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RESEARCH ARTICLE

Maritime international trade and bioinvasions: A three-year long survey of small mammals in Autonomous Port of Cotonou, Benin

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IRD

Handling Editor: Bárbara Langdon**Abstract**

1. International trade has been favouring the dissemination of a wide suite of invasive alien species. Upstream prevention through the monitoring of entry points is identified as an appropriate strategy to achieve control of bioinvasions and their consequences. Maritime transportation has been responsible for the introduction worldwide of exotic rodents that are major pests for crops and food stocks as well as reservoirs of many zoonotic pathogens. In order to limit further dissemination, the International Health Regulation constrains decisions makers and socio-economic stakeholders to manage ship-mediated import/export of rodents within seaports.
2. Unfortunately, eco-evolutionary insights into rodent introduction events that could guide preventive actions in seaports are very scarce. In order to bridge this gap, we here describe the results of a 3 year-long survey of small mammals conducted in the Port of Cotonou, Benin.
3. Our aim was to assess the spatiotemporal distribution, diversity and relative abundance of invasive and native rodents.
4. 960 small mammal individuals were captured in nine within-seaport sites. We found (i) a marked predominance of invasive species (84% of the individuals belonging to *Mus musculus*, *Rattus rattus*, *R. norvegicus*), (ii) with native species (i.e. *Mastomys natalensis* and the shrew *Crocidura olivieri*) essentially restricted to

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peripheral non-industrial areas, as well as (iii) a fine-scale spatial segregation stable over time between the invasive Norway rats and house mice on the one hand, and the black rats and shrews on the other hand.

5. Furthermore, trapping before and after two successive rodent control campaigns indicates that they were ineffective and that subsequent rodent recolonisation occurred 6–12 months following intervention.
6. *Synthesis and applications.* Our results are discussed in terms of ecological processes at play (e.g. interspecific interactions) and operational recommendations (e.g. assessment of proper eradication units, environmental modifications).

KEYWORDS

biological invasions, community ecology, international health regulation, invasive rodents, *Mus*, *Rattus*, seaport, West Africa

1 | INTRODUCTION

Invasive alien species (IAS) represent a significant threat to global food security through the introduction of major pests to crops and food stocks (Early et al., 2016), to biodiversity through the perturbation of invaded environments (Doherty et al., 2016), to public health through the dissemination of reservoirs, vectors and pathogens (e.g. Lin et al., 2012; Meda et al., 2016) as well as to human infrastructures (e.g. Walther et al., 2011). Altogether, these processes translate into massive yet still under-evaluated economic losses (Diagne, Leroy, et al., 2021), more likely in low-income regions (see Diagne, Turbelin, et al., 2021 for a synthesis in Africa). Over the past centuries, the development of transport by road, air and sea has significantly contributed to the unintentional and exponential spread of a large number of plants, animals and microbes across the globe (Seebens et al., 2015). Such new introductions—and their associated impacts—are expected to increase with ever-growing global trade (Bellard et al., 2016; Early et al., 2016) and climate change (e.g. Hulme, 2016).

Among the most heavily-impacting IAS, three anthropophilic rodent species—namely, the house mice (*Mus musculus*), the black (*Rattus rattus*) and Norway rats (*Rattus norvegicus*)—have been disseminated worldwide following goods and people movements (e.g. Aplin et al., 2011; Bonhomme et al., 2011; Song et al., 2014). They are now listed among 100 of the world's worst IAS having highly deleterious socio-environmental impacts (Lowe et al., 2000; www.iucnedlist.org) and ranking in the top 15 rodent pest taxa of the world (Capizzi et al., 2014). Rodents may be unintentionally embarked on ships either together with merchandise, or by climbing mooring cables, then nesting onboard where they often feed on the transported goods. They may swim toward the shore following shipwrecks that occur close to landmasses (e.g. Russell et al., 2005). They may also land down along mooring cables and pontoons within seaports (e.g. Russell et al., 2005; Vincent, 2000). As a consequence, international and highly connected harbours are expected to be privileged entry points for the introduction of rats and mice. For instance, from January 1990 to December 1998, a surveillance campaign showed

that 270 out of 1093 (24.7%) inspected ships in Shanwei seaport, China, contained rodents (Song et al., 2003). As another example, a one-day inspection on a single ship that docked in the port of Qingdao, China, revealed the presence of 266 rodents from five different species (*Rattus norvegicus*, *R. tanezumi*, *R. rattus*, *Mus musculus* and *Cricetulus triton*) (Song et al., 2003), thus suggesting that large embarkations may even represent travelling ecosystems, hence potential 'multi-species propagules'.

The introduction of invasive rodents into seaports can cause significant damage to the harbour facilities as well as to locally stored goods. In the Autonomous Port of Cotonou (hereafter APC), Benin, *R. norvegicus* and *M. musculus* are responsible for the destruction >100 tons of imported rice (i.e. >58k€) per warehouse and per year (Dossou et al., 2020). Though not precisely estimated, gnawing-induced damages to electric networks and large equipment (e.g. unloading machines) are likely to represent a significant economic loss (APC and Bolloré Company staff, pers. comm.). Furthermore, introductions of rodents may be accompanied by the importation of associated zoonotic pathogens (e.g. hantavirus in Asia and beyond: Lin et al., 2012; Wang et al., 2022; murine typhus in Taiwan: Kuo et al., 2017; plague worldwide: Barbieri et al., 2020). This seems to have also been the case in APC where Seoul hantavirus have been recently described (Castel et al., 2021).

The International Health Regulation (World Health Organization, 2006), inherited from quite old international debates (Howard-Jones & World Health Organization, 1975) and texts (e.g. the 1903 International Sanitary Convention already preconized rat control on ships), was adopted in 2005 and applied in July 2007. It compels each WHO member state to establish procedures for the surveillance and control of human pathogens' vectors and reservoirs (especially rodents) at all entry points in their national territory. Among other issues, this legislation imposes seaport and airport authorities to implement a state-of-art, the set-up and follow-up of management of IAS within and 400m around their infrastructures. This aims at avoiding the unintended import/export of infectious microbial, vector and reservoir species, hence at decreasing the associated risks of zoonotic emergence and pandemics. However, the

development of such surveillance and control strategies at entry points is not trivial. In particular, it requires a good understanding of the mode and rate of potential biological invasions as well as of the spatiotemporal dynamics of newly introduced species or newly introduced individuals of already present invasive species. Unfortunately, only very few studies have focused on small mammal communities in/around seaports. The rare existing ones include taxonomic inventories (e.g. Voelckel & Varieras, 1960), phylogeography or population genetics surveys (e.g. Gatto-Almeida et al., 2021; Kaleme et al., 2011; Song et al., 2003), pathogen detection (e.g. Castel et al., 2021; Kuo et al., 2017; Rahelinirina et al., 2018; Wang et al., 2022) or evaluation of damage-associated costs (e.g. Dossou et al., 2020). However, none of these studies focused on the fine structure of rodent species assemblages themselves, *a fortiori* on their dynamics over time.

In order to bridge this knowledge gap, the present study explores the structure and dynamics of small mammal communities within APC over a 3-year-long period. More specifically, our aims were to (i) describe the specific composition of these small mammal communities in relation with fine-scale habitats, (ii) compare the relative distribution of native vs. invasive species, and (iii) determine the spatiotemporal distribution and co-existence of these species. We also took advantage of an anti-rat campaign implemented by the seaport stakeholders during our survey to evaluate the effects of such treatment on the rodent populations.

2 | MATERIALS AND METHODS

2.1 | Ethical and regulatory aspects

Research agreements were signed between the Republic of Benin and the French Institute of Research for Sustainable Development (IRD) (renewed on 6 April 2017 and available upon request) as well as between the IRD and University of Abomey-Calavi (signed on 30 September 2010 and renewed on 3 July 2019). All field work sessions were written-authorized by the APC authorities. During field trapping campaigns, explanations about the program were systematically provided to the workers present on-site. No trap was ever

set without the explicit oral consent of the owners, operators and/or personnel working in the surveyed sites.

Rodents were treated in accordance with the American Society of Mammalogists guidelines (Sikes & Gannon, 2011), and then sacrificed by cervical dislocation after diethyl-ether anaesthesia, as recommended (Mills et al., 1995). None of the trapped species had IUCN protected status (IUCN red list category). Permit for access and fair sharing of knowledge and data was delivered by the Beninese national competent authorities (Nagoya protocol, permit 608/DGEFC/DCPRN/PF-APA/SA).

