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ORIGINAL ARTICLE

Habitat mosaic as a driver of the resilience of native species: The case of the assemblage of small mammals from the city of Franceville, Gabon

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Keywords
urban rodents; introduced rodents; community composition; habitat gradient; landscape heterogeneity; central African city.

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Abstract

Rodents (Rodentia) are the most abundant and diverse order of mammals, present in all habitats, including urban areas. The traffic linked to globalisation has favoured their involvement in biological invasions that have an impact on local biodiversity, the economy and human health. In Franceville, Gabon, little is known about the rodent community. We therefore studied the composition and distribution of rodents along a gradient highlighting the heterogeneity of the city's landscape. The three habitat types studied showed no difference in small mammal abundance, while the diversity index was higher in the vegetated habitat (SDI = 0.73) compared to the outdoor (SDI = 0.71) and indoor (SDI = 0.45) habitats. Our work shows the importance of vegetal remnants in the city for the maintenance of native species. It also highlights the impact of introduced species on small mammal assemblages and the need for management to reduce the factors of their proliferation.

Introduction

Understanding the determinants of species community assemblages influencing the composition, structure and species richness of these communities remains a central issue in ecology, especially for biodiversity conservation. This is even more true in urban areas where native fauna face many challenges in adapting to human-modified landscapes, including habitat loss (fragmentation by urbanization) and species introduction (Grimm et al., 2008; McKinney, 2002, 2008). Indeed, urbanization is the fastest growing of many anthropogenic pressures worldwide, contributing to biodiversity loss and biological homogenization, that is, the replacement of native species by widespread non-native species (Aronson et al., 2014; McKinney, 2006). The need for conservation of native fauna in urban areas is growing. However, despite the fact that urbanization is a major threat to biodiversity, more and more studies show that cities can also harbour a high diversity of species (Spotswood et al., 2021; Van Helden et al., 2021). Indeed, the preservation of residual natural habitat as well as the increased heterogeneity by cities can help conserve native species, in order to reduce the impacts of urbanization on native ecosystems. Urban areas can provide opportunities for biodiversity conservation as they may contain rare and threatened species (McKinney, 2002; Spotswood et al., 2021; Van Helden et al., 2021).

Rodents are the most diverse and abundant group in the mammalian class (Carleton & Musser, 2005). They are distributed globally in all types of habitats ranging from deserts to tropical forests, tundras and mountains, including human rural and urban housing areas (Assefa & Chelmala, 2019; Carleton & Musser, 2005; Granjon & Duplantier, 2009). Two decades ago, studies on urban rodent communities in the world were scarce. However, the past decade has seen an increase in the number of studies on rodent assemblage in urban landscapes. Many of these focused on the comparison of rodent communities according to an urbanization gradient, that is, natural environments (parks/nature reserves), rural or urban areas (Cavia et al., 2009; Fernández & Simonetti, 2013; Garba et al., 2014). Other studies focused on the distribution of rodents in waste sites and slums generated by ever-growing urbanization (Buzan et al., 2016).

Regardless of the geographical area and the objectives of the research, these studies highlight a shift in rodent composition and distribution in favour of introduced species in urban areas. This pattern observed in most cities reflects a biotic homogenization in response to global changes, especially human activities such as urbanization (Aronson et al., 2014; McKinney, 2006, 2008). Indeed, urbanization has a significant impact on biodiversity. It is responsible for radical changes in the environment that lead to changes in climate, hydrology, light, soil or noise levels that affect biological communities (McKinney, 2008). Urbanization mainly drives changes in species assemblages, by replacing specialized species with generalist ones. Thus, these environmental changes, resulting from urbanization, affect the rodent community and can result in population shifts. Native rodent species are progressively replaced by introduced species including rats, *Rattus rattus* and *Rattus norvegicus*, and the house mice *Mus musculus*, which are much more adapted to environments highly modified by humans (Feng & Himsworth, 2014).

In Africa, very little data are available on the characteristics of rodent assemblages in urban areas. The few existing studies on the subject are limited to the Sahel region along the coast (Garba et al., 2014; Garba & Dobigny, 2014; Hima et al., 2019; Houemenou et al., 2014).

The aim of this study is to analyse the urban rodent community in the city of Franceville, Gabon. It is a continental city with a tropical climate, located in central Africa and characterized by a mosaic landscape consisting of savannah, forest and urban areas. It has no navigable rivers and the city is accessed either by road or railway.

The heterogeneity of habitat, high diversity of habitats, generally results in a great diversity of species (Cramer & Willig, 2002). Thus, the heterogeneity of the landscape of the city of Franceville suggests a high species richness within the community of small mammals as indicated in the literature (Cavia et al., 2009). Indeed, the forest–savannah ecotone areas like those observed in and around Franceville (Barriere et al., 2000) contain a great diversity among wildlife communities (Kark, 2013). However, the presence of the introduced black rat *R. rattus*, reported in previous surveys (Ebang Ella, 2011; Maganga Mboga, 2012) and the destruction of natural habitats, both as a result of anthropogenic activity, could impact the level of diversity and influence the distribution of small mammals within the city (McKinney, 2002). At the city scale, a high diversity of small mammals is expected, while for the three habitats analysed (Inside, outside and vegetation), a decrease in diversity and conversely an increase in the abundance of commensal species from the vegetation habitat to the inside habitat are expected.

This study provides much needed knowledge on urban and semi-urban rodents assemblage in Gabon, especially since only forest and savannah rodents had been previously studied in the country (Duplantier, 1989; Mboumba et al., 2020; Nicolas & Colyn, 2003). We recommend preservation of vegetation habitat to promote the conservation of native species and limit the spread of introduced species. Our study also improves our knowledge of urban rodent assemblage in sub-Saharan Africa.

Materials and methods

Study area

Franceville is a Gabonese city located 500 km southeast of the capital Libreville with a population of 129 000 inhabitants (Population Data.net, 2020). This recent city grew in the 1960s due to the presence of nearby mines and the creation of the university (Pourtier, 1980). Franceville is characterized by a diffuse spatial organization composed of islets of savannah and forests as well as human housing areas (Fig. 1). Franceville is linked to the capital city Libreville (where the main seaport is located) by asphalting roads and a railway.

