M. m. domesticus* and from November 2013 to February 2014 for *R. rattus*. The detailed description of the standardized rodent trapping protocol used here was provided in Dalecky *et al.* (2015). Briefly, we set at least 120 traps (two traps per house, with sampled houses chosen to cover a significant part of the inhabited area) during one to three nights, in order to ensure that 20 adult individuals per rodent species were caught in each locality. Rodents were captured alive and sacrificed by cervical dislocation, weighted to the nearest 0.5 g, sexed and dissected. Finally, digestive tracts were removed, unrolled and individually stored until examination in plastic universal vials containing 95% ethanol. Rodents were aged on the basis of body weight and/or reproductive status following Granjon and Duplantier (2009). They were identified with morphometric and genetic tools (cytochrome b gene-based RFLP for specific identification in *Mastomys* spp.; ZFY2 gene-based RFLP for subspecific identification in *M. musculus*).

2.3. GIH collection and identification

For each rodent, the different sections of the digestive tract (stomach, small intestine, large intestine and caecum) were scrutinized following Ribas *et al.* (2011). GIH were carefully removed and counted, then classified by morphotype and stored in 95% ethanol. For accurate GIH identification at the most precise taxonomic level, we combined morphological and molecular approaches as diagnosis tools. Morphological identification was firstly carried out

using conventional microscopy and generalist identification keys (Khalil, Jones & Bray 1994; Anderson, Chabaud & Willmott 2009) or specific literature when available. At least one specimen of each taxon identified per rodent species and locality category was then sequenced for Cytochrome Oxidase 1 (CO1) for nematodes (Cross *et al.* 2007) and acanthocephalan, and Nicotinamide Adenine Dinucleotide subunit 1 (NAD1) for cestodes (Littlewood, Waeschenbach & Nikolov 2008). For this purpose, total DNA was extracted from the mid-body region of individual GIH, with the anterior and posterior regions retained in 95% ethanol to complete the morphological examination if necessary. DNA extraction was achieved using the DNeasy blood and tissue Kit (Qiagen) according to manufacturer's instructions slightly modified with a final elution of 200µl of AE buffer. Tissue samples were digested in 180µl of lysis buffer with 20µl of proteinase-K incubated at 56°C overnight. PCR amplifications were performed using the primers 5'-TTGRTTTTTTGGTCATCCTGARG-3' and 5'-WSYMACWACATAATAAGTATCATG-3' for CO1, and 5'-GGNTATTSTCARTNTCGTAAGGG-3' and 5'-TTCYTGAAGTTAACAGCATCA-3' for NAD1, in 25 µl reactions containing 2 µl of DNA extract, 1X of Dream Taq buffer (included 2mM of MgCl2), 0.2 mM of dNTP, 0.5 µM of each primer and 1 Unit of Dream Taq (ThermoFischer). Cycling conditions in Mastercycler gradient (Eppendorf) were the following: 94 °C 3 min, followed by 40 cycles of 94 °C 30s, 50 °C 60s for CO1 and 55°C 60s for NAD1, 72 °C 90s, and a final extension at 72 °C 10 min. PCR products were run on a 1.5% agarose gel to ensure amplification and then sequenced in both direction by Eurofins MWG (Germany). Sequences obtained were processed (cleaning, assembling and alignment) then compared to both public (Genbank) and personal molecular databases. The personal reference sequence database was developed by sequencing nematodes and acanthocephalans of rodents from different West-African areas (Burkina Faso, Mali, Senegal; Supplementary Fig. S1) that had been already identified morphologically to the species level.

2.4. Data analysis

The analyses were carried out independently for each invasion route.

Structure of GIH assemblages. Using the software Quantitative Parasitology 3.0 (Rózsa, Reiczigel & Majorost 2000), prevalence (i.e., percentage of infected hosts) and mean abundance of each GIH taxon were estimated per host species in each locality (Table 2). We also investigated whether the GIH community was structured according to host species and/or invasion status along each invasion route. We thus performed a Principal Component Analysis (PCA) on the restricted dataset including infected hosts only and the presence/absence of GIH taxa showing prevalence higher than 5%. The significance of host species and invasion status was tested independently using Between/Within-groups Analysis (BWA) and Monte-Carlo tests (999 permutations). Note that the influence of invasion status was analyzed by considering four groups to avoid a host-species bias in recently invaded localities: A) invasive hosts in localities of long-established invasion, B) invasive hosts in localities at the invasion front, C) native hosts in localities at the invasion front and D) native hosts in non-invaded localities.

Testing factors affecting GIH assemblages. We used Generalized Linear Models (GLMs) to evaluate whether variations in GIH communities along each invasion route were consistent with the hypotheses relating parasitism and invasion success. We conducted separate analyses for native and invasive host species as we expected different outcomes for these rodents. In invasive rodents, we expected a loss of parasites on the invasion fronts (PR hypothesis) and/or acquisition of local parasites (SB hypothesis); in native rodents, we expected an increase of prevalence, abundance and/or diversity of parasites between non-invaded localities and invasion front under the SO and/or SB hypotheses. Analyses were performed on the following response variables: overall prevalence (percentage of infected hosts combining all GIH taxa; presence/absence data), individual species richness (number of GIH taxa found in one host

individual), specific prevalence (percentage of hosts infected by a GIH taxon; presence/absence data) and specific abundance (number of individuals of a GIH taxon per examined host including uninfected ones). For specific indicators, only GIH taxa that exhibited prevalence levels higher than 10% were considered. We assumed a binomial distribution for prevalence data and a Poisson distribution for abundance data and species richness, using then respectively quasibinomial and negative binomial distributions in case of overdispersion. The full models included individual host factors (sex and body mass), the invasion status of the locality (long-established invasion *vs* invasion front for invasive hosts, invasion front *vs* not invaded localities for native hosts) and their pairwise interactions as possible predictors. As some GIH of terrestrial mammals spend at least one part of their life-cycle in the external environment as egg or larvae, we also included the climate (temperature and rainfall) as environmental predictor at the scale of the locality. For this purpose, climatic data, i.e. temperature (recorded from local weather stations closest to sampled localities and available on http://www.ncdc.noaa.gov/cdo-web/datasets; in degrees Celsius for each year: monthly mean, mean minimum and maximum, daily minimum and maximum) and rainfall (recorded from satellite products available on http://richardis.univ-paris1.fr/precip/rainser1.html with GPCP-1DD as date source; in millimeters for each year: annual accumulative, accumulative, monthly minimum and maximum rainfall in rainy season) were retrieved between 1997 and 2012. We first carried out PCA on these data (Supplementary Fig. S2, Fig. S3),. Then, we included the first PCA axis coordinates of each locality in the starting model. If strong association was graphically observed between the first PCA axis and invasion status, the coordinates on the second axis were included. Model selection was then performed from full models based on the Akaike information criterion with correction for samples of finite size (AICc). The most parsimonious model among those selected within two AIC units of the best model was chosen. *P-values* were obtained by

stepwise model simplification using likelihood-ratio tests. The final models were validated by checking the model dispersion and ensuring normality, independence and variance homogeneity of the residuals. All analyses were performed using the packages ade4 v1.4-16, MuMIn v1.15.1 and lme4 v1.1-8 implemented in R software v3.2.1 (R Core Team 2015).