2.2 | Study area

The APC was created in 1964 and represents today a 400,000 m² area within Cotonou. Its geographical location and the topography of the surrounding seabed make it a favourable site to serve as a maritime hub, particularly toward landlocked Sahelian countries such as Mali, Niger, Burkina-Faso and Chad as well as toward the neighbouring Nigeria. In 2018, almost half of the total traffic in the APC was associated with the trade toward or from these countries. In total, 1000 to 2000 ships dock at APC annually, and the cumulative amount of imported and exported merchandises averages 11 million tons, with a strong dominance of importations (Statistics and Economic Studies Service/SOBEMAP). APC activities participate to 90% of Benin international trade and generate up to 60% of its GDP; it also contributes significantly to the country's customs revenue (80%–90%) and tax income (40%–50%) (Le Monde.fr, 2019/08/02). As such, it currently represents one of the main drivers of Benin's socio-economic development.

We studied two distinct zones within the APC: the 'industrial port' on the one hand, and the so-called 'artisanal port' on the other hand. The industrial port includes restaurants and canteens, dockside warehouses and various handling and APC administrative services. The artisanal port is located next to the industrial one (Figure 1): it gathers the traditional fishing port, a wholesale market of fresh fish, associated traditional fish storage infrastructures stand as well as a few durable buildings (such as the facades of walls, buildings and fences).

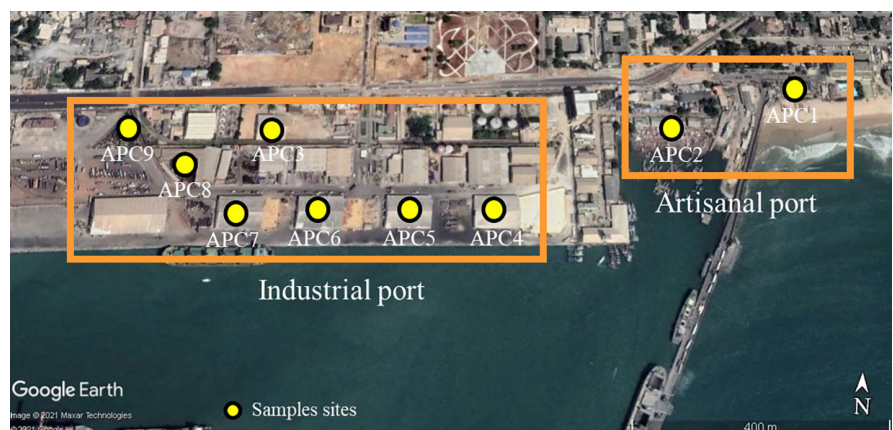


FIGURE 1 Trapping sites in Cotonou Seaport.

2.3 | Sampling design

Our trapping sessions consisted of two successive survey phases. The first one was carried out between August 2014 and December 2015 in various places within the artisanal and industrial ports to identify relevant candidate sites that were representative of contrasted habitats, easily accessible and favourable to small mammal populations. This campaign (data not shown) allowed us to select nine observatory sites for longitudinal monitoring per se. The second phase of our survey then consisted in a series of trapping campaigns (sessions 1 to 6) planned each semester between 2017 and 2020 in each of the nine sites described here below.

Sites in the traditional port included:

APC1 (6.351°N, 2.434°E)—an assemblage of traditional stores that lies along the beach on a sandy soil, gathers several durable buildings where fishes and fishing material are stocked in unsanitary contiguous rooms and where fishes are prepared for sale.

APC2 (6.351°N, 2.432°E)—the fresh fish market where sea products are directly brought from the adjacent wharf, prepared, ice-stored and sold on-site to consumers.

Inside the industrial port area, seven sites were surveyed:

APC3 (6.350°N, 2.426°E)—a cemented alley of abandoned and dirty durable rooms as well as restaurants and outdoor canopies where women cook food that is consumed on-site by local workers.

APC4-7 (6.349°N, 2.429°E; 6.349°N, 2.428°E; 6.349°N, 2.427°E; 6.349°N, 2.426°E)—four large non-joined industrial storehouses managed by the Port Handling Society of Benin (SOBEMAP) where imported goods (mostly Asian rice) are permanently brought in and out by trucks and workers.

APC8 (6.349°N, 2.425°E)—an ensemble of durable buildings around a vast cemented courtyard that serve as fuel station, garage and mechanical equipment storage rooms for the SOBEMAP.

APC9 (6.350°N, 2.423°E)—a vast area (half-cemented, half-fallow with many waste around) where large equipment (including out-of-service equipment) are parked or abandoned.

Pictures are available in see Appendix S1 and a map is shown on Figure 1.

Importantly, all trapping sites are quite similar from a rodent ecology perspective. In particular, they are all characterised by human presence and extensive human activities, the absence of plant cover, the absence of dumping sites, the omnipresence of human infrastructures made of durable materials as well as abundant and permanently available food resources on-site (APC1-7) or in the close surroundings (APC8 and APC9), all factors that are known to drive rodent infestation within urban environments (Cavia et al., 2015; de Masi et al., 2009; Murphy & Marshall, 2003). That said, we assumed

that (other) specific environmental features that may influence rodent community diversity and dynamics over space and time have been taken into account in our subsequent analyses through including a 'site' effect (see below).

At each session, all sites were sampled within the same 3 weeks (i.e. Session 1: September–October 2017; Session 2: March–April 2018; Session 3: September–October 2018; Session 4: March–April 2019; Session 5: September–October 2019; Session 6: March–April 2020) and using a standardised protocol (Garba et al., 2014).

2.4 | Trapping and identification of small mammals

In order to maximise the probability of capturing individuals of different species and sizes (Dalecky et al., 2015; Garba et al., 2014; Lucaccioni et al., 2016), two types of traps were systematically used together in almost equal numbers: locally made wire mesh (30 cm × 10 cm × 10 cm) and Sherman traps (23.2 cm × 7.3 cm × 8.8 cm; ©Sherman Inc., USA). A mixture of peanut butter and sardines in oil was used as bait. The traps were set for three consecutive nights and checked each morning. *R. rattus* is originally an arbicolous species, meaning that this species is a good climber. Actually, we systematically placed traps on high grounds when it was possible. Rodents captured were 'sacrificed by cervical dislocation' and processed in the same day. Coordinates of traps that captured rodents were systematically recorded.

Of note, two rodent control campaigns were carried out by a SOBEMAP-hired firm in 8–11 October 2018 (hence just before our Session 3) then 12–24 December 2018 (hence a bit less than 2 months before our Session 4) in the warehouses (APC4-7) and the garage (APC8). The first campaign involved Zinc Phosphide in baits made of mixed fish and maize. Baits were placed in polystyrene bowls every 10 m. Unfortunately, despite our demands, no piece of information could be obtained from the private firm in charge on the second control campaign except dates and sites.

Small mammal species often include morphologically similar species difficult to distinguish. This may be particularly true for mice, shrews, *Mastomys* spp. and very juveniles of *Rattus* spp. In addition to morphological identifications (Granjon & Duplantier, 2009), all *Rattus* and *Mus* individuals were genotyped with species-specific microsatellite markers (Badou et al., 2021; Desvars-Larrive et al., 2017; Lippens et al., 2017; Loiseau et al., 2008) while some *Mastomys natalensis* ($N=2$ of 14) and shrews (at least two individuals per site × trapping session; $N=29$ of 141) individuals were barcoded through for mitochondrial cytochrome b gene sequencing and subsequent comparison to available reference datasets (Dobigny et al., 2008; Jacquet et al., 2015) according to previously described protocols (Dobigny et al., 2008). PCR-RFLP permitted the unambiguous identification of the other 12 *Mastomys* individuals (Lecompte et al., 2005).

2.5 | Trapping data analysis

2.5.1 | Trap-specific and species-specific trapping effort

We used Chi-squared tests to evaluate whether and how our trapping effort affected the outcomes of our sampling survey. First, the respective numbers of each type of traps set in each site (pooled for the six sessions) were compared to ensure that our trapping effort in each site was similar between sessions. Second, we tested if the species-specific trapping success (calculated as follows: $100 \times Nm/NTN$, where Nm and NTN are the total number of individuals of each species and the total number of trap-nights, respectively) differed between the two types of traps (i.e. wire mesh vs. Sherman) for each rodent species.

2.5.2 | Species-specific relative abundance according

Given that no significant differences were detected in the trapping efforts (see Section 3), we compared the number of rodent individuals captured (therefore defined as relative abundance) at both inter- and intraspecific levels. We compared the relative abundance (for all the six sessions) between species in each site using a Chi-squared test, that is between *R. rattus* and *C. olivieri* in APC1, APC2 and APC9; between *R. rattus* and *R. norvegicus* in APC3 and APC8; between *R. rattus* and *M. musculus* and between *R. norvegicus* and *M. musculus* in APC4, APC5, APC6, APC7 and APC8.

