diversity

MDPI

Article

Native and Invasive Small Mammals in Urban Habitats along the Commercial Axis Connecting Benin and Niger, West Africa

Karmadine Hima [1,*], Gualbert Houémenou [2], Sylvestre Badou [2], Madougou Garba [3], Henri-Joel Dossou [2], Jonas Etougbétché [2], Philippe Gauthier [4], Emma Artige [4], Odile Fossati-Gaschignard [4], Sama Gagaré [5], Gauthier Dobigny [2,4] and Ambroise Dalecky [6,*]

[1] Faculté des Sciences et Techniques, Université Abdou Moumouni, Niamey BP 10662, Niger
[2] Ecole Polytechnique d'Abomey-Calavi, Laboratoire de Recherche en Biologie Appliquée, Université d'Abomey-Calavi, Cotonou 01 BP 2009, Benin; gualbert.houemenou@gmail.com (G.H.); sylvestrebadou@yahoo.fr (S.B.); dossou_hjoel@yahoo.fr (H.-J.D.); starjer22@gmail.com (J.E.); gauthier.dobigny@ird.fr (G.D.)
[3] Direction Générale de la Protection des Végétaux, Niamey BP 323, Niger; garba_madougou@yahoo.fr
[4] Centre de Biologie pour la Gestion des Populations, UMR IRD-INRA-Cirad-Montpellier SupAgro-MUSE, Campus International de Baillarguet, 755 avenue du Campus Agropolis, CS 30016, 34988 Montferrier-sur-Lez, France; philippe.gauthier@ird.fr (P.G.); emmanuelle.artige@inra.fr (E.A.); odile.fossati@ird.fr (O.F.-G.)
[5] Centre Régional Agrhymet, Rue de l'Université, Niamey BP 11011, Niger; sama.gagare@cilss.int
[6] IRD, Aix Marseille Université, LPED, 13331 Marseille Cedex 3, France
* Correspondence: karmadine@gmail.com (K.H.); ambroise.dalecky@ird.fr (A.D.)

Received: 18 October 2019; Accepted: 4 December 2019; Published: 10 December 2019

Abstract: Based on compiled small mammal trapping data collected over 12 years from Benin and Niger (3701 individual records from 66 sampling sites), located in mainland Africa, we here describe the small mammal community assemblage in urban habitats along the commercial axis connecting the two countries, from the seaport of Cotonou to the Sahelian hinterland, with a particular focus on invasive species. In doing so, we document extant species distributions, which highlight the risks of continuing the range expansion of three synanthropic invasive rodent species, namely black rats (*Rattus rattus*), brown rats (*R. norvegicus*), and house mice (*Mus musculus*). Using various diversity estimates and community ecology approaches, we detect a latitudinal gradient of species richness that significantly decreased Northward. We show that shrews (*Crocidura*) represent a very important component of micro-mammal fauna in West African towns and villages, especially at lower latitudes. We also demonstrate that invasive and native synanthropic rodents do not distribute randomly in West Africa, which suggests that invasive species dynamics and history differ markedly, and that they involve gradual, as well as human-mediated, long distance dispersal. Patterns of segregation are also observed between native *Mastomys natalensis* and invasive rats *R. rattus* and *R. norvegicus*, suggesting potential native-to-invasive species turn over. Consequences of such processes, especially in terms of public health, are discussed.

Keywords: synanthropic rodents; biological invasion; community ecology; *Rattus*; *Mus*; West Africa

1. Introduction

In addition to the various effects of global changes such as climate modification [1], shift in land-use [2,3], and urbanization [4–7], West Africa faces great impacts from international trade, such as biological invasions [8,9]. Biological invasions occur from the rapid development of major commercial hubs (like international seaports and airports), as well as the densifying of road and river transportation networks [10,11].

Arrival, proliferation, and spatial expansion of invasive species can deeply alter an ecosystems functioning [12] and the community structure of species [13–16]. In the case of successful bioinvasions, communities tend to be simplified and homogenized [17–19] and exotic species usually become numerically dominant [20]. The bioinvasion of rodent species are usually intimately associated with urbanization, human trade, and transportation [21–24]. *Rattus* spp. and *Mus musculus* are widely introduced rodent species [25], and when established, they may cause very severe damage to crops and food stocks [26]. They may also deeply impact public health through the worldwide dissemination of pathogens [27–30] and greatly threaten native biodiversity through predation, competition, and extinction of local species, as well as the modification of host/parasite interactions [31–37].

Rats and mice were first introduced in West Africa in coastal cities, probably from the pre-colonial period to the present day, and they disseminated within lands, following human movements and goods trade [23,24,38–40]. These invasive rodents expanded rapidly inland over the last decades, with their dispersal being tightly associated with fluvial and road networks, transport improvement, as well as growing urbanization [22–24,38,40–45]. As such, history was important in shaping current distributions of invasive rodent species in West Africa.

Niger is a land-locked country that operates its import and export products from the closest seaports, in particular Cotonou seaport in Benin [46], through which nearly 80% of its international trade transits [47]. As a consequence, the Benin–Niger corridor is one of the main transnational trade routes for Niger, especially for cereals and other food products [48,49]. In such a context, recent surveys have highlighted the probable role of road and fluvial traffic in the invasion and progression of black rats in Southwest Niger [24,41].

Based on extensive trapping data obtained in recent years (see methods), we here present a survey of small mammal faunas in a series of cities and villages from Benin and Niger. In doing so, we aim to describe the distribution and the spread of commensal small mammals along the coast–hinterland commercial axis connecting Benin and Niger, with a particular focus on three invasive rodent species, namely black rats (*Rattus rattus*), brown rats (*Rattus norvegicus*), and house mice (*Mus musculus*). Using these baseline data, we discuss the implications of bioinvasions on small mammal communities and alert sanitary and agricultural authorities about the potentially ongoing and rapid geographic expansion of these commensal invasive species. As such, this study contributes to Aichi Biodiversity Target #9 on invasive alien species.

2. Material and Methods

2.1. Sampling

Between 2005 and 2017, terrestrial small mammal (i.e., including rodents and shrews) sampling was conducted in commensal habitats in Benin and Niger during the course of different research programs. Sampling sites were distributed along a South–North gradient that included several coastal localities of Southern Benin (i.e., Porto-Novo, Ganvié, Togbin, Ouidah, and Cotonou, including its international seaport), a few inland cities of central and Northern Benin (i.e., Bohicon, Dassa-Zoumé, Parakou, and Kandi), as well as South-Western Niger, along the Niger River (i.e., Boumba, Say, and Hamma Dendi), and the main tarred roads connecting Niamey, the capital city of Niger, to the surrounding countries (i.e., Makalondi at the Burkinabè border; Dosso and Dogondoucthi along the national road towards Eastern Niger and Northern Nigeria; Gaya at the Benin/Niger border; and Tillabery on the road to Mali) (Figure 1). Our dataset thus includes 18 localities from Southern Guinean to Northern Sahelian localities. Localities refer to prospected villages and cities. In terms of surface area, they ranged from small villages of less than one square kilometre (i.e., Hamma Dendi, and Ganvié) to large urban agglomerations extended over several tens of square kilometres (i.e., Cotonou, Niamey). Sites corresponded to sampling points within these localities. We aimed to sample each site within an area of the same order of magnitude. Thus, villages and small cities were here considered as single sites, when in the two large cities, sites referred to different urban neighborhoods/districts. In total, 66 sampling sites, with a minimum of 10-captured small mammal individuals (36 sites in Benin, 30 in Niger), were considered in the present study. In particular, the two largest cities, i.e., Cotonou and Niamey, were both intensively and extensively sampled (28 and 22 different sites in Cotonou and Niamey, respectively).

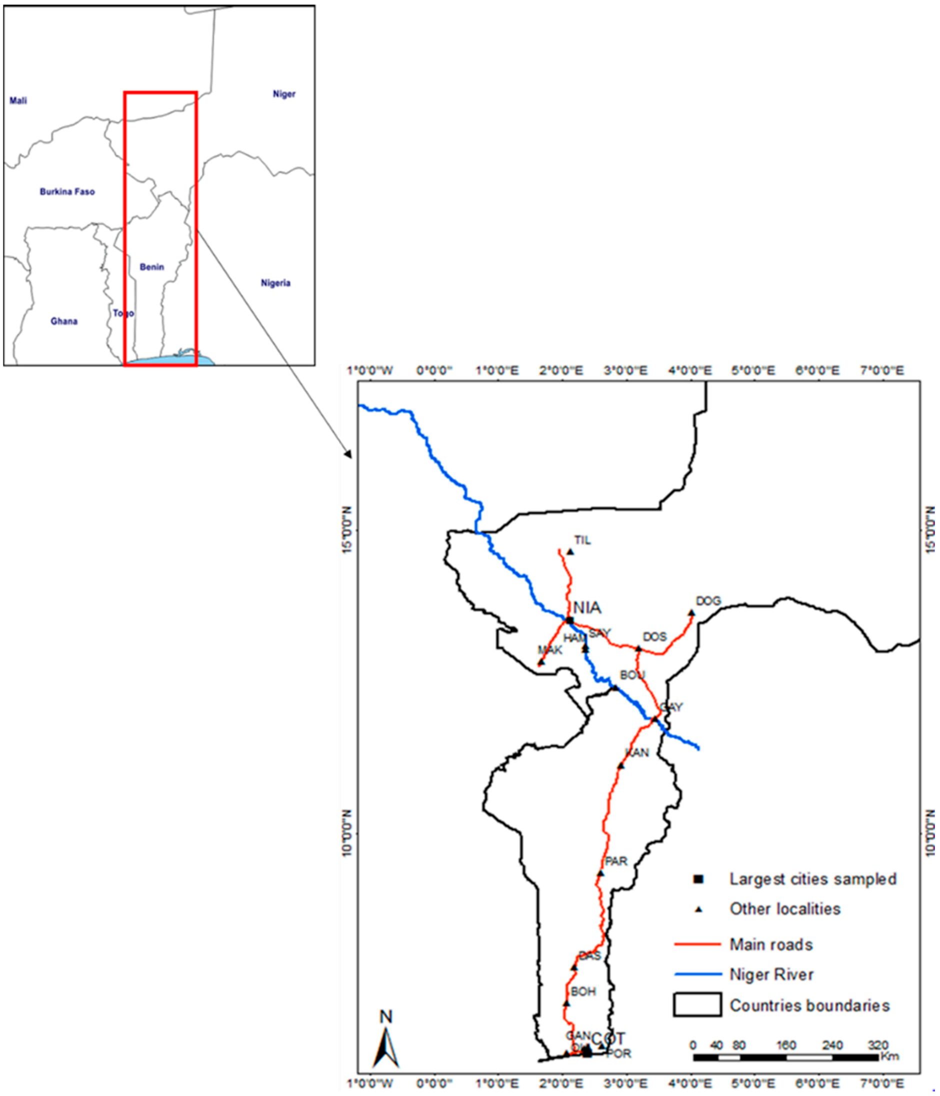

Figure 1. Map summarizing the different sampled localities and their distribution along the corridor axis, from South (Cotonou, Benin) to North (Tillabery, Niger). Squares represent the two largest cities (Cotonou and Niamey), which include several sampling sites (see text for details). The other localities, considered as one sampling site, are represented by triangles. BOH = Bohicon; BOU = Boumba; COT = Cotonou; DAS = Dassa-Zoumé; DOG = Dogondoutchi; DOS = Dosso; GAN = Ganvié; GAY = Gaya; HAM = Hamma-Dendi; KAN = Kandi; MAK = Makalondi; NIA = Niamey; OUI = Ouidah; PAR = Parakou; POR = Porto-Novo; SAY= Say; TIL = Tillabery; and TOG = Togbin.