Rodent capture took place in houses from six districts in the city of Franceville (Fig. 1): four peripheral districts (Mangoungou, Mbaya, Sable and Yéné) and two central districts (Ombélé and Potos). The sampled districts were chosen according to their location, their proximity to the main transportation axes (roads and railway) and their urban landscape, to represent variable levels of connectivity and building aggregation. Mbaya includes several industries. Potos is the central trade district; it includes large storehouses and the main open-air food market. All other districts are essentially residential areas. It should also be noted that these districts are located along the main access points to the city (roads and railway). The various characteristics of these districts (connectivity, aggregation of buildings and presence or absence of vegetation) highlight the diversity of areas in the city of Franceville. The rodents were also captured in the vegetation in the town centre and on the periphery of the town. These included a forest and savanna patch. Each of the patches was, respectively, 1.5 ha and 0.83 ha in area and 555 m and 371 m in perimeter. The distance between the patches was approximately 7 km and the nearest houses were about 200 m away.

Sampling design and ethical statement

Rodents were captured during four sampling campaigns in 2013 (from March to April and from July to August) and in 2014 (from March to April and from June to July), according to a standardized live-trapping protocol as previously described

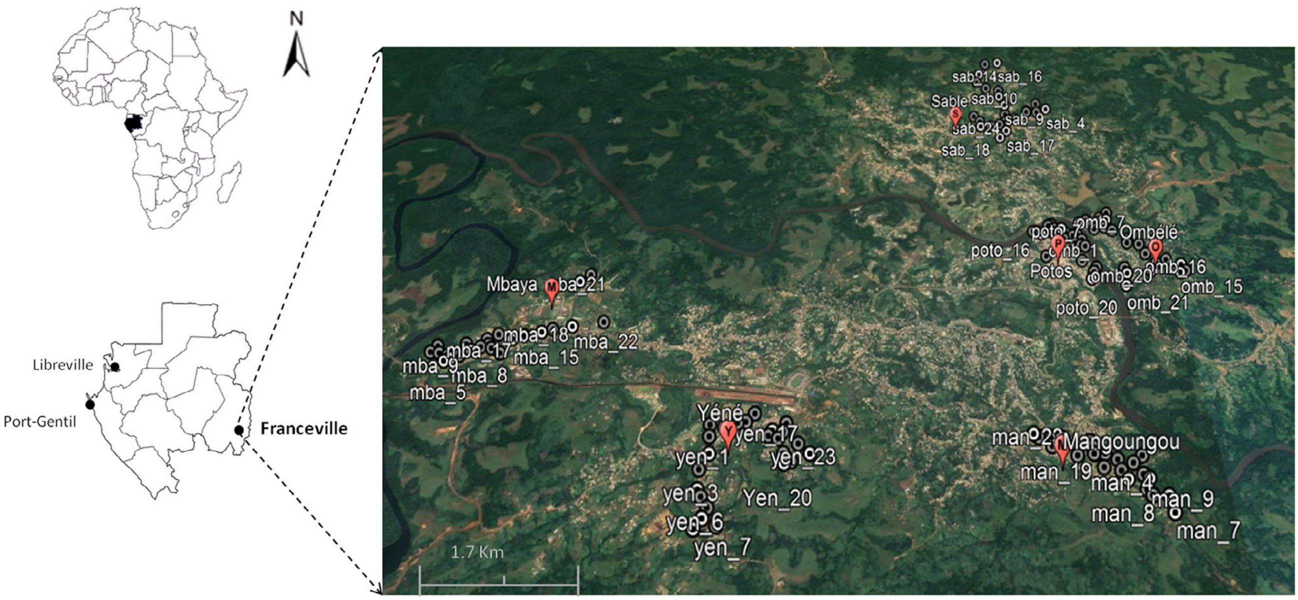

Figure 1 Location of the study area. Satellite image showing the location of the city of Franceville on the map of Gabon and highlighting the mosaic of habitats present within the city. The districts and sites sampled are shown with red and white dots respectively.

(Mangombi et al., 2016). Two traps, a Tomahawk and a Sherman trap were set in rooms inside the house (kitchen, bedroom or living room), along walls or furniture. Two other traps (one of each type) were set outside at a distance of 0–30 m from the house, in the garden, near the latrines or garbage bins. The traps measured 25 × 8 × 8 cm and 23.2 × 7.3 × 9 cm (L × W × H), respectively, for Tomahawk and Sherman. Palm nuts and peanut butter were placed in the traps to serve as bait every late afternoon. The traps were set for 5 consecutive days and checked every morning. In each district, rodents were collected in 44–48 houses, during the same week, resulting in a total of 278 capture sites (houses). The houses were selected according to the owner's consent and were at least 30–100 m from each other. The sites were usually homes or houses with a shop dedicated to trading. In 2014, point sampling was also conducted for 10 days in a patch of forests and savannah patches among those which are scattered throughout the city. This involved placing four trap lines of 10 traps, two in the forest and two in the savannah. Each pair of trap lines consisted of a Tomahawk trap and another Sherman trap. Living rodents were brought back to the laboratory of the Centre Interdisciplinaire de Recherches Médicales de Franceville (CIRMF), euthanized with a halothane solution, autopsied in accordance with the guidelines of the American Society of Mammalogists (Sikes, Gannon and the animal care and use committee of the American Society of Mammalogists, 2011), weighed, sexed and measured for species identification purposes. Euthanasia was necessary as these rodent samples were used in other aspects of our project, including the study of zoonoses and the genetics of rodent populations. Furthermore, we judged it unethical to release potentially infected rodents into residential areas. However, none of the rodent species investigated in this study has protected status (see IUCN and CITES lists). Trapping campaigns were performed with prior agreement from local authorities (the Mayor of Franceville and the chiefs of the districts) and all sampling procedures were approved by the Gabonese National Ethical Committee for Research (Comité National d'Ethique pour la Recherche; Prot n° 0020/2013/SG/CNE).

Species identification

Specific species identification was conducted with the identification keys provided by Jean-Marc Duplantier (Unpublished data) and Violaine Nicolas following their various studies on rodents in Gabon (Duplantier, 1982, 1987, 1989; Nicolas, 2003a, 2003b; Nicolas et al., 2002, 2008, 2012).