3. Results

3.1. Rodent trapping

A total of 752 rodents belonging to four species (268 *M. m. domesticus* and 169 *Mastomys erythroleucus* on the mouse invasion route; 193 *R. rattus*, 29 *Ma. erythroleucus* and 93 *Mastomys natalensis* on the rat invasion route) were collected in 25 localities (Table 1). In long-established localities, only invasive rodents were generally captured except on the rat invasion route where few *Ma. erythroleucus* individuals (n = 24) have been trapped but not included in further analyses due to low sample size. As expected in localities at the invasion front, native rodents co-occurred with invasive ones, although being nearly systematically less abundant. Along the mouse invasion route, native rodent communities were largely dominated by *Ma. erythroleucus*, whereas *Ma. erythroleucus* and *Ma natalensis* dominated along the rat invasion route. These two native sister species did not co-occur, except in a single non-invaded locality (Bransan). We therefore did not disentangle the potential impact of these *Mastomys* sibling species in the analyses focusing on the rat invasion route.

3.2. Structure of GIH assemblages

We recorded eight taxa of GIH along the mouse invasion route (Table 2). Five nematode taxa (*Aspiculuris tetraptera*, *Gongylonema* sp., *Pterygodermatites senegalensis*, *Syphacia obvelata*, Trichostrongylid) were found in *M. m. domesticus* only, and two species (*Anatrichosoma* sp., *Asp. africana*) were found in *Ma. erythroleucus* only. The dominant *Asp. tetraptera* was the only nematode found in *M. m. domesticus* populations from long-established and recently established invasion. *Asp. africana* was restricted on native rodents

from invasion front localities. Only the cestode *Mathaevotaenia symmetrica* was found in both host species whatever the invasion status of the sampled locality. The overall prevalence varied from 0.3% (Trichostrongylid) to 11.6% (*Asp. tetraptera*) in *M. m. domesticus*, and from 15.4% (*Asp. africana*) to 36.1% (*M. symmetrica*) in *Ma. erythroleucus*.

We recorded 14 taxa of GIH within rodents sampled along the rat invasion route (Table 3). Three nematodes (*Aspiculuris* sp., *Gongylonema* sp., *Protospirura muricola*) and the acantocephalan *Moniliformis moniliformis* were strictly found within *R. rattus* sampled in localities of long-established invasion. Three nematodes (*Asp. africana, Pterygodermatites* sp., *Trichuris mastomysi*) and one cestode (*Raillietina baeri*) were specifically found in *Mastomys* spp. Two nematodes (*Neoheligmonella granjoni, Physaloptera* sp.) and four cestodes (*Hymenolepis diminuta, Hymenolepis sp., M. symmetrica, Raillietina trapezoides*) were found both in *R. rattus* and *Mastomys* spp., but only two species (*N. granjoni., R. trapezoides*) were shared by sympatric invasive and native rodent populations at the invasion front. *Aspiculuris* sp. in *R. rattus* would be a new species (Ribas et al.unpublished work). The overall prevalence ranged from 1% (*R. trapezoides*) to 30.1% (*H. diminuta*) in *R. rattus*, and from 0.8% (*Pterygodermatites* sp., *H. diminuta*) to 26.2% (*T. mastomysi*) in *Mastomys* spp.

Multivariate analyses revealed that the GIH communities along both invasion routes were structured with regard to host species, with distinct GIH communities between native and invasive rodents (Figs. 2b, 3b), even on invasion fronts (Figs. 2a, 3a).

3.3. Testing factors affecting GIH assemblages

Mouse invasion route. For *M. m. domesticus*, GLMs revealed significant association between invasion status and, respectively, GIH overall prevalence ($F_{1,166} = 23.19$, $p < 0.0001$), species richness ($F_{1,166} = 25.22$, $p < 0.0001$), and *Asp. tetraptera* prevalence ($F_{1,166} = 48.71$, $p < 0.0001$), with higher values in host populations from long-established localities than in those from invasion front (Table 4a). Climate was systematically included in the most parsimonious

models, explaining GIH overall prevalence ($F_{1,165}$ = 25.80, p < 0.0001), species richness ($F_{1,165}$ = 33.48, p < 0.0001), prevalence of *Asp. tetraptera* ($F_{1,265}$ = 40.28, p < 0.0001) and abundance of *M. symmetrica* ($F_{1,265}$ = 4.99, p = 0.0254). For *Ma. erythroleucus*, invasion status was a significant predictor for GIH overall prevalence ($F_{1,167}$ = 9.26, p = 0.0023) and species richness ($F_{1,166}$ = 25.22, p < 0.0001), as well as *Asp. africana* prevalence ($F_{1,167}$ = 33.60, p < 0.0001) and abundance ($F_{1,167}$ = 53.47, p < 0.0001), with native hosts from the invasion front being more infected than those from non-invaded localities (Table 4a). Climate also influenced variations in GIH overall prevalence ($F_{1,166}$ = 26.89, p < 0.0001), *M. symmetrica* prevalence ($F_{1,166}$ = 17.79, p < 0.0001) and abundance ($F_{1,165}$ = 15.88, p < 0.0001), and *Anatrichosoma* sp. prevalence ($F_{1,165}$ = 6.82, p < 0.009). GLM also showed that native female rodents exhibited higher abundance of *M. symmetrica* than males ($F_{1,167}$ = 7.17, p = 0.0074).

Rat invasion route. For *R. rattus*, GLMs revealed that GIH overall prevalence ($F_{1,191}$ = 37.57, p < 0. 0001) and species richness ($F_{1,191}$ = 31.84, p < 0. 0001) as well as *H. diminuta* prevalence ($F_{1,191}$ = 39.69, p < 0. 0001) and abundance ($F_{1,191}$ = 26.18, p < 0. 0001) were lower in localities of long-established invasion than in those at the invasion front (table 4b). Climatic features also affected significantly GIH overall prevalence ($F_{1,190}$ = 8.95, p = 0.0027), species richness ($F_{1,190}$ = 10.06, p = 0.0015) and *H. diminuta* abundance ($F_{1,190}$ = 14.79, p = 0.0001). For *Mastomys* species, invasion status was found to influence *Asp. africana* prevalence ($F_{1,120}$ = 8.13, p = 0.0043), *M. symmetrica* prevalence ($F_{1,120}$ = 31.53, p < 0. 0001) and abundance ($F_{1,120}$ = 39.54, p < 0. 0001) which were lower at the invasion front than in non-invaded localities (Table 4b). Variations in GIH overall prevalence ($F_{1,120}$ = 22.13, p < 0. 0001) and species richness ($F_{1,120}$ = 26.88, p < 0. 0001) as well as *T. mastomysi* prevalence ($F_{1,120}$ = 11.06, p = 0. 0009), *Asp. africana* prevalence ($F_{1,119}$ = 26.91, p < 0. 0001), *M. symmetrica* prevalence ($F_{1,120}$ = 6.40, p = 0.0114) and abundance ($F_{1,120}$ = 39.54, p < 0.