Two to four traps were set inside each sampled room in a building (houses, storehouses, shops, offices, and markets) for three–five consecutive nights. Commensal habitats were irregular and complex, and given that traps were set indoor, ethical guidelines imposed that trapping procedures strictly respect the everyday life of people living there. As a consequence, it was not feasible to arrange lines or grids when trapping inside buildings. Investigated households were targeted, following the acceptance of inhabitants as well spatial coverage, with buildings separated by 10–200 m, according to site spatial organization. Baits consisted of peanut butter, usually supplemented with fish or 'soumbala' (local spice made from the *Néré* tree, *Parkia biglobosa*). Minimal overall sampling effort, of approximately 27,142 trap-nights, was deployed (Table 1). In order to capture small (e.g., *Mus* spp., etc.), medium-sized (e.g., *Mastomys* spp.), to moderately large rodent species (e.g., *Rattus* spp., etc.), as well as shrews (*Crocidura* spp.), two models of traps were most often used in combination and in similar proportions: Sherman folding box traps (8 × 9 × 23 cm; H.B. Sherman Traps, Inc., Tallahassee, FL, USA) and locally made wire-mesh live traps (10 × 10 × 25 cm), with the exception of a subset of the most ancient sampling sessions (23 sites) in Benin, where only wire-mesh live traps (Firobind model, 8 × 8 × 25 cm, and locally made model, 10 × 10 × 25 cm), baited with a mixture of wheat flour and caned sardine or smoked fish, were used.

Small mammals were captured alive and immediately brought to the lab where they were processed the same day or the day after. They were euthanatized with diethyl–ether or chloroform for the most ancient sampling sessions, and sacrificed by cervical dislocation, as recommended by Mills et al. [50] for the most recent sessions. Sex and standard body measurements (weight, head + body, tail, ear, and hindfoot lengths) were recorded. The reproductive status was also noted for both sexes. Tissue samples were collected for further analyses, such as taxonomic barcoding, population genetics, and pathogen screening, etc. All samples were deposited in CBGP Small Mammal Collection, Montpellier, France (https://doi.org/10.15454/WWNUPO) and in LARBA sample collection, Cotonou, Benin.

2.2. *Species-Specific Identifications*

Due to the frequent coexistence of cryptic species in West Africa [51], we were cautious to provide unambiguous specific assignments, in particular for most if not all rats, mice, and multi-mammate rats, which were of primary interest for the purposes of the present study. As such, our species-specific identifications relied on morphological grounds when no ambiguity existed (e.g., adult rats and house mice). However, very young individuals or individuals belonging to sibling species complexes were identified through laboratory methods [41,52]. To do so, we performed karyotyping (e.g., *Mastomys* spp. [34]), nuclear microsatellite genotyping (e.g., *Rattus rattus*, *R. norvegicus* and *Mastomys natalensis*), or cytochrome b mitochondrial gene sequencing (e.g., *Rattus* spp., *Mastomys* spp., *Praomys* spp., *Arvicanthis* spp., and *Crocidura* spp. [24,34,53]; our unpublished data).

2.3. *Ethics Statements*

All trapping sessions were conducted under explicit agreements with local, traditional (e.g., family and household heads, shops, and firm owners), as well as administrative (i.e., Cotonou City Hall services, Crop Protection Division in Niger, urban district chiefs) authorities. None of the rodent species captured in the present study had a protected status (see IUCN and CITES lists). All animals were treated in a humane manner, in accordance with the guidelines from the American Society of Mammalogists [54]. Fieldwork in Benin was conducted under the research agreement between the Republic of Benin and the French National Research Institute for Sustainable Development (IRD), which was signed on 30th September 2010 (available upon request). Those in Niger were authorized by the scientific partnership agreement (number 301027/00) between IRD and the Republic of Niger.

Table 1. Small mammal species sampled in 66 sites of urban habitats along the commercial axis connecting Benin and Niger, from South to North. PAC refers to the Autonomous international Port of Cotonou. For each site, an estimate of the trapping effort is provided. For each taxon, the number of trapped individuals is provided. Invasive species: *R. ra.*: *Rattus rattus*, *R. no.*: *Rattus norvegicus*, *M. mus.*: *Mus musculus*. Native species: *M. nat.*: *Mastomys natalensis*, *Cro.*: *Crocidura* spp., *Arvi.*: *Arvicanthis* spp., *Prao.*: *Praomys* spp., *Cri.*: *Cricetomys* spp., and *M. ery.*: *Mastomys erythroleucus*. Diversity indices: *S*(10), number of species in a subsample of 10 individuals; 1-*D*, Simpson index; and *H*, Shannon entropy.

Localities	Sites	Latitude (°N)	Longitude (°E)	Sampling Date(s)	Trapping Effort (Trap-Nights)	Invasive Species			Native Species						Total Captures	Diversity Indices		
						R. ra.	*R. no.*	*M. mu.*	*M. nat.*	*Cro.*	*Arvi.*	*Prao.*	*Cri.*	*M. ery.*		*S*(10)	*1-D*	*H*
Cotonou	PAC	6.348	2.431	2006, 2014, 2015	840	38	99	12	3	87	0	0	0	0	239	3.35	0.67	1.23
Cotonou	Wlacodji	6.351	2.442	2006	270	9	7	0	3	3	0	0	0	0	22	3.71	0.69	1.27
Cotonou	Marché Ganhi	6.355	2.437	2005	60	0	18	0	0	7	0	0	0	0	25	1.99	0.40	0.59
Togbin	Togbin	6.355	2.305	2017	262	6	0	0	35	4	0	0	0	0	45	2.45	0.37	0.68
Cotonou	Jacques	6.358	2.457	2006	45	13	0	0	2	3	0	0	0	0	18	2.75	0.44	0.78
Cotonou	Enagnon	6.362	2.453	2006	180	17	9	0	3	3	0	0	0	0	32	3.36	0.62	1.14
Cotonou	St-Jean	6.363	2.418	2010, 2016, 2017	1791	128	0	0	17	93	0	14	12	0	264	3.28	0.63	1.19
Cotonou	Abokicodji	6.363	2.442	2009, 2010	240	37	1	0	3	2	0	0	0	0	43	2.21	0.25	0.55
Cotonou	Bokossi	6.365	2.438	2009, 2010	150	9	10	0	0	7	0	0	0	0	26	2.98	0.66	1.09
Cotonou	Tokpa	6.365	2.434	2006	150	18	7	0	0	2	0	0	0	0	27	2.59	0.48	0.81
Cotonou	Dédokpo	6.369	2.439	2006	210	16	8	0	1	1	0	0	0	0	26	2.76	0.52	0.91
Ouidah	Ouidah	6.372	2.076	2015	720	115	6	0	39	36	4	0	0	0	200	3.22	0.60	1.13
Cotonou	Kpankpan	6.373	2.439	2006	270	1	8	0	12	3	0	0	0	0	24	3.23	0.62	1.11
Cotonou	Marché Tokpa	6.374	2.430	2006	60	22	7	0	1	1	0	0	0	0	31	2.60	0.44	0.80
Cotonou	Agla	6.375	2.363	2010, 2016, 2017	1728	168	27	0	57	82	0	6	1	0	341	3.54	0.66	1.28
Cotonou	Chankpamè	6.378	2.486	2006	270	18	0	0	4	6	0	0	0	0	28	2.80	0.52	0.89
Cotonou	Zogbohouè	6.379	2.389	2006	430	46	0	0	1	1	0	0	0	0	48	1.42	0.08	0.20
Cotonou	Adogléta	6.381	2.438	2005, 2006	60	5	2	0	2	4	0	0	0	0	13	3.92	0.71	1.31
Cotonou	Suru-Léré	6.382	2.462	2006	240	35	0	0	2	1	0	0	0	0	38	1.73	0.15	0.33
Cotonou	Djidjè	6.384	2.434	2006	210	6	8	0	0	4	0	0	0	0	18	2.98	0.64	1.06
Cotonou	Kowégbo	6.387	2.469	2006	210	28	1	0	0	0	0	0	0	0	29	1.34	0.07	0.15
Cotonou	Ahouansori	6.388	2.423	2005	210	22	0	0	1	1	0	0	0	0	24	1.83	0.16	0.34
Cotonou	Ladji	6.389	2.433	2010, 2016, 2017	1744	182	16	0	5	101	0	1	0	0	305	2.59	0.53	0.91
Cotonou	Avotrou	6.389	2.476	2005	360	40	0	0	13	1	0	0	0	0	54	2.14	0.39	0.64
Cotonou	Minonchou	6.391	2.457	2006	150	23	0	0	1	4	0	0	0	0	28	2.21	0.30	0.56
Cotonou	Ayimlonfidé	6.392	2.567	2017	210	28	2	0	0	0	0	0	0	0	30	1.56	0.12	0.24
Cotonou	Gankpodo	6.393	2.456	2006	150	28	0	0	5	4	0	0	0	0	37	2.55	0.40	0.72
Cotonou	Fifadji	6.395	2.398	2006, 2016	210	69	19	0	1	6	0	0	0	0	95	2.51	0.43	0.78
Cotonou	Vossa Kpodji	6.397	2.400	2006	250	48	5	0	2	1	0	0	0	0	56	2.15	0.26	0.54
Cotonou	Godomey	6.413	2.312	2006	480	14	0	0	1	1	0	0	0	0	16	2.25	0.23	0.46
Ganvié	Ganvié	6.469	2.397	2017	230	36	6	0	0	1	0	0	0	0	43	2.05	0.28	0.51
Porto Novo	Porto Novo	6.497	2.629	2015	580	129	4	0	30	67	0	0	0	0	230	2.89	0.58	1.02
Bohicon	Bohicon	7.192	2.076	2017	276	44	0	0	21	8	0	0	0	0	73	2.69	0.54	0.91
Dassa-Zoumé	Dassa-Zoumé	7.785	2.199	2017	169	15	2	0	9	5	0	0	0	0	31	3.41	0.65	1.18
Parakou	Parakou	9.376	2.630	2017	190	34	0	0	1	4	0	0	0	0	39	1.97	0.23	0.45
Kandi	Kandi	11.135	2.936	2017	280	38	0	0	1	0	0	0	0	0	39	1.26	0.05	0.12
Gaya	Gaya	11.877	3.451	2011	304	32	0	0	6	0	2	0	0	0	40	2.29	0.34	0.61
Boumba	Boumba	12.409	2.840	2011	201	8	0	0	41	0	3	0	0	0	52	2.32	0.35	0.64
Makalondi	Makalondi	12.836	1.687	2012	334	0	0	0	15	0	0	0	0	0	15	1.00	0.00	0.00
Hamma Dendi	Hamma Dendi	13.0327	2.3785	2011	326	30	0	0	0	0	0	0	0	0	30	1.00	0.00	0.00
Dosso	Dosso	13.042	3.198	2011	543	31	0	0	5	0	0	0	0	0	36	1.83	0.24	0.40