In addition, molecular identification was performed for all small mammals by 16S ribosomal RNA gene amplification as previously described (Nicolas et al., 2012) and sequenced with a BigDyeTM Terminator V3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA, Perkin-Elmer) in an ABI PRISM 3130XL Genetic Analyser (Applied Biosystems, Thermo Fisher Scientific, France). The obtained sequences were analysed using ChromasPro version 1.3 (Technelysium Pty, Ltd., Tewantin, Queensland, Australia) for assembly, and were aligned using CLUSTALW, implemented in BioEdit v7.2 (Hall, 1999). A threshold of 98% similarity for the same species was defined according to the results of BLASTn search. Nevertheless, for complex species of the *Mus Nannomys*, *Praomys* and *Lophuromys* groups, which require more specific identification tools than the 16S gene, we considered identification only at the genus level. All sequences from this study have been deposited in GenBank under accession numbers MT256376 to MT256385 for rodent species and MT677677 to MT677695 for shrew species.

Data analysis

Trap success and biodiversity measures

Animals captured in each district were counted and trap success (T, defined as the number of individuals caught per 100 trap nights) was calculated on the basis of the total number of rodents trapped (N) divided by trapping effort (Te, the product of the number of traps used and number of trapping nights) (Nicolas & Colyn, 2006). Here, it is computed as (T) = [(N/Te) × 100]. Rodent assemblages in each district/habitat were characterized by the species richness and the Simpson diversity index (SDI), using the Paleontological Statistics software (PAST; Hammer et al., 2013). The Kruskal–Wallis test was used to compare the relative abundance ra (i.e. T) between the three habitat types, and Renyi diversity profiles were plotted using PAST software to obtain a visual perspective of rodent diversity differences between the three habitats. Abundance and diversity analyses were conducted in two ways: the first by considering the three inside, outside and vegetation habitats; the second by considering inside and outside habitats, taking into account the districts sampled. Rodent taxa with collection numbers of less than five were extracted from the analyses.

To determine whether most common taxa were found in the dataset, the species rarefaction curve was conducted with the Estimate S 9.1.0. program (Colwell, 2013).

Landscape of Franceville

The landscape of the city of Franceville shows the disparate distribution of the main elements such as the forest, the savannah and the buildings, although certain districts present higher proportions of these elements compared to others (Fig. 2a). Chi^2 test performed (X-squared = 42.489, d.f. = 10, $P < 0.0001$) show a significant difference in the landscape structure between the districts of Franceville. Indeed, built areas are dominant in Potos, Ombélé and Mangoungou (57, 47 and 49% of the district area, respectively). Savannah is dominant in Mbaya and Yéné (54 and 51%, respectively). In the sable district, the three main habitats have similar rates (forest 38%, savannah 27% and buildings 35%). These associations between the dominant element of the landscape and the district are presented by the principal component analysis (PCA) (Fig. 2b). This description has been made previously to describe the spatial landscape of the city. 'Spatial analysis' and 'image processing' extensions of ArcGIS software 10.3 (Environmental Systems Research Institute) were used to elaborate the land use maps based on the supervised classification method (Appendix S1).

Environmental factors of habitat

During capture, for each sampled house, we collected several environmental factors located between 0 and 30 m from the house: the presence of a food stock, a road, a watercourse, domestic animals and the rooms in the house (see Table 1). All these variables highlight the potential characteristic factors of each of the districts using multiple correspondence analysis (MCA) (Fig. 2c). These variables were also used to understand their potential relationship to the presence or relative abundance of rodents or a given species. For this purpose, generalized linear mixed models (GLMM) with a Poisson distribution (Hosmer et al., 1989) were parameterized using the R 4.2.0 software (https://cran.r-project.org), with the *glmer* function of the *lme4* package. Models with a ΔAIC < 2 (Burnham & Anderson, 2004) were retained, and the model with the lowest AIC value was considered the best model. AIC changes were evaluated when model terms were added or removed using the *dredge* function in the MuMIn package (Barton, 2020). Given the identical sampling effort at each site, the response variable was the number of individuals per rodent species in each site and, as predictors, environmental variables. The 'District' variable was taken as random effect.

Results

Composition of small mammal community

A total effort of 11.520 trap nights in the city of Franceville resulted in the capture of 832 small mammals (7.2% trap success). Among these, 454, 325 and 53 small mammals were sampled inside, outside and in vegetation islets respectively. These comprise at least 13 different taxa (Table 2).

Overall, the introduced rodent *R. rattus* was the most captured small mammal (N = 485), followed by shrews (N = 103), the native species *Mus Nannomys* sp. (N = 70), *M. domesticus* (N = 58) another introduced species and the other native species *Lemniscomys striatus* (N = 48), *Lophuromys* sp. (N = 32), *Praomys* sp. (N = 31), *Cricetomys* sp. (N = 3) and *Oenomys hypoxanthus* (N = 2) (Table 2). The plotted species accumulation curve (Fig. 3a) showed sufficient sampling effort as it tends to stabilize after the capture of nearly 700 individuals, in terms of standard sampling, especially in inside and outside habitats. Thus, our survey effort was most likely enough to gain a sample of the species present. Nevertheless, it also indicates that some additional species may still be trapped. Conversely, the absence of a plateau for the rarefaction curve of sampling in vegetation habitat suggests that the most common taxa are missing from the collection (Fig. 3b). This is not unexpected because the sampling effort in this habitat was lower than in inside and outside habitats. However, these data provide an overview and show the need to preserve the vegetation habitat within a city for the conservation of native small mammals.