At the intraspecific level, the relative abundance at each site was compared between sessions through Kruskal–Wallis rank sum tests, and, when needed, through pairwise comparisons using Wilcoxon rank sum tests (95% family-wise confidence level). These analyses included the sites where at least one individual of a given species had been captured (i.e. APC4–8 for *R. norvegicus* and *M. musculus*; APC1 and APC2 for *R. rattus*; APC1 for *Crociodura olivieri*).

A particular attention was paid to the impact of rodent control campaigns on the species-specific trapping success, taking into account the effect of trap types (see Section 3). To do so, *Rattus rattus*-specific wire-mesh trapping success was compared at each session between the untreated APC1 and APC2 sites on the one hand, and the treated APC8 site on the other hand. In the same manner, *R. norvegicus*-specific wire-mesh and *Mus musculus*-specific Sherman trapping success were calculated at each session in the treated APC4–8 sites.

All analyses were performed under the R software (R Core Team, 2011) and p -values < 0.05 were considered significant.

2.5.3 | Specific diversity

Smoothed sample-based rarefaction curves rescaled by the total number of individuals were computed for both the artisanal (APC1 and APC2) and industrial (APC3–9) seaport sites using EstimateS

v.9.1.0 (Colwell, 2013) to verify that sampling was sufficient to detect most common species, as well as to compare the two areas in terms of species richness (Gotelli & Colwell, 2001). Species diversity estimates were expressed as Hill numbers of orders 0, 1 and 2 to quantify diversity in equivalent numbers of equally abundant species (Gotelli & Chao, 2013; Hill, 1973; Jost, 2006, 2007). For each port area, three estimates of rodent species diversity were computed: species richness (0D), exponential Shannon entropy (1D) and Simpson index (2D) for rarefied subsamples of ca. 100 individuals. To do so, each subsample (i.e. each trapping site within a session) was randomised without replacement. Differences in specific diversity estimates between industrial vs. artisanal sets of sites were considered significant when a lack of overlap between 95% confidence intervals (mean ± 1.96 standard error) was observed (Colwell et al., 2012; Gotelli & Colwell, 2011). Community diversity between the artisanal (APC1 and APC2) and the industrial (APC3–9) areas were compared using EstimateS v.9.1.0 (Colwell, 2013).

2.5.4 | Co-occurrence analyses

Co-occurrence analyses of small mammal species were performed for the nine sites in order to investigate putative deterministic associations within small mammal assemblages (Gotelli & Entsminger, 2003). In brief, they test whether each pair of taxa is found in an aggregated or segregated manner more often than by chance (Gotelli, 2000; Gotelli & Entsminger, 2003). To do so, data were organised as matrices of capture events: each row indicated the number of trapped individuals of a given species while each column corresponded to a trapping site at a given session. We first looked at sites \times sessions with at least one individual captured ($N=54$ columns), then at sites \times sessions where at least 10 individuals were sampled ($N=35$). We then tested the observed versus expected patterns under the null hypothesis of random assembly (Gotelli, 2000) using the standardised C-score (SCS) (Stone & Roberts, 1990) as a quantitative index of co-occurrence, with significant negative and positive SCS indicating aggregation and segregation, respectively (Gotelli, 2000). To assess statistical significance, the observed SCS was compared to values obtained from 10,000 iterations using two recommended null-models: first with random matrices constrained to have row and column totals identical to our data matrix (see the 'fixed-fixed' algorithm model 1 in Gotelli, 2000), and second by checking whether the result was identical to the 'fixed-equiprobable' algorithm model (see model 2 in Gotelli, 2000). We estimated pairwise co-occurrence scores using the program Pairs v.1.0 (Ulrich, 2008) and applied the 95% confidence limit criterion (Gotelli & Ulrich, 2010) to determine whether a particular pair of species was statistically aggregated, segregated or randomly associated.

2.5.5 | Occupancy modelling

Detection probability is imperfect and heterogeneous between species, traps and also nights. The probabilities of detection and occupancy

of a species at a trapping site were therefore estimated using a site occupancy model (MacKenzie et al., 2002) that takes the trapping sessions into account. Such a model of site occupancy relies on spatial and temporal replicates to estimate jointly the probability of detection of the species given its presence at a site as well as the probability of occupancy of the site by this particular species. This modelling was conducted only for the most frequently trapped species (*Crocidura olivieri*, *M. musculus*, *R. norvegicus* and *R. rattus*; see below) under R using the unmarked v.0.13-2 package (Fiske et al., 2015). The spatial replicates were the traps at a given session while the temporal replicates were the three consecutive nights of trapping during a given field session. In such a context, a trap is 'triplicated' across multiple rows for the different sessions (Garba et al., 2014). Occupancy models were applied at the session level and site was added as a covariate to handle the fact that traps were not independent. The sampling units used in the site occupancy analysis were the traps-sessions. The sample size was thus 6569 (around 1094 traps over the entire study area for 6 sessions) instead of only 9 sites. The temporal replicates were the three successive nights of the same sessions. We fitted models with sessions and sites as covariates (in interaction or addition) to deal with potential spatial correlations. As traps were not exactly at the same locations from one session to another, we could not use dynamic occupancy models. For each species, analyses were conducted on two different data sets: dataset 1 includes all nine sampling sites while dataset 2 included only sites with significant numbers of captures, that is at least 15 individuals captured during the six sessions, namely APC1 and APC2 for *R. rattus*, APC4-8 for *M. musculus* and *R. norvegicus*, and APC1 for *Crocidura olivieri*. APC4-7 sites being warehouses with the same characteristics, they were grouped together and considered as one locality, and APC8 as another independent one.

The effects of a suite of parameters on the detection and occupancy probabilities were investigated using a model comparison procedure (Burnham & Anderson, 2002): Dataset 1 was used to test the effect of sessions, trap types and nights (with no interaction) on detection probabilities, as well as of sessions and sites (with interaction) on occupancy probabilities, thus leading to 16 models combining different sets of covariates that were fitted on dataset 1 (see Appendix S2). The effects of sessions, trap types and nights on detection probabilities were also explored using Dataset 2, thus leading to 16 other models fitted on Dataset 2 (see Appendix S2). The best-fitted models were determined following the AIC criterion (Burnham et al., 2011).

3 | RESULTS

3.1 | Trapping success and relative abundance of small mammal species

Between 2017 and 2020, 6569 trap nights were set over the whole trapping survey, with 960 small mammals caught in the nine sites sampled (global trapping success of 14.6%). A large proportion of the individuals collected ($N=805$ out of 960, i.e. 83.8%) belonged to invasive species, namely *Rattus rattus* ($N=369$, i.e. 38.4% of all captures), *Rattus*

norvegicus ($N=189$, i.e. 19.7%) and *Mus musculus* ($N=247$, i.e. 25.7%), while the remaining ones (16.2%) belonged to native species, namely the shrew *Crocidura olivieri* ($N=141$, i.e. 14.7%) and the multi-mammate rat *Mastomys natalensis* ($N=14$, i.e. 1.5%) (Table 1). The number of small mammals per site and per session ranged between 46 and 244 (median=93), and between 107 and 208 (median=168), respectively. Details of all trapping results per species, site, session and trap type are provided in Table 1 and see Appendix S3.

A comparison of the proportion of the two types of traps set in our different sites shows that difference between the proportion of Sherman and wire mesh traps used during the whole study was only significant in APC3 where a higher number of wire mesh traps was used ($p=0.02$; see Appendix S4).

We observed strong and significant differences in trapping success depending on the type of trap used for the four most captured species: *R. rattus* ($\chi^2=100.95$, $p<0.001$) and *Rattus norvegicus* ($\chi^2=119.17$, $p<0.001$) were better captured by wire-mesh traps while trapping of *M. musculus* ($\chi^2=187.69$, $p<0.001$) and *Crocidura olivieri* ($\chi^2=18.45$, $p=0.001$) was significantly more successful with Sherman traps.

The comparison of species-specific relative abundances (represented by the species-specific trapping success) showed no difference between *R. rattus* and *Crocidura olivieri* in APC1 ($\chi^2=3.21$, $p=0.07$), while *R. rattus* was more abundant than *Crocidura olivieri* in APC2 ($\chi^2=53.48$, $p=0.001$). *R. rattus* was trapped more often than *R. norvegicus* in APC3 ($\chi^2=40.5$, $p=0.001$). *R. norvegicus* was more abundant than *M. musculus* in APC4 ($\chi^2=6.33$, $p=0.01185$) while both species were found in similar relative abundance in APC5 ($\chi^2=1.04$, $p=0.31$) and APC6 ($\chi^2=3.67$, $p=0.05$). *M. musculus* was more abundant than *R. norvegicus* ($\chi^2=11.64$, $p=0.001$) in APC7. Relative abundances of *M. musculus* and *R. rattus* were similar in APC8 ($\chi^2=0.12$, $p=0.72$) where both species were more abundant than *R. norvegicus* (*R. rattus* and *R. norvegicus*: $\chi^2=9.98$, $p=0.001$; *M. musculus* and *R. norvegicus*: $\chi^2=8.00$, $p=0.005$). Finally, *R. rattus* was more abundant than *Crocidura olivieri* in APC9 ($\chi^2=18.67$, $p=1.55E-05$).