Table 1. *Cont.*

Localities	Sites	Latitude (°N)	Longitude (°E)	Sampling Date(s)	Trapping Effort (Trap-Nights)	Invasive Species			Native Species						Total Captures	Diversity Indices		
						R. ra.	*R. no.*	*M. mu.*	*M. nat.*	*Cro.*	*Arvi.*	*Prao.*	*Cri.*	*M. ery.*		*S*(10)	*1-D*	*H*
Say	Say	13.096	2.360	2011	338	0	0	0	18	0	7	0	0	0	25	1.99	0.40	0.59
Niamey	Gnalga	13.479	2.114	2010	400	0	0	0	27	3	0	0	0	0	30	1.72	0.18	0.33
Niamey	Pont Kennedy	13.485	2.102	2010	448	0	0	0	40	4	0	0	0	0	44	1.66	0.17	0.30
Niamey	Abattoirs	13.490	2.123	2010	478	77	0	0	0	0	0	0	0	0	77	1.0	0.00	0.00
Niamey	Karadje 1–2	13.494	2.097	2009, 2011	1290	0	0	0	50	8	0	0	0	0	58	1.80	0.24	0.40
Niamey	Gamkalé Q	13.494	2.125	2010	452	0	0	0	23	0	0	0	0	0	23	1.00	0.00	0.00
Niamey	Kirkissoye	13.495	2.110	2010	725	24	0	0	13	0	4	0	2	0	43	3.07	0.59	1.05
Niamey	CGA	13.502	2.112	2010	326	19	0	0	1	0	0	0	0	0	20	1.50	0.10	0.20
Niamey	Lamorde	13.507	2.077	2010	418	0	0	0	36	1	0	0	0	0	37	1.27	0.05	0.12
Niamey	CYA	13.512	2.099	2010	500	4	0	0	61	0	0	0	0	0	65	1.50	0.12	0.23
Niamey	Petit Marché	13.514	2.110	2011	374	13	0	0	24	0	0	0	0	0	37	1.99	0.46	0.65
Niamey	Wadata	13.518	2.144	2010	497	0	0	0	11	6	0	0	0	0	17	2.00	0.46	0.65
Niamey	Grand Marché	13.519	2.115	2011	305	7	0	61	0	3	0	0	0	0	71	2.04	0.25	0.49
Niamey	Entrepôt CYA	13.520	2.081	2009	661	19	0	0	0	0	3	0	0	0	22	1.86	0.24	0.40
Niamey	Route Filingué	13.521	2.152	2011	370	0	0	0	15	15	0	0	0	0	30	2.00	0.50	0.69
Niamey	Yantala Bas	13.527	2.082	2010	449	0	0	0	27	1	0	0	0	0	28	1.36	0.07	0.15
Niamey	Yantala Haut	13.534	2.082	2010	484	0	0	0	23	0	0	0	0	0	23	1.00	0.00	0.00
Niamey	Boukoki	13.537	2.113	2010	449	0	0	0	47	2	0	0	0	0	49	1.37	0.08	0.17
Niamey	Banifandou	13.544	2.136	2010	370	0	0	0	33	8	0	0	0	0	41	1.92	0.31	0.49
Niamey	Daressalam	13.546	2.096	2010	531	0	0	0	40	1	0	0	0	0	41	1.24	0.05	0.11
Niamey	Koubia	13.552	2.054	2010	378	0	0	0	26	2	0	0	0	0	28	1.60	0.13	0.26
Niamey	Koirategui	13.589	2.109	2010	266	0	0	0	10	2	0	0	0	0	12	1.98	0.28	0.45
Niamey	Tchangare	13.589	2.101	2010	228	0	0	0	16	0	0	0	0	0	16	1.00	0.00	0.00
Dogondoutchi	Dogondoutchi	13.644	4.034	2012	193	16	0	0	22	0	0	1	0	0	39	2.25	0.51	0.78
Tillabery	Tillabery	14.218	1.455	2011	619	0	0	0	6	0	1	0	0	8	15	2.67	0.55	0.88
				Total	27,142	1765	272	73	912	610	24	22	15	8	3701			

2.4. Data Analyses

A smoothed sample-based rarefaction curve, rescaled by individuals, was computed with the program Estimate S 9.1.0 [55] to determine whether most common taxa were been detected in the dataset [56]. Correlations, e.g., between a species relative abundance and latitude, were tested with the nonparametric Spearman rank correlation coefficient (r_S). *P*-values were two-tailed.

2.4.1. Distribution of Native and Invasive Small Mammals

Geographical maps were produced to illustrate species-specific distributions. We analyzed spatial variations of the distribution of the different species. To do so, we approximated, for each site, estimates of relative abundances of the different species in the samples as the proportions of the total number of individuals trapped within a site belonging to a given species, hereafter designed as *p*(species). For each species, we explored spatial variation in *p*(species) along the South–North axis by testing for a correlation with latitude. The dataset, being a compilation of trapping results from different research programs, was not appropriate to investigate temporal variation. This study nevertheless provides baseline data so that this could be an area for future research.

The association between sampling sites and trapped species was then described through a factorial correspondence analysis (FCA), implemented in R, using the Ade4 package [57,58] as well as cartography graphics designed in the R-adegraphics package [59]. The multivariate analyses presented here focused on the most frequently trapped taxa (i.e., detected in ≥25% of the trapping sessions), namely: *M. natalensis*, *R. rattus*, *R. norvegicus*, and *Crocidura* spp.

2.4.2. Species Diversity

The variation of species diversity, both within sites (alpha-diversity) and between sites (beta-diversity), was investigated. For each trapping site, small mammal species richness was computed as an estimate of alpha-diversity using the rarefaction method implemented in the software BiodivR [60], using a subsample of 10-trapped individuals drawn at random. The Simpson (1-*D*) index of diversity and Shannon *H* entropy were estimated using PAST v.3.25 software [61]. We investigated the spatial variation of species richness and the Simpson and Shannon diversity indices by testing for a correlation with latitude. The comparison of species richness between groups of sampling sites was done using a Mann–Whitney non-parametric test.

Beta-diversity was a measure of change in the diversity of species between sites: High beta-diversity indicated a low level of similarity, while low beta-diversity showed a high level of similarity. For each pair of sites, the similarity of trapped small mammal communities was estimated using two indices: The incidence-based Jaccard and the abundance-based Morisita–Horn indices [62], both implemented in the software EstimateS 9.1.0 [55]. The Jaccard index was based on presence–absence data, and thus estimated the similarity of species lists. The Morisita–Horn index was based on a species relative abundance, gave a strong weight to the most abundant species, and was not sensitive to variations in species richness or sample size [63].

We explored the respective influence of the spatial distribution of sites and of the presence–absence of invasive species on the similarity of communities. The influence of each explanatory variable (pairwise spatial distance between sites and invasion status) was first tested separately and then tested in combined analyses. The matrix of pairwise similarity of invasion status was based on the presence–absence of invasive species; it was coded as 1 when two sites shared either the detection of any invasive species (i.e., both sites were invaded) or none of them (i.e., in both sites, only native species were detected), and as 0 when two sites differed in the detection of invasive species (i.e., one site with at least one of the three invasive species and the other site only with native species). The variation explained by two variables may be correlated and therefore partly redundant. In order to determine the proportion of community similarity, explained by each explanatory variable when controlling for the effect of the other variable, we used the method of variance partitioning [64–66], thus allowing us to calculate the part of the variance explained by each variable, the variation shared between variables, and the residual variance. In doing so, we inferred the relative and independent statistical effects of each variable in structuring community similarity. Statistical significance was investigated using partial Mantel tests (10,000 permutations) under the program FSTAT 2.9.3.2 [67].

2.4.3. Co-Occurrence Patterns

Patterns of co-occurrence of commensal small mammal species were compared at the regional level as follows. Data were organized as matrices of the occurrence of captured events: Each row referred to the number of trapped individuals of a given species, while each column corresponded to a trapping site. We compared the observed and expected patterns under the null hypothesis of random assembly [68], using the standardized C-score (SCS) [69] as a quantitative index of co-occurrence, with a significant negative and positive SCS, indicating aggregation and segregation, respectively. To assess the statistical significance, the observed SCSs were compared to the values obtained from 10,000 iterations using null models with random matrices constrained for row and column totals to match the original matrix ('fixed-fixed' algorithm, model 1). We checked that the outcome of the 'fixed-equiprobable' algorithm (model 2), another recommended model [68], was identical. We estimated pairwise co-occurrence scores using Pairs 1.1 [70] and applied the confidence limit criterion [71] to determine whether a particular pair of species was statistically aggregated, segregated, or randomly associated. Results of this co-occurrence analysis are presented for four taxa that were frequently trapped (in ≥25% of the trapping sites for each taxon), namely *M. natalensis*, *R. rattus*, *Crocidura* spp., and *R. norvegicus*. We also investigated possible species association among all sampled sites through the test of a correlation between pairs of *p*(species) for the different species pairs.

3. Results

3.1. Trapping Results

The sample-based rarefaction curve, rescaled by individuals, was based on small mammal trapping data in the 66 urban sites and approached a plateau, suggesting that the most common taxa have been sampled in the whole investigated area (Figure 2). However, sampling was not intensive enough in some sites to assess how the rarefaction curve differed between sites. Trapping resulted in a total of 3701 captured individuals (Table 1), including three invasive species: *Rattus rattus* (1765 individuals), *Rattus norvegicus* (272), and *Mus musculus* (73), as well as six native taxa: *Mastomys natalensis* (912 individuals), *Crocidura* spp. (610), *Arvicanthis* spp. (24), *Praomys* spp. (22), *Cricetomys* spp. (15), and *Mastomys erythroleucus* (8). For each of the rarely collected rodent genera, a minimum of two different species have been identified along the commercial axis connecting Benin and Niger: *Arvicanthis niloticus* from the "C2–C4" clade (sensu [72]) in the Northern sites, and *Arvicanthis* species from the "ansorgei evolutionary group" in the Southern sites (possibly ANI-2 cytotype of *A. rufinus*, though we note that *A. ansorgei* has also been previously detected in sympatry with *A. niloticus* in Gaya at the border between Niger and Benin) ([72,73], Gauthier and Dobigny, unpublished data); and *Praomys daltoni* in Niger and *P. derooi* in Benin ([53,74], Mikula et al., submitted). *Cricetomys* individuals from Niamey were unambiguously diagnosed as *C. gambianus,* but molecular data of those from Cotonou was lacking. Most captured shrews of genus *Crocidura* were made of large size individuals, usually referred to as *C. olivieri* species complex (clades I and II in Jacquet et al. [75]), along with a few *C. viaria* (clade III in Jacquet et al. [75]) small individuals in Niamey. To be more cautious, given that the taxonomy of *Crocidura* warrants a throughout revision, and because some of the *Crocidura* and of the rarely trapped rodent specimens have only been identified by morphology, we decided to conservatively refer to individuals from these genera as undetermined (i.e., 'spp.'). Hereafter, we confidently made the hypothesis that the results were not strongly biased by this taxonomic lumping.