Distribution of small mammals across habitats

Considering the three types of habitats analysed, the relative abundances (ra, i.e. T) of small mammals in these habitats showed no significant difference (Kruskal–Wallis test, P = 0.15) (Fig. 4a). However, the introduced rodents, *R. rattus* and *M. musculus*, were not captured in the vegetation habitat, while most of the native species were captured in all study habitats. Sampling also included rare native species such as *Cricetomys* sp., *Lophuromys* sp. and *Oenomys hypoxanthus*,

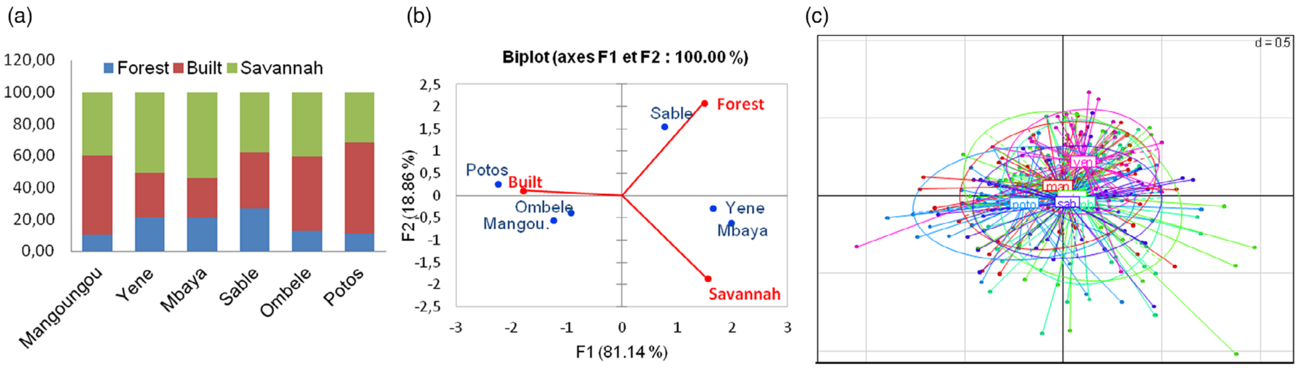

Figure 2 Landscape and habitat of the city of Franceville. The histogram (a) and ACP analysis (b) describe the landscape structure of Franceville across forest, savannah and built. The Multiple component analysis (c) presents the characteristics of the districts according to the environmental factors collected. The points are the modalities (see Table 1) of the factors that were identified in the field at each site within the districts in order to describe its environment. The analysis shows that there is not a single group of terms that are separate from each other. However, Yéné and Potos appear somewhat opposed as Yéné is characterized by a formal subdivision of hard houses and Potos an informal development. Mangou is for Mangoungou district.

Table 1 Set of environmental variables collected and used to assess relationships between rodent abundance/diversity and environmental factors

Category of variable	Variable	Type	Modalities
Houses	House	Numeric	Number within 30 m of the sampled site
	Inhabitants	Numeric	Number in the house
	Rooms	Numeric	Number by house
	Bedrooms	Numeric	Number by house
	Shop	0/1	0: no shop, 1: shop
Kitchen	Kitchen indoor	0/1	0: absence or 1: presence of indoor kitchen
	Kitchen outdoor	0/1	0: absence or 1: presence of outdoor kitchen
Surroundings	Market	0/1	0: absence or 1: presence of market
	Road	0/1	0: absence or 1: presence of road
	River	0/1	0: absence or 1: presence of river
	Savannah	0/1	0: absence or 1: presence of savannah
	Forest	0/1	0: absence or 1: presence of forest
	Vegetable garden	0/1	0: absence or 1: presence of garden
	Fence	0/1	0: absence or 1: presence of fencing
Property	Garbage	0/1	0: absence or 1: presence of garbage
	Latrine	0/1	0: absence or 1: presence of latrine
	Unsanitary	Qualitative	1: Low unsanitary
		Qualitative	2: Mean unsanitary
		Qualitative	3: High unsanitary
Animals	Cat	0/1	0: absence or 1: presence of cat
	Dog	0/1	0: absence or 1: presence of dog
	Poultry	0/1	0: absence or 1: presence of poultry
	Cattle	0/1	0: absence or 1: presence of cattle

and *Crocidura poensis* and *Crocidura hildegardeae* which were found in outside and vegetation habitats respectively (Table 2). Indeed, the descriptive analysis of the observations of the taxa of small mammals according to the habitats showed the association between the native species and the vegetation habitat. This association is all the more highlighted when the black rat is excluded from the analysis (Fig. 4b,c). Renyi diversity profiles (Fig. 5) for the three study habitats and SDI suggested that species diversity was highest in vegetation habitat (SDI = 0.73), followed by outside habitats (SDI = 0.71) and lowest in the inside habitats (SDI = 0.45).

The same patterns of abundance/diversity were observed when analyses only took into account the inside and outside habitats following the sampled districts. Between inside and outside habitats, no significant difference in relative abundance was found (Mann–Whitney test, W = 1, $P = 0.10$). Conversely, species diversity was greater outside compared to inside (Mann–Whitney test on SDI, W = 1, $P = 0.004$).

Table 2 Inventory of small rodent taxa and Soricidae in the six districts of Franceville. Various richness estimates are indicated

	Indoor							Outdoor							Vegetation	
	Mangoungou	Mbaya	Ombélé	Potos	Sable	Yéné	*N* Indoor (ra % or T)	Mangoungou	Mbaya	Ombélé	Potos	Sable	Yéné	*N* Outdoor (ra % or T)	*N* Forest & Savannah (ra % or T)	Overall
Rodents																
Cricetomys sp.	0	0	0	0	0	0	**0**	1	1	0	0	1	0	**3 (0.05)**	**0**	3 (0.03)
Lophuromys sp	0	1	0	0	0	0	**1 (0.01)**	2	1	0	0	3	5	**11 (1.2)**	**20 (5)**	32 (0.27)
Lemniscomys striatus	1	2	2	0	0	1	**6 (0.1)**	2	2	8	1	7	6	**26 (0.5)**	**16 (4)**	48 (0.42)
M. m. domesticus[a]	0	46	0	8	0	0	**54 (1)**	0	0	0	0	4	0	**4 (0.07)**	**0**	58 (0.5)
Mus Nannomys	4	2	1	0	6	7	**20 (0.4)**	10	4	8	0	13	13	**48 (0.9)**	**2 (0.5)**	70 (0.61)
Oenomys hypoxanthus	0	0	0	0	0	0	**0**	0	0	1	0	0	1	**2 (0.03)**	**0**	2 (0.02)
Praomys sp.	3	0	0	0	2	1	**6 (0.1)**	3	2	4	2	2	2	**15 (0.3)**	**10 (2.5)**	31 (0.27)
R. rattus[a]	58	50	75	63	54	30	**330 (6.0)**	27	27	42	32	18	9	**155 (2.8)**	**0**	485 (4.21)
Shrews																
Crocidura goliath	1	0	1	2	2	0	**6 (0.1)**	2	0	1	0	1	2	**6 (0.1)**	**1 (0.25)**	13 (0.11)
Crocidura poensis	0	0	0	0	0	0	**0**	0	1	0	0	0	0	**1 (0.0)**	**3 (0.75)**	4 (0.03)
Sylvisorex ollula	0	0	0	0	0	1	**1 (0.0)**	0	0	0	0	0	0	**0**	**0**	1 (0.01)
Crocidura hildegardeae	0	0	0	0	0	0	**0**	0	0	0	0	0	0	**0**	**1 (0.25)**	1 (0.01)
Unidentified shrews	7	6	5	7	4	1	**30 (0.5)**	9	10	10	16	4	5	**54 (1)**	**0**	84 (0.73)
Diversity measures																
Total	74	107	84	80	68	41	**454**	56	48	74	51	53	43	**325**	**53**	832
Number of sites	48	45	48	44	46	47	**278**	48	45	48	44	46	47	**278**	**2**	280
Trapping effort (2 years)	960	900	960	880	920	940	**5560**	960	900	960	880	920	940	**5560**	**400**	11 520
Trap success (T)	7.7	11.9	8.8	9.1	7.4	4.4	**8.2**	5.8	5.3	7.7	5.8	5.8	4.6	**5.8**	**13.3**	7.2
Richness	6	6	5	4	5	6	**9**	8	8	7	4	9	8	**11**	**7**	11
Simpson Diversity Index	0.37	0.59	0.2	0.36	0.36	0.43	**0.45**	0.7	0.63	0.63	0.51	0.79	0.81	**0.71**	**0.73**	–
Evenness	0.38	0.49	0.32	0.52	0.43	0.41	**0.30**	0.58	0.49	0.55	0.59	0.68	0.78	**0.46**	**0.63**	–