Species-specific trapping success (see Appendix S5) did not show significant differences between sessions for *R. rattus* in the APC1 and APC2 sites that were not treated with anticoagulant. However, significant temporal variations were observed for the three other most captured species: for *R. norvegicus*, trapping success during Sessions 5 and 6 were significantly larger than during sessions 3 and 4 in treated sites APC4-8. For *M. musculus*, trapping success of Sessions 1, 2, 5 and 6 were significantly larger than sessions 3 and 4, and that of session 6 was more important than during session 5 in APC4-8. For *C. olivieri* in the non-treated APC1, trapping success of session 1 was significantly larger than during the other five sessions.

In addition, even when trap- and species-specific trapping successes were considered in order to investigate specifically the impact of rodent control campaigns, no variation were observed for *R. rattus* in non-treated sites APC1 and APC2 (Figure 2a,b) while no capture occurred in the treated site APC8 during sessions 3 and 4 (corresponding to the rat control campaign period) before increasing again at post-treatment sessions 5 and 6 (Figure 2c). In the same

TABLE 1 Summary of trapping results per species, sessions and sites of Cotonou Seaport.

Sites	APC1						APC2						APC3								
	S1	S2	S3	S4	S5	S6	Total	S1	S2	S3	S4	S5	S6	Total	S1	S2	S3	S4	S5	S6	Total
Trapping effort	118	210	189	215	215	199	1146	77	104	84	81	94	73	513	74	72	74	58	70	72	420
RRA	16	14	27	21	30	27	135	8	8	8	12	17	19	72	1	10	20	11	16	6	64
RNO	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	6	1	9
MMU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
MNA	0	0	0	0	0	0	0	2	1	1	0	0	0	4	0	0	0	1	0	2	3
COL	30	15	21	19	13	10	108	0	0	0	3	2	2	7	3	1	1	0	0	0	5
Total	46	29	49	40	43	37	244	10	9	9	15	19	21	83	5	12	22	12	22	9	82
Sites	APC4						APC5						APC6								
	S1	S2	S3	S4	S5	S6	Total	S1	S2	S3	S4	S5	S6	Total	S1	S2	S3	S4	S5	S6	Total
Trapping effort	136	107	88	141	152	115	739	129	118	102	142	139	104	734	122	152	104	173	108	93	752
RRA	0	0	0	0	3	2	5	0	0	0	0	1	3	4	0	0	0	2	4	5	11
RNO	5	5	2	7	10	9	38	4	9	2	4	4	20	43	8	17	6	5	10	9	55
MMU	3	10	1	0	0	5	19	23	7	3	2	3	15	53	13	10	4	6	25	19	77
MNA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COL	1	0	0	0	0	2	3	0	2	1	0	0	1	4	0	1	1	0	0	0	2
Total	9	15	3	7	13	18	65	27	18	6	6	8	39	104	21	28	11	13	39	33	145
Sites	APC7						APC8						APC9								
	S1	S2	S3	S4	S5	S6	Total	S1	S2	S3	S4	S5	S6	Total	S1	S2	S3	S4	S5	S6	Total
Trapping effort	120	139	103	152	120	102	736	127	152	181	308	190	134	1092	55	67	71	113	51	80	437
RRA	1	0	0	0	1	3	5	7	15	0	0	12	4	38	4	17	3	4	5	2	35
RNO	3	10	2	3	5	5	28	1	0	1	1	5	7	15	0	0	0	0	0	0	0
MMU	13	12	2	1	16	16	60	9	3	1	2	10	10	35	1	1	0	0	0	0	2
MNA	0	1	0	0	1	0	2	1	0	0	0	2	0	3	0	1	0	1	0	0	2
COL	2	0	0	1	0	0	3	0	1	0	0	0	1	2	2	1	0	1	0	3	7
Total	19	23	4	5	23	24	98	18	19	2	3	29	22	93	7	20	3	6	5	5	46

Note: COL, *Crocidura olivieri*; MMU, *Mus musculus*; MNA, *Mastomys natalensis*; RNO, *Rattus norvegicus*; RRA, *Rattus rattus*.

manner, the lowest trap-specific species-specific trapping successes for *R. norvegicus* and *M. musculus* in the treated sites APC4-8 were also observed during sessions 3 and 4 (Figure 2d,e) but, for both species, Sessions 1 and 2's relative abundance levels were recovered immediately after, that is, during sessions 5 and 6, hence 6 months to 1 year later (Figure 2d,e).

3.2 | Species diversity

The plateaus observed on biodiversity accumulation curves (Figure 3) indicate that the small mammal communities were correctly sampled in both the artisanal (APC1 and APC2) and industrial (APC3-9) seaport areas. Regardless species richness index used, the comparison of random sub-samples of about 200 individuals shows that the species diversity is significantly higher in the industrial than the artisanal seaport (species richness $^0D=4.98\pm 0.02$ vs. 3.73 ± 0.19 ; exponential entropy of Shannon $^1D=3.52\pm 0.17$ vs. 2.32 ± 0.25 ; the inverse of Simpson's index $^2D=3.16\pm 0.19$ vs. 2.10 ± 0.21 ; see also Figure 3).

3.3 | Species-specific spatial distributions

From Table 1, it can be noted that *R. rattus* was collected in all sites, though in much higher numbers in the artisanal seaport (APC1 and APC2) and, to a lesser extent, in the canteens area (APC3) as well as in the SOBEMAP garage (APC8).

Rattus norvegicus and *Mus musculus* were not captured in the artisanal port, with the only exception of one single Norway rat in APC1 during session 3. In the contrary, these two species largely dominated the trapping results in the warehouses located along the

unloading docks (APC4-7). A few individuals of *M. musculus* and *R. norvegicus* were also collected in APC8, and two house mice were caught in APC9. The native shrew *Crocidura olivieri* was almost exclusively restricted to the artisanal seaport (APC1 and APC2), with only a few individuals being trapped in the industrial port. The native *Mastomys natalensis* was found in very rare instances, especially in the warehouses where only two animals were captured during our 3-year-long survey (Figure 4).

3.4 | Co-occurrence analyses

Two statistical models were used to investigate species co-occurrence relying on all species pairs in all 54 possible site x session combinations with at least one individual captured: both of them indicated significant patterns of segregation between *Rattus rattus* and *Rattus norvegicus* ($SCS1=3.48$, $p<0.001$ and $SCS2=4.48$, $p<0.001$), *R. rattus* and *Mus musculus* ($SCS1=3.42$, $p<0.001$ and $SCS2=4.45$, $p<0.001$) as well as between *Crocidura olivieri* and *Mastomys natalensis* ($SCS1=1.82$, $p=0.06$ and $SCS2=2.56$, $p=0.01$). Only model 2 showed significant segregation between *R. norvegicus* and *Crocidura olivieri* ($SCS1=1.19$, $p=0.23$; $SCS2=2.16$, $p=0.03$). In contrast, *R. norvegicus* and *M. musculus* were caught more often together than randomly (i.e. aggregation; $SCS1=-3.82$, $p<0.001$ and $SCS2=-3.18$, $p=0.001$). Finally, only model 1 showed aggregation between *R. rattus* and *Mastomys natalensis* ($SCS1=-2.14$, $p=0.03$; $SCS2=-1.66$, $p=0.09$).