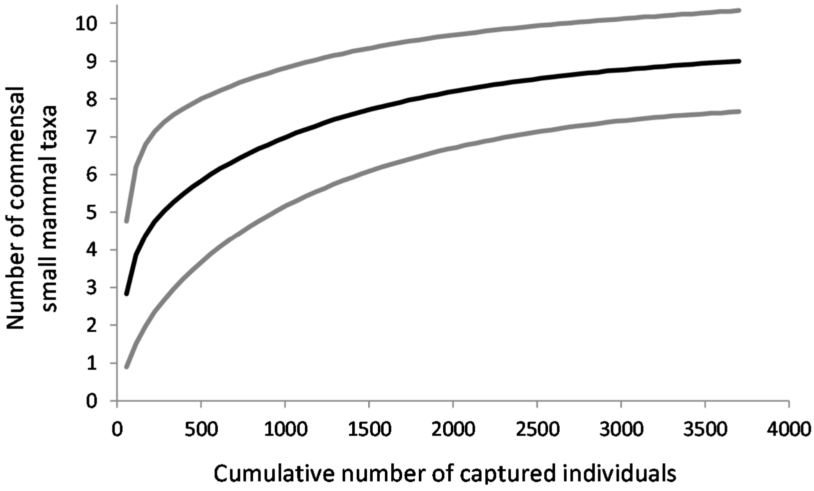

Figure 2. Sample-based rarefaction curve rescaled by individuals representing the number of commensal small mammal taxa for a given number of captured individuals over 66 urban sites from Benin and Niger. Grey lines refer to the 95% confidence intervals.

A median number of 34 small mammal individuals were captured per site (range: 12 to 341). *Mastomys natalensis* was detected in 86.4% of the 66 sites, followed by *R. rattus* (71.2% of sites), *Crocidura* spp. (69.7%), *R. norvegicus* (33.3%), *Arvicanthis* spp. (10.6%), *Praomys* spp. (6.1%), *Cricetomys* spp. (4.5%), *Mus musculus* (3.0%), and *Mastomys erythroleucus* (1.5%).

3.2. Distribution of Native and Invasive Small Mammals

Invasive species were captured in most of the sampled trapping sites (48/66 = 73%) and localities (15/18 = 83%), with the invasive *R. rattus* being the most frequently captured species of the whole dataset (Table 1).

Factorial correspondence analysis (Figure 3A) revealed two distinct groups of sites that were discriminated along the F1 axis: On the left (negative values), mainly Nigerien sites were characterized by *M. natalensis* abundance, while sites where *R. rattus* numerically dominated, mostly from Benin, lie on the right side, i.e., towards positive values. Clear exceptions were the localities of Togbin in Benin where *M. natalensis* was found to be more abundant than *R. rattus* and Hamma Dendi in Niger where only *R. rattus* was captured (Table 1).

We found a rather strong and significant correlation between site coordinates on the F1 axis of the FCA and their respective latitude ($r_S = -0.588$, $P < 10^{-3}$, $n = 66$), suggesting a latitudinal variation of the community structure.

The cartography of species distribution (Figure 3B) showed that two species, *R. rattus* and *M. natalensis*, were found in most sampling sites in both Benin and Niger. In terms of abundance, *M. natalensis* dominated in Northern sites (Niger), while *R. rattus* dominated in Southern sites (Benin) where *R. rattus* had been detected in every site, except in the Ganhi market of Cotonou, in which *R. norvegicus* was the most frequently trapped species. Data from Cotonou (South) and Niamey (North), the two localities where extensive and fine-grained data have been collected, suggest that *R. rattus* populations are distributed as "continuous nappes" in the South, but only in isolated patches in the North.

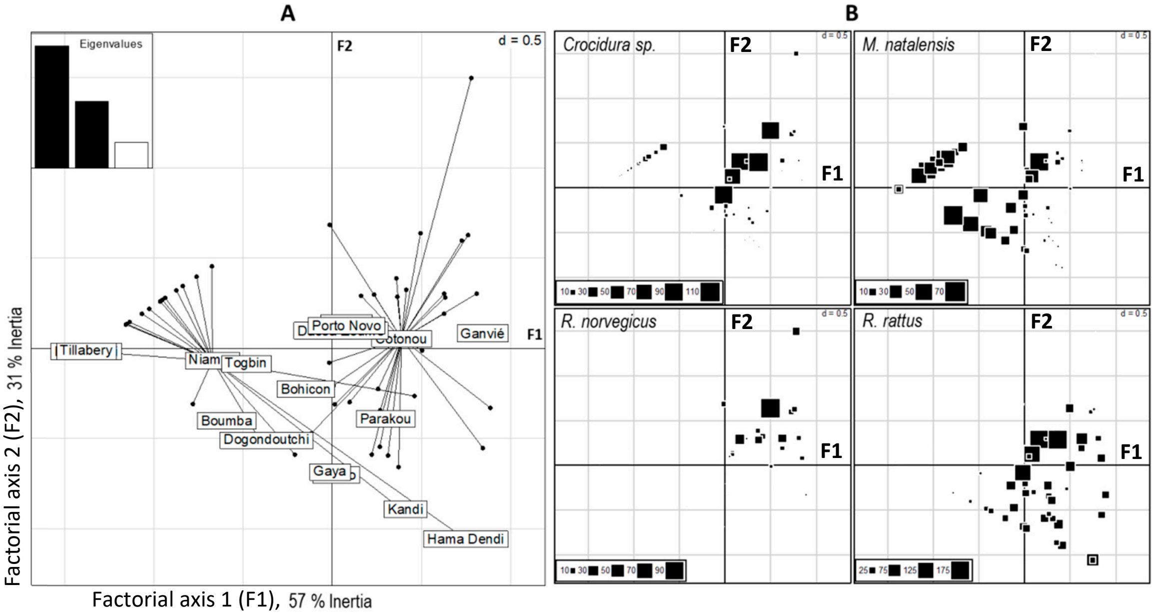

Figure 3. Factorial analysis results. **A** (left panel): Factorial map of the two first axes of the factorial correspondence analysis on the most frequently trapped taxa at 66 sites of urban habitats along the commercial axis connecting Benin and Niger, revealing two distinct groups of sites, on the left (negative values), from Northern Nigerien sites characterized by *M. natalensis* abundance to Southern Beninese sites on the right (towards positive values), where *R. rattus* dominates numerically. Lines connect sites from the same country. **B** (right panel): Cartography of species and their abundance distribution on the two first axes of the factorial correspondence analysis.

As to *R. norvegicus* captures, they were mostly restricted to sites in coastal, Southern Benin; the Northernmost locality where the species have been detected (Dassa-Zoumé in 2017) is 210 km North from the coast. *Mus musculus* species was unambiguously detected in only two sites: The Autonomous Port of Cotonou and the Great Market of Niamey.

The native species *M. natalensis* was detected in all Northern and Southern sampled localities, except Hamma Dendi in Niger (where, only *R. rattus* was found) and Ganvié in Benin (where the rodent community largely consists of *R. rattus*, and to a lesser extent, *R. norvegicus*). However, this is in opposition to the *R. rattus* distribution, where it was found that *M. natalensis* distributions were continuous in the North sites, particularly in the well-sampled city of Niamey [34], and in patches in Benin, especially in the well-sampled city of Cotonou (our own unpublished data).

Crocidura spp. were more abundant in Southern sites of Benin than in Niger sites; this was particularly noticeable in the cities of Niamey and Cotonou (6.9% and 22.2%, respectively), where large and equivalent trapping efforts were made.

Cricetomys spp. were only captured occasionally in Cotonou and Niamey. However, this may not reflect its real abundance and distribution due to the likely low probabilities of trapping this large animal with the models and sizes of traps employed here.

A statistically significant latitudinal gradient of relative abundances of the different species, expressed as p(species), was detected for four taxa: *M. natalensis* ($r_S = 0.538$, $P < 10^{-3}$, $n = 66$), *R. rattus* ($r_S = -0.404$, $P < 10^{-3}$, $n = 66$), *R. norvegicus* ($r_S = -0.648$, $P < 10^{-3}$, $n = 66$), and *Crocidura* spp. ($r_S = -0.429$, $P < 10^{-3}$, $n = 66$). From South to North, p(*M. natalensis*) increased, while p(*R. rattus*), p(*R. norvegicus*) and p(*Crocidura* spp.) decreased. For the other taxa that were much less frequently trapped, no significant spatial variation could be detected (all $P \geq 0.09$).

3.3. Species Diversity

A non-random spatial community structure was retrieved along a latitudinal (i.e., South–North) gradient. Local species richness of captured commensal small mammals, i.e., including both native and invasive species, was estimated by rarefaction for 10 sampled individuals and ranged between one and four species, with a mean ± SE of 2.17 ± 0.09 species per trapping site ($n = 66$). Estimated species richness decreased significantly Northward ($r_S = -0.589$, $n = 66$, $P < 10^{-3}$), with higher values in most of Beninese sites (mean ± SE = 2.56 ± 0.11, $n = 36$) than those observed in Nigerien sites (mean ± SE = 1.71 ± 0.10, $n = 30$; Mann-Whitney test $P < 10^{-3}$). Notably, this pattern of latitudinal variation was also observed for native species richness (sites from Benin: mean ± SE = 2.00 ± 0.13, $n = 12$; Niger: 1.58 ± 0.11, $n = 23$; Mann-Whitney test $P = 0.0178$; estimates based on 10 sampled individuals of native species). The number of shared species between sites varied from zero to five species. The same pattern of spatial variation was observed for the Simpson (1-D) index of diversity ($r_S = -0.487$, $n = 66$, $P < 10^{-3}$) and for the Shannon H entropy ($r_S = -0.552$, $n = 66$, $P < 10^{-3}$).

The similarity of commensal small mammal assemblages varied with the invasion status, and to a lesser extent, with spatial distance, showing a distance decay of species similarity (Table 2).

Table 2. Variance partitioning into "spatial" and "invasion status" components of the small mammal community similarity in urban habitats along the commercial axis connecting Benin and Niger. The similarity was estimated using the Morisit–Horn and the Jaccard indices. [I + S] = total variation explained by the invasion status and spatial variables together, [I] = variation explained by invasion status variable, [S] = variation explained by spatial variable, [I|S] = pure invasion status variation, [S|I] = pure spatial variation, [I∩S] = spatial structuring in the similarity data that is shared by the invasion status data, and 1 − [I + S] = unexplained variation.