In bold, data according to the three habitat types analysed. Relative abundance is designated by ra and trap success by T.
[a]Invasive rodents.

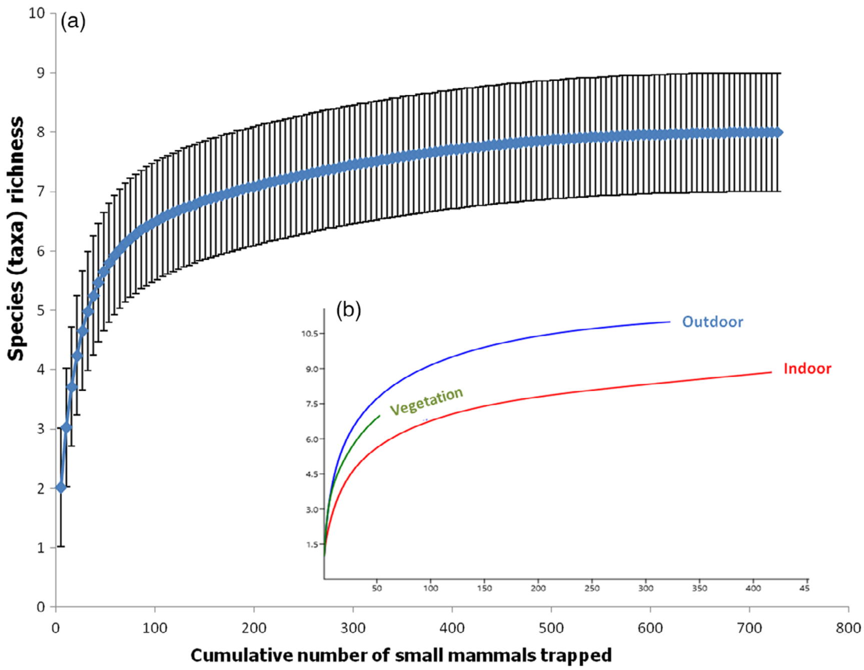

Figure 3 Species accumulation curve. (a) Rarefaction curve by individuals representing the number of small mammal taxa for a given number of captured individuals, with ± standard deviation and (b) rarefaction curve for the separately studied habitats.

Rodents and habitat of Franceville

The description of the sites according to environmental factors by the multiple component analysis (MCA) does not reveal any group of houses (sites). Indeed, all the modalities of the evaluated variables are centred towards the origin of the axes. The axes, therefore, do not discriminate any group of houses associated with any factor, showing that there is no significant divergence of environmental variables between the districts (Fig. 2c).

L272–274: The results of the GLMM analysis of the standard sampling revealed socio-environmental factors that significantly determine the abundance of certain rodents, notably *R. rattus*, *M. musculus*, *Mus Nannomys* sp., *Lemniscomys striatus* and shrews (Table 3). Indeed, the presence of the introduced rodent *R. rattus* was significantly and positively associated with a higher number of houses around the sampled house, a high number of inhabitants in the house, the presence of latrines, unsanitary conditions and negatively correlated with the presence of fences and cattle. Moreover, the presence of *domesticus* was positively associated with the presence of markets and cats; and negatively associated with the presence of unsanitary conditions, a stream, a high number of houses, latrines, savannah and dogs. The presence of *M. Nannomys* was positively associated with the presence of latrines and negatively associated with the presence of savannah and garbage. *Lemniscomys striatus* was associated with the presence of savannah which is its natural environment and negatively associated with the presence of a high number of houses. Shrews showed an association with the presence of stream.

Discussion

Relative abundance and diversity of small mammals

Our study on small mammals in the city of Franceville across three different habitats recorded at least 13 taxa of small mammals, which shows a large diversity for 832 captured animals. Our results showed no differences in the abundance of small mammals among habitats. Conversely, species composition between these habitats was different, with a higher diversity index for the outside and vegetation habitat. The absence of difference in relative abundance could be explained by the weights of the species that make up each habitat. Introduced rodents are more abundant in the inside habitat and absent from the vegetation habitat, while native rodents are more abundant in the vegetation habitat which is their natural environment. Obviously, introduced rodents are commensal species highly adapted to the urban environment (inside) (Feng & Himsworth, 2014).