0001) appeared to be influenced by climatic conditions. GLMs also revealed that heavier individuals were more infected by *T. mastomysi* ($F_{1,120}$ = 6.97, p = 0. 0083) and *M. symmetrica* burden was more important in females than in males ($F_{1,120}$ = 3.89, p = 0. 0485).

4. Discussion

In this study, we found nineteen GIH taxa in four rodent species indicating a great GIH diversity, consistently with previous studies in commensal rodents from Africa (e.g., Brouat *et al.* 2007; Elshazly *et al.* 2008). The majority of these GIH taxa occurred anecdotally in their hosts (prevalence < 5% for twelve taxa). Some of the taxa recorded here are known to infect a wide variety of rodent species throughout the world. More specifically, it is likely that *Asp. tetraptera* and *H. diminuta*, the dominant GIH recovered in *M. m. domesticus* and *R. rattus* respectively, were brought in Senegal with these rodents. Indeed, it has been showed that *Asp. tetraptera* is a typical parasite of *M. m. domesticus* worldwide (Behnke *et al.* 2015) and *H. diminuta* was retrieved in *R. rattus* in many other regions where black rats were introduced (Elshazly *et al.* 2008). Alternatively, *Asp. africana, P. senegalensis*, *N. granjoni* and *T. mastomysi* were first described in African rodents and should thus be local parasites, some of which may have been acquired by invasive rodents during their range expansion. However, making unambiguous assumptions on the local/exotic origin of some parasites is not straightforward. As such, *H. diminuta* was also retrieved here in one native *Ma. natalensis* individual captured in non-invaded localities. The origin (i.e., local *vs* exotic) of other GIH found exclusively in *M. m. domesticus* (e.g., *S. obvelata*) and *R. rattus* (e.g., *Gongylonema* sp.) is also confusing. For instance, *S. obvelata* was regularly found in house mouse elsewhere (e.g., Milazzo *et al.* 2010), but was also reported in local non-commensal rodents *Arvicanthis niloticus* and *Mastomys huberti* in Senegal (Diouf). Yet, the cestode *M. symmetrica* was found in native and invasive rodent species on both invasion routes, whatever the invasion status of the locality. To date, this GIH species was associated with invasive *R. rattus* and *M. m.*

domesticus in America, Europe and Asia (Beveridge 2008); its first report in Africa from a South-African endemic rodent *Micaelamys namaquensis* was very recent (V. Haukisalmi, personal observations). In this study, the concomitant use of morphological and molecular tools allowed to have some confidence in the fact that some GIH taxa are shared by invasive and native rodents. The difficulties to assess the precise status of parasites as local or exotic is however still there, resulting from the important temporal gap between the increasing of human-mediated transport of animal organisms and the establishment of taxonomic surveys and species monitoring programs (Lymbery *et al.* 2014).

Under the hypotheses of SO or SB, we expected to detect some GIH taxa only at the invasion front for native hosts or for invasive hosts, respectively. No such typical pattern was detected along the mouse invasion route. Indeed, the only GIH species (*M. symmetrica*) found in both native and invasive rodents along the mouse invasion route was recorded in all sampled localities. In most of the selected GLMs but not in the most parsimonious one (data not shown), the abundance of *M. symmetrica* was found to be higher in *Ma. erythroleucus* populations from the invasion front than from non-invaded areas. . Providing that this cestode is native, it may however have been acquired by invasive rodents at the time of their establishment in coastal localities before spread. In this case, the increased infection level in *Ma. erythroleucus* at the invasion front would thus be a pattern compatible with the SB hypothesis.

On the rat invasion route, some GIH taxa were recorded in a rodent species exclusively at the invasion front, such as *Hymenolepis* sp. and *R. trapezoides* in *R. rattus* and *Ma. natalensis*, *R. baeri* in *M. natalensis* or *N. granjoni* in *R. rattus* (Table 3). Nevertheless, these GIH taxa occurred in only a few localities with low infection levels and were not therefore considered in GLMs. These data indicated that host acquisition may have occurred at the invasion front as expected under SO/SB hypotheses. However, competence of the new host may be too low

for the parasite acquisition has an impact on infection levels in native hosts. Lower infection levels of *M. symmetrica* observed in *Mastomys* populations from the invasion front compared to non-invaded localities were not consistent with SO or SB hypotheses, and would rather suggest a dilution of this parasite (Johnson *et al.* 2008) when both host species occurred.

One can imagine that the detection of SO or SB patterns along mouse and rat invasion routes would be prevented by the involvement of highly virulent parasites causing the rapid death of the host acquiring them. However, this argument is not likely for GIH that are generally not lethal for their hosts (Bordes & Morand 2011). The absence of typical SO or SB patterns may rather lie in the fact that many GIH taxa could be specialists or, at least, exhibit high host preferences, this latter potentially explaining the contrasted specific prevalences recorded for some GIH in different rodent species (e.g., *R. trapezoides* on rat invasion route). GIH may thus not be an accurate model to evaluate the importance of SO and SB processes in rodent invasion success. By the way, previous studies suggesting a role of parasites in the invasion success of *M. m. domesticus* and *R. rattus* mainly focused on protozoans or microparasites (e.g., Wyatt *et al.* 2008; Harris 2009), but see Smith and Carpenter (2006).

Both *M. m. domesticus* and *R. rattus* exhibited lower rates of parasitism in localities sampled at the invasion front compared to long-established localities in Senegal, consistently with the PR hypothesis. This pattern was detected when considering the whole GIH community (overall prevalence and species richness) as well as specific taxa (*Asp. tetraptera* prevalence in *M. m. domesticus* and *H. diminuta* prevalence and abundance in *R. rattus)*. PR was already shown in expanding populations of *R. rattus* in other invasion contexts (Morand *et al.* 2015). To our knowledge, our work is the first providing such evidence of parasite release in *M. m. domesticus.* Subsequently, our results raise obvious questions about the precise causes and outcomes of this parasite loss.

The decrease of parasitism levels in invading rodent populations may be explained either because the limited number of host individuals involved in spread does not carry the complete range of parasites found in source localities (founder effect), or because parasites that spread with their host are unable to establish and persist in the new environment of the invasion front (MacLeod *et al.* 2010). Distinguishing between these two types of processes is often difficult mainly because data on host and parasites close before and after the invasion spread are often lacking (Lymbery *et al.* 2014).