Variation	**Morisita-Horn Similarity Index**		**Jaccard Similarity Index**	
	Variance (%)	***P***	**Variance (%)**	***P***
[I + S]	44.6	<0.0001	24.4	<0.0001
[I]	41.1	<0.0001	19.2	<0.0001
[S]	18.9	<0.0001	15.0	<0.0001
[I|S]	25.7	<0.0001	9.4	<0.0001
[S|I]	3.5	<0.0001	5.2	<0.0001
[I∩S]	15.4	-	9.9	-
1 − [I + S]	55.4	-	75.6	-

Community similarity differs according to the invasion status: Pairs of sites where only native species were detected showed high a similarity (median value for Morisita–Horn index = 0.978 and for Jaccard index = 0.500, 153 pairs of sites), like the pairs of sites there were both invaded (median value for Morisita–Horn index = 0.813 and for Jaccard index = 0.500, 1128 pairs of sites). On the contrary, pairs of sites that differed in the detection of invasive species (one site with at least one of the three invasive species and the other site only with native species) exhibited low similarity (median value for Morisita–Horn index = 0.082 and for Jaccard index = 0.333, 864 pairs of sites). Taken together, the invasion status and spatial distance variables explained 44.6% of Morisita–Horn similarity and 24.4% of Jaccard similarity. The pure component explained by the invasion status showed the highest contribution (25.7% of Morisita–Horn similarity and 9.4% of Jaccard similarity). Overall, 15.4% of Morisita–Horn and 9.9% of Jaccard similarity variation was shared between the invasion status and spatial variables.

3.4. Co-Occurrence Patterns

The two null models for testing species co-occurrence at the regional level showed a pattern of segregation between native *M. natalensis* and invasive *Rattus* spp. This pattern of segregation was significant for *R. norvegicus* (model 1: $P = 0.003$, model 2: $P = 0.014$), while only marginally non-significant for *R. rattus* for one of the models (model 1: $P = 0.14$, model 2: $P = 0.088$). Notably, a significant negative correlation between *R. rattus* and *M. natalensis* relative abundance (i.e., p(*R. rattus*) and p(*M. natalensis*)) was found ($r_S = -0.730$, $P < 10^{-3}$). We found significant aggregation patterns between *R. norvegicus* and *R. rattus*, and between *R. norvegicus* and *Crocidura* spp. (Table 3).

Table 3. Patterns of co-occurrence of small mammal species in urban habitats along the commercial axis connecting Benin and Niger. Four commensal taxa were considered: The native *M. natalensis* and *Crocidura* spp., and the invasive *R. rattus* and *R. norvegicus*. The standardized C-score (SCS) measured the extent to which pairwise taxa co-occurred: Significant negative and positive SCS indicates aggregation and segregation, respectively, whereas the SCS that does not deviate significantly from the null distribution suggests random associations. The results from two randomization models are presented: Model 1: fixed row-fixed column and model 2: fixed row-equiprobable column. Significant *P*-values, using the 95% confidence limit criterion, are in bold. $N = 66$ sites.

Species 1	Number of Occurrences	Species 2	Number of Occurrences	Number of Joint Occurrences	Model 1		Model 2	
					SCS	*P*	SCS	*P*
M. natalensis	55	*R. rattus*	47	37	1.49	0.14	1.70	0.088
M. natalensis	55	*Crocidura* spp.	46	40	−1.42	0.16	−1.18	0.24
M. natalensis	55	*R. norvegicus*	22	15	2.91	**0.003**	2.46	**0.014**
R. rattus	47	*Crocidura* spp.	46	33	−0.33	0.74	−0.21	0.83
R. rattus	47	*R. norvegicus*	22	21	−2.62	**0.009**	−2.65	**0.008**
Crocidura spp.	46	*R. norvegicus*	22	20	−2.20	**0.027**	−2.35	**0.018**

4. Discussion

4.1. Distributions of Native and Invasive Small Mammals

We detected a total of nine taxa, including the three invasive species *Rattus rattus*, *R. norvegicus*, and *Mus musculus*, and at least six native taxa, namely *Mastomys natalensis* and *Crocidura* spp. (≥2 species), and at a much lower frequency, *Arvicanthis* spp. (2–3 species), *Praomys* spp. (2 species), *Cricetomys* spp., and *Mastomys erythroleucus*. While additional species were expected in the community (e.g., *Xerus erythropus* was observed outdoor in Niamey; the pygmy mice *Mus hausa* was captured by hand indoor in Hamma Dendi and *Mus baoulei* was trapped in peri-urban areas of Cotonou that were not included in the present study), such a set of more than 12 trapped species is typical of commensal West African Sudano–Sahelian small mammal communities [51]. As a comparison, in Senegal, a total of 17 taxa of commensal small mammals have been recorded over three decades, including the same three invasive species [23]. In Nigeria, 19 small mammal species, including invasive *R. rattus*, were detected from nine localities across three ecological zones [76]. Similar diversity estimates and species assemblages have already been reported in recent surveys conducted in commensal habitats in other West African countries [77–79].

M. natalensis, *R. rattus*, and *Crocidura* spp. were the most abundantly trapped species as they have been detected in both Benin and Niger, with, respectively, 86.4%, 71.2%, and 69.7% of the 66 sites sampled. Apart from a few exceptions (Togbin in Benin a peri-urban site that still remains separated from Cotonou city by mangroves, and Hamma Dendi in Niger located along the Niger River away from main road axes), two distinct groups of localities were identified: One group consisting mainly of Nigerien localities characterized by *M. natalensis* numerical dominance on the one hand, and another group of Beninese localities where *R. rattus* was more frequently trapped on the other hand.

The most abundant native species, *M. natalensis,* was detected in both Northern and Southern localities. Similar distribution patterns, including low abundances of most other native species, have been observed elsewhere, thus indicating that *M. natalensis* is the most frequently captured native commensal small mammal species in various ecological zones in West Africa [34,51,76,80]. Its distribution was found to be locally continuous in the Northern sites, particularly in the well-sampled city of Niamey [34], while in Benin, especially in the well-sampled city of Cotonou, where invasive species dominate, it was rather in patches (see Table 1). Invasive species were found in most of the sampled sites and localities.

The most frequently trapped invasive species was *R. rattus*. We cannot formally exclude that this could partly result from a non-random choice of trapping sites in several localities (Gaya, Dosso in Niger; Kandi, Parakou, Bohicon, and Dassa-Zoumé in Benin), which were prospected essentially as part of a research program focusing on invasive *R. rattus*. However, the observed high frequency of *R. rattus* was not surprising, given the worldwide geographic distribution of this species and the suggestion that it is well adapted to warm and humid climates [19,22]. This species is already widely distributed in West African villages and cities [51], although it is probably still expanding in the area, especially Northward within the Sahelian region, following the road and river traffic [24].

In other parts of the world, several studies have reported that, when established, *R. norvegicus* is the most common species in urban rodent communities [81–84]. However, in the present study, *R. norvegicus* was mostly restricted to coastal cities and one village (i.e., Ganvié) in Southern Benin, less than ca. 200 km from the coast. This could indicate that its Northward expansion is currently in progress, but is still limited, or alternatively, that it has not found favorable environmental conditions to establish and proliferate further North. The last hypothesis is congruent with the fact that *R. norvegicus* is generally the most abundant at sites with a large proportion of highly vegetated urban coverage and the presence of permanent bodies of water [19]. Indeed this species has long been thought to be restricted to seaports and the islands of Africa, and not to be adapted to dry Sahelian cities (but see Rosevear [85], p. 278). Nevertheless, we propose that further attention should be paid to this species, since many localities with shallows between Dassa–Zoumé and Niger exist and were not investigated, while they may well be favorable for the brown rat. We highly recommend the monitoring of sites in these areas and along the river of Niger, including Niamey, to detect *R. norvegicus* at the earlier stages of possible introductions. Indeed, *R. norvegicus* clearly has the potential to establish inland in West Africa, as already observed in Bamako, Mali [86], the Office du Niger area in Mali (our own unpublished observations), Podor, Senegal [23], and Kano, Nigeria [53]; it may then dominate the other small mammal species, massively affect human infrastructures and food resources, and act as a reservoir of many zoonotic pathogens of public health importance [87,88].

Another major invasive species, the house mouse, *Mus musculus*, was only detected in Cotonou and Niamey, where, despite extensive samples, it was restricted to industrial–commercial sites, i.e., the Autonomous Port of Cotonou and the Great Market of Niamey. We argue that these trading sites may act as 'invasion hubs' and as bridgeheads towards neighboring localities (see Dalecky et al. [23] for a proposed role of markets in the range expansion of *M. musculus* in Senegal). This suggests that house mice may have been transported to Niamey directly from Cotonou harbor where many trucks embark crops and other goods that are exported by the road directly to the Niger capital city. This would represent a >1000 km long-distance inland jump for this species that has not been observed elsewhere in Niger to date ([89]; this study). Population genetic studies should test this hypothesis.

Crocidura spp. was significantly more abundant in Southern localities of Benin than in Niger localities. This was particularly noticeable in Niamey and Cotonou, which were investigated through very large trapping efforts. A similar abundance of shrews in urban assemblages of small mammals has already been reported in West Africa [76]. Note that some *Crocidura* species are known to be synanthropic, tightly associated with human dwellings, and very dependent on human resources [75,90]. We cannot exclude that parts of the *Crocidura* species found in Niamey could have had a human-assisted origin. Shrews are very numerous in the outdoor and in the commensal environments from Southern Benin, notably Cotonou (22.2% of all captures), while they were found at much lower frequencies in Niamey (6.9%). This suggests that they may prefer subequatorial rather than Sahelian climates. Cities may provide buffered conditions, allowing them to colonize drier regions such as Niger. As for invasive rodent species, their dissemination could also be associated with human trade and transportation. This would reinforce the hypothesis that the possible mechanism of dispersal in some large *Crocidura* species could be associated with human-mediated transportation [75,91], but it deserves to be fully demonstrated in West Africa.

4.2. Species Diversity and Co-Occurrence Patterns

The estimated local species richness in commensal habitats is typically low, as already observed for small mammals in other studies [23,92]. We found that the species richness is higher in Southern localities than in Northern ones, which warrants considering all taxa, and when the analysis is restricted, to native taxa. This suggests that the observed decrease of diversity Northward cannot be explained merely by the impact of invasive species, but that other historical, ecological, and biogeographical processes may be acting as well. A non-random spatial community structure was retrieved along a latitudinal gradient. Spatial variation of relative abundances of the different species was detected for the four most frequently trapped taxa; from South to North, it increased for *M. natalensis*, while it decreased for *R. rattus*, *Crocidura* spp., and *R. norvegicus*. Finally, we found that the similarity of commensal small mammal assemblages varies strongly with the status of invasion, and to a lesser extent, with the spatial distance between sites. Differences in species composition and relative abundance within small mammal assemblage in relation to geographical and environmental factors have been previously reported in several other studies [93–99].