This low level of diversity in the inside habitat can be explained by the impacts of human activities that can modify the functioning of ecosystems and therefore animal assemblages (McKinney, 2002; Tylianakis et al., 2008). Indeed, across a gradient of human-impacted environments, species diversity decreases from less impacted environments towards urban core areas which are the centres of human activity such as buildings and houses (McKinney, 2008). Our results, different from this assertion, would be explained by the process of urbanization currently in progress and the particularity of the

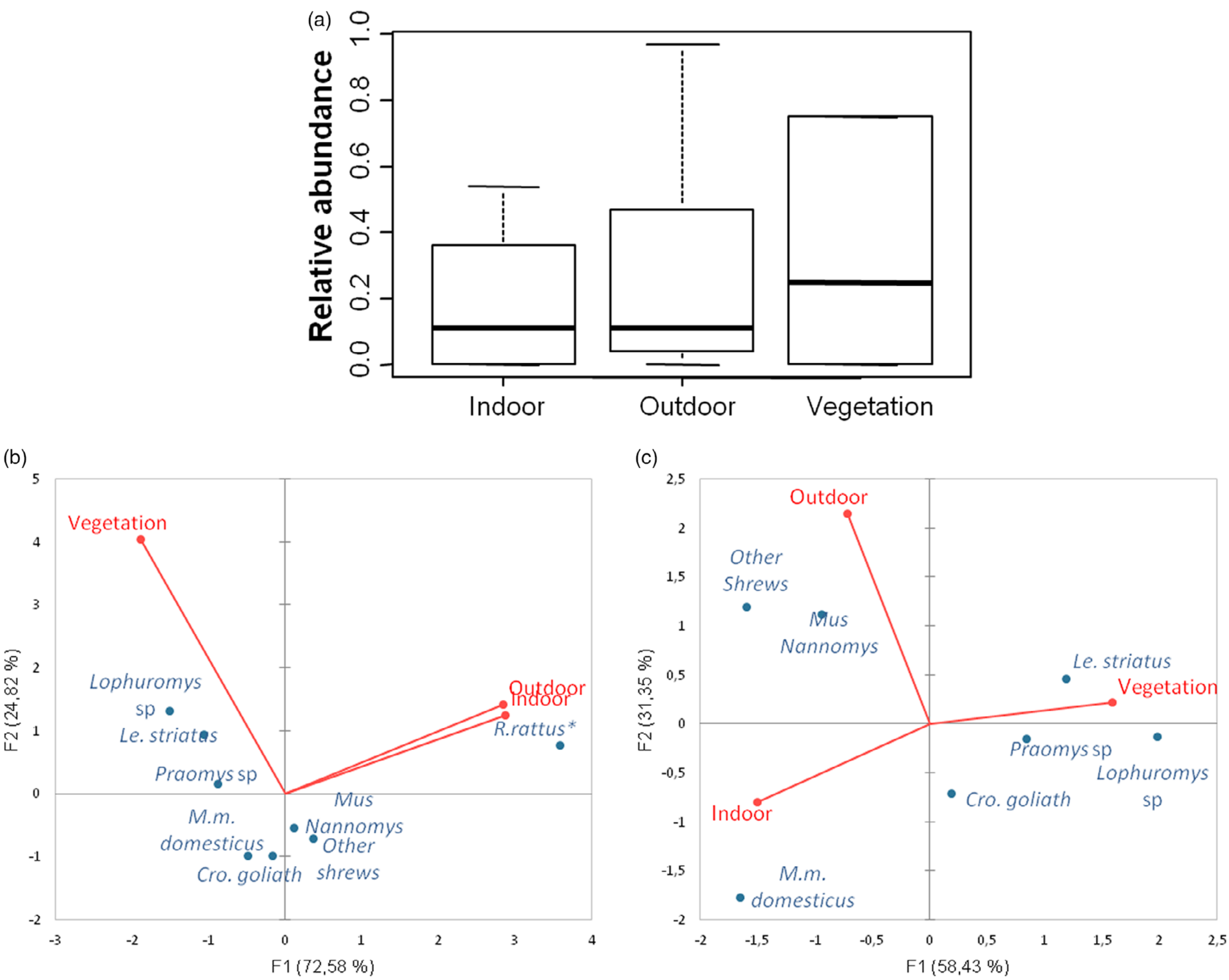

Figure 4 Distribution of small mammals within Franceville. (a) Boxplots without outliers of relative abundance of small mammals across the three habitats in Franceville; and plots showing rodent species associated with the three habitats of the city: (b) with *R. rattus* and (c) without *R. rattus* whose high proportion masks the distribution of other small mammals.

habitat of Franceville which is located at a double crossroads between urban/rural and forest savannah.

In comparison with cities in other African countries, the richness of small mammals observed in Franceville (13 taxa) was similar to that found by Houemenou et al. (2014) in Cotonou (11 taxa) in Benin, but our study showed a much higher diversity than the one observed in Niamey (7 taxa) in Niger, (Garba et al., 2014). It should be noted that in both Cotonou and Franceville, sampling was carried out both in houses and in vegetation areas, unlike in Niamey. Our data clearly show the association between the presence of vegetation habitats in urban areas and the diversity of rodent species (Fig. 5) as shown in other studies (Cavia et al., 2009; Wells et al., 2014). In Franceville, due to the heterogeneity of the landscape and especially the areas of forest–savannah ecotone, there is a great diversity of small mammals.

As expected, the small mammal community in Franceville was more diverse than what was found in the forest areas of Gabon (Franceville: 13 species, Monts Doudou: 11 species) (Nicolas & Colyn, 2003). However, the community of small mammals in Franceville was expected to be even more diverse than we found based on previous studies. These previous studies showed the presence of six other species that we did not capture during our study: *Deomys ferrugineus*, *Stochomys longicaudatus*, *Malacomys longipes*, *Heimyscus fumosus*, *Hybomys univittatus* and *Mastomys natalensis*. These are all forest species (Duplantier, 1989; Nicolas et al., 2002; Nicolas & Colyn, 2003) except *M. natalensis* which is a commensal species (Dobigny, 2000; Granjon & Duplantier, 2009; Monadjem et al., 2015). Their absence from our sampling could indicate that they have been supplanted by introduced species, in particular *R. rattus* (Shiels et al., 2014). The species *R. rattus* is

