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ORIGINAL PAPER

Association between temporal patterns in helminth assemblages and successful range expansion of exotic *Mus musculus domesticus* in Senegal

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Abstract Relationships between parasitism and invasion success are increasingly evidenced in the literature. However, the dynamic nature of the major parasite-related processes has been rarely taken into account until now, while the residence time of invaders in colonized regions was shown to be associated to crucial changes in parasite communities. Here, we strive to bridge this gap using a temporal survey of rodent populations along one invasion route of the exotic house mouse *Mus musculus domesticus* that currently invades North Senegal. In this study, we investigated whether gastrointestinal helminth (GIH) assemblages changed over time in native (*Mastomys erythroleucus*) and/or invasive (*M. m. domesticus*) rodent populations sampled at an invasion front, and whether these potential changes may be associated to the invasion success of the exotic mouse. Four years separated two rodent sampling campaigns (2013 and 2016/17) in six localities. Despite being relatively short, the timeframe considered here allowed to evidence significant patterns in rodent communities and their GIH assemblages. At the host community level, we showed that the exotic mouse was now established at all sites, becoming the dominant species in sites where it was not recorded before. At the GIH community level, increased infection of the single shared cestode (*Mathevotaenia symmetrica*) in both rodent species brought support to the "spill-back" hypothesis. Infection levels of GIH that remained low at the invasion front in invading mice over time also supported the "enemy release" hypothesis. Both hypotheses should deserve further experimental work to demonstrate their role in the invasion success of the house mouse in Senegal.

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Introduction

The evidence of a strong relationship between parasitism and invasion success is increasingly growing (Prenter et al. 2004; Dunn and Hatcher 2015; Dunn et al. 2012). By exerting selection pressures on host life-history traits, micro- and macroparasites influence the ecology, evolution and dynamics of their host populations (Deter et al. 2007; Vandegrift and Hudson 2009; Telfer and Bown 2012; Tuttle et al. 2017; Young et al. 2017), shaping indirectly a range of interactions among native and invading host species (Dunn and Hatcher 2015). Parasites may thus mediate the successful range expansion of introduced species in different ways. First, newly established host populations may benefit from a parasite loss ("enemy release" hypothesis) through impoverishment of their original parasite communities or reduced infection levels (Keane and Crawley 2002; Torchin et al. 2003; Colautti et al. 2004). By enhancing invader fitness and performance (e.g. through reallocation of energetic resources from unnecessary defence mechanisms into competitive abilities: Blossey and Nötzold 1995), this parasite release may translate into advantage against co-occurring native competitors. Second, competing native hosts may be negatively affected by the acquisition of exotic parasites from introduced hosts (''spill-over hypothesis) because of lack of evolved resistance or tolerance (Taraschewski 2006; Bell et al. 2009; Hatcher et al. 2012; Lymbery et al. 2014; Blackburn and Ewen 2017). Finally, introduced species may increase infection of native hosts ("disease facilitation") by amplification, as reservoirs or vectors, of local parasites (''spillback" hypothesis; Carolus et al. 2019; Kelly et al. 2009; Mastitsky and Veres 2010) or indirectly through habitat alteration (Chalkowski et al. 2018) or stress induction in competing native hosts (Christe et al. 2006). Recent studies have exhibited the potential contribution of these hypotheses in the successful spread of several exotic taxa (e.g. Strauss et al. 2012; Sheath et al. 2015; Goedknegt et al. 2017; Tuttle et al. 2017; Costa et al. 2018). However, it was recently highlighted that the dynamic nature of these processes has rarely been taken into account up to now, partly explaining contradictory findings evidenced from previous works investigating the above mentioned hypotheses in similar systems (Schultheis et al. 2015).

Yet, the increasing residence time of invasive species in colonized regions was shown to be associated to crucial changes in parasite communities (Perkins et al. 2017), which may have consequences on the parasite-related processes. Indeed, new host-parasite associations are known to form over time in the invaded range (Krakau et al. 2006). The potential advantage acquired by invaders experiencing parasite release during their spread might thus be more or less rapidly offset by subsequent accumulation of either previously escaped parasites (that catch up with their original host through delayed spread), and/or novel parasites from the introduced range, with different potential outcomes (Liebhold and Bascompte 2003; Platvoet and Rigaud 2007; Gendron et al. 2012; Jones and Brown 2014; Wattier et al. 2007). Therefore, the magnitude of "enemy release" could be predicted to decrease over time and with range expansion into new habitats (Hawkes 2007; Mitchell et al. 2010). Also, "spill-over" and "spill-back" processes might occur long after introduction of the exotic host, if local adaptation is needed for the parasite to exploit a naïve host species as a novel resource (Gossner et al. 2009). Hence, the parasite-related patterns identified in one-time surveys could represent only snapshot pictures captured from a transitory situation, where a diachronic approach may reveal evolving patterns in terms of host-parasite interactions with subsequent consequences on between-host interactions.