A non-random pattern of species associations was observed along the Benin–Niger commercial axis. As such, segregation between native *M. natalensis* and the two invasive rat species (i.e., *R. rattus* and *R. norvegicus*) was detected. We also found a significant negative correlation between *R. rattus* and *M. natalensis* relative abundances. The results of co-occurrence analyses, including *M. musculus*, were not significant ($P \geq 0.11$, data not shown), probably due to the very low number of sites (2/66) where this species was detected, thus providing too low of a statistical power. Segregation between invasive *R. rattus* and *M. musculus*, and native *M. natalensis*, has been previously detected on commensal rodents at a local scale in specific districts of Niamey city [34]. Here, we also found aggregation patterns within species assemblages at the regional level, particularly between *R. norvegicus* and *R. rattus*, on the one hand, and between *R. norvegicus* and *Crocidura* spp. on the other. At that stage, the determinants underlying the latter patterns remain unexplained; fine-scale resolution eco-ethological studies are required to address such an issue.

Our results suggest that the dissemination of invasive rodent species (rats and mice) is most probably ongoing in this part of West Africa. We provide evidence that the introduction and proliferation of these invasive organisms has a negative impact on the native commensal *M. natalensis*, as this was already suggested at the scale of Niamey [34] or in other parts of Africa (e.g., Senegal) [38]. If confirmed, such a native-to-invasive turn over in rodent species would have important consequences in terms of public health. For instance, *M. natalensis* is the main reservoir of the Lassa virus, which is responsible for annual epidemics of Lassa hemorragic fevers in West Africa (review in Monath [100]), including Benin [101]. To date, the virus has never been identified in *Rattus* spp., thus likely precluding widespread circulation of the zoonotic agents in Southern Benin cities where *R. rattus* have largely replaced *M. natalensis*. Similar shifts in epidemiological dynamics probably concern many other rodent-borne zoonotic pathogens, which may interact differently with various small mammal species. Such consequences could be more severe given the growing and ongoing urbanization [102], which is known to lead to many challenges for global health and the epidemiology of infectious diseases [103,104].

5. Conclusions

At that stage, we found that native *M. natalensis* is still a major component of the synanthropic small mammal assemblages along the commercial axis connecting Benin and Niger, although the species may be locally replaced by invasive taxa where the latter settle. Our results also show that shrews may represent a very important component of micro-mammal fauna in West African towns and villages, especially at lower latitudes. As a conclusion, invasive and native synanthropic rodents do not distribute randomly in West Africa. Our results also suggest that invasive rodent species (rats and mice) dynamics and history differ markedly, and their dissemination is most probably ongoing in this part of West Africa.

In such a context, we firmly recommend that further studies and monitoring programs should be implemented to infer the sources, routes, and tempo of colonization of the three invasive rodent species, as well as to document their impact in terms of biodiversity and sanitary risks in urban ecosystems.

Author Contributions: Conceptualization, G.D., K.H., G.H., and A.D.; methodology, A.D., G.D., K.H. and G.H.; formal analysis, A.D., K.H., and O.F.-G.; investigation, G.H., S.B., M.G., K.H., G.D., P.G., H.-J.D., J.E., S.G., E.A.; writing original draft preparation, K.H., A.D. and G.D.; writing, review and editing, G.D., A.D. and K.H.

Funding: This research was supported by the French National Research Institute for Sustainable Development (IRD, France), Abomey-Calavi University (UAC, Benin) and Abdou Moumouni University (UAM, Niger). KH has been supported by visiting researcher grants from AMU and IRD during the writing of this paper.

Acknowledgments: This work could not be accomplished without the joint collaborative effort of the members of the "Observatoire des petits Mammifères Indicateurs des Changements Environnementaux" (ObsMiCE) and the "Jeune Equipe Associée à l'IRD—Invasions Biologiques en Afrique de l'Ouest" (JEAI-IBAO). We thank all colleagues and collaborators for their respective contribution in collecting and/or analysing data included in this study. We would also like to thank Caroline Tatard for her help for the molecular identification of many of the specimens collected. Thanks to Souley Yero K. from Regional Center Agrhymet for drawing the map of the investigated localities. Tasnime Adamjy is thanked for her reading and English editing. Four reviewers are thanked for their helpful comments. We are particularly grateful to all householders and local authorities from Benin and Niger for allowing us to set traps inside their homes and workplaces.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Lebel, T.; Cappelaere, B.; Galle, S.; Hanan, N.; Kergoat, L.; Levis, S.; Vieux, B.; Descroix, L.; Gosset, M.; Mougin, E.; et al. AMMA-CATCH studies in the Sahelian region of West-Africa: An overview. *J. Hydrol.* **2009**, *375*, 3–13. [CrossRef]
2. Sarr, B. Present and future climate change in the semi-arid region of West Africa: A crucial input for practical adaptation in agriculture. *Atmos. Sci. Lett.* **2012**, *13*, 108–112. [CrossRef]
3. Ahmed, K.F.; Wang, G.; You, L.; Yu, M. Potential impact of climate and socioeconomic changes on future agricultural land use in West Africa. *Earth Syst. Dyn.* **2016**, *7*, 151–165. [CrossRef]
4. Hitimana, L.; Heinrigs, P.; Tremolieres, M. West African urbanization trends. *West Afr. Futures* **2011**, *1*, 1–8.
5. Denis, E.; Moriconi-Ebrard, F.; Harre-Roger, D.; Thiam, O.; Séjourné, M.; Chatel, C. Dynamique de l'urbanisation, 1950–2020: Approche géo-statistique Afrique de l'ouest. In *Africapolis*; HAL Id: Hal-00357271; Paris, 2008; 124p, Available online: https://hal.archives-ouvertes.fr/hal-00357271 (accessed on 13 March 2019).
6. Bocquier, P.; Mukandila, A.K. African urbanization trends and prospects. *Afr. Popul. Stud.* **2011**, *25*, 337–361. [CrossRef]
7. Guillaumont, P.; Simonet, C. To What Extent Are African Countries Vulnerable to Climate Change? Lessons from a New Indicator of Physical Vulnerability to Climate Change. Ferdi Working Paper I08. 2011. Available online: https://ferdi.fr/publications/to-what-extent-are-african-countries-vulnerable-to-climate-change-lessons-from-a-new-indicator-of-physical-vulnerability-to-climate-change (accessed on 7 October 2019).
8. Early, R.; Bradley, B.A.; Dukes, J.S.; Lawler, J.J.; Olden, J.D.; Blumenthal, D.M.; Gonzalez, P.; Grosholz, E.D.; Ibañez, I.; Miller, L.P.; et al. Global threats from invasive alien species in the twenty-first century and national response capacities. *Nat. Commun.* **2016**, *7*, 12485. [CrossRef]
9. Pratt, C.F.; Contantine, K.L.; Murphy, S.T. Economic impacts of invasive alien species on African smallholder livelihoods. *Glob. Food Secur.* **2017**, *14*, 31–37. [CrossRef]
10. Hulme, P.E. Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *J. Appl. Ecol.* **2009**, *46*, 10–18. [CrossRef]
11. Ascensão, F.; Capinha, C. Aliens on the Move: Transportation Networks and Non-native Species. In *Railway Ecology*; Ebook; de Água, B., Borda-de-Água, L., Barrientos, R., Beja, P., Pereira, H.M., Eds.; Springer International Publishing: Cham, Switzerland, 2017; pp. 65–80. [CrossRef]

12. Tylianakis, J.M.; Didham, R.K.; Bascompte, J.; Wardle, D.A. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* **2008**, *11*, 1351–1363. [CrossRef]
13. Kotliar, N.B.; Wiens, J.A. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. *Oikos* **1990**, *59*, 253–260. [CrossRef]
14. Levin, S.A. The problem of pattern and scale in ecology. *Ecology* **1992**, *73*, 1943–1967. [CrossRef]
15. Ricklefs, R.E. Community diversity: Relative roles of local and regional processes. *Science* **1987**, *235*, 167–171. [CrossRef] [PubMed]
16. Wiens, J.A.; Stenseth, N.C.; Van Horne, B.; Ims, R.A. Ecological mechanisms and landscape ecology. *Oikos* **1993**, *66*, 369–380. [CrossRef]
17. Alberti, M.; Marzluff, J.M. Ecological resilience in urban ecosystems: Linking urban patterns to human and ecological functions. *Urban Ecosyst.* **2004**, *7*, 241–265. [CrossRef]
18. Shochat, E.; Stefanov, W.L.; Whitehouse, M.E.A.; Faeth, S.H. Urbanization and spider diversity: Influences of human modification of habitat structure and productivity. *Ecol. Appl.* **2004**, *14*, 268–280. [CrossRef]
19. Cavia, R.; Cueto, G.R.; Suárez, O.V. Changes in rodent communities according to the landscape structure in an urban ecosystem. *Landsc. Urban Plan.* **2009**, *90*, 11–19. [CrossRef]
20. Melles, S.; Glenn, S.M.; Martin, K. Urban bird diversity and landscape complexity: Species–environment associations along a multiscale habitat gradient. *Conserv. Ecol.* **2003**, *7*, art5. [CrossRef]
21. Audoin-Rouzeau, F.; Vigne, J.D. La colonisation de l'Europe par le rat noir. *Rev. Paléobiol.* **1994**, *13*, 125–145.
22. Aplin, K.P.; Suzuki, H.; Chinen, A.A.; Chesser, R.T.; ten Have, J.; Donnellan, S.C.; Austin, J.; Frost, A.; Gonzalez, J.P.; Herbreteau, V.; et al. Multiple Geographic Origins of Commensalism and Complex Dispersal History of Black Rats. *PLoS ONE* **2011**, *6*, e26357. [CrossRef]
23. Dalecky, A.; Bâ, K.; Piry, S.; Lippens, C.; Diagne, C.A.; Kane, M.; Sow, A.; Diallo, M.; Niang, Y.; Konečný, A.; et al. Range expansion of the invasive house mouse *Mus musculus domesticus* in Senegal, West Africa: A synthesis of trapping data over three decades, 1983–2014. *Mammal Rev.* **2015**, *45*, 176–190. [CrossRef]
24. Berthier, K.; Garba, M.; Leblois, R.; Navascues, M.; Tatard, C.; Gauthier, P.; Gagare, S.; Piry, S.; Brouat, C.; Dalecky, A.; et al. Black rat invasion of inland Sahel: Insights from interviews and population genetics in south-western Niger. *Biol. J. Linn. Soc.* **2016**, *119*, 748–765. [CrossRef]
25. Drake, D.R.; Hunt, T.L. Invasive rodents on islands: Integrating historical and contemporary ecology. *Biol. Invasions* **2009**, *11*, 1483–1487. [CrossRef]
26. Paini, D.R.; Sheppard, A.W.; Cook, D.C.; De Barro, P.J.; Worner, S.P.; Thomas, M.B. Global threat to agriculture from invasive species. *Proc. Natl. Acad. Sci. USA* **2016**, *113*, 7575–7579. [CrossRef] [PubMed]
27. Vogler, A.J.; Chan, F.; Nottingham, R.; Andersen, G.; Drees, K.; Beckstrom-Sternberg, S.M.; Wagner, D.M.; Chanteau, S.; Keim, P. A Decade of Plague in Mahajanga, Madagascar: Insights into the Global Maritime Spread of Pandemic Plague. *mBio* **2013**, *4*, e00623. [CrossRef]
28. Wu, Y.W.; Hsu, E.L.; Lin, T.H.; Huang, J.H.; Chang, S.F.; Pai, H.H. Seaports as a source of Hantavirus: A study in isolated islands. *Int. J. Environ. Health Res.* **2007**, *17*, 25–32. [CrossRef]
29. Lin, X.D.; Guo, W.P.; Wang, W.; Zou, Y.; Hao, Z.Y.; Zhou, D.J.; Dong, X.; Qu, Y.G.; Li, M.H.; Tian, H.F.; et al. Migration of Norway rats resulted in the worldwide distribution of Seoul Hantavirus today. *J. Virol.* **2012**, *86*, 972–981. [CrossRef]
30. Kuo, C.C.; Wardrop, N.; Chang, C.T.; Wang, H.C.; Atkinson, P. Significance of major international seaports in the distribution of murine typhus in Taiwan. *PLoS Trop. Negl. Dis.* **2017**, *11*, e5430.
31. Olson, L.J. The economics of terrestrial invasive species: A review of the literature. *Agric. Res. Econ. Rev.* **2006**, *35*, 178–194. [CrossRef]
32. Suarez, V.A.; Tsutsui, N.D. The evolutionary consequences of biological invasions. *Mol. Ecol.* **2008**, *17*, 351–360. [CrossRef]
33. Pyšek, P.; Richardson, D.M. Invasive species, environmental change and management, and health. *Ann. Rev. Environ. Res.* **2010**, *35*, 25–55. [CrossRef]
34. Garba, M.; Dalecky, A.; Kadaoure, I.; Kane, M.; Hima, K.; Veran, S.; Gagare, S.; Gauthier, P.; Tatard, C.; Rossi, J.P.; et al. Spatial segregation between invasive and native commensal rodents in an urban environment: A case study in Niamey, Niger. *PLoS ONE* **2014**, *9*, e110666. [CrossRef] [PubMed]
35. Harper, G.A.; Bunbury, N. Invasive rats on tropical islands: Their population biology and impacts on native species. *Glob. Ecol. Conserv.* **2015**, *3*, 607–627. [CrossRef]