Particular features have been identified to render some parasites more prone to be lost during invasion (MacLeod *et al.* 2010). For instance, rare, patchily distributed or strongly virulent parasites have less opportunity to follow their host during its spread. Also, parasites with complex life cycles may fail to establish in a novel area because of sub-optimal environmental factors such as the absence of one of their required intermediate hosts. GIH have usually low pathogenic effects due to co-evolution of immunoregulatory processes with their hosts (Dobson & Foufopoulos 2001), suggesting that strong virulence is not a key trait to explain their loss by invasive rodents. In this study, the two GIH that have been lost during mouse and rat expansions, i.e., *Asp. tetraptera* and *H. diminuta* respectively, were highly prevalent in localities of long-established invasion. However, the absence of *Asp. tetraptera* in some of these localities (THL, NDB) may explain why this nematode is less prevalent at the invasion front of *M. m. domesticus*. Also, this directly transmitted parasite whose transmission depend on host density might have been brought by first introduced *M. m. domesticus* at the invasion front but then lost because of small host population size (Lippens *et al.* in revision). On the contrary, *H. diminuta* was homogeneously distributed in long-established invasion localities of *R. rattus*. The life cycle of this GIH requiring intermediate hosts might explain its loss during rat invasion. However, its intermediate hosts may be various arthropod species

including beetles (Andreassen *et al.* 2004) that are *a priori* widely distributed in Senegal (Sembène *et al.* 2008).

Contrasted environmental conditions between localities of long-established invasion and invasion front may also explain spatial variations in helminth prevalence either directly (as GIH of terrestrial mammals spend at least one part of their life-cycle in the external environment outside their host) or indirectly through their impact on host demography or life-history traits (Krasnov *et al.* 1998). Consistently, climate has been systematically found to be significant in most of the models explaining variations in infection levels or community structure of GIH on both invasion routes.

Parasite loss does not necessarily mean parasite release (Prior *et al.* 2015). The extent to which parasite loss actually translates into a competitive advantage remains difficult to demonstrate because it involves subtle and complex impacts (Marcogliese & Pietrock 2011). For instance, a decrease in parasite species richness -as expected when PR occurs- may theoretically lead to lower inter-specific competition within parasite infracommunities, and thus increased abundance of the remaining parasites (Roche *et al.* 2010) or higher occurrence of over-regulated parasites within host populations. Assuming higher impacts of remaining parasites, this loss phenomenon should not have any positive effect on the host population. The loss of common parasites, such as *A. tetraptera* in *M. m. domesticus* or *H. diminuta* in *R. rattus*, is more likely to result in an effective "release" for their host (Colautti *et al.* 2004). It has been advocated that PR may lead to positive outcomes in host either through regulatory (release of a parasite regulating host demographic parameters such as survivorship and fecundity) and/or through compensatory (reallocation of resources from defense to population growth over ecological time, or counter-selection of genotypes with costly defenses during invasion over evolutionary time) pathways (Colautti *et al.* 2004). Understanding how parasite loss may translate into effective release requires therefore a better understanding of the effects

of specific enemies on their host (Colautti *et al.* 2004). Up to now, the advantage conferred by a parasite loss has more often been assumed than concretely addressed in animal models (Prior *et al.* 2015). Some studies provided field evidence that GIH may impact host population dynamics (Hudson 1998; Albon *et al.* 2002; Newey *et al.* 2005; Vandegrift & Hudson 2009; Rosà *et al.* 2011). Previous laboratory studies suggested relatively low effects of *Asp. tetraptera* on laboratory house mouse probably due to the selection of an immunological resistance (Derothe *et al.* 1997), but also negative effects on fitness in the case of heavy worm burdens (reviewed in Taffs, 1976). For *H. diminuta*, experimental infestations suggested expensive immunological responses accompanied with pathophysiological changes in hosts (Kosik-Bogacka, Baranowska-Bosiacka & Salamatin 2010). However, these studies focused on laboratory models that could differ from field-caught rodents in many ways. Further experimental infestations on *M. m. domesticus* and *R. rattus* individuals sampled in natural populations in Senegal should be actually the best way to ascertain the GIH release-related benefices at the host population level, even if we are aware that the specific effects of a parasite in natural populations -as co-infections with other parasite taxa may occur in host infracommunities- could differ from those in common garden conditions (Telfer *et al.* 2010).

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Table 1: Number of individuals analyzed per host species for each locality along a) the mouse invasion route and b) the rat invasion route. The code used for each sampling locality is indicated in parentheses. LI: localities of long-established invasion; IF: localities at invasion fronts; NI: non-invaded localities. '-' indicates that no rodent was trapped or analyzed.

a)

Categories	**Localities (code)**	**Host species**	
		M. m. domesticus	*Ma. erythroleucus*
LI	Dagathie (DAG)	28	-
	Mbakhana (MBA)	27	-
	Thilene (THL)	19	-
	Ndombo (NDB)	21	-
IF	Dodel (DOD)	22	25
	Aere Lao (AEL)	28	20
	Galoya (GAL)	42	10
	Dendoudi (DEN)	18	21
	Lougue (LOU)	26	19
	Croisement Boube (CRB)	37	-
NI	Doumnga Lao (DOL)	-	25
	Lambago (LAM)	-	16
	Thiewle (THW)	-	21
	Diomandou walo (DIW)	-	12

b)

Categories	**Localities (code)**	**Host species**		
		R. rattus	*Ma. erythroleucus*	*Ma. natalensis*
LI	Marsassoum (MAR)	24	-	-
	Diakene-Wolof (DIK)	24	-	-
	Diattacounda (DIT)	27	-	-
	Tobor (TOB)	20	-	-
IF	Badi Nieriko (BAN)	24	9	-
	Boutougoufara (BOU)	29	7	-
	Kedougou (KED)	22	-	24
	Soutouta (SOU)	23	10	-
NI	Bransan (BRA)	-	3	22
	Mako (MAK)	-	-	26
	Segou (SEG)	-	-	21

Table 2: Prevalence in % [with 95% confidence intervals calculated with Sterne's exact method] and abundances (mean ± standard deviation) of GIH taxa collected from *M. m. domesticus* (*Mm*) and *Ma. erythroleucus* (*Mae*) for each sampling locality (codes are provided in Table 1) along the mouse invasion route. Taxa in bold are those chosen for performing GLMs. No abundance data was reported for both *Anatrichosoma* sp. and *Gongylonema* sp as they were difficult to quantify. The type of lifecycle, direct (only one host in the cycle) or complex (at least one intermediate host, mainly insects), is also provided for each GIH taxon. Legend: Loc = Locality. Cestoda: Mat = *Mathevotaenia symmetrica*. Nematoda: Ana = *Anatrichosoma* sp.; Aspa = *Aspiculuris africana*; Aspt = *Aspiculuris tetraptera*; Gong = *Gongylonema* sp.; Pte = *Pterygodermatites senegalensis*; Syp = *Syphacia* obvelata; Tric = Trichostrongylid.