To date, studies that attempted to assess time effect on parasite-mediated processes in biological invasions are scarce and focused on few taxa (e.g. fish: Gendron et al. 2012, Gagne and Blum 2016; insects: Jones and Brown 2014; plants: Schultheis et al. 2015; mammals: Tompkins et al. 2002; Kołodziej-Sobocińska et al. 2018). Furthermore, most of them relied on biogeographical and/or interspecific comparisons, while parasite changes promoting invasion success may be species-specific, transient and rapidly blurred by local factors and eco-evolutionary changes following host establishment (Sakai et al. 2001; Colautti et al. 2004). In this context, temporal surveys in a spatially well-delimited context appear crucial to link potential changes in host communities (following range

expansion of exotic species) with loss, acquisition and/or sharing of both exotic and local parasites over time. Particularly, well-characterized ongoing expansion ranges may enable to investigate in relevant ways the role of parasite-mediated changes in the invasion success (Cornet et al. 2016). Substantial knowledge of invasion history and current progress of expansion range (Miura 2007), but should help to understand long-term ecological processes as well as those that might occur early upon introduction in novel areas. However, such study systems have been scarcely considered in a temporal frame to the best of our knowledge.

Here, we strive to bridge this gap using a diachronic survey of rodent populations along one invasion route of the exotic invasive house mouse *Mus musculus domesticus* in North Senegal. The house mouse is a worldwide commensal invader that was introduced during the colonial period in western coastal cities of Senegal, from where it has spread eastwards since the beginning of the twentieth century, taking advantage of the increase in human activities and the improvement of transport infrastructures in inner Senegal (Dalecky et al. 2015; Lippens et al. 2017). The house mouse now occurs in most villages and cities of northern and central Senegal, from where the native Guinea multimammate mouse, *Mastomys erythroleucus* has been concomitantly excluded. Currently, both species coexist in localities at the invasion front. A previous study investigated gastrointestinal helminth (GIH) communities from both native and invasive rodent populations sampled in 2013 along the northern invasion route of the house mouse in Senegal (Diagne et al. 2016). Patterns were consistent with the predictions of the "enemy release" hypothesis, with a decrease in overall GIH prevalence and richness as well as lower prevalence/abundance of the exotic nematode *Aspiculuris tetraptera* in mouse populations at the invasion front compared with anciently invaded areas at coastal sites. Conversely, no GIH "spill-over" signal was detected, which was interpreted as reflecting the high host specificity of the GIHs collected (only one cestode species was shared by exotic and native rodents). Finally, some patterns were consistent with disease facilitation, such as the increase of GIH infracommunity species richness as well as those of prevalence and abundance of the native parasite *Aspiculuris africana* in native rodents at invasion front compared to non-invaded areas.

We investigated four years later GIH assemblages of native and invasive rodent populations in localities that had been sampled in 2013, with the aim to evaluate the potential changes that have occurred in both host and parasite communities. The temporal dynamics of the house mouse invasion was shown to be rapid in Senegal, with changes detectable over a few years at the local and even regional scales (Dalecky et al. 2015). Besides, rapid variations in helminth community structure have been shown to occur in invasion contexts (e.g. Gendron and Marcogliese 2016). We used a field-based correlative approach to investigate the following questions: (i) do the rodent communities change at the invasion front (i.e. extirpation of native populations in already invaded sites, arrival/establishment of exotic rodents in previously non-invaded sites)? (ii) are GIH assemblages of exotic and native rodent species more similar as a result of parasite sharing when co-existence time between native and exotic host increases? (iii) does the "enemy release" pattern disappear in the exotic mouse with increased residence time and geographic spread, and do parasitism levels increase in native rodents under "spill-back", "disease facilitation" and/or "spill-over" expectations? More specifically, we expected to confirm the low prevalence of the nematode *A. tetraptera* in exotic mice in all invaded sites, and no substantial increase of this GIH prevalence and/or abundance between 2013 and 2016/17 at sites already invaded in 2013, under the "enemy release" hypothesis; we expected to detect increased prevalence and/or abundance of the shared cestode *Mathevotaenia symmetrica* in native and invasive rodents between 2013 and 2016/17 at all sites invaded by the exotic mouse, under the "spill-back" or "spill-over" hypotheses; and we expected to detect increased prevalence and/or abundance of the native nematode *A. africana* in native rodents between 2013 and 2016/17 at all sites invaded by the exotic mouse under the "disease facilitation" hypothesis.

Materials and methods

Study sites

We focused on the invasion route that was previously surveyed in 2013 for GIH assemblages in the house mouse and in native rodents (Diagne et al. 2016). At

that time, the choice of sampled sites was based on historical records and ongoing longitudinal surveys of rodent communities in villages and towns of Senegal (later published in Dalecky et al. 2015). New sampling sessions were realized between November 2016 and February 2017 (period referred as '2016/17' hereafter) within six sites which proved to be representative of two situations (Fig. 1): (i) *previously invaded* sites (Aere Lao, Dendoudi, Dodel), where the house mouse arrived just before 2013 and co-existed in stable populations with native *M. erythroleucus*; (ii) *newly invaded* sites (Diomandou Diery, Diomandou Walo, Lambago), where the exotic mouse was not yet established in 2013 (only two individuals were sampled in Diomandou Diery), but where it is now established (see "Results").