36. Young, H.S.; Parker, I.M.; Gilbert, G.S.; Guerra, A.S.; Nunn, C.L. Introduced Species, Disease Ecology, and Biodiversity–Disease Relationships. *Trends Ecol. Evol.* **2017**, *32*, 41–54. [CrossRef] [PubMed]
37. Diagne, C.; Galan, M.; Tamisier, L.; d'Ambrosio, J.; Dalecky, A.; Bâ, K.; Kane, M.; Niang, Y.; Diallo, M.; Sow, A.; et al. Ecological and sanitary impacts of bacterial communities associated to biological invasions in African commensal rodent communities. *Nat. Sci. Rep.* **2017**, *7*, 14995. [CrossRef] [PubMed]
38. Duplantier, J.-M.; Granjon, L.; Bâ, K. Répartition biogéographique des petits rongeurs au Sénégal. *J. Afr. Zool.* **1997**, *111*, 17–26.
39. Kaleme, P.K.; Bates, J.M.; Belesi, H.K.; Bowie, R.C.K.; Gambalemoke, M.; Kerbis-Peterhans, J.; Michaux, J.; Mwanga, J.M.; Ndara, B.R.; Taylor, P.J.; et al. Origin and putative colonization routes for invasive rodent taxa in the Democratic Republic of Congo. *Afr. Zool.* **2011**, *46*, 133–145. [CrossRef]
40. Lippens, C.; Estoup, A.; Hima, M.K.; Loiseau, A.; Tatard, C.; Dalecky, A.; Bâ, K.; Kane, M.; Diallo, M.; Sow, A.; et al. Genetic structure and invasion history of the house mouse (*Mus musculus domesticus*) in Senegal, West Africa: A legacy of colonial and contemporary times. *Heredity* **2017**, *119*, 64–75. [CrossRef]
41. Dobigny, G.; Poirier, P.; Hima, K.; Cabaret, O.; Gauthier, P.; Tatard, C.; Costa, J.M.; Bretagne, S. Molecular survey of rodent-borne *Trypanosoma* in Niger with special emphasis on *T. lewisi* imported by invasive black rats. *Acta Trop.* **2011**, *117*, 183–188.
42. Tollenaere, C.; Brouat, C.; Duplantier, J.-M.; Rahalison, L.; Rahelinirina, S.; Pascal, M.; Moné, H.; Mouahid, G.; Leirs, H.; Cosson, J.-F. Phylogeography of the introduced species *Rattus rattus* in the western Indian Ocean, with special emphasis on the colonization history of Madagascar. *J. Biogeogr.* **2010**, *37*, 398–410. [CrossRef]
43. Bonhomme, F.; Orth, A.; Cucchi, T.; Rajabi-Maham, H.; Catalan, J.; Boursot, P.; Auffray, J.C.; Britton-Davidian, J. Genetic differentiation of the house mouse around the Mediterranean basin: Matrilineal footprints of early and late colonization. *Proc. R. Soc. Lond. B* **2011**, *278*, 1034–1043. [CrossRef]
44. Konečný, A.; Estoup, A.; Duplantier, J.-M.; Bryja, J.; Bâ, K.; Galan, M.; Tatard, C.; Cosson, J.-F. Invasion genetics of the introduced black rat (*Rattus rattus*) in Senegal, West Africa. *Mol. Ecol.* **2013**, *22*, 286–300. [CrossRef] [PubMed]
45. Stragier, C.; Piry, S.; Loiseau, A.; Kane, M.; Sow, A.; Niang, Y.; Diallo, M.; Ndiaye, A.; Gauthier, P.; Borderon, M.; et al. Interplay between historical and current features of the cityscape in shaping the genetic structure of the house mouse (*Mus musculus domesticus*) in Dakar (Senegal, West Africa). *bioRxiv* **2019**. [CrossRef]
46. Sounouvou, M.G.J. Contribution à L'amélioration du Transport International de Marchandises: Cas du Corridor Bénin-Niger. Bachelor's Thesis, Université Internationale du Benin (UPIB), Benin, Benin, 2007; 57p.
47. Chambre de Commerce d'Industrie et d'Artisanat du Niger. Organisation des trafics routiers et échanges commerciaux le long du corridor Bénin-Niger. In *Rapport D'Etudes*; Chambre de Commerce d'Industrie et d'Artisanat du Niger: Niamey, Niger, 2018; 34p.
48. Boluvi, G.M. Malanville-Gaya: Comptoir commercial et couloir de spéculations (pays-frontière de l'informel). Club du Sahel et de l'Afrique de l'ouest. In *West African Borders and Integration*; Paris, 2004; 29p. Available online: http://www.hubrural.org/IMG/pdf/wabi_malanville_gaya.pdf (accessed on 7 October 2019).
49. Sougue, E. Malanville-Gaya, une dynamique de territorialisation à la frontière Benin-Niger. *Territ. En Mouv. Rev. Géogr. Aménage.* **2016**, *29*. [CrossRef]
50. Mills, J.N.; Yates, T.L.; Childs, J.E.; Parmenter, R.R.; Ksiazek, T.E. Guidelines for Working with Rodents Potentially Infected with Hantavirus. *J. Mammal.* **1995**, *76*, 716–722. [CrossRef]
51. Granjon, L.; Duplantier, J.-M. *Les Rongeurs de L'Afrique Sahélo-Soudanienne*; IRD, MNHN: Marseille, France, 2009; 215p.
52. Dobigny, G.; Lecompte, E.; Tatard, C.; Gauthier, P.; Bâ, K.; Duplantier, J.-M.; Granjon, L.; Denys, C. An update on the taxonomy and geographic distribution of the cryptic species *Mastomys kollmannspergeri* (Muridae, Murinae) using combined cytogenetic and molecular data. *J. Zool.* **2008**, *276*, 368–374. [CrossRef]
53. Tatard, C.; Garba, M.; Gauthier, P.; Hima, K.; Artige, E.; Dossou, H.J.; Gagaré, S.; Genson, G.; Truc, P.; Dobigny, G. Rodent-borne *Trypanosoma* from cities and villages of Niger and Nigeria: A special role for the invasive genus *Rattus*? *Acta Trop.* **2017**, *17*, 151–158. [CrossRef]
54. Sikes, R.S.; Gannon, W.L. and the Animal Care and Use Committee of the American Society of Mammalogists. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.* **2011**, *92*, 235–253. [CrossRef]