	Phylum	Cestoda	Nematoda						
	Cycle	Complex	Direct	Direct	Direct	Direct	Direct	Direct	Complex
Loc	Host	**Mat**	***Ana***	*Aspa*	***Aspt***	*Gon*	*Syp*	*Tric*	*Pte*
DAG	*Mm*	17.9% [6.1 – 36.9] (0.5 ± 1.26)			71.4% [51.8 - 85.8] (23.93 ± 36.71)		10.7% [3 – 28.2] (0.71 ± 3.22)	17.9% [7.3 – 35.7] (0.71 ± 1.8)	17.9% [7.3 – 35.7] (0.71 ± 1.8)
MBA	*Mm*	7.4% [1.3 – 23.7] (0.15 ± 0.53)			22.2% [10.2 - 41.5] (9.07 ± 36.62)				
THL	*Mm*						21.1% [7.5 – 44.6] (0.84 ± 2.22)		
NDB	*Mm*	4.8% [0.3 – 23.3] (0.05 ± 0.22)							
CRB	*Mm*	7.5% [2.1 – 19.8] (0.10 ± 0.38)							
GAL	*Mm*	14.3% [6.4 – 28.4] (0.33 ± 1.07)			2.4% [0.1 – 12.7] (0.02 ± 0.15)	4.8% [0.9 - 16.3]	4.8% [0.9 – 16.3] (0.12 ± 0.55)		
DOD	*Mm*	9.1% [1.6 – 29.1] (0.59 ± 2.56)			4.5% [0.2 – 22.2] (0.05 ± 0.21)				
AEL	*Mm*	32.1% [17.5 – 51.8] (0.68 ± 1.16)			7.1% (1.3 – 22.9] (8.04 ± 36.59)				
DEN	*Mm*	5.6% [0.3 – 27.1] (0.06 ± 0.24)							
LOU	*Mm*	7.7% [1.4 – 24.6] (0.19 ± 0.69)				3.8% [0.2 - 8.8]			
DOD	*Mae*	40% [22.2 – 60.2] (1.48 ± 2.42)		56% [35.8 – 74.4] (10.32 ± 17.03)					
GAL	*Mae*	60% [29.1 – 85] (3.30 ± 3.92)		30% [8.7 – 61.9] (7.80 ± 14.81)					
AEL	*Mae*	65% [42.4 - 83.3] (1.95 ± 3.14)	30% [14 – 52.5]	45% [24.4 - 68] (13.90 ± 40.68)					
DEN	*Mae*	4.8% [0.25 - 23.3] (0.33 ±1 .53)							
LOU	*Mae*	42.1% [22.2 - 65.5] (0.84 ± 1.26)	52.6% [31.2 – 74.3]						
DOL	*Mae*	56% [35.8 - 74.4] (2.76 ± 3.97)							
LAM	*Mae*		18.8% [5.3 – 43.6]						
THW	*Mae*	28.6% [13.3 – 50.6] (0.91 ± 1.81)	33.3% [15.9 – 55.1]						
DIW	*Mae*	33.3% [12.3 - 63] (0.33 ± 0.49)							

Table 3: Prevalence in % [with 95% confidence intervals calculated with Sterne's exact method] and abundances (mean ± standard deviation) of GIH taxa collected from *R. rattus* (*Rr*), *Ma. erythroleucus* (*Mae*) and *Ma. natalensis* (*Man*) for each sampling locality (codes are provided in table 1) along the rat invasion route. Taxa in bold are those chosen for performing GLMs. No abundance data was reported for *Gongylonema* sp. as it was difficult to quantify. The type of lifecycle, direct (only one definitive host) or complex (at least one intermediate host, mainly insects), is also provided for each GIH taxon. Legend: Loc = locality code. Acanthocephalan: Mon = *Moniliformis moniliformis*. Cestoda: Hym = *Hymenolepis* sp.; Hymd = *Hymenolepis diminuta*; Mat = *Mathevotaenia symmetrica*; Raib = *Raillietina baeri*; Rait = *Raillietina trapezoides*. Nematoda: Asp = *Aspiculuris* sp.; Aspa = *Aspiculuris africana*; Gong = *Gongylonema* sp.; Neo = *Neoheligmonella granjoni*; Phy = *Physaloptera* sp.; Pro = *Protospirura muricola*; Pte = *Pterygodermatites* sp.; Tri = *Trichuris mastomysi*.

	Phylum	Acanthocephala	Cestoda					Nematoda							
	Cycle	Complex	Complex	Complex	Complex	Complex	Complex	Direct	Direct	Direct	Direct	Complex	Complex	Complex	Direct
Loc	Host	*Mon*	*Hym*	***Hymd***	***Mat***	*Raib*	*Rait*	*Asp*	***Aspa***	*Gon*	*Neo*	*Phy*	*Pro*	*Pte*	***Tri***
MAR	*Rr*			54. 2% [34-73] (3.4 ± 4.3)									4.2% [0-20] (0.1 ± 0.6)		
DIK	*Rr*	37.5% [20-58] (6.7 ± 13.3)		25% [11-46] (1 ± 1.8)						8.3% [1-27]			4.2% [0-20] (0.1 ± 0.2)		
DIT	*Rr*			59. 3% [40-76] (3.8 ± 4.2)	3.7% [0-18] (0.2 ± 1)			3.7% [0-18] (1.1 ± 5.6)				3.7% [0-18] (0.1 ± 0.3)			
TOB	*Rr*			65% [42-83] (4.2 ± 4.6)				5% [0-24] (0.1 ± 0.4)				5% [0-25] (0.1 ± 0.2)			
BOU	*Rr*		3.4% [2-17] (0.1 ± 0.2)	3.4% [2-17] (0.1 ± 1)							3.4% [2-17] (0.1 ± 0.2)				
KED	*Rr*			41% [22-62] (2.4 ± 4.3)			4.5% [0-22] (0.1 ± 0.21)				4.5% [0-22] (0.2 ± 0.8)	4.5% [0-22] (0.1 ± 0.2)			
BAN	*Mae*										11.1% [1-44] (0.1 ± 0.3)	11% [1-44] (0.1 ± 0.3)			
BOU	*Mae*										14.3% [1-55] (0.3 ± 0.4)				
BRA	*Mae*														33.3% [2-86] (1.7 ± 0.78)
KED	*Man*		8.3% [1-27] (0.1 ± 0.5)			8.3% [1-27] (0.2 ± 0.7)	16.7% [6-37] (1.4 ± 4.9)		12.5% [3-31] (0.7 ± 2.9)		4.2% [0-20] (0.1 ± 0.4)				45.8% [27-66] (3.3 ± 5.1)
BRA	*Man*				54.5% [34-74] (1.6 ± 1.9)										18.2% [6-39] (1.1 ± 2.6)
MAK	*Man*			3.8% [0-19] (0.1 ± 0.2)	23.1% [11-42] (0.6 ± 1.4)				50% [30-63] (12 ± 29.5)		3.8% [0-19] (0.1 ± 0.2)	3.8% [0-19] (0.1 ± 0.4)		3.8% [0-19] (0.1 ± 0.4)	19.2% [8-38] (0.4 ± 0.9)
SEG	*Man*				14.3% [4-35] (0.5 ± 1.3)				38.1% [20-60] (15.9 ± 65.6)		29.6% [13-51] (1.0 ± 2.3)				52.4% [31-72] (1.8 ± 3.9)