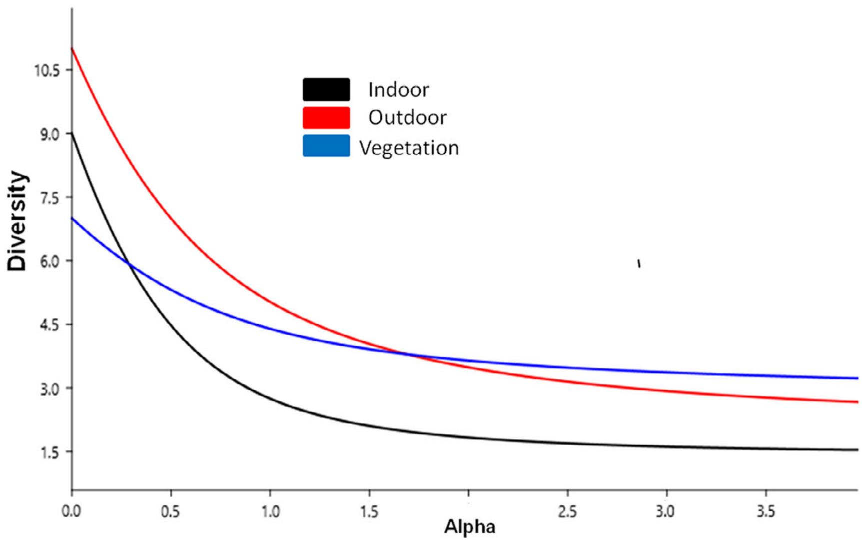

Figure 5 Renyi diversity profiles for the three study habitats in Franceville.

competitive and has characteristic traits (e.g. aggressiveness, high reproductive rate and large body mass) (Feng & Himsworth, 2014) that allow it to outcompete most of the often small native species. Furthermore, it is a species that is well adapted to native vegetation and uses patches of forest in cities to move around (Wells et al., 2014). The fact that *R. rattus* was found abundant both inside and outside would support the hypothesis that it has locally supplanted native rodents absent from our sampling. However, this could only be a lack of detection. On the other hand, the alteration of the natural habitat of these species due to the progression of urbanization could also explain their absence within our sampling. Habitat alteration is a consequence of human activity responsible for the loss of biodiversity (McKinney, 2002, 2008). To support this, for example, we noted during our collections, the presence of a market in the Mbaya district which was absent during the previous sampling (Maganga Mboga, 2012) showing the evolution of the city. Therefore, other sites within the city should be sampled. Another hypothesis would be the insufficient trapping effort to capture these species. Indeed, the accumulation curve suggests that species could still be taken. Also, for this, it would be necessary to increase the trapping effort (i.e. time and sites) (Colwell et al., 2012) to increase the possibility of having a more representative sampling of rodent species of Franceville. The absence of commensal rodent *M. natalensis*, known to live close to humans, is surprising. Its absence in all sampling areas may also suggest extirpation by the black rat *R. rattus* with which it is generally segregated (Garba et al., 2014; Hima et al., 2019). Further sampling campaigns must be made to validate this hypothesis. In Franceville, so far, the islands of forests and savannas that dot the city allow the survival of native species (Fig. 4b,c) but without ensuring their long-term survival in front of the predominant introduced species *R. rattus* which will continue to spread with the progression of urbanization.

Structure of small mammal community

Analysis of the small mammal community structure in the city of Franceville through the similarity Morisita–Horn index showed the presence of four clusters of small mammal assemblages (Fig. 6). The specificity of these groups lies in the presence and numerical abundance of introduced rodent species. This structure highlights the major influence of introduced species and their impact on local species communities.

These findings show the influence of humans, through urbanization, deforestation and/or biological invasions, on local small mammal communities. These results are consistent with studies which already demonstrated the impact of urbanization on species communities (Cavia et al., 2009; Łopucki et al., 2013). The existence of fragments of forests and savannah in Franceville allows the maintenance of native species for the moment, despite the presence of introduced species in the city.

Species abundance and environmental factors

The abundance of rodents depends on the resources available in their habitat. Commensal species are generally abundant because of the continuous availability of resources and shelter provided by humans, unlike rodent populations in the natural environment (Singleton et al., 2003). The commensal rodent *R. rattus* was the most abundant small mammal. The presence of this introduced species is not surprising, it has already been reported in many African cities (Granjon & Duplantier, 2009; Hima et al., 2019; Olayemi et al., 2018).

Several environmental factors were associated with *R. rattus* abundance in the city, the aggregation of houses, the high number of inhabitants, the presence of latrines and a high level of unsanitary conditions. These factors are generally related to

Table 3 Factors influencing the richness and relative abundance of small mammals within the city of Franceville

Species	Model no. (rank)	Fixed effects: Intercept	Market	Waterway	Garbage	Latrine	Unsanitary	Savannah	Cattle	Dog	Cat	Fence	Inhabitant	Number of room	Number of house	D.f.	ΔAIC	Akaike weight
Small mammals	**1306 (1)**	0.464	+			+						+	0.028		0.257	7	0	0.039
Rattus rattus	**1686 (1)**	−0.541				+	+		+			+	0.037		0.422	9	0	0.044
Mus musculus sp.	**764 (1)**	−1.972	+	+		+	+	+		+	+				−1.043	11	0	0.151
Mus Nannomys sp.	**557 (1)**	−1.017			+	+		+							−0.425	6	0	0.020
Lemniscomys striatus	**6 (1)**	−1.406							+						−0.786	4	0	0.295
Soricidae	**241 (1)**	−1.462		+									0.056	−0.137	0.428	6	0	0.065

Only models having significant explanative factors were presented. Significant factors are those from the most parsimonious generalized linear mixed model obtained after model selection and residuals-based validation procedures carried out for each response variable. AICc: Akaike's information criterion with correction for finite sample size. Δ indicates the difference between the model selected and the model with the lowest AICc.

Means of the best estimated models and the rank are represented here by model n° (Rank) in bold.