Field sampling and helminth collection

Rodent trapping was carried out inside human dwellings in each targeted site. For each site, we used the same standardised sampling protocol described in detail elsewhere (Dalecky et al. 2015; Diagne et al. 2016), with the aim to capture alive 20 adult rodents per species. At least 120 locally made wire-mesh live traps (8.5 × 8.5 × 26.5 cm) and Sherman folding box traps (8 × 9 × 23 cm) were set, checked in the following morning then re-baited if necessary for 1–3 successive nights at each site. Captured rodents were morphologically identified (following keys provided in Granjon and Duplantier 2009), euthanized by cervical dislocation then weighed to the nearest 0.5 g, sexed and dissected. We assessed the reproductive status (active *vs* inactive) of the autopsied rodents (active males: scrotal testes and developed seminal vesicles; active females: pregnant or suckling state, or perforated vagina). In order to compare the population structure between sampling years and category of sites, we carried out Pearson's Chi-squared test with Yates' continuity correction for the reproductive status and the host gender, and Kruskal–Wallis rank sum test (KW test) for the body mass, separately for both host species. The analyses were performed using the MASS package (R Core Team 2015.

The digestive tract of each rodent was removed and immediately stored in 95% ethanol for further examination. In the lab, GIHs were carefully extracted, counted (except for helminths recovered from the stomach wall that were not straightforward to quantify) and classified by morphotype then stored in 95% ethanol for further accurate identification. This latter relied on the combination of morphological and molecular (Cox1 marker) tools, as previously described (Diagne et al. 2016 and references therein).

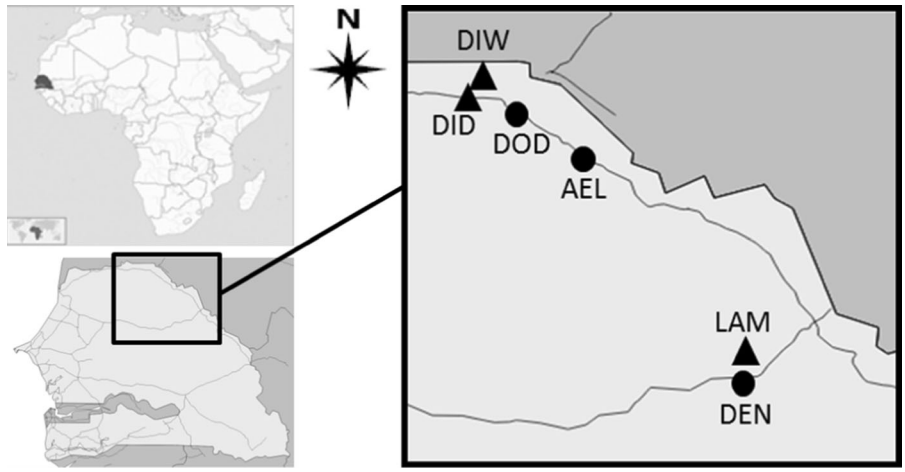


Fig. 1 Geographic location of the six sampling sites in North Senegal. Circles and triangles are used to indicate, respectively, *previously invaded sites* (where the exotic house mouse arrived just before 2013 and co-existed in stable populations with native *Mastomys erythroleucus*) and *newly invaded sites* (where the exotic house mouse was not yet established in 2013 but occurred in 2016/17). AEL: Aere Lao; DEN: Dendoudi; DOD: Dodel; DID: Diomandou Diery; DIW: Diomandou Walo; LAM: Lambago

Structure of GIH assemblages

For each GIH species identified, we determined prevalence (percentage of infected rodents within the entire host population) and mean abundance (number of helminths per rodent, infected or not) separately for both rodent species (the invasive *Mus m. domesticus* and the native *Mastomys erythroleucus*—which represented the widely dominant species of the indigenous commensal rodent communities, see "Results") at each sampling site. To identify how the GIH assemblages were structured at both inter- and intra-specific levels, we constructed dissimilarity matrices of GIH assemblages among host populations, using Jaccard (Jac) β-diversity index. This index was chosen as we considered datasets with GIH presence/absence information, to prevent bias related to the GIH taxon for which exact counting could not be ensured (i.e., *Gongylonema*-like taxon; see results). We performed permutational multivariate analyses of variance (PERMANOVA) on these dissimilarity matrices using *host species* as an explanatory factor, in order to evaluate whether GIH assemblages differed between invasive and native host species. PERMANOVAs were then performed separately for each host-specific dissimilarity matrices considering *sampling year* and *category of site* as explanatory factors, in order to evaluate changes in GIH assemblages within host species. As there were no data for *M. m. domesticus* in 2013 in the *newly invaded* sites (only two individuals sampled), we considered two distinct datasets for the house mouse: one focusing on house mice captured at all sampling sites in 2016/17 to test for the *category of site* factor; and another focusing on house mice sampled in *previously invaded* sites between 2013 and 2016/17 to test for the *sampling year* factor.

All these analyses were carried out using the software Quantitative Parasitology 3.0 (Rózsa et al. 2000) and the packages Vegan v2.4.239 (Oksanen et al. 2010) and Phyloseq v1.19.140 (McMurdie and Holmes 2013) implemented in the R software v3.2.1 (R Core Team 2015).