Table 4: Most parsimonious Generalized Linear Models (GLMs) for the a) mouse and b) rat invasion routes. AICc: Akaike's information criterion corrected for finite sample size. Δ: difference between the model chosen and the model with the lowest AICc. LRT: Likelihood-ratio test. LI: localities of long-established invasion; IF: invasion front; NI: non-invaded localities. F: Females; M: Males. Aspa: *Aspiculuris africana*; Aspt: *Aspiculuris tetraptera*; Mat: *Mathevotaenia* sp.; Tri: *Trichuris mastomysi*.

a)

Host species	**Response variable**	**AICc (Δ)**	**Significant factors**	**Df**	**LRT**	***p-value***
M. m. domesticus	Overall prevalence	258.5 (1.19)	Status (LI > IF)	1	23.188	< 0.0001
			Climate	1	25.798	< 0.0001
	Species richness	327.8 (0.86)	Status (LI > IF)	1	25.218	< 0.0001
			Climate	1	33.476	< 0.0001
	Aspt prevalence	115.4 (0.00)	Status (LI > IF)	1	48.714	< 0.0001
			Climate	1	40.279	< 0.0001
	Mat abundance	296.9 (1.29)	Climate	1	4.994	0.0254
Ma. erythroleucus	Overall prevalence	209.8 (0.92)	Status (IF > NI)	1	9.263	0.0023
			Climate	1	26.891	< 0.0001
	Species richness	337.4 (0.00)	Status (IF > NI)	1	15.521	< 0.0001
			Climate	1	18.635	< 0.0001
	Mat prevalence	207.3 (1.62)	Climate	1	17.789	< 0.0001
	Mat abundance	466.4 (1.00)	Sex (F > M)	1	7.166	0.0074
			Climate	1	15.876	< 0.0001
	Aspa prevalence	115.6 (0.00)	Status (IF > NI)	1	33.602	< 0.0001
	Aspa abundance	332.0 (0.00)	Status (IF > NI)	1	53.469	< 0.0001
	Ana prevalence	145.7 (0.03)	Climate	1	6.819	0.009

b)

Host species	**Response variable**	**AICc (Δ)**	**Significant factors**	**Df**	**LRT**	***p-value***
R. rattus	Overall prevalence	200.9 (1.89)	Status (LI > IF)	1	37.574	< 0. 0001
			Climate	1	8.945	0.0027
	Species richness	277.1 (0.21)	Status (LI > IF)	1	31.842	< 0. 0001
			Climate	1	10.059	0.0015
	Hymd prevalence	200.3 (0.00)	Status (LI > IF)	1	39.685	< 0. 0001
	Hymd abundance	550.9 (0.00)	Status (LI > IF)	1	26.179	< 0. 0001
			Climate	1	14.792	0.0001
Ma. erythroleucus *Ma. natalensis*	Overall prevalence	150.3 (0.53)	Climate	1	22.13	< 0. 0001
	Species richness	269.4 (1.03)	Climate	1	26.878	< 0. 0001
	Tri prevalence	122.8 (0.44)	Body mass (+)	1	6.9712	0.0083
			Climate	1	11.062	0.0009
	Aspa prevalence	88.9 (0.00)	Status (IF < NI)	1	8.1322	0.0043
			Climate	1	26.913	< 0. 0001
	Mat prevalence	86.7 (0.22)	Status (IF < NI)	1	31.532	< 0. 0001
			Climate	1	6.399	0.0114
	Mat abundance	174.1 (0.00)	Status (IF < NI)	1	39.541	< 0. 0001
			Sex (F > M)	1	3.893	0.0485
			Climate	1	5.894	0.0152

Figure legends

Figure 1. Rodent sampling localities on house mouse (symbols in white) and black rat (symbols in black) invasion routes. Locality codes are given in Table 1. Triangles, squares and circles correspond respectively to localities of long-established invasion, recently invaded localities and non-invaded localities.

Figure 2. Principal component analysis showing GIH assemblages structure based on (a) the invasion status of the locality and (b) the host species on the mouse invasion route. Between-within analysis showed significant structuration for both factors (Monte-Carlo test, $p < 0.05$). The variables (GIH taxa having overall prevalence > 10%) are projected on the correlation circle between the two graphs (the codes used refer to those from table 2).

Legend: A: *Mus (Mus musculus domesticus)* of long-established localities (red); B: *Mus* on invasion front (orange); C: *Mastomys* (*Mastomys erythroleucus*) on invasion front (blue); D: *Mastomys* in non-invaded localities (green).

Figure 3. Principal component analysis showing GIH assemblages structure based on (a) the invasion status of the locality and (b) the host species on the rat invasion route. Between-within analysis showed significant structuration for both factors (Monte-Carlo test, $p < 0.05$). The variables (GIH taxa of which overall prevalence > 10%) are projected on the correlation circle between the two graphs (the codes used refer to those from table 3). This analysis considered only *Ma. natalensis* as native species because of too low GIH prevalence in *M. erythroleucus*.

Legend: A: *Rattus rattus* of long-established rats (red); B: *R. rattus* on invasion front (orange); C: *Mastomys erythroleucus* on invasion front (blue); D: *Ma. erythroleucus* in non-invaded localities (green).

Supplementary Fig. S1. Molecular phylogenetic tree of nematode sequences used as reference sequence database. The tree construction (Tamura-Nei model, Gamma distribution) was based on the mitochondrial Cytochrome Oxidase subunit 1 (CO1) following maximum-likelihood analysis with 100 bootstrap replicates implemented via the software MEGA6 (Molecular Evolutionary Genetics Analysis version 6.0). All worm samples were retrieved from rodent hosts collected in Senegal, Mali or Burkina Faso. Samples are identified by the host species and the code used to refer it in our collection. A number was added to "sp" when more than one undetermined species were expected for a particular nematode genus. Outgroup is sequences of the ac acanthocephalan Moniliformis moniliformis collected from R. rattus in Senegal. Scores at nodes represent bootstrap support for that node. Scale bar is proportional to the genetic distance in substitutions per site.