Results were very similar when the same analyses were conducted on species pairs from the 35 site x session combinations with at least 10 individuals captured since both models resulted in significant segregation patterns for species pairs *R. norvegicus* and

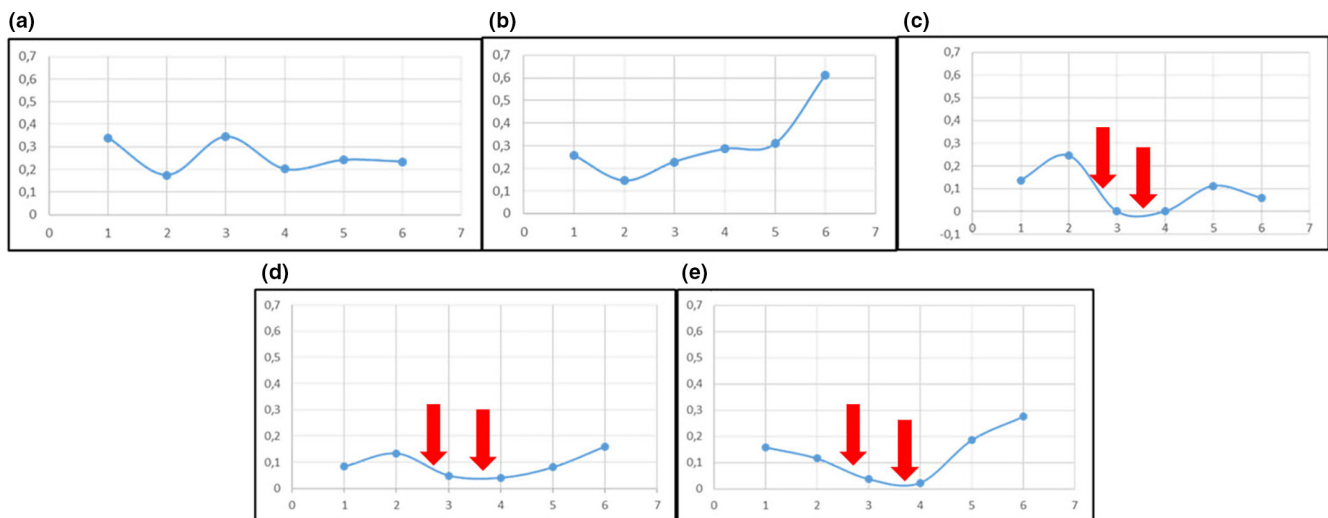


FIGURE 2 Trap-specific and species-specific trapping success (x-axis) during the six field sessions (y-axis) in the best sampled sites (see the text for details): (a) wire mesh trap-specific trapping success for *R. rattus* in APC1; (b) wire mesh trap-specific trapping success for *R. rattus* in APC2; (c) wire mesh trap-specific trapping success for *R. rattus* in APC8; (d) wire mesh trap-specific trapping success for *R. norvegicus* in APC4-8; and (e) Sherman trap-specific trapping success for *M. musculus* in APC4-8. Red arrows indicated rodent control campaigns conducted before our trapping campaigns.

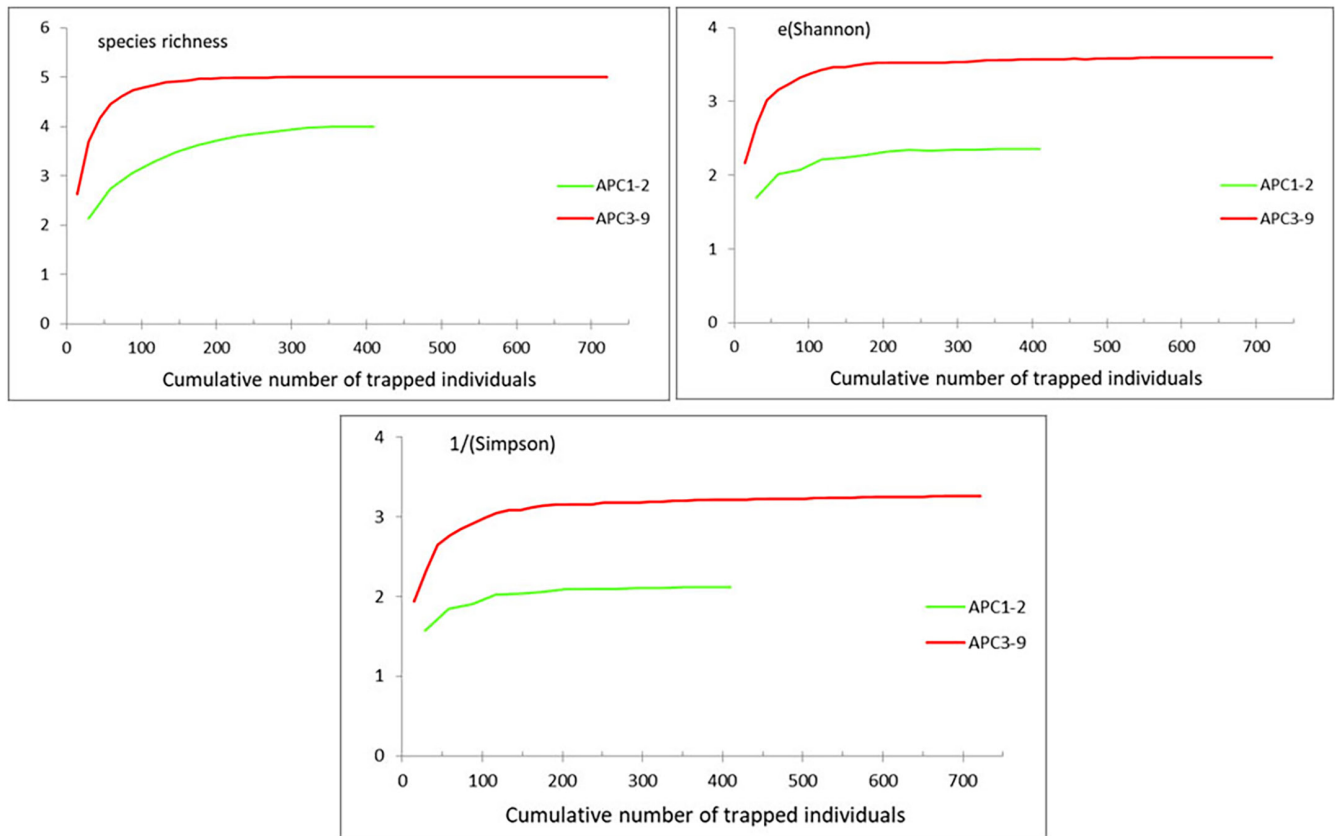


FIGURE 3 Sample-based rarefaction curves, rescaled by individuals, representing the number of commensal small mammal taxa for a given number of individuals captured in the nine sites of the Cotonou Seaport.

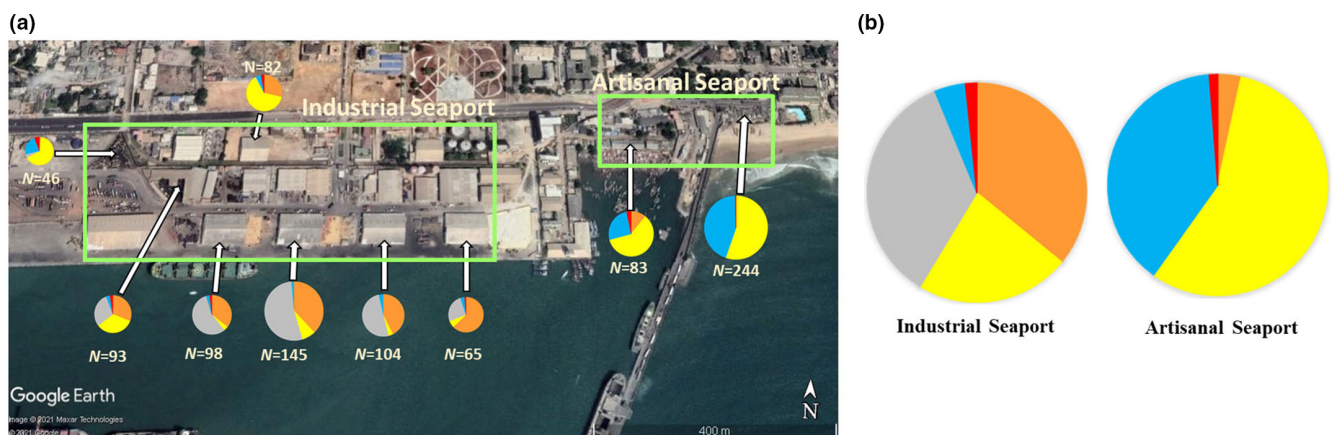


FIGURE 4 (a) Small mammal sampled in the Autonomous Port of Cotonou from 2017 to 2019. Circle sizes are proportional to the raw number of captures. Yellow, orange, grey, blue and red colours correspond to *R. rattus*, *R. norvegicus*, *M. musculus*, *Crocidura olivieri* and *Mastomys natalensis*, respectively. (b) Relative proportion of each species in the artisanal and industrial areas.

Crocidura olivieri ($SCS1=1.97$, $p=0.04$ and $SCS2=2.93$, $p=0.003$), *R. norvegicus* and *R. rattus* ($SCS1=2.09$, $p=0.03$; $SCS2=2.82$, $p=0.004$), *R. rattus* and *M. musculus* ($SCS1=2.23$, $p=0.02$; $SCS2=3.12$, $p=0.001$), *Crocidura olivieri* and *Mastomys natalensis* ($SCS1=2.05$, $p=0.03$ and $SCS2=2.86$, $p=0.004$) while significant aggregation was retrieved for *R. norvegicus* and *Mus musculus* ($SCS1=-3.05$, $p=0.002$; $SCS2=-2.50$, $p\leq 0.01$) (Table 2).