Testing hypotheses about the role of GIHs on invasion success

We used Generalised Linear Mixed Models (GLMMs) to further assess whether temporal variations in GIH assemblages support a role of parasitism in the house mouse invasion success. Prevalence and abundance levels of GIH species for which global prevalence exceeded 10% in each dataset were considered as response variables, assuming a binomial distribution for prevalence data and a Poisson distribution for abundance data. A model selection approach was performed, using the Akaike information criterion with correction for samples of finite size (AICc). The starting models included host factors (*gender*, *reproductive status* and *body mass*), *sampling year* (2013 vs 2016/17), *category of sites* (previously invaded *vs* newly invaded) as well as their pairwise interactions as possible predictors. Rodent specific densities should have been interesting potential explanatory variables to take into account, but they were poorly related to trapping success (Castañeda et al. 2018), and were thus not considered in the models. Models performed for *M. m. domesticus* include either *sampling year* or *category of sites* as explanatory variable according to the dataset considered (i.e. those considered for PERMANOVA above). For the house mouse, *body mass* was not considered together with the *category of sites* as potential predictors in the same starting models, as both variables were found to be correlated (see "Results"). Similarly for native *M. erythroleucus*, models did not include the *reproductive status* as a potential predictor because most of the native rodents (n = 177) were reproductively active. Models with all possible combinations of the terms included in the starting model were generated with the MuMIn ver. 1.10.5 R package (dredge function). Models with a ΔAICc < 2 with respect to the model with the lowest AICc were selected and the most parsimonious of these models was chosen. The significance of explanatory variables and their interactions was determined by deletion testing and log-likelihood ratio tests. The assumptions of each final model were checked graphically, by an analysis of their residuals. When needed, post-hoc comparisons were carried out with pairwise Wilcoxon rank sum tests (95% family-wise confidence level). All analyses were performed using the R packages MuMIn v1.43.6 (Barton and Barton 2019) and lme4 v1.1-8 (De Boeck et al. 2011).

Results

Rodent communities

In 2016/17, we captured 245 rodents (165 M. *m. domesticus*, *73 M. erythroleucus*, seven *Arvicanthis*

niloticus) in the six localities sampled (Table 1), leading to a total of 437 rodents (235 M. *m. domesticus*, 202 M. *erythroleucus*) analysed among both periods (2013 and 2016/17). The seven individuals belonging to the other local rodent species, *A. niloticus* were not included in these analyses. As expected, the exotic house mouse was found in 2016/17 at all sampling sites; in *previously invaded* sites, rodent communities were largely dominated by the house mouse (108 M. *m. domesticus* vs. 20 M. *erythroleucus*), while they were dominated by native *M. erythroleucus* in two out of three of these sites in 2013 (Dendoudi, Dodel). The Dendoudi site is quite representative of this rapid variation as no native rodent was captured there in 2016/17. In *newly invaded* sites, invasive rodents co-occurred with native ones (57 M. *m. domesticus*, 53 Ma. *erythroleucus*) in different ways according to the site considered. Invasive and native rodents co-existed in Diomandou Diery at similar abundance levels (16 M. *m. domesticus*, 17 Ma. *erythroleucus*), but *M. m. domesticus* (n = 9 individuals) was dominated by native *M. erythroleucus* (n = 33) in the neighbouring site (smaller village) of Diomandou Walo. Conversely, the house mouse already became the dominant rodent species (n = 32) in Lambago where only three native *M. erythroleucus* were trapped in 2016/17.

In both host species, sex ratio and reproductive status did not differ between the two categories of sites. Regarding the body mass, only mice from newly invaded sites appeared lighter than their congeners from previously invaded sites (KW test = 4.8985; *p-value = 0.0269*).

Helminth species in host populations

Six helminth species (five nematodes, one cestode) were collected from the rodents analysed in 2016/17 (see Table 1 for specific prevalence and abundance levels), among them five were already found in 2013 in North Senegal. Similarly to 2013, helminth assemblages strongly differed among host species, the cestode *Mathevotaenia symmetrica* being the single GIH shared by both invasive (24.2%) and native (34.2%) rodents. In *M. m. domesticus*, we found that three nematode species (*A. tetraptera*, *Pterygodermatites senegalensis* and *Syphacia obvelata*) circulated at very low prevalence levels in 2016/17. Two of these species (*P. senegalensis* and *S. obvelata*)) that were found in one mouse from Diomandou Walo (*newly invaded* site) and three mice from Dodel (*previously invaded* site), respectively, were not retrieved in 2013 at any of the six sites sampled while they were collected at coastal sites of long-established invasion. The nematode *A. tetraptera*—which was the main parasite lost along its invasion route by the exotic mouse in 2013—was found in five mice from two *previously invaded* sites only (Aere Lao, Dodel). In *M. erythroleucus*, we found two nematode taxa at about 10% of prevalence: *Aspiculuris africana* that was restricted to the same *previously invaded* sites (Aere Lao, Dodel) than in 2013, and a *Gongylonema*-like taxon, which was not identified in 2013 (Table 1). For the latter, the quality of available GIH samples did not enable to morphologically identify (at the species level) and quantify all the specimens. Nonetheless, successfully amplified sequences for six individuals showed that they belong to a single distinct clade. Surprisingly, we did not retrieve the nematode *Anatrichosoma gerbilis*, which was reported as one of the main local helminth in two populations of native rodents in 2013 (Table 1).