Legend: *A. niloticus: Arvicanthis niloticus; Ma. erythroleucus: Mastomys erythroleucus; Ma. huberti: Mastomys huberti; Ma. natalensis: Mastomys natalensis; M. m. domesticus: Mus musculus domesticus; P. daltoni: Praomys daltoni; P. rostratus: Praomys rostratus; R. rattus: Rattus rattus.*

Supplementary Fig. S2. Principal component analysis (PCA) of climatic data for categories of localities sampled along the house mouse invasion route (b) based on the uncorrelated climatic variables (temperatures in °C, rainfall in mm, recorded between 1997 and 2012) remaining after a first PCA (a). Between-within analysis showed significant classes (Monte-Carlo test, $p < 0.05$). Legend: max rain: maximum monthly rainfall during rainy season (mean per year); mn MnTM: lowest monthly minimum temperature (mean per year); localities of long-established invasion (red); localities of invasion front (blue); non-invaded localities (green).

Temperature data were recorded from local weather stations closest to sampled localities and available on http://www.ncdc.noaa.gov/cdo-web/datasets; rainfall data were recorded from satellite products available on http://richardis.univparis1.fr/precip/rainser1.html with GPCP-1DD as date source.

Supplementary Fig. S3. Principal component analysis (PCA) of climatic data for categories of localities sampled along the black rat invasion route (b) based on the uncorrelated climatic variables (temperatures in °C, rainfall in mm, recorded between 1997 and 2012) remaining after a first PCA (a). Between-within analysis showed significant classes for both factors (Monte-Carlo test, $p < 0.05$). Legend: max MMxT: highest daily maximum temperature (mean per year); min MMnT: lowest daily minimum temperature (mean per year); min Rain: minimum monthly rainfall during rainy season (mean per year); localities of long-established invasion (red); localities of invasion front (blue); non-invaded localities (green).

Temperature data were recorded from local weather stations closest to sampled localities and available on http://www.ncdc.noaa.gov/cdo-web/datasets; rainfall data were recorded from satellite products available on http://richardis.univparis1.fr/precip/rainser1.html with GPCP-1DD as date source.

