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DIVERSITY PATTERNS OF RODENT ASSEMBLAGES ALONG HABITAT GRADIENTS IN THE DAHOMEY GAP (TOGO, WEST AFRICA)

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Abstract.

The rodent assemblages were studied in different habitat types of the Fazao-Malfakassa National Park located in Togo, West Africa. A suite of different methods was applied, including face-to-face interviews with local hunters, live trapping along standardized transects and opportunistic observations. A total of 20 rodent species were recorded based on the surveys carried out in villages. There was a clear gradient pattern in the univariate diversity indices by habitat type: Dominance index was remarkably higher in urban/plantation than in the other habitat types whereas Evenness index was remarkably higher in gallery forest than in the other habitat types. According to a Canonical Correspondence Analysis, three "ecological groups" (= guilds) of species were formed: a group from wooded habitats (savannahs and semiforests), a group from grassy savannah and a group from urban/plantation habitats. Null model analyses revealed that species tend to non-randomly congregate in some habitat types and/or localities.

Key words: Rodentia, specific diversity, community ecology, Fazao-Malfakassa National Park, West Africa.

Introduction

Savannah ecosystems are among the most ecologically important in Africa, for example as they host a massive biomass, unrivaled in the world, as far as large mammals are concerned (see East, 1984; Hatton et al. 2015). Savannah ecosystems are threatened globally by human-derived factors causing broad shifts in woody vegetation with a tendency towards homogenization of their structure (McCleery et al. 2018). However, despite their ecological importance and the precarious conservation status of large strips of grassland territory (Pour la Nature 2001), savannahs have been thoroughly studied with regard to communities of large mammals, birds and vegetational successions, while the assemblages of many other groups, including vertebrates, have received little scientific attention so far. These considerations apply more to the "Dahomey Gap" savannahs of the southern region of Benin, Togo, and eastern Ghana (West Africa) which are also home to a partly exclusive fauna (Mallon et al. 2015). In fact, the "Dahomey Gap" savannah separates the Guinea-Congolian forest zone into two separate forest blocks (i.e. the Upper Guinean and the Lower Guinean forests, Saltzmann and Hoelzmann 2005; Mallon et al. 2015) and represented an area of isolation, speciation and endemism for forest species that found themselves isolated in the forest islands scattered in the region's wide savanistic matrix (Mallon et al. 2015).

Savannah environments also house a remarkable diversity of rodent species (e.g., Happold and Happold 1991; Decher and Bahian 1999; Happold, 2013), which are also of considerable ecological importance, for example being *Acacia* seed dispersers (Kuechly et al. 2011). Nonetheless, studies on the community ecology of rodent communities in African savannahs remain scarce, and very little is known on the diversity patterns and the assembly rules (Gotelli 2001; Gotelli and McCabe 2002) governing these communities. Composition and diversity of savannah rodent communities are apparently affected by landuse and habitat type (Blaum et al. 2007), with significant changes in relative abundance of species among habitats that were observed between periods, suggesting seasonal trends in habitat preferences (Bâ et al. 2013). These changes may help resource partitioning and species coexistence in these species-rich rodent communities (Amori and Luiselli 2011; Bâ et al. 2013). However, null model analyses with Monte Carlo simulations revealed that spatial resource partitioning is unlikely to be a main assembly rule for rodent communities in tropical African forests (Amori and Luiselli 2011), and no competition was uncovered by a South African study on savannah small mammals (Rautenbach et al. 2014). In addition, a recent meta-analysis on the community ecology of these animals in West African savannahs has shown that studies using a combination of methods (e.g., live trapping, pitfalls, cover boards, visual encounter) detected more species per site than studies utilizing single methods (Amori et al. 2021), and that there was no effect of trapping design (transect versus grid) on species richness per site (Amori et al. 2021). The number of sympatric rodents per site was relatively stable, suggesting that the ecological conditions of the various West African savannah sites are functionally similar and support a inter-site similar number of sympatric species although not necessarily the same taxa (Amori et al., 2021).