Structure of GIH assemblages

For these analyses (and for further statistics below), rodent populations comprising less than 10 individuals were excluded to avoid potential bias. This concerned the house mouse population from Diomandou Diery in 2013 (only 2 individuals captured) and the native *M. erythroleucus* from Lambago in 2016/17 (only 3 individuals captured). PERMANOVAs carried out on Jaccard dissimilarity index-based matrices revealed that the GIH assemblages differed significantly between invasive *M. m. domesticus* and native *M. erythroleucus* ($F = 10.73$, $p < 0.0001$). Within each host species, we found contrasted patterns regarding the level of similarity of GIH assemblages over time. For invasive *M. m. domesticus* the GIH assemblages were significantly different in 2016/17 between *previously invaded* and *newly invaded* sites ($F = 5.02$, $p = 0.0187$), but not in *previously invaded* sites between 2013 and 2016/17 ($F = 3.51$, $p = 0.06$). In native *M. erythroleucus*, significant dissimilarities were highlighted between GIH assemblages from *previously invaded* versus *newly invaded* sites ($F = 19.96$, $p = 0.0001$), as well as between 2013 and 2016/17 ($F = 6.03$, $p = 0.0048$). These results

Table 1 Prevalence (in percentage with 95% confidence intervals calculated with Sterne's exact method) and abundances (mean ± S.D.) of gastrointestinal helminth (GIH) taxa collected from each rodent population (Mus: *Mus musculus domesticus*; Mastomys: *Mastomys erythroleucus*) sampled in previously invaded sites (in bold) or in newly invaded sites (in italics)

Host	Site	Sampling year	*Gon*	*Ana*	*Aspa*	*Aspt*	*Mat*	*Pte*	*Syp*
Mus (n = 235)	**AEL**	2013 (n = 28)				7.1% [1.3 – 22.9] (8.04 ± 36.59)	32.1% [17.5 – 51.8] (0.68 ± 1.16)		
		2016/17 (n = 32)				12.5% [4.39–28.14] (0.625 ± 1.91)	43.8% [27.85–61.04] (0.91 ± 1.49)		
	DEN	2013 (n = 18)					5.6% [0.3 – 27.1] (0.06 ± 0.24)		
		2016/17 (n = 39)					17.9% [8.60–33.16] (1.15 ± 3.38)		
	DOD	2013 (n = 22)				4.5% [0.2 – 22.2] (0.05 ± 0.21)	9.1% [1.6 – 29.1] (0.59 ± 2.56)		
		2016/17 (n = 37)				2.7% [0.14–14.37] (0.03 ± 0.16)	29.7% [17.17–45.91] (0.43 ± 0.83)		8.1% [2.25–21.35] (0.32 ± 1.51)
	DID	2016/17 (n = 16)					12.5% [2.27–37.16] (0.32 ± 1.01)		
	DIW	2016/17 (n = 9)					11.1% [0.57–44.34] (0.67 ± 2)	11.1% [0.57–44.34] (0.67 ± 2)	
	LAM	2016/17 (n = 32)					15.6% [6.37–32.57] (0.25 ± 0.62)		
Mastomys (n = 202)	**AEL**	2013 (n = 20)		30% [14 – 52.5]	45% [24.4—68] (13.90 ± 40.68)		65% [42.4–83.3] (1.95 ± 3.14)		
		2016/17 (n = 13)	23.1% [6.61–51.96]		53.8% [26.05–77.60] (24.31 ± 35.96)		46.2% [22.40–73.95] (5.08 ± 9.71)		
	DEN	2013 (n = 21)					4.8% (0.33 ± 1.53)		
	DOD	2013 (n = 25)			56% [35.8 – 74.4] (10.32 ± 17.03)		40% [22.2 – 60.2] (1.48 ± 2.42)		
		2016/17 (n = 7)			14.3% [0.74–55.42] (0.71 ± 1.89)		42.9% [12.88–77.46] (1.14 ± 2.19)		
	DID	2013 (n = 35)							
		2016/17 (n = 17)	23.5% [8.47–48.87]				35.3% [16.64–59.37] (7.12 ± 19.79)		
	DIW	2013 (n = 12)					33.3% [12.3–63] (0.33 ± 0.49)		
		2016/17 (n = 33)	3.0% [0.16–16.11]				30.3% [16.12–48.46] (2.67 ± 7.09)		
	LAM	2013 (n = 16)		18.8% [5.3 – 43.6]					

n: rodent sample size. AEL: Aere Lao; DEN: Dendoudi; DOD: Dodel; DID: Diomandou Diery; DIW: Diomandou Walo; LAM: Lambago. *Mat*: *Mathevotaenia symmetrica*; *Aspa*: *Aspiculuris africana*; *Aspt*: *Aspiculuris tetraptera*; *Pte*: *Pterygodermatites senegalensis*; *Syp*: *Syphacia obvelata*. No abundance data was reported for both *Anatrichosoma* sp. (*Ana*) and *Gongylonema*-like taxon (*Gon*) as they were difficult to quantify

suggest that native hosts experienced more changes in the composition and/or prevalence levels of their GIH assemblages among *categories of sites* and over *sampling years* than *M. m. domesticus*.