Figure 1

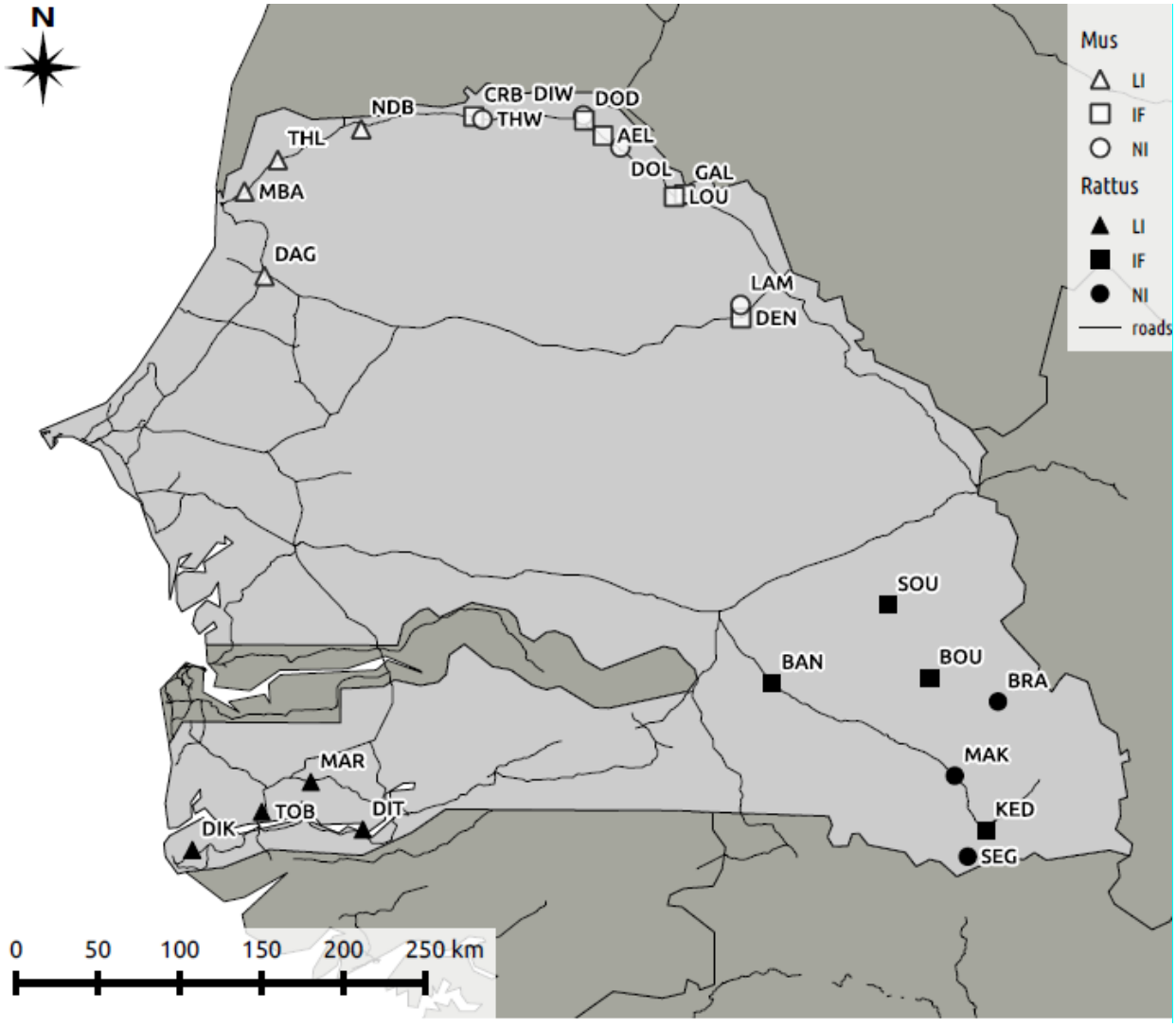


Figure 2

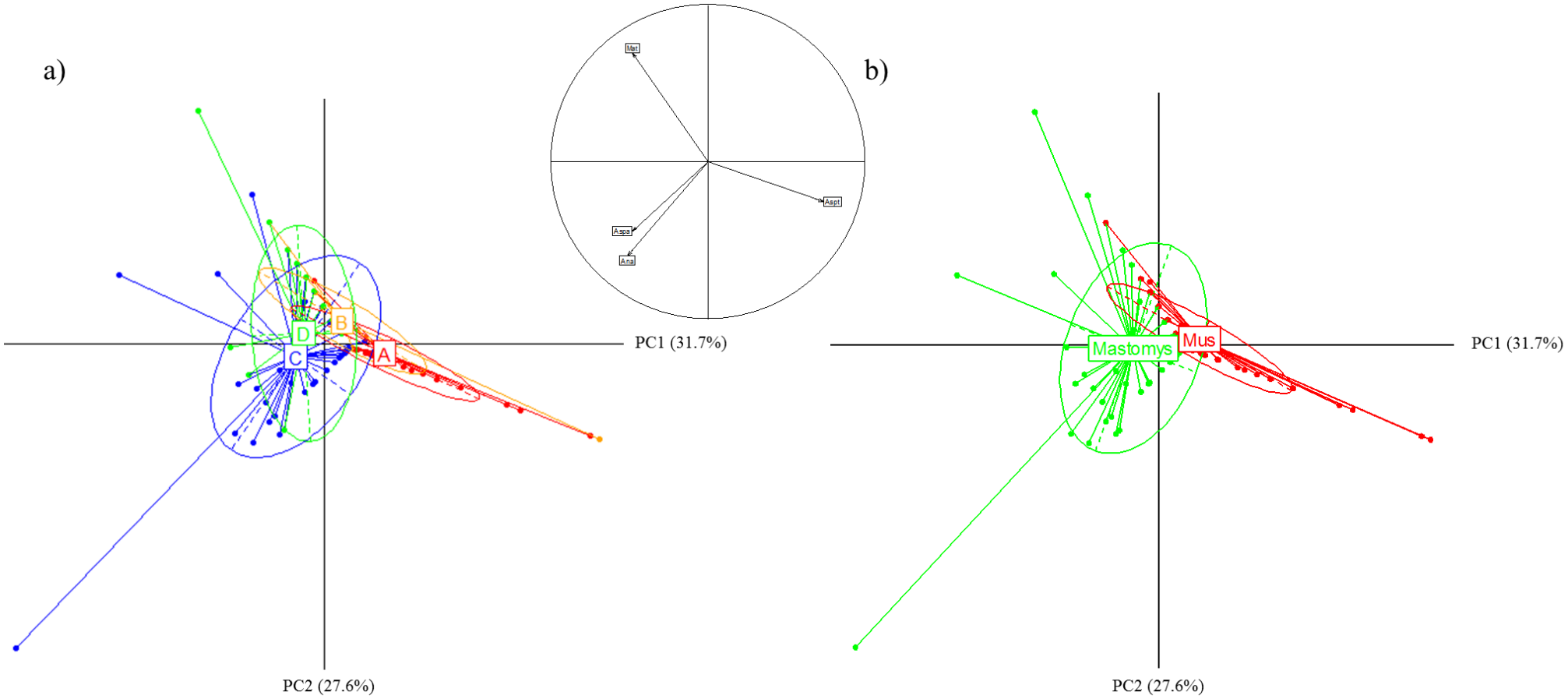
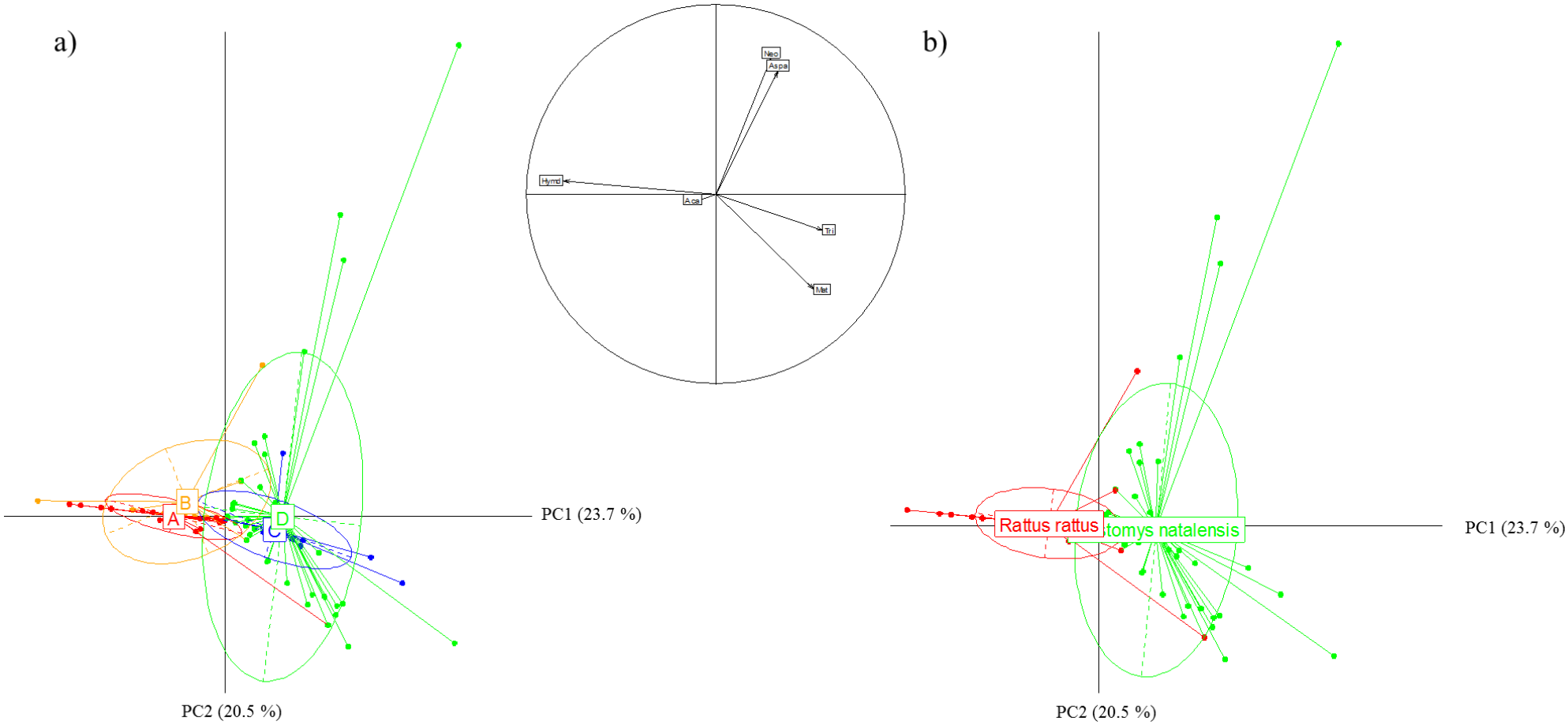

a)
b)
Mat
Aspt
Aspa
Ana
D
B
C
A
PC1 (31.7%)
PC2 (27.6%)
Mastomys
Mus
PC1 (31.7%)
PC2 (27.6%)

Figure 3


a)
b)
Neo
Aspa
Hymd
Aca
Tri
Met
B
A
D
C
PC1 (23.7 %)
PC2 (20.5 %)
Rattus rattus
tomys natalensis
PC1 (23.7 %)
PC2 (20.5 %)