In Togo (West Africa), apart for general studies on mammalian diversity and ecology (e.g., Amori et al. 2016; Agbessi et al. 2017; Segniagbeto et al. 2017, 2018a, 2018b, 2020; Assou et al. 2021), there is a shortage of data concerning rodents. However, Amori et al. (2016) provided an updated commented checklist of all the mammalian species known to be present in Togo including small non-flying mammals. According to these authors, 52 species of rodents are reported for Togo. Of all Togolese rodents, *Leimacomys buettneri* Matschie, 1893 is particularly intriguing as it is an endemic forest species known from only two specimens that were collected in Bismarckburg (now Adélé area) in 1890 (Matschie 1893). According to Denys (1993) and Amori et al. (2016), this species would probably be extinct although the remains of its habitats (islands of mature hilly forests) are still occurring in the Adélé region (Assoukoko, Diguengue, Yégué, Dikpeleou, etc.).

In this paper, we focus on describing the diversity patterns (species richness, abundance, dominance, evenness) and the assembly rules (Gotelli 2001; Gotelli and McCabe 2002) of rodents in a suite of habitat types within a Dahomey Gap savannah area of western Togo, the Fazao-Malfakassa National Park (hereby FMNP). Following the conclusions by Amori et al. (2021), we applied a multidisciplinary approach to evaluate these ecological features of the rodent communities in FMNP, including trapping (with different types of live traps), transect surveys and face-to-face interviews with local persons.

More specifically, we aim at answering to the following key questions:

(i) How many sympatric rodent species do occur in the various habitat types of the FMNP?

(ii) Are there any differences in the assemblage characteristics and community metrics (dominance, evenness) of rodents in the different habitat types of this savannah area? We hypothesize that there should be a gradient effect between the various habitats: forest spots should be richer in terms of number of sympatric species and with communities more equiverse than savannah and anthropized/cultivated sites (e.g., Delcros et al. 2015; Luiselli et al. 2022).

(iii) Are the rodent assemblages non-randomly structured? That is, do the various sympatric species partition the available spatial niche? We hypothesize that rodent communities should be randomly structured at the study area given that a previous meta-analysis revealed little evidence for interspecific competition along the habitat niche axis in West African small mammals (Amori and Luiselli 2011; Rautenbach et al. 2014; Delcros et al. 2015).

(iv) What are the main conservation implications of our study for the management of rodent populations in the Dahomey Gap savannahs?

We used a suite of analytical methods (including multivariate analyses and null models with Monte Carlo simulations) to explore the above-mentioned key questions.