Testing hypotheses about the role of GIHs on invasion success

For *M. m. domesticus*, model selection was carried out for *M. symmetrica* only, as it was the only species whose mean prevalence exceeded 10% (Table 1). The prevalence (LRT = 4.67, $p < 0.031$) and abundance (LRT = 5.41, $p = 0.0019$) of *M. symmetrica* increased over time in mouse populations of *previously invaded* sites, and its prevalence was higher at *previously invaded* sites compared to *newly invaded* ones (LRT = 3.76, $p = 0.0434$) (Table 2; Fig. 2). Host gender (LRT = 10.26, $p = 0.0013$) and body mass (LRT = 9.08, $p = 0.0025$) were also correlated with *M. symmetrica* abundance, with higher infection levels in female and lighter house mice (Table 2).

For *M. erythroleucus*, model selection was carried out for *M. symmetrica* and *A. africana*, but not for the *Gongylonema*-like taxon that was not found in 2013 and for which specific identity was not ensured. Only *M. symmetrica* prevalence was significantly found to be correlated with one of the explanatory variables (Table 2; Fig. 2). Indeed, the best model selected revealed a significant effect of the interaction between *sampling year* and *category of sites* (LRT = 4.61, $p = 0.0316$). Post-hoc comparisons indicated that native host populations from *newly invaded* sites were more parasitized by the cestode in 2016/17 than in 2013 ($p = 0.00167$).

Discussion

In this study, we investigated whether GIH assemblages changed over time in native and invasive rodent populations sampled at an invasion front, and whether these changes may be related to the invasion success of the exotic house mouse in North Senegal. Despite being relatively short (about four years between the 2013 and the 2016/2017 samplings), the timeframe considered here enabled us to evidence significant changes in rodent communities and their GIH assemblages. At the host community level, the house mouse was established at all sites sampled in 2016/17, and

Table 2 Summary of the most parsimonious Generalised Linear Mixed Models (GLMs) finally selected

Dataset considered	Response variable	AICc (Δ)	Predictors	LRT	*p-value*
M. m. domesticus (previously invaded sites)	*M. symmetrica* prevalence	196.2 (0.01)	Year (2016/17 > 2013)	4.6703	0.03069
	M. symmetrica abundance	648.8 (0)	Year (2016/17 > 2013)	5.4165	0.019947
			Host gender (F > M)	10.2628	0.001357
			Host body mass (−)	9.0769	0.002589
M. m. domesticus (2016/17 samples)	*M. symmetrica* prevalence	183.4 (0)	Category of sites (PIS > NIS)	3.7591	0.0434
M. erythroleucus	*M. symmetrica* prevalence	211.80 (0)	Year*Category of sites (NIS2017 > NIS2013)	4.6188	0.03162

The sampling site was considered as a random factor. Legend: AICc: Akaike's information criterion corrected for finite sample size. Δ: difference between the model selected and the model with the lowest AICc. LRT: Likelihood-ratio test. F: Females; M: Males. PIS: previously invaded sites; NIS: newly invaded sites. '−' indicates a negative correlation

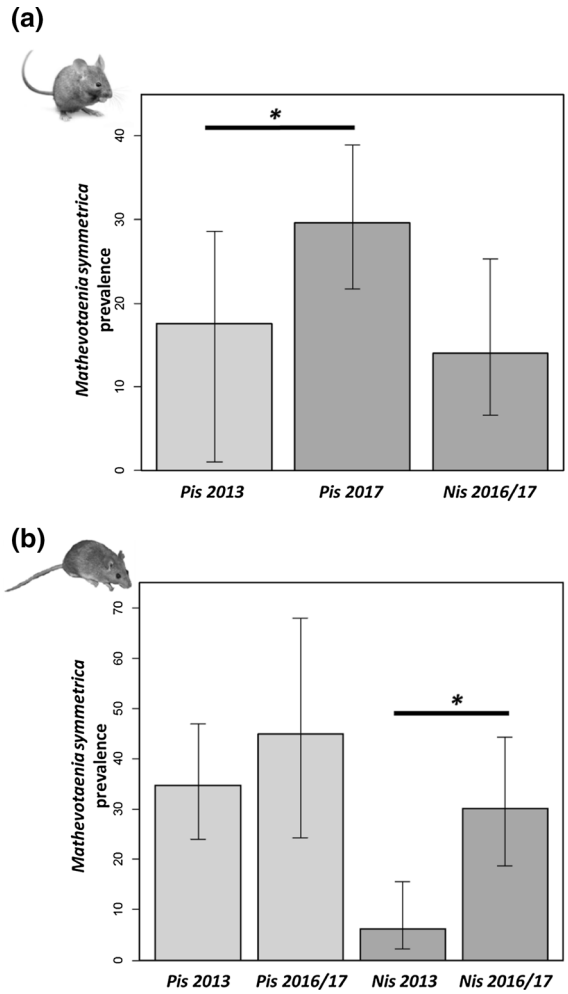


Fig. 2 Prevalence (%) of hosts infected by *Mathevotaenia symmetrica* in **a** invasive and **b** native rodent populations sampled from the different categories of sites (*Pis: Previously invaded sites*; *Nis: Newly invaded sites*) in 2013 and 2016/17. Error bars represent 95% confidence intervals calculated with Sterne's exact method

became the dominant species in sites where it was not recorded four years ago. At the GIH community level, we showed that the infection levels of the single shared cestode, *M. symmetrica*, increased in both rodent species, but we found no significant change for helminths previously lost by invading mice between 2013 and 2016/17.