55. Colwell, R.K. *Estimate S* Version 9.1: Statistical Estimation of Species Richness and Shared Species from Samples (Software and User's Guide). Freeware for Windows and Mac OS. 2013. Available online: http://viceroy.eeb.uconn.edu/Colwell/#Software (accessed on 20 February 2019).
56. Gotelli, N.J.; Colwell, R.K. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **2001**, *4*, 379–391. [CrossRef]
57. Chessel, D.; Dufour, A.B.; Thioulouse, J. The ade4 package-I-One-table methods. *R News* **2004**, *4*, 5–10.
58. Dray, S.; Dufour, A.B. The ade4 package: Implementing the duality diagram for ecologists. *J. Stat. Softw.* **2007**, *22*. [CrossRef]
59. Dray, S.; Siberchicot, A. Adegraphics: An S4 Lattice-Based Package for the Representation of Multivariate Data. 2017. Available online: https://CRAN.R-project.org/package=adegraphics (accessed on 20 February 2019).
60. Hardy, O.J. BiodivR 1.2. A Program to Compute indices of Species Diversity within Sample and Species Similarity between Samples Using Rarefaction Principles to Reduce Sampling Bias. 2010. Available online: http://ebe.ulb.ac.be/ebe/Software.html (accessed on 22 February 2019).
61. Hammer, Ø.; Harper, D.A.T.; Ryan, P.D. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontol. Electron.* **2001**, *4*, 1–9.
62. Magurran, A.E. *Measuring Biological Diversity*; Blackwell Publishing: Oxford, UK, 2004; 256p.
63. Chao, A.; Chazdon, R.L.; Cowell, R.K.; Shen, T.J. Abundance-Based Similarity Indices and Their Estimation When There Are Unseen Species in Samples. *Biometrics* **2006**, *62*, 361–371. [CrossRef] [PubMed]
64. Borcard, D.; Legendre, P.; Dapeau, P. Partialling out the spatial component of ecological variation. *Ecology* **1992**, *73*, 1045–1055. [CrossRef]
65. Cottenie, K.; Michels, E.; Nuytten, N.; De Meester, L. Zooplankton metacommunity structure: Regional vs. local processes in highly interconnected ponds. *Ecology* **2003**, *84*, 991–1000. [CrossRef]
66. Cottenie, K. Integrating environment and spatial processes in ecological community dynamics. *Ecol. Lett.* **2005**, *8*, 1175–1182. [CrossRef] [PubMed]
67. Goudet, J. *FSTAT, Version 2.9.3, a Program to Estimate and Test Gene Diversities and Fixation Indices*; Lausanne University: Lausanne, Switzerland, 2001; Available online: https://www2.unil.ch/popgen/softwares/fstat.htm (accessed on 9 December 2019).
68. Gotelli, N.J. Null model analysis of species co-occurrence patterns. *Ecology* **2000**, *81*, 2606–2621. [CrossRef]
69. Stone, L.; Roberts, A. The checkerboard score and species distributions. *Oecologia* **1990**, *85*, 74–79. [CrossRef]
70. Ulrich, W. Pairs—A FORTRAN Program for Studying Pair-Wise Species Associations in Ecological Matrices. 2008. Available online: http://www.keib.umk.pl/pairs/ (accessed on 31 January 2019).
71. Gotelli, N.J.; Ulrich, W. The empirical Bayes approach as a tool to identify non-random species associations. *Oecologia* **2010**, *162*, 463–477. [CrossRef]
72. Dobigny, G.; Tatard, C.; Gauthier, P.; Bâ, K.; Duplantier, J.-M.; Granjon, L.; Kergoat, G.J. Mitochondrial and Nuclear Genes-Based Phylogeography of *Arvicanthis niloticus* (Murinae) and Sub-Saharan Open Habitats Pleistocene History. *PLoS ONE* **2013**, *8*, e77815. [CrossRef]
73. Bryja, J.; Colangelo, P.; Lavrenchenko, L.A.; Meheretu, Y.; Šumbera, R.; Bryjová, A.; Verheyen, E.; Leirs, H.; Castiglia, R. Diversity and evolution of African Grass Rats (Muridae: *Arvicanthis*)—From radiation in East Africa to repeated colonization of northwestern and southeastern savannas. *J. Zool. Syst. Evol. Res.* **2019**, *57*, 970–988. [CrossRef]
74. Bryja, J.; Granjon, L.; Dobigny, G.; Patzenhauerova, H.; Konečný, A.; Duplantier, J.-M.; Gauthier, P.; Colyn, M.; Durnez, L.; Lalis, A.; et al. Plio-Pleistocene history of West African Sudanian savanna and the phylogeography of the *Praomys daltoni* complex (Rodentia): The environment/geography/genetic interplay. *Mol. Ecol.* **2010**, *19*, 4783–4799. [CrossRef] [PubMed]
75. Jacquet, F.; Denys, C.; Verheyen, E.; Bryja, J.; Hutterer, R.; Kerbis Peterhans, J.C.; Stanley, W.T.; Goodman, S.M.; Couloux, A.; Colyn, M.; et al. Phylogeography and evolutionary history of the *Crocidura olivieri* complex (Mammalia, Soricomorpha): From a forest origin to broad ecological expansion across Africa. *BMC Evol. Biol.* **2015**, *15*, 71. [CrossRef] [PubMed]
76. Olayemi, A.; Obadare, A.; Oyeyiola, A.; Fasogbon, S.; Igbokwe, J.; Igbahenah, F.; Ortsega, D.; Günther, S.; Verheyen, E.; Fichet-Calvet, E. Small mammal diversity and dynamics within Nigeria, with emphasis on reservoirs of the Lassa virus. *Syst. Biodivers.* **2018**, *16*, 118–127. [CrossRef]

77. Lecompte, E.; Fichet-Calvet, E.; Daffis, S.; Koulémou, K.; Sylla, O.; Kourouma, F.; Doré, A.; Soropogui, B.; Aniskin, V.; Allali, B.; et al. *Mastomys natalensis* and Lassa Fever, West Africa. *Emerg. Infect. Dis.* **2006**, *12*, 1971–1974. [CrossRef] [PubMed]
78. Coulibaly-N'Golo, D.; Allali, B.; Kouassi, S.K.; Fichet-Calvet, E.; Becker-Ziaja, B.; Rieger, T.; Gunther, S. Novel arenavirus sequences in *Hylomyscus sp*. And *Mus* (*Nannomys*) *setulosus* from Côte d'Ivoire: Implications for evolution of arenaviruses in Africa. *PLoS ONE* **2011**, *6*, e20893.
79. Kronmann, K.C.; Nimo-Paintsil, S.; Guirguis, F.; Kronmann, L.C.; Bonney, K.; Obiri-Danso, K.; Fichet-Calvet, E. Two novel arenaviruses detected in pygmy mice, Ghana. *Emerg. Infect. Dis.* **2013**, *19*, 1832–1835. [CrossRef] [PubMed]
80. Fichet-Calvet, E.; Becker-Ziaja, B.; Koivogui, L.; Gunther, S. Lassa serology in natural populations of rodents and horizontal transmission. *Vector Borne Zoonotic Dis.* **2014**, *14*, 665–674. [CrossRef] [PubMed]
81. Traweger, D.; Travnitzky, R.; Moser, C.; Walzer, C.; Bernatzky, G. Habitat preferences and distribution of the brown rat (*Rattus norvegicus* Berk.) in the city of Salzburg (Austria): Implications for an urban rat management. *J. Pest Sci.* **2006**, *79*, 113–125. [CrossRef]
82. Langton, S.; Cowan, D.; Meyer, A. The occurrence of commensal rodents in dwellings as revealed by the 1996 English House Condition Survey. *J. Appl. Ecol.* **2001**, *38*, 699–709. [CrossRef]
83. Feng, A.Y.T.; Himsworth, C.G. The secret life of the city rat: A review of the ecology of urban Norway and black rats (*Rattus norvegicus* and *Rattus rattus*). *Urban Ecosyst.* **2014**, *17*, 149–162. [CrossRef]
84. Kajdacsi, B.; Costa, F.; Hyseni, C.; Porter, F.; Brown, J.; Rodrigues, G.; Farias, H.; Reis, M.G.; Childs, J.E.; Ko, A.I.; et al. Urban population genetics of slum-dwelling rats (*Rattus norvegicus*) in Salvador, Brazil. *Mol. Ecol.* **2013**, *22*, 5056–5070. [CrossRef] [PubMed]
85. Rosevear, D.R. *The Rodents of West Africa*; British Museum (Natural History): London, UK, 1969; 604p.
86. Meinig, H. Notes on the mammal fauna of the southern part of the Republic of Mali, West Africa. *Bonn. Zool. Beitr.* **2000**, *49*, 101–114.
87. Meerburg, B.G.; Singleton, G.R.; Kijlstra, A. Rodent-borne diseases and their risks for public health. *Crit. Rev. Microbiol.* **2009**, *35*, 221–270. [CrossRef] [PubMed]
88. Kosoy, M.; Khlyap, L.; Cosson, J.-F.; Morand, S. Aboriginal and Invasive Rats of Genus *Rattus* as Hosts of Infectious Agents. *Vector Borne Zoonotic Dis.* **2015**, *15*, 3–12. [CrossRef] [PubMed]
89. Dobigny, G.; Nomao, A.; Gautun, J.C. A cytotaxonomic survey of rodents from Niger: Implications for systematics, biodiversity and biogeography. *Mammalia* **2002**, *66*, 495–523. [CrossRef]
90. Klimant, P.; Klimantová, A.; Baláž, I.; Jakab, I.; Tulis, F.; Rybanský, L.; Vadel, L.; Krumpálová, Z. Small mammals in an urban area: Habitat preferences and urban rural gradient in Nitra City, Slovakia. *Pol. J. Ecol.* **2017**, *65*, 144–157. [CrossRef]
91. McDevitt, A.D.; Montgomery, W.I.; Tosh, D.G.; Lusby, J.; Reid, N.; White, T.A.; McDevitt, C.D.; O'Halloran, J.; Searle, J.B.; Yearsley, J.M. Invading and Expanding: Range Dynamics and Ecological Consequences of the Greater White-Toothed Shrew (*Crocidura russula*) Invasion in Ireland. *PLoS ONE* **2014**, *9*, e100403. [CrossRef]
92. Fichet-Calvet, E.; Lecompte, E.; Veyrunes, F.; Barriere, P.; Nicolas, V.; Koulemou, K. Diversity and dynamics in a community of small mammals in coastal Guinea, West Africa. *Belg. J. Zool.* **2009**, *139*, 93–102.
93. Khanam, S.; Mushtaq, M.; Kayani, A.R.; Nadeem, M.S.; Beg, M.A. Small mammal community composition and abundance in rural human habitations of Pothwar, Pakistan. *Trop. Ecol.* **2017**, *58*, 515–524.
94. Wells, K.; Lakim, M.B.; O'Hara, R.B. Shifts from native to invasive small mammals across gradients from tropical forest to urban habitat in Borneo. *Biodivers. Conserv.* **2014**, *23*, 2289–2303. [CrossRef]
95. Cully, J.F.; Collinge, S.K.; Van Nimwegen, R.E.; Ray, C.; Johnson, W.C.; Thiagarajan, B.; Conlin, D.B.; Holmes, B.E. Spatial variation in keystone effects: Small mammal diversity associated with black-tailed prairie dog colonies. *Ecography* **2010**, *33*, 667–677. [CrossRef]
96. Jing-yuan, L.; Hong, D.; Geng-bai, T.; Pin-hong, Y.; Shen-wen, W.; Hong, P. Community Structure and Diversity Distributions of Small Mammals in Different Sample Plots in the Eastern Part of Wuling Mountains. *Zool. Res.* **2008**, *29*, 637–645.
97. Butet, A.; Paillat, G.; Delettre, Y. Factors driving small rodents assemblages from field boundaries in agricultural landscapes of western France. *Landsc. Ecol.* **2006**, *21*, 449–461.
98. Andrade, A.; Monjeau, A. Patterns in community assemblage and species richness of small mammals across an altitudinal gradient in semi-arid Patagonia. *J. Arid Environ.* **2014**, *106*, 18–26. [CrossRef]

99. Krasnov, B.R.; Shenbrot, G.I.; Mouillot, D.; Khokhlova, I.S.; Poulin, R. Spatial Variation in Species Diversity and Composition of Flea Assemblages in Small Mammalian Hosts: Geographical Distance or Faunal Similarity? *J. Biogeogr.* **2015**, *32*, 633–644. [CrossRef]
100. Monath, T.P. A short history of Lassa fever: The first 10–15 years after discovery. *Curr. Opin. Virol.* **2019**, *37*, 77–83. [CrossRef]
101. Attinsounon, C.A.; Ossibi, I.B.R.; Alassani, A.; Adé, S.; Saké, K.; Glèlè-Kakaï, C.; Dovonou, A. Report of a fatal case of Lassa fever in Parakou in 2018: Clinical, therapeutic and diagnostic aspects. *BMC Infect. Dis.* **2018**, *18*, 667. [CrossRef]
102. Güneralp, B.; Lwasa, S.; Masundire, H.; Parnell, S.; Seto, K.C. Urbanization in Africa: Challenges and opportunities for conservation. *Environ. Res. Lett.* **2018**, *13*, 015002. [CrossRef]
103. Neiderud, C.J. How urbanization affects the epidemiology of emerging infectious diseases. *Infect. Ecol. Epidemiol.* **2015**, *5*, 27060. [CrossRef]
104. Eskew, E.A.; Olival, K.J. De-urbanization and Zoonotic Disease Risk. *EcoHealth* **2018**, *15*, 707–712. [CrossRef]