3.5 | Occupancy modelling: Detection and occupancy probabilities

The detection probability of *R. rattus* was higher with the wire-mesh than with the Sherman traps as well as during the first night of trapping (N1) than during the two following nights (N2 and N3). For *R. norvegicus*, detection probabilities were higher with the wire-mesh

TABLE 2 Co-occurrence patterns of the five small mammal species in the 54 sites with at least one individual captured.

Sp1	s1	Sp2	s2	Com	Model 1		Model 2	
					SCS1	p	SCS2	p
RRA	37	RNO	35	18	3.48	<0.001	4.48	<0.001
RRA	37	MMU	31	15	3.42	<0.001	4.45	<0.001
RRA	37	COL	27	20	-1.62	0.10	-0.91	0.36
RRA	37	MNA	11	10	-2.14	0.03	-1.66	0.09
RNO	35	MMU	31	28	-3.82	<0.001	-3.18	0.001
RNO	35	COL	27	14	1.19	0.23	2.16	0.03
RNO	35	MNA	11	5	0.80	0.42	1.53	0.12
MMU	31	COL	27	14	-0.04	0.96	0.78	0.43
MMU	31	MNA	11	5	0.19	0.85	0.89	0.37
COL	27	MNA	11	2	1.82	0.06	2.56	0.01

Note: Sp1: species 1; s1: number of occurrences where Sp1 was observed; Sp2: species 2; s2: number of occurrences where Sp2 was observed; Com: number of instances when Sp1 and Sp2 were observed together in the same site/session combination (i.e. number of joint occurrences). Significant *p*-values using the 95% confidence limit criterion are indicated in bold.

traps and at nights N1 and N2, while it was higher for Sherman traps but similar among nights for *M. musculus*. *Crocidura* showed higher detection probabilities on the first night and with Sherman traps.

The best models on occupancy probabilities gave identical results with the analysis performed on all nine sites (Dataset 1) or only on sites with the highest number of captures (≥ 15 ; Dataset 2). For *R. norvegicus* and *M. musculus*, the best-fitted model for occupancy probabilities included the interaction of sessions and sites (Table 3). For *R. norvegicus*, occupancy probability was also a function of trap type, session and night whereas only trap type was included in the best-fitted model retrieved for *M. musculus*. For *R. rattus* and *Crocidura sp.*, the best model selected was the interaction between trap type, session and night (Table 3).

Taking sessions into account, models showed similar occupancy rates of APC1 and APC2 by *R. rattus* (Table 4). The variation over time is similar with 100% occupancy in Sessions 1 and 2. The *R. norvegicus* occupancy rate was almost constant with close to 100% occupancy during all the six sessions in APC4 to APC7 (Table 4). It was slightly lower in APC8 (Table 4). For *M. musculus*, occupancy of sites APC4-7 was moderate with lower occupancy rates in Session 4 (Table 4). For *Crocidura sp.*, the occupancy rate in APC1 was much higher in Sessions 3 and 6 than in Sessions 2 and 5 (Table 4).

4 | DISCUSSION

Five small mammal species were detected during our 3-year-long monitoring of nine APC sites: three invasive species, namely *Rattus rattus*, *Rattus norvegicus* and *Mus musculus*, as well as two native species *Mastomys natalensis* and *Crocidura olivieri*. The three invasive species were by far the most abundant (83.9% of all captures), with *R. rattus*, *M. musculus* and *R. norvegicus* representing 38.4%, 25.7% and 19.7% of all captures, respectively. Our results in APC were strongly similar to those observed in other African seaport settings.

For instance, both *R. rattus* and *R. norvegicus* were sampled in Douala (Cameroon), with a predominance of *R. norvegicus* within the rodent community (Voelckel & Varieras, 1960). In Kinshasa seaport and Kisangani river-port (Democratic Republic of Congo), the four rodent species captured included the same three invasive species than those found here (Kaleme et al., 2011). Similarly, the four small mammal taxa mentioned in the seaports of Mahajanga (Madagascar) and Mayotte Island (Comores), included rats and mice, with *R. norvegicus* and *R. rattus* being the most dominant species in both locations (Rahelinirina et al., 2018). However, these surveys are either old (in the 1950s for the data from Cameroon) or based on much lower trapping effort and/or captures (for the data from DR Congo, Madagascar and Comores) than the present work. In addition, we underline that our study is the first to provide knowledge on the spatiotemporal distribution of small mammal species within a seaport at such a fine scale.

Several studies have already shown that important biases in small mammal diversity assessment and monitoring may exist if the type of traps used (Garba et al., 2014) as well as the successive trapping nights (Lucaccioni et al., 2016) are taken into account. Accordingly, our study shows that the probability of detecting the most captured species significantly varied according to these parameters. For instance, chances of detecting *R. rattus* and *R. norvegicus* were higher with wire-mesh traps while *M. musculus* and *Crocidura olivieri* were more trapped using Sherman traps. This was particularly striking for Norway rats (only 16 captures out of 3279 night traps using Sherman traps) and house mice (only 14 captures out of 3290 night traps using wire mesh traps). Furthermore, contrary to what is widely assumed (e.g. neophobia; Modlinska & Stryjek, 2016), higher probabilities of captures of shrews and both rat species were associated with the first trapping nights. This suggests that the presence of new traps in the environment did not frighten these species, which were rapidly attracted by our baits. This may be explained by the habituation of APC small mammals to forage within a permanently changing and human-influenced environment (e.g. in-and-out

TABLE 3 Occupancy (*psi*) and detection (*p*) probabilities of the top-ranked models for each well sampled species, namely *R. rattus*, *R. norvegicus*, *M. musculus* and *Crocicidura* sp.

Models	AIC	ΔAIC	nPars	AICwt	Models	AIC	ΔAIC	nPars	AICwt	
<i>Rattus rattus</i>										
<i>psi</i> (.) <i>p</i> (trap + session + night)	1128.34	0.00	10	91%	<i>Rattus norvegicus</i>					
<i>psi</i> (session + loc) <i>p</i> (trap + session + night)	1133.69	5.35	16	6%	<i>psi</i> (session + loc) <i>p</i> (trap + session + night)	932.07	0.00	16	75%	
<i>psi</i> (session) <i>p</i> (trap + session + night)	1136.38	8.04	15	1%	<i>psi</i> (session + loc) <i>p</i> (trap)	934.68	2.61	14	20%	
<i>psi</i> (session * loc) <i>p</i> (trap + session + night)	1139.11	10.77	21	0.4%	<i>psi</i> (session + loc) <i>p</i> (trap)	939.24	7.17	9	2%	
<i>Mus musculus</i>										
<i>psi</i> (session + loc) <i>p</i> (trap)	1184.10	0.00	9	47%	<i>psi</i> (session * loc) <i>p</i> (trap)	939.97	7.90	14	1%	
<i>psi</i> (session + loc) <i>p</i> (trap + session + night)	1185.05	0.95	16	29%	<i>Crocicidura</i> sp.					
<i>psi</i> (session + loc) <i>p</i> (trap + session)	1186.19	2.09	14	16%	<i>psi</i> (.) <i>p</i> (trap + session + night)	668.96	0.00	10	90%	
<i>psi</i> (session * loc) <i>p</i> (trap)	1189.24	5.13	14	3%	<i>psi</i> (session) <i>p</i> (trap + session + night)	674.65	5.69	15	5%	
					<i>psi</i> (.) <i>p</i> (trap + session)	676.54	7.58	8	2%	
					<i>psi</i> (session) <i>p</i> (trap)	677.63	8.67	8	1%	

Note: 'Trap' refers to the two trap models, 'session' to the six temporal sessions and 'night' for the three consecutive nights of trapping. '+' means that the covariates were tested in interaction while '*' that they were tested in addition. ΔAIC is the difference between the retrieved and the best models. 'nPars' and 'AICweight' correspond to the number of parameters in the model and the AIC weight, respectively.

TABLE 4 Species-specific occupancy probabilities (Pred) estimated by site and session for the four best-sampled species, namely *R. rattus*, *R. norvegicus*, *M. musculus* and *Crocicidura* sp.