GIH assemblages still differed between both rodent species

The concomitant use of morphological and molecular tools enabled us to be confident with the identification at the species level of GIH helminths. Such identification is necessary to establish whether parasites are shared by both host species especially in the case of closely related and morphologically similar helminth species (e.g. *A. tetraptera* and *A. africana*) in order to test adequately some hypotheses (*i.e.* "spill-over", "spill-back"). The only uncertainty concerned the specific identification of the *Gongylonema*-like taxon in *M. erythroleucus* at newly invaded sites. This helminth was only detected in 2016/17, whereas another nematode, *Anatrichosoma gerbilis* was only detected in 2013. This underlines that helminth assemblages of rodents may change over time, even for species that are not rare (Behnke et al. 2008). As they both live in the stomach, it is tempting to suggest within-host competition between these GIHs sharing the same micro-habitat (Behnke et al. 2009; Telfer et al. 2010), but this hypothesis is highly speculative at this stage.

As in 2013, GIH assemblages were significantly different between *M. m. domesticus* and *M. erythroleucus* in 2016/17. Indeed, only one GIH species, the cestode *M. symmetrica*, was shared among host species. Strong host specificity may partly explain such distinct GIH assemblages between sympatric *M. m. domesticus* and *M. erythroleucus*. *A. tetraptera* has already been identified as a typical parasite of house mice in several parts of the world (Behnke et al. 2015). Similarly, to the best of our knowledge, *A. africana* was only retrieved in African rodents, and was never found to circulate in *M. musculus* anywhere. On the contrary, strict host specificity should not characterise *S. obvelata* and *P. senegalensis* (found here in mice only), as they were already described in *Mastomys* species elsewhere (e.g. Julius et al. 2018), and even in *M. erythroleucus* at significant prevalence levels in South-eastern Senegal (Brouat et al. 2007). Some helminth species are known to be associated to several confamilial host species, but their distribution among host populations in both space and time can be mediated by extrinsic factors related to the local environment (Spickett et al. 2019 and references therein). The phylogenetic (both rodent species analysed here belong to the same sub-family) and

ecological (invasive and native individuals live in very close proximity) proximity should facilitate host-switching (Landaeta-Aqueveque et al. 2018) for such species. Hence, host switching of helminths between native and introduced rodents was already evidenced in other studies (e.g. Smith and Carpenter 2006; Romeo et al. 2014; Loxton et al. 2017), but they concerned introductions older than a few years. Maybe the timeframe considered in this study is too short to observe host-switching, since host-parasite compatibility allowing a parasite to establish inside a novel host may require numerous generations to evolve (Paterson et al. 2012). Also, low helminth burden of invasive mice at the invasion front could not favour the acquisition of novel helminths by *M. erythroleucus*, since host switching is facilitated by high parasitic abundances (Landaeta-Aqueveque et al. 2018).

Persistency of parasite loss in the exotic mouse is consistent with the enemy release hypothesis

Parasite loss was evidenced in *M. m. domesticus* at its invasion front in our previous study (Diagne et al. 2016). The new results presented here confirmed this pattern. First, GIH prevalence and abundance levels in *M. m. domesticus* were found to be low (no prevalence level exceeding 10%, except for *M. symmetrica*: Table 1) in all sites, even in sites that were previously invaded. Second, GIH assemblages did not change over time in *M. m. domesticus*. Third, the parasite that was shown to experience significant reduction along the invasion route sampled in 2013 (i.e., *A. tetraptera*) was totally absent at *newly invaded* sites in 2016/17, and did not significantly increase in prevalence and abundance at *previously invaded* sites between 2013 and 2016/17. Although the persistency of this parasite loss may relate to the short timeframe considered in this study, exotic parasites had already been shown to catch up their original invasive host within only few years following introduction in novel ecosystems (e.g. Wattier et al. 2007; Hajek and Tobin 2011). Besides, such a parasite recovery could have been more expected regarding the direct (monoxenous) life cycle (Anya 1966) and the low virulence (Taffs 1976) of *A. tetraptetra*, these parasite traits being associated to a greater likelihood of parasite persistence in exotic hosts during range expansion (Prenter et al. 2004). The hypothesis of abiotic environmental conditions that would impair establishment of *A. tetraptera* in the invasion front area cannot be excluded. Alternatively, biotic factors, such as the concomitant presence of native rodents that could act as sink reservoirs ('dilution effect'; Keesing et al. 2006, Johnson and Thieltges 2010, Gendron and Marcogliese 2016), might contribute to this reduced infection by exotic parasites. Hence, long-established house mouse populations from source sites were shown to exhibit higher infection levels by *A. tetraptera* in sites where native rodents no longer occupied indoor habitats (Diagne et al. 2016). Nevertheless, the more plausible explanation for the pattern exhibited here may rely on the fact that parasites having patchy distribution in original host populations are more susceptible to be lost along invasion routes (MacLeod et al. 2010; Phillips et al. 2010; Coates et al. 2017). Consistently, available data showed that, despite its high prevalence in coastal source sites from North Senegal, *A. tetraptera* was distributed patchily there (Diagne et al. 2016).