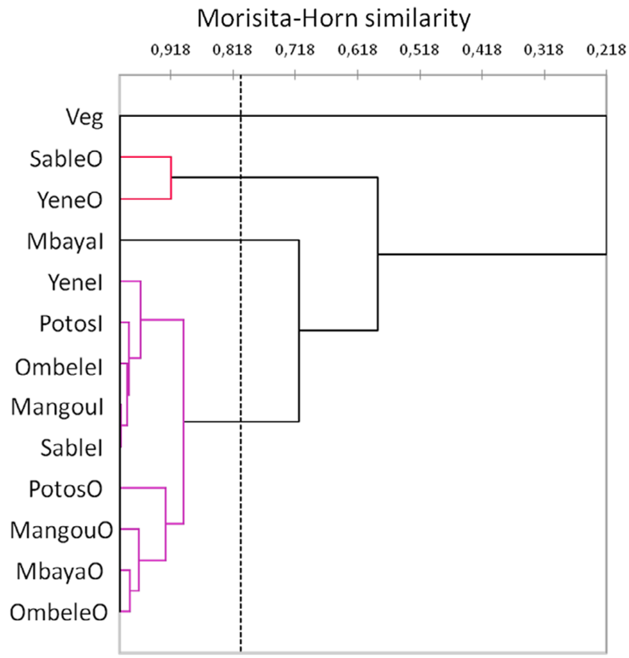

Figure 6 Dendrogram based on the Morisita–Horn similarity index in district/habitat pairs, as shown in Table 4. It measures the similarity in taxa composition between two districts or habitats. I, Inside; O, Outside; Mangou, Mangongou.

informal urbanization (i.e. precarious housing, slum, etc.), favoured by black rat infestations (Alirol et al., 2011; Buzan et al., 2016). Conversely, a significant negative association between rats and factors such as the presence of fences and cattle was shown. While this negative association with fences (mostly walls) can be explained by the fact that these obstacles limit the movement of rats, the underlying processes that lead to a negative association between rats and cattle cannot yet be explained and will need to be investigated.

The other introduced species captured in Franceville is the house mouse *M. m. domesticus*. Although not very abundant in the city (58/832) our results show the presence of this species in only one district of the city, which is highly intriguing. As mentioned above, we suppose that this species is probably in the early stages of its invasion into the urban environment. It was previously captured in the city in very small numbers in the Potos district, where the large central market is located (Ebang Ella, 2011). It is also possible that this species is absent due to competition with *R. rattus*, which is aggressive and supplants the other species. Indeed, the house mouse is not detected where *R. rattus* is the most widespread rodent species (Dalecky et al., 2015). The relative abundance of *M. m. domesticus* is significantly dependent on factors such as markets and cats (Table 4). This association supports the major role of markets and roads in the expansion of the range of this species (Dalecky et al., 2015). Indeed, this species was found in the Mbaya district (located on the road axis leading to the edge of the city), in the Potos district (a place where storing containers are unloaded) and the Sable district supplied by Potos. The link between mice

Table 4 Morisita–Horn's index measuring the similarity of small mammal composition among districts across the different habitats of Franceville

	MangouI	MbayaI	OmbeleI	PotosI	SableI	YeneI	MangouO	MbayaO	OmbeleO	PotosO	SableO	YeneO	Vegetation
MangouI	1												
MbayaI	0.72	1											
OmbeleI	0.99	0.70	1										
PotosI	0.99	0.80	0.98	1									
SableI	1.00	0.72	0.99	0.99	1								
YeneI	0.98	0.71	0.96	0.96	0.99	1							
MangouO	0.88	0.68	0.81	0.84	0.87	0.90	1						
MbayaO	0.94	0.71	0.88	0.91	0.92	0.92	0.97	1					
OmbeleO	0.94	0.72	0.89	0.91	0.93	0.94	0.97	0.98	1				
PotosO	0.93	0.69	0.89	0.92	0.91	0.88	0.90	0.97	0.94	1			
SableO	0.69	0.66	0.62	0.67	0.70	0.76	0.91	0.81	0.85	0.68	1		
YeneO	0.48	0.38	0.41	0.43	0.49	0.56	0.77	0.64	0.67	0.51	0.92	1	
Vegetation	0.03	0.03	0.02	0.00	0.02	0.04	0.15	0.10	0.15	0.04	0.32	0.46	1

Abbreviations: I, Inside; O, Outside; Mangou, Mangongou.

and cats remains difficult to explain, since in this study the presence of cats seems to attract rodents. Initially, cats are natural predators of rodents and their presence repels them (Herbreteau, 2007). However, recent observations show the contrary (Garba, 2012) and this association corroborates this fact.

Some species of African pygmy mice are known to inhabit houses (Happold, 2013), its predominant presence outside could reflect an exclusion by introduced species. This assertion can be supported by the fact that the African pygmy mice have not been collected in other African cities including Cotonou and Niamey (Hima et al., 2019), where the invasion of *R. rattus* and *M. musculus* is rather advanced compared to Franceville. However, it should be remembered that Franceville is a double crossroads between urban/rural and forest/savannah and that the ecology of species of the subgenus *Nannomys* mainly includes savannahs and rural areas (Granjon & Duplantier, 2009). The presence of African pygmy mice mainly outside could therefore be due to the structure of the city and the ecology of the latter.

The association between *Mus Nannomys* sp. and latrines could be explained by the fact that latrines provide shelter for these pygmy mice.

Shrews, the most abundant small mammals after rats, have already been reported in other African cities, especially in West Africa (Hima et al., 2019). Many shrews appear to be associated with the human environment (Jacquet et al., 2015). Shrews, whether in forest or savannah, are strongly correlated with wetlands and streams. In our study, we did identify positive associations between shrews and several factors such as the stream, a high number of houses, inhabitants and rooms in the house. The wet microhabitat found in the tropical and subequatorial African region is favourable to shrews compared to the Sahelian region as previously reported (Hima et al., 2019). In our sampling, *Crocidura goliath* was the most captured species among the 20 shrew species identified by molecular biology (12/20; 60%, Figure S1).

Conclusion

The three types of habitats studied showed no difference in the abundance of small mammals, while the diversity index was higher in the vegetation habitat (SDI = 0.73) compared to outside (SDI = 0.71) and inside (SDI = 0.45) habitats. Our work shows that the presence of vegetative remains in the city allows the maintenance of native species. They also emphasize the impact of introduced species on the small mammal assemblages and the need for management that reduces the factors conducive to the proliferation of introduced species particularly *R. rattus* which dominates the community. In terms of conservation, our results highlight the importance of vegetation in cities to preserve native species and reduce the impacts of human activities such as urbanization on biodiversity.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Brief description of the methodology for classifying landscape elements, forest, savannah and urban area of the city of Franceville.

Figure S1. Phylogenetic tree for taxonomy of shrews.