<i>Rattus rattus</i>	<i>Rattus norvegicus</i>				<i>Mus musculus</i>				<i>Crocicidura olivieri</i>			
	Pred ± SE	Session	Localities	Locality	Pred ± SE	Session	Localities	Locality	Pred ± SE	Session	Localities	Locality
0.99 ± 0.05	1	APC1	APC4-7	APC8	0.55 ± 0.1	1	APC4-7	APC8	0.59 ± 0.1	1	APC4-7	APC1
0.99 ± 0.07	2	APC1	APC4-7	APC8	0.41 ± 0.09	2	APC4-7	APC8	0.28 ± 0.1	2	APC4-7	APC1
0.64 ± 0.3	3	APC1	APC4-7	APC8	0.50 ± 0.3	3	APC4-7	APC8	0.99 ± 0.03	3	APC4-7	APC1
0.44 ± 0.15	4	APC1	APC4-7	APC8	0.14 ± 0.1	4	APC4-7	APC8	0.40 ± 0.2	4	APC4-7	APC1
0.54 ± 0.16	5	APC1	APC4-7	APC8	0.43 ± 0.06	5	APC4-7	APC8	0.26 ± 0.1	5	APC4-7	APC1
0.45 ± 0.1	6	APC1	APC4-7	APC8	0.73 ± 0.08	6	APC4-7	APC8	0.99 ± 0.2	6	APC4-7	APC1
0.99 ± 0.02	1	APC2	APC8	APC8	0.26 ± 0.08	1	APC8	APC8				
0.99 ± 0.02	2	APC2	APC8	APC8	0.17 ± 0.06	2	APC8	APC8				
0.82 ± 0.3	3	APC2	APC8	APC8	0.22 ± 0.2	3	APC8	APC8				
0.66 ± 0.2	4	APC2	APC8	APC8	0.04 ± 0.03	4	APC8	APC8				
0.75 ± 0.1	5	APC2	APC8	APC8	0.17 ± 0.04	5	APC8	APC8				
0.68 ± 0.1	6	APC2	APC8	APC8	0.43 ± 0.1	6	APC8	APC8				

goods transports, workers' movements, high levels of noise due to voices and trucks, permanent lights, etc). Indeed, there is little doubt that the so-called 'landscape of fear' (reviewed in Bedoya-Pérez et al., 2019) of rodents evolving in harbours and other industrial-like sites is very different from their counterparts living in other habitats. Alternatively, the higher trapping success associated with first nights may also be partly explained by the fear generated by the first captured individuals to their congeners, the latter ones subsequently avoiding traps during the following nights, as already observed in rats (Kondrakiewicz et al., 2019). From the former, we highlight the importance of well-tailored protocols when setting up small mammals monitoring programs (e.g. using the more adapted type of traps as well as an accurate number of trapping nights depending on the species present).

Rattus rattus and *C. olivieri* over-dominate the small mammal community within the artisanal part of the port, with 63.3% and 35.2% of the total captures in APC1 and APC2, respectively. *C. olivieri* is a synanthropic shrew species that was astonishingly abundant in this particular habitat displaying sandy corridors and durable but unsanitary and encumbered buildings. We speculate that its insectivorous diet is well adapted to the abundance of insects that may be attracted by the large amounts of fresh fish as well as constant humidity that characterise APC1 and APC2 sites. Regarding *R. rattus*, this rodent is the most abundant species within Cotonou and other southern cities in Benin (Dossou et al., 2015; Hima et al., 2019; Houéménou et al., 2019). Therefore, this was not surprising to find highly abundant populations of this species in APC1 and APC2 sites (artisanal zone port), which are likely to be more similar to the urban areas of Cotonou than does the industrial part of the seaport—where dominant *R. rattus* populations were restricted to 'peripheral' areas (canteens at APC3, 78.1% of the total captures and parking area at APC9, 76.1%). Consistently, *R. rattus* was almost absent from the purely industrial seaport sites, such as warehouses (APC4-7) and garage (APC8) where Norway rats and house mice largely dominated (APC4-7: 90.5% of the total captures; APC8: 53.8%).

This spatial exclusion between *R. rattus* on the one hand, and *R. norvegicus* and *M. musculus* on the other hand, remains quite stable over our monitoring campaigns and may be explained by the fact that Norway rats and house mice are better adapted to industrial-like environments (Gatto-Almeida et al., 2021), while black rats prefer surrounding urban landscapes (Berthier et al., 2016) despite contrasted patterns have already been showed elsewhere (e.g. black rats have abundantly colonised industrial settings within Niamey slaughterhouse in Niger; Garba et al., 2014). In any case, our findings represent a novel illustration of species-specific segregations that have already been observed elsewhere in African commensal habitats facing with biological invasions of exotic rodents. For instance, (i) *M. musculus* and *R. rattus* have almost completely replaced native species in many cities and villages of Senegal (Dalecky et al., 2015; Stragier et al., 2019); (ii) *R. norvegicus* tended to displace *R. rattus* as early as in the 1950s in Douala, Cameroon (Voelckel & Varieras, 1960); and (iii) the usually highly prolific native *Mastomys natalensis* was locally replaced by invasive black rats and/or house

mouse in Niamey, Niger (Garba et al., 2014). An alternative, non-exclusive explanation could rely on local predator-prey interactions, which may also drive contrasted spatial distributions of the rodents. A dedicated survey on rodents' potential predators would be a relevant perspective in that sense, particularly to assess whether the presence of natural predators may be responsible for this marked segregated distribution. At this stage, however, this argument is hardly supported by our field observations and information from the local staff of the seaport, from which we noticed that (i) snakes and birds seem absent or very rare in the sites sampled, and (ii) cats were present in moderate numbers within both industrial and artisanal zones. Consistently, a previous study has evidenced that cats alone do not significantly impact rodent foraging activities, except when they are associated with dogs—which is not the case in Cotonou Seaport (Mahlabia et al., 2017).

Also, mouse and rat individual movements within urban environments are considered to be only a few dozens of meters long, although some rare longer dispersal events may exist (Combs et al., 2018; Feng & Himsworth, 2014; Gardner-Santana et al., 2009). Adjacent APC sites are all >40 to ~200m away from each other. In addition, urban rat territories are particularly narrow (30–40m), especially when population density is high (Combs et al., 2018), which is clearly the case in Cotonou seaport. Moreover, most APC sites are separated by wide bare soil-cemented areas and/or durable walls which may greatly gene flow between them, as paved streets were shown to do in some cities (e.g. Combs et al., 2018). Finally, it has been recently shown that the three invasive species (*R. norvegicus*, *R. rattus* and *M. musculus*) show very strong levels of population structuring at the very fine (i.e. APC) scale within Cotonou seaport (Badou, Hima, et al., 2023).

While habitat preference or features may (at least partly) explain the spatial segregations observed here, other eco-evolutionary processes—such as interspecific competition and/or historical factors—could also contribute to this distribution pattern. In Benin, *Rattus rattus* is widely distributed (Hima et al., 2019) and supposed to have been introduced at least twice, with its first introduction probably dating back to the 15th or 16th century (Etougbétché et al., 2020). On the contrary, Norway rats are limited to the southern part of the country and has never been observed further north than Dassa city (7.785°N, 2.199°E; Hima et al., 2019). This species also occurs in some restricted areas of the Sahel, such as in Mali (Meinig, 2000), Senegal (Dalecky et al., 2015) and Nigeria (e.g. Tatard et al., 2017), but it has never been observed in Niger yet (Hima et al., 2019). This suggests that Norway rats may be of more recent origin than black rats, and currently expanding in West Africa (Hima et al., 2019; Dalecky et al., unpublished data)—although knowledge on phylogeographic/demogenetic facets and the origin and invasion dynamics of this species is currently scarce in the African context. Furthermore, house mice have been sampled only in the industrial zone of APC where it was highly abundant. On the contrary, a previous study detected a very low presence of this species from the surrounding area (four individuals in Abomey-Calavi; Dossou et al., 2015) and the core city of Cotonou (one individual in Ladji; Dossou et al., 2022).

House mice have never been collected elsewhere despite massive prospecting in villages and towns as well as along a latitudinal transect across southern Benin (Dossou et al., 2015; Houéménou et al., 2019; Hima et al., 2019). Importantly, this species was found to occur in the great market of Niamey (Niger), where many trucks discharge imported food and products that are loaded inside the APC (Hima et al., 2019). This very peculiar pattern of distribution strongly suggests that the house mice was very recently introduced into Benin—very likely through maritime trade—and house mice are currently encroaching further inland through road transport, as already depicted elsewhere in West Africa (Dalecky et al., 2015).

From the foregoing, such a maintained segregation pattern may therefore result from both historic and ecological factors, with shrews and black rats first on-site and then replaced by subsequently introduced Norway rats and house mice populations. The reasons underlying the exclusion of black rats on the one hand, and the coexistence of Norway rats and house mice on the other hand, remain to be elucidated. One may speculate that it could involve (i) a better adaptation of Norway rats and house mice to strictly industrial habitats, (ii) elimination of medium-sized (i.e. *R. rattus* and *C. olivieri*) by larger (i.e. *R. norvegicus*) species, (iii) limited competition between two species of very different sizes (i.e. *R. norvegicus* and *M. musculus*) in a context of abundant food resources and/or (iv) a higher probability of pathogen spill-over (leading to elimination of the less resistant or more naïve host species; Wyatt et al., 2008) between rat species than between the more distantly related Norway rats and mice. In case of sequential invasion events of several invasive species (or populations), the order of arrival and successful settlement may be important for subsequent (population- or) species-specific distributions. In particular, it may be that the presence of an already proliferating invasive organism prevents the proliferation of a newly introduced one. This was supported by some surveys on black rats at the population level (Granjon & Cheylan, 1989). However, data to ascertain the proper succession of house mice, black and Norway rats' introduction events in Benin and in Cotonou are missing. Available data (see here above) rather suggest that black rats were first, and that Norway rats and mice arrived more recently. One would thus expect that, if only arrival order matters, black rats would be dominant in all Cotonou seaport areas, which was not observed here.