Given the generation time of the house mouse (4 months; Nachman and Searle 1995) and longitudinal data indicating introduction of *M. m. domesticus* since at least 2012 in sites of the *previously invaded* category (Dalecky et al. 2015), our results suggest that *M. m. domesticus* could benefit from "enemy release" for at least 20 generations, which might be sufficient to play a role in invasion success. Common garden experiments (de Villemereuil et al. 2016) are needed to evaluate the net effect of *A. tetraptera*, and assess if this parasite loss may translate into actual advantage (Colautti et al. 2004; Prior and Hellmann 2013).

Temporal increase of *M. symmetrica* in native and exotic rodents is consistent with the spill-back hypothesis

The cestode *M. symmetrica* was the only GIH shared by native and exotic rodents. This cestode is a cosmopolitan generalist (Beveridge 2008) that was already found in invasive mice elsewhere (e.g. Europe: Murai 1974; Asia: Kalyankar and Deshmukh 1980) as well as in (non-invaded) African rodent communities (e.g. South Africa: Spickett et al. 2019). The first evidence of this cestode in exotic rodents in Africa was recently published by Diagne et al. (2016) in North Senegal, and was supported by new data collected here. Assessing whether this helminth was initially brought or captured by the house mouse upon

introduction thus appears not straightforward. Our data suggest that *M symmetrica* infected native rodents prior to the arrival of the house mouse at the invasion front, since it was abundant in native rodents from sites not yet invaded by the house mouse in 2013 (Diagne et al. 2016). One plausible explanation could be that this cestode was introduced by house mice in Senegal, but spread prior to its original host across the country. Indeed, generalist parasites like *M. symmetrica*, with complex life cycle have great chances to be transmitted and/or to adapt to novel hosts, because they tend to be very resistant to changes in the environment and may be acquired by feeding on common insects that act as intermediate hosts (Lafferty et al. 2010; Poulin et al. 2011; Roy et al. 2011).

We found an increase of *M. symmetrica* infection between 2013 and 2016/17, both in native rodent populations from *newly invaded* sites, *i.e.* after the arrival of the house mouse, and in house mouse populations from *previously invaded* sites. This suggests that the longer the time of coexistence between native and invasive rodents, the higher the parasitism with this cestode in native rodents. Whatever the origin of this parasite (either native or invasive), it was found to occur at high prevalence levels in native rodents of non-invaded sites. The observed pattern could thus correspond to that expected under a "spill-back" hypothesis, with increased levels of infection by an "already local" parasite following the arrival of an exotic host. "Spill-back" has still largely been overlooked and/or barely supported in the current literature, notably because it requires quantitative comparisons of local parasite infection levels and exotic host abundances (Kelly et al. 2009; Chalkowski et al. 2018). Demonstrating a role of M. *symmetrica* "spill-back" in the invasion success of the house mouse would require evidencing a greater susceptibility of native rodents to this parasite.

In conclusion, our study provides empirical supports for two major hypotheses in invasion ecology, namely "enemy release" and parasite "spill-back". Indeed, our findings suggest that (i) escape from parasites, mainly the ancestral *A. tetraptera*, and (ii) higher local parasitism mediated by the single shared cestode *M. symmetrica* may contribute to the successful ongoing range expansion of the exotic mouse in Senegal. To the best of our knowledge, our study is the first to connect both—not mutually exclusive—processes to a contemporary range expansion within the same temporal frame. The extent of the temporal frame considered here is however too short to enable firm conclusions. Demonstrating the role of "enemy release" and "spill-back" in the invasion success of the house mouse would also require further studies about the effects of the parasites that are lost or gained on invasive and native rodents. These effects could range from acute to almost benign infections following the specific context, including community composition, within-host interactions and local competition (Telfer et al. 2010; Leggett et al. 2017). In addition to future (semi) experimental works, the next step should be to extend parasite surveys (e.g. on another mouse invasion route in Senegal, or for other invasive rodents such as the black rat (*Rattus rattus*)) in order to evaluate if we could observe similar signals when studying parasitism and invasion success. This would allow to strengthen the conclusions drawn in this study, or alternatively to bring supports for the stochastic nature of the invasion process of exotic rodents within the same areas. Moreover, our study focused only on one parasite community, while it is known that several parasite communities interact antagonistically and/or synergistically within each host (Lello et al. 2004; Graham 2008; Telfer et al. 2010). For instance, helminths and bacteria, which largely infect rodents, interact frequently with unpredictable outcomes at both ecological and sanitary levels (Kreisinger et al. 2015; Ezenwa 2016). Thus, it would be interesting to move beyond the single parasite community approach (used here with GIH assemblages) to a 'multicommunity' approach involving the preliminary identification of between-parasite assemblages as a first investigation step.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Prior explicit agreement from relevant local authorities and individual owners was systematically obtained for each sampling campaign within private dwellings. Trapping sessions and transfer of biological samples were carried out in accordance with requirements of Senegalese and French legislations. Every realized protocol received explicit approval from the relevant institutional comitee (Centre de Biologie pour la Gestion des Populations (CBGP): Agrément pour l'utilisation d'animaux à des fins scientifiques D-34-169-1). All animal-related procedures were performed according to official ethical guidelines provided by the American Society of Mammalogists (Sikes and Gannon 2011). None of the rodent species investigated here has any protected status from the International Union for Conservation of Nature.

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