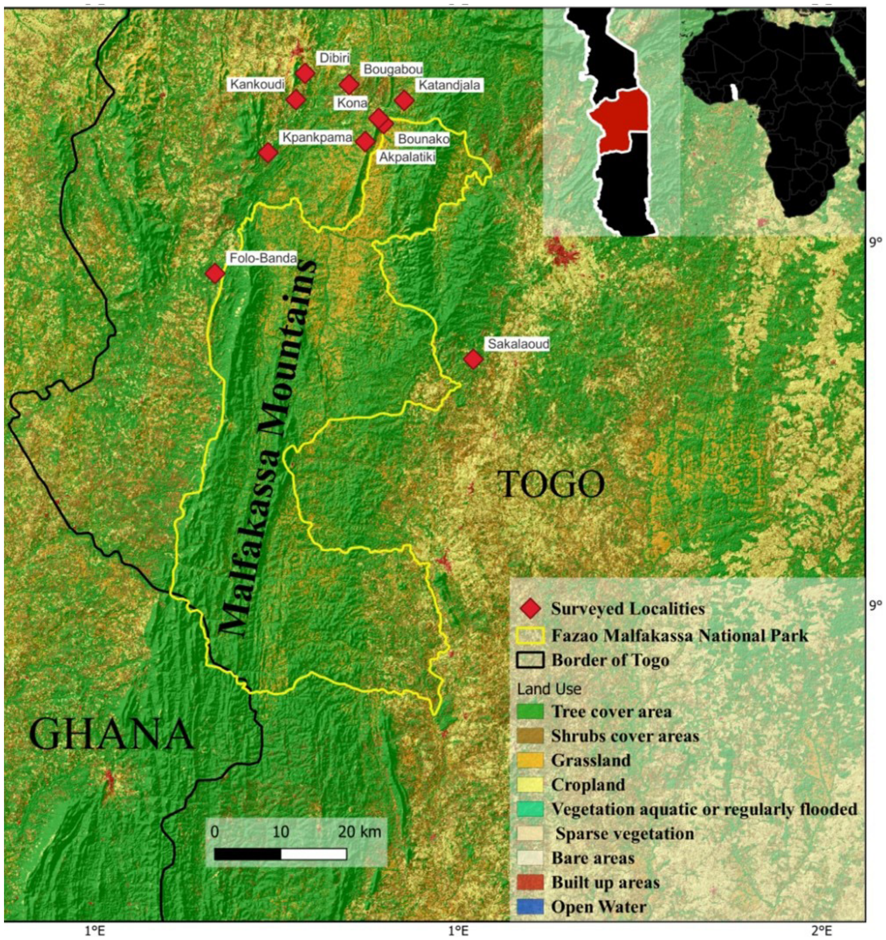
Materials and Methods

Study Area

FMNP extends between eastern longitudes 0 ° 36 "and 1 ° 2" and northern latitudes 8 ° 21 "and 9 ° 10" and covers an area of 192,000 ha, in the western part of the central region of Togo (Figure 1). It is located in the Guinea-Sudanese transition zone (Segniagbeto et al. 2017; Atsri et al. 2018), within the ecological zone II (Segniagbeto et al. 2017; Atsri et al. 2018). The territory is hilly and is dominated by the Fazao Mountains forming a rocky ridge all along the western edge, culminating at 813m elevation.

The FMNP soils are mainly ferruginous and

Figure 1: Map of Togo showing the main study areas in the surroundings of the Fazao Malfakassa National Park, and the landuse patterns of the surveyed territory.



tropical ferrous, and its main vegetation is a mosaic of savannahs and forests (Atsri et al. 2018). The habitats within the park are diverse, and consist of patches of open forests with *Isoberlinia doka* and *Anogeissus leiocarpus* as dominant species, dry forests dominated by *Detarium microcarpum* and *Monotes kerstingii*, gallery forests with *Berlinia grandiflora*, *Afzelia africana,* and *Daniellia oliveri* , and wide savannahs. These savannahs are dominated mainly by species of the Andropogonae subfamily but also by grass species of the genus *Hyparrhenia* (Astri et al., 2018). The hilltops are mainly covered by *Parinari curatellifolia*, *Crossopteryx febrifuga* and *Pteleopsis suberosa* (Atsri et al. 2018). The climate is hot and humid and is characterized by a rainy season from April to October and a dry season from November to March. The average annual temperature is around 25°C and the total rainfall varies between 1,200 and 1,500 mm (Adjoussi 2000).

Fieldwork was limited in the northern part of Fazao-Malfakassa National Park, in the patches of territory belonging to the villages of Bounako, Kona, Bougabou, Kankoudi, Sakalaoudè, Akpalatiki, Folo-Banda, Katandjala, Kpankpama and Dibiri (Figure 1).

Protocol

The field study was based on a multidisciplinary approach, including (i) face-to-face interviews with local persons, (ii) transect surveys (for detecting squirrels and large rodents) and (iii) live-trapping sessions.

Face-to-face interviews were carried out in the villages of Bounako, Kona, Bougabou, Kounkoudi and Dibiri. In total, 100 local persons were interviewed. They were divided into nine groups of 7-13 persons per group, generally comprising the village chiefs and their notables, farmers, eco-guards, teachers and gravel vendors. Each group was subjected to 11 questions, made in the local language (Kotokoli) to facilitate communication (Appendix 1). Photos of the different species from a small mammal field guide (De Visser et al. 2001) were shown to the respondents to choose those they often encounter in their area. On average, the interview survey lasted 20 minutes per group.

Field survey using the recce method, with the help of eco-guards, were carried out in January 2019 and between January and July 2020. To apply the recce method, we formed teams of two people supported by two experienced trackers to reduce noise. Because of logistic constraints, we could not open line transects for this study. Instead, recces were conducted following the paths already created by local hunters. Observation work started very early in the morning (04h to 11h) and/or in the late afternoon (15h to 19h). The beginning start and end of the censuses were noted to calculate the observation effort as well as the number of kilometres travelled. The team walked at an average speed of 1 km/h searching for signs of mammal activity. When a rodent individual was encountered, the following information was recorded: species, time, GPS location, group size and structure, behaviour and habitat type. Other presence indicators were also considered e.g. footprints, faeces, carcasses, etc.

Live trapping was carried out during the rainy season from July 20 to 31, 2020, in each habitat type (see below for the description of the various habitats). We selected this period because the beginning of the rainy season is by far the best period of the year to trap small mammals in tropical West Africa (Amori and Luiselli 2011). Fifty live traps were used, out of which 6 Sherman traps (aluminum traps measuring 9 x 7.5 x 23 cm) and 44 home-made traps (mesh and wooden traps measuring 10 x 10 x 30 cm) (Online Supplementary Figure S1). Due to logistic constraints (poor accessibility to various sectors of the park due to flooding of rivers and the very high vegetation during this period of data collection), the trapping sessions were carried out in only three sectors (Bounako, Akpalatiki, Kankoudi). Akpalitiki sector was partially anthropized with fields of corn, sesame and cassava, and with grassy plots and many *Vitellaria paradoxa* trees. In Bounako, there was a mosaic of vegetation ranging from teak plantations through gallery forest to grassy savannas. Kankoudi was a mainly savannah area, with the grass cover being very dense. In each locality, we placed 21 traps (including 3 Shermans), that were set between 4:00 p.m. and 5:00 p.m. for six consecutive trapping nights. Akpalatiki and Kankoudi sectors were sampled simultaneously. Due to the insufficient number of traps available, Bounako was sampled after sampling the first two localities. We used a mixture of peanut butter and roasted peanut seeds as bait. The traps were checked every day in the morning between 7:00 a.m. and 8:00 a.m. and the baits were renewed. The traps that captured any rodent individual were delicately emptied into a jar containing cotton wool soaked in ether to anesthetize the animal. The live specimens collected were photographed for later identification. The specimens were also anesthetised to take their external morphometric measures (with a calliper with 1 mm precision) and body weight. The following morphometric data (in millimetres) were collected: head and body length (LTC), tail length (LQ), ears length (Or), and hind leg length (Pp). These morphological data were not used in the present paper. The GPS coordinates of each trap, and of each eventually captured rodent individual, were recorded, and the habitat type of each captured individuals was recorded. Specimens were identified on the basis of their morphological and morphometric characters using the keys and descriptions provided in De Visser et al. (2001) and Granjon and Duplantier (2009).

Recce transects and live trapping were carried out along a gradient of five habitat types with different tree coverage density (Figure 2):

(a) Gallery forest, with at least 50% of the landscape being covered by large trees (*Detarium microcarpum* , *Monotes kerstingii*, *Berlinia grandiflora*, *Afzelia africana, Daniellia oliveri,* etc.).
(b) Wooded savannah, similar as the previous habitat but with tree coverage of 30-49%, and the remaining landscape being dominated by grassy vegetation.
(c) Shrub savannah, with less than 10-29% of tree coverage and with large trees being essentially isolated or in small groups; shrubs and bushes covering at least 30% of the landscape.
(d) Grassy savannah, with 0-9% of tree coverage, and with shrubs and bushes covering less than 30% of the landscape.
(e) Plantation/urban, with at least 60% of the landscape with human settlements and plantations (cassava, etc).

In order to minimize biases in data gathering, trapping sessions, number of trap-days and recce transects were arranged in such a way that there was a nearly even field effort across habitat types and study sites.

Figure 2. Photos of the trap types and the habitats where rodents were studied at the study areas in western Togo

Data analysis

Trapping efficiency was evaluated by considering both the trapping effort and the trapping success (%) according to the following formulas (Souttou et al. 2012):

$$\text{Trapping effort} = \textit{number of trapping nights} \times \textit{number of traps used}$$

$$\text{Trapping success (\%)} = \frac{\textit{total number of specimens caught}}{\textit{total number of trapping nights}} \times 100$$

We performed individual rarefaction curves to evaluate the completeness of the samples done for each habitat type and for each study station. This module estimates how many taxa you would expect to find in samples with a smaller total number of individuals (Krebs 1989). In other words, by this method it is possible to read out the number of expected taxa for any smaller sample size.

The dissimilarity among rodent species in terms of clustering of the centroids of the various species with habitat associations, was evaluated by Canonical Correspondence Analysis. In order to illustrate patterns of species composition, evenness and dominance, and to interpret diversity patterns among the stations and/or habitat types, we calculated the following univariate metrics (Magurran 1983; Hammer 2012):

(1) Number of observed taxa (*S*); this is the total number of species directly observed (in recce transects or in live traps) in each station/habitat type.

(2) Total number of individuals (*n*); this is the total sample size, with all species pooled, that was recorded at each station/habitat type.

(3) Dominance index:

$$D = 1\text{-}Simpson\ index$$

with this index ranging from 0 (all taxa are equally abundant) to 1 (one taxon dominates the entire community).

(4) Shannon's index, varying from 0, for communities with only a single taxon, to high values, for communities characterised by many taxa but each having few individuals:

$$H' = -S(fr) \times [ln(fr)]$$

where *S* is the total number of rodent species recorded, $fr = n/N$, with *n* is the number of individuals of each species in each habitat type and *N* is the total number of individuals of each species in the study area.

(5) Pielou's Evenness index, calculated as:

$$e = H'/H_{max}$$

where:

$$H_{max} = lnS$$

with *H'* representing Shannon's index, and *S* the total number of rodent species recorded. H_{max} corresponds to the maximum value of diversity (i.e., when all species are equally represented in our samples).

(6) Chao-1 index:

$$\text{Chao-1} = S + F1(F1 - 1)/(2\ (F2 + 1)$$

where *F1* is the number of singleton species and *F2* the number of doubleton species. A singleton is a species occurring only once in the total sample, and doubleton is a species occurring just twice in the total sample. This index was used in order to predict the theoretical number of sympatric species that can occur at a given site/habitat type on the basis of the performed field effort.

In order to explore the community structure (i.e. the occurrence of non-random resource partitioning patterns between sympatric species) of rodents by site and by habitat type, we calculated Pianka's (1986) overlap formula on the study assemblages based on the raw number of captured individuals. In this formula, values close to 0 (no overlap) would indicate resource partitioning and hence competitive structure, whereas values close to 1 (total overlap) would suggest an aggregated use of the available resources and hence no competition (Pianka, 1986). In the original data matrices, each row represented a different species in the assemblage being analysed, and each column represented a different habitat-type, or locality of trapping, category. The original species utilization matrices from which Pianka's overlap was calculated were randomized by shuffling the original values among habitat (or sites) resource states, with 30,000 random Monte Carlo simulations (=null matrices) of the original observed matrix being generated by EcoSim 7.0 software. Each of these null matrices was built using two randomization algorithms (RA2 and RA3) after Lawlor (1980), using the same methodology as in Amori and Luiselli (2011). Niche overlap values were calculated for each of these randomly generated matrices, thus obtaining a mean overlap value (with associated variance estimates) resulting from the simulated null matrices. Overlap values from the observed dataset were then compared with the simulated mean overlap values, and the nonrandom (= competitive) structure of the community was assumed when P(observed ≤ expected) = 0.05 or less (Gotelli and Graves 1996). In all cases, equiprobable habitat resource use was assumed a priori in the analyses.

Statistical analyses were performed by PAST 4.0 (Hammer 2012) and SPSS version 20.0 (Levesque 2007) softwares, and the Monte Carlo simulations with EcoSim 7.0 software (Gotelli 2011), with all tests being two tailed and alpha set at 5%.

Results

The list of species previously recorded from the study area (Amori et al., 2016) is given in Appendix2. Based on this bibliographic evidence, a total of 15 rodent species, divided into four families and ten genera, were expected to be present in the FMNP.

Interviews

During the interview surveys about 77% of respondents indicated that *Dendromus messorius, Arvicanthis niloticus*, *Xerus erythropus* and *Cricetomys gambianus* were the most frequently captured rodents, that mirrored the fact that these species were indeed captured at all sites during our surveys (Table 1). 23% of the interviewees stated that they did not notice any predominance of one rodent over another. *Aethomys stannarius, Arvicanthis niloticus* and *Protoxerus stangeri* are becoming increasingly rare in catches according to 78% of the interviewees, whereas 22% of them declared that they did not notice an increased rarity of any species.

During the dry season, the number of rodents captured by trapping night was between 1 and 5 according to 49% of respondents, while 21% affirmed that this number was between 6 and 10; 7% between 11 and 15; and 23% did not report any precise number. During the rainy season, 25% of interviewees affirmed that they did not capture any rodents by trapping night, while 75% of them reported this number being below 5. Thus, there was a consensus for a higher amount of rodents caught routinely during the dry season.

Community composition

Overall, with a trapping effort of 378 trap nights at a rate of 126 trap nights per site, we captured 208 individuals belonging to 20 rodent species, distributed in 6 families and 17 genera (Table 2), with an overall trapping success of 6.88%. The number of sympatric species per study area varied between 5 and 18 (Table 1) and averaged 13 ± 4.9. The number of strictly sympatric species per habitat type varied between 4 and 14 (Tables 2 and 3) with a mean of 7.6 ± 4.3. Overall, there were three singletons (*Aethomys stennarius, Gerbilliscus kempi, Mus musculus*) and one doubleton (*Praomys deeroi*). *Aethomys stennarius* was the first country record for Togo (see Amori et al., 2016).

The distribution of the captures of the various species in the five habitat types is given in Table 2. A rarefaction analysis based on the relationships between captured samples (= number of individuals captured per habitats) and number of discovered taxa

Table 1: List of the rodent species recorded in the various localities of Fazao Malfakassa National Park.
+ = ascertained presence

Family	Species	Locality				
		Kona	Bougabou	Konkoudi	Bounako	Dibiri
Sciuridae	*Funisciurus leucogenys* (Waterhouse, 1842)	+	+	+	+	
	Funisciurus substriatus De Winton, 1899	+	+	+	+	
	Heliosciurus gambianus (Ogilby, 1835)	+	+	+	+	
	Heliosciurus rufobrachium (Waterhouse, 1842)	+	+	+	+	
	Paraxerus poensis (A. Smith, 1830)	+	+	+	+	
	Protoxerus stangeri (Waterhouse, 1842)	+	+	+	+	+
	Xerus erythropus Desmarest, 1817	+	+	+	+	+
Hystricidae	*Hystrix cristata* Linnaeus, 1758	+	+		+	
Thryonomyidae	*Thryonomys swinderianus* (Temmink, 1827)	+		+	+	
Nesomyidae	*Cricetomys gambianus* Waterhouse, 1840	+	+	+	+	
	Dendromus messorius Thomas, 1903	+	+	+	+	+
	Steatomys caurinus Thomas, 1912			+	+	+
Muridae	*Gerbilliscus kempi* (Thomas, 1897)	+				
	Aethomys stannarius (Thomas, 1913)	+				
	Arvicanthis niloticus (E. Geoffroy, 1803)	+	+	+	+	+
	Lemniscomys zebra (Heuglin, 1864)	+	+	+		
	Mus musculus Linnaeus, 1758				+	
	Rattus rattus (Linnaeus, 1758)	+	+			
Anomaluridae	*Anomalurus beecrofti* Fraser, 1853	+			+	
	Anomalurus derbianus (Gray, 1842)	+			+	

Table 2. Synopsis of the total number of individuals, captured or seen during recce transects, for the various rodent species, in relation to the habitat types at the study area

	Symbol	Habitat types				
		wooded savannah	shrub savannah	grassy savannah	plantations/urban	gallery forest
Aethomys stannarius	AES	0	0	0	0	1
Arvicanthis niloticus	ARN	9	0	0	0	0
Gerbilliscus guineae	GEG	0	0	0	0	1
Gerbilliscus kempi	GEK	0	4	0	0	0
Lemniscomys zebra	LEZ	3	0	0	0	0
Mastomys erythroleucus	MAE	0	0	1	0	0
Mastomys natalensis	MAN	8	0	0	0	0
Mus (Nannomys) haoussa	NAH	6	0	0	0	0
Mus (Nannomys) setulosus	NAS	1	0	0	0	0
Mus musculus	MUM	0	0	0	1	0
Praomys derooi	PRD	1	0	1	0	0
Rattus rattus	RAR	0	0	0	6	0
Taterillus gracilis	TAG	13	0	0	0	0

Cricetomys emini	CRE	0	0	0	0	3
Cricetomys gambianus	CRG	0	0	0	26	0
Dendromus messorius	DEM	16	0	0	0	0
Steatomys caurinus	STC	0	9	0	0	0
Thryonomys swinderianus	THS	0	0	0	22	1
Hystrix cristata	HYC	2	3	0	0	0
Funisciurus anerythrus	FUA	0	0	0	0	4
Funisciurus leucogenys	FUL	0	0	0	0	4
Funisciurus substriatus	FUS	0	0	0	0	5
Heliosciurus gambianus	HEG	0	3	0	0	8
Heliosciurus rufobrachium	HER	0	0	0	0	4
Paraxerus poensis	PAP	0	0	0	0	4
Protoxerus stangeri	PRS	0	2	4	0	9
Xerus erythropus	XEE	1	3	3	0	6
Anomalurus beecrofti	ANB	0	0	0	0	4
Anomalurus derbianus	AND	0	0	0	0	6
TOTAL		60	24	9	55	50

Table 3. Synthesis of the diversity indices calculated for each surveyed habitat type in Fazao Malfakassa National Park, Togo

	grassy savannah	Lower	Upper	shrub savannah	Lower	Upper	wooded savannah	Lower	Upper	plantations/ urban	Lower	Upper	gallery forest	Lower	Upper
Species richness	10	9	10	6	5	6	4	4	4	4	4	4	14	14	14
No. Individuals	60	60	60	24	24	24	9	9	9	55	55	55	60	60	60
Dominance	0.1728	0.1444	0.2211	0.2222	0.184	0.3819	0.3333	0.2593	0.4815	0.3957	0.3421	0.4704	0.09278	0.08611	0.125
Simpson	0.8272	0.7789	0.8556	0.7778	0.6181	0.816	0.6667	0.5185	0.7407	0.6043	0.5296	0.6579	0.9072	0.875	0.9139
Shannon	1.935	1.764	2.071	1.653	1.258	1.738	1.215	1.003	1.369	1.035	0.8905	1.17	2.478	2.316	2.529
Evenness	0.6925	0.6062	0.8012	0.8707	0.6215	0.9473	0.8425	0.6814	0.9828	0.704	0.6091	0.8054	0.8512	0.7237	0.8958
Chao-1	11.5	9	16	6	5	7	5	4	7	4	4	4	17	14	20

in each study area (Figure 3A) and in each habitat type (Figure 3B), revealed that the species richness was adequately described by our study. This pattern was also highlighted by Chao-1 estimates indicating that the number of theoretically expected species per habitat was very close to that effectively observed by us in the field (Table 3). There was a clear gradient pattern in the univariate diversity indices by habitat type: Dominance index was remarkably higher in Urban/plantation than in the other habitat types whereas Evenness index was remarkably higher in gallery forest than in the other habitat types (Table 3).

A Canonical Correspondence Analysis revealed that 89.2% of the total variance was explained by the first three axes (Axis 1: 34.6%, Axis 2: 32.8%, Axis 3: 21.8%), and that three "ecological groups" (= guilds) of species were formed: a group from wooded habitats (savannahs and semiforests), a group from grassy savannah and a group from urban/plantation habitats (Figure 4). However, two species (*Hystrix cristata* and *Praomys derooi*) were not attributable to any well defined habitat type, and are therefore excluded from further null model analyses.

Null model analyses

The mean observed niche overlap for habitat types among species was 0.294, whereas the expected niche overlap for the RA3 algorithm was

Figure 3. Saturation curves (including upper and lower 95% Condifence Intervals) showing the number of newly encountered rodent species in relation to the number of captured individuals in each study station (a) and habitat type (b).

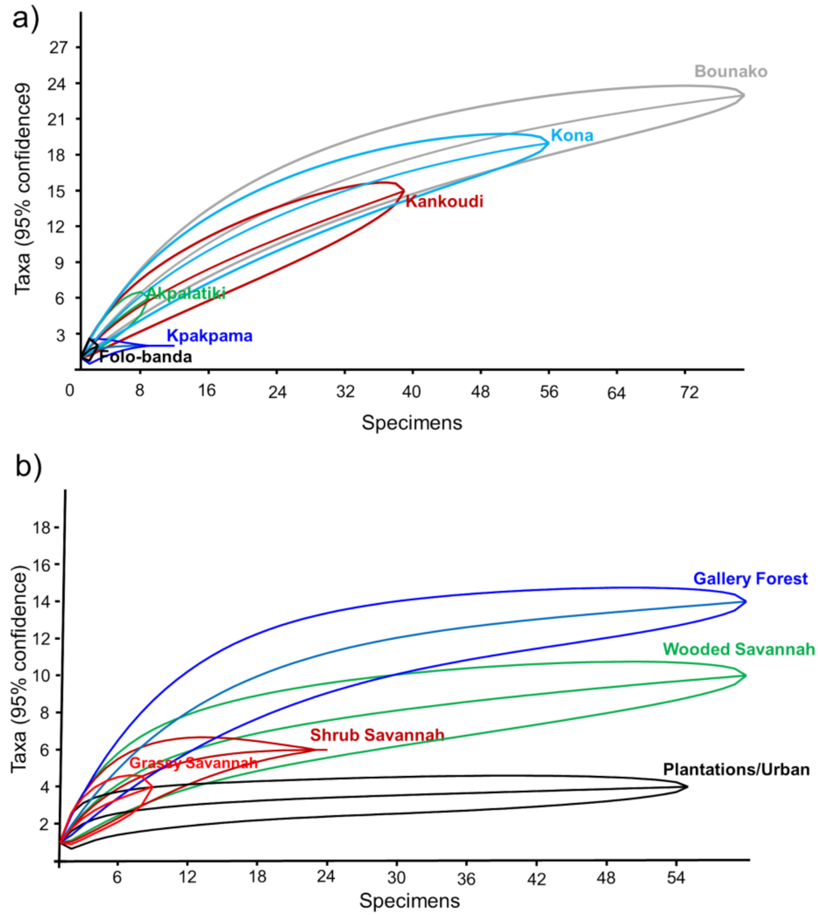
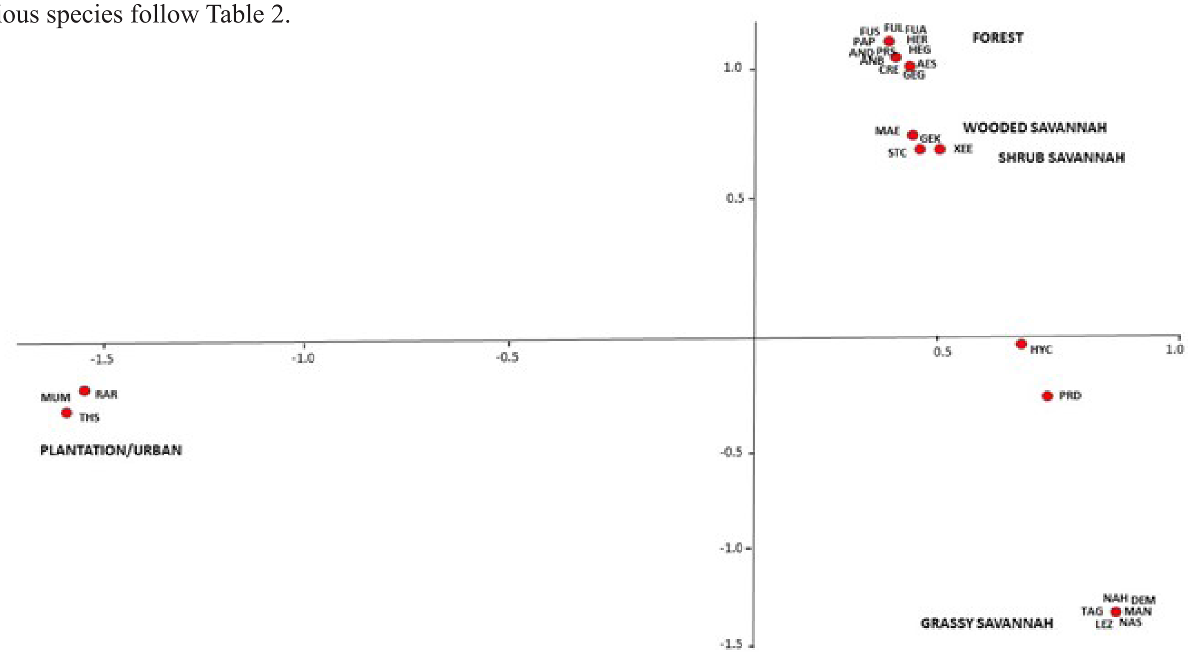


Figure 4. Output of a Canonical Correspondence Analysis showing the clustering among the centroids of rodent species and habitat associations at the study area in western Togo. For more details, see the text. Red dots would indicate species, and blue dots would indicate the habitat categories from which the various individuals were captured. Symbols for the various species follow Table 2.



0.234 (Variance = 0.00035). RA3 algorithm revealed a non-random congregated resource use in the studied rodent assemblages for the habitat type simulations ($P_{(obs.\leq exp.)}$= 0.99, $P_{(obs.\geq exp.)}$= 0.01), whereas RA2 algorithm (simulated mean overlap = 0.171, variance = 0.00005) revealed no structure at all ($P_{(obs.\leq exp.)}$= 0.909, $P_{(obs.\geq exp.)}$= 0.091).

A similar output was observed also when analysing the rodent assemblage structure by locality. In this case, the mean observed niche overlap was 0.486, whereas the expected niche overlap for the RA3 algorithm was 0.277 (variance = 0.00022). RA3 algorithm revealed a non-random congregated resource use in the studied rodent assemblages for the localities simulations ($P_{(obs.\leq exp.)}$= 0.999, $P_{(obs.\geq exp.)}$= 0.001), whereas RA2 algorithm (simulated mean overlap = 0.456, variance = 0.00071) revealed no structure at all ($P_{(obs.\leq exp.)}$= 0.897, $P_{(obs.\geq exp.)}$= 0.103).

Discussion

How many rodent species do occur in the FMNP?