Regardless of eco-historical origin, this non-random species-specific spatial distribution of invasive rodents probably implies that, nowadays, only Norway rats or House mice are capable to climb onto docked ships and get disseminated overseas from Cotonou seaport. Conversely, it suggests that no black rats have successfully walked down docked ships and successfully settled within the industrial area of APC during the 3 years of our study. This could be due either to their absence aboard docked ships, their non-disembarking from docked ships, or their unsuccessful settlement within already installed communities, especially communities dominated by Norway rats and house mice. The relatively recent observations in UK where black rats seem to live on ships and to land down from time to time (Twigg, 1992) could make the latter hypothesis plausible. Hence, this assumption and should be tested given its possibly detrimental

consequences in terms of rodent control (e.g. advantage to newly introduced rodents following the elimination of already present ones).

Interestingly, two rodent control campaigns were organised in the industrial warehouses (APC4-7) and the garage (APC8) before our trapping sessions 3 and 4. These controls consisted in the installation of anticoagulant-poisoned baits in the crevices; unfortunately, a full description of the protocol used and a proper evaluation of its effect were not made available by the program implementers. Anyway, the marked decrease in the relative abundance of Norway rats and house mice as well as the absence of black rats in APC8 (something not observed for black rats in the non-treated APC1 and APC2 sites) during Sessions 3 and 4 in those treated sites strongly suggest some efficiency of this rodent control operation. Unfortunately, this effect was clearly short-term since high (and sometimes even higher abundances) were systematically retrieved only 6 months to 1 year later (Sessions 5 and 6) following treatment. This indicates that poisoning campaigns alone are not sufficient to achieve long-term eradication, and that accompanying measures, such as environmental modifications toward less rodent-favouring habitats (e.g. rearrangement and physical protection of food stocks within local infrastructures), appear necessary to avoid rapid post-control re-infestation, as already suggested in other settings (e.g. sewer networks: Channon et al., 2006; United States: Witmer & Shiels, 2017; Brazilian slum: Hacker et al., 2016; Richardson et al., 2019).

Controls (through the use of trapping or anticoagulants) are also expected to have an impact on the spatial distribution of coexisting rodent species, thus potentially leading to a—potentially transitory—reshuffling of intraspecific as well as interspecific interactions (Richardson et al., 2019). As such, rat control campaigns could have led to the disruption of the observed species-specific spatial segregation patterns in APC. Interestingly, black rats were slightly more abundant within the four industrial storehouses (APC4-7; see Table 1) during the trapping sessions 5 and 6, that is following the poison-based treatment of these sites. It is thus possible that black rats from the surrounding areas took advantage of the local Norway rat mortality to partly (re)infest these particular areas. Unfortunately, our stand-alone data are not robust enough to test for this hypothesis, and longer-term investigations will be necessary to reach a convincing conclusion. Note that documenting such multi-species recolonisation events following rodent control campaigns are crucial for the implementation of efficient rodent control strategies and the avoidance of rodents and associated-pathogens dispersals between the seaport and the surrounding urban landscape.

An interesting perspective would be to properly integrate the rodent control (e.g. method used, temporal aspects) as a potential explanative factor of the rodent community structure, which implies integrative research built with local stakeholders.

5 | CONCLUSIONS

This original longitudinal survey of small mammal communities in an African sea harbour led us to provide two main applied

recommendations for further efficient prevention and management under two perspectives—especially more relevant for developing regions. First, we advocate for a novel paradigm based on improved science-society interactions, where scientists and stakeholders will ever-increasingly engage in a more concerted implementation of context-adapted management of pest organisms. Our study allowed us to highlight that partnership-based approach between scientists and local stakeholders is instrumental to help improve future studies. We strongly recommend that such concerted approach should be systematised to promote more efficient and sustainable management operations dedicated to rodent populations in seaports. Indeed, unambiguously identifying species and dynamics (across space and over time) of small mammal populations is crucial to setup and adapt relevant prevention and control strategies (e.g. type of traps to prioritise for long-term surveys and/or mechanical removal; assessments of rodent ecology to assess the most appropriate timing of control measures; evaluation of re-infestation risk; delineation of functional eradication/management units). Moreover, our data suggest that the effect of currently organised rat control campaigns is limited and that population recovers quickly after poisoning (probably within 6–12 months). While we did not get precise information on how this operation was carried out (something that could be easily improved by a better communication between rodent academic experts and rodent management operators), we can safely assume that no specific assessment was planned by the local managers prior to it. Integrating scientific expertise (e.g. species on-site; fine-scale species-specific spatial distributions and relative abundances; rodent resistance to anticoagulants) at early stages of the design and implementation of treatment would have probably increase the probability to achieve a more sustainable control effect. For instance, population genetic analyses of APC rodents are currently underway to investigate whether the re-infestation observed here is endogenous and/or depends on newly introduced individuals from surrounding areas. Furthermore, evidence-based environmental modifications within the port as well as locally maintained procedures against new introductions from docking ships are key to limit rodent proliferation after control programs. This echoes the approaches relying on Ecologically-Based Rodent Management (EBRM). The latter method aims at making the environment unsuitable for rodents through science-guided and integrated actions (such as habitat modification and/or biological control through indigenous predators) in order to make the environment unsuitable for rodents (Constant et al., 2020).

Second, we stress the need to move the problem of biological invasions higher in the official agendas of African regional organisations, with a special focus on the introduction points such as sea harbours. Here, we found that invasive rodents (namely house mice, Norway and black rats) dominate the sampled communities, thus confirming that seaports have represented—and probably still represent—major entry points for such invading pest organisms, which may subsequently disseminate inland through other transportation means (Hima et al., 2019). We also demonstrated clear spatial segregation patterns at a very fine scale over the 3 years of our survey,

particularly between some invasive species within the heart of the seaport. Taking into account the major impacts that invasive rodents may have on food security, economics and health, their abundant populations in APC make it urgent to set proactive control strategies. A recent study evidenced that IAS represent a significant economic burden in Africa, and that their costs are largely driven by damage—while management expenditures remain scarce (Diagne, Turbelin, et al., 2021). The adoption and implementation of biosecurity measures (e.g. early detection and eradication) appear as the most relevant and efficient strategy for African countries where economic capacities are often limited (Faulkner et al., 2020). The ultimate objective is to act against invaders before they become widely established, since controlling widespread invasions is often impossible or may require a high amount of resources afterward.

We hope that our study will serve as a sound basis for further, complementary efforts in that sense.

AUTHOR CONTRIBUTIONS

Study design and supervision: Sylvestre Badou, Philippe Gauthier, Gualbert Houéménou, Arlette Tchabi, Laurent Faton, Karmadine Hima, Clément Agbangla and Gauthier Dobigny. *Field work:* Sylvestre Badou, Philippe Gauthier, Henri-Joël Dossou, Jonas Etougbéché, Tasnime Adamjy, Camille Evenamia and Gauthier Dobigny. *Statistical analyses:* Sylvestre Badou, Aurélien Besnard, Ambroise Dalecky and Christophe Diagne. *Writing and revision:* Sylvestre Badou, Antoine A. Missihoun, Ambroise Dalecky, Christophe Diagne and Gauthier Dobigny.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.bg79cnp4> (Badou, Missihoun, et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: (A) Assemblage of traditional stores (APC1), (B) fresh fish market (APC2), (C) restaurants and outdoor canteens (APC3), (D) four large non-joined industrial storehouses (APC4-7), (E) garage and mechanical equipment storage rooms (APC8) and (F) storage area for large equipment (APC9).

Appendix S2: Small mammal species sampled during the seven sessions in the nine sites of the International Autonomous Port of Cotonou (APC). For each session and site, an estimate of the trapping effort is provided according to the type of trap. For each site and taxon, the number of individuals trapped is indicated. nG: number of wire mesh, nS: number of Sherman traps, G+S: total number of traps (nG+nS), cG: captures in wire mesh, cS: captures in Sherman traps, cT: total captures (cG+cS).

Appendix S3: Estimation of the difference in the proportion of each type of trap (wire and sherman) set at the nine sites during sessions 2 to 7.

Appendix S4: A comparison of the two types of traps in APC3.

Appendix S5: Species-specific success for *Rattus rattus* in APC1 and APC2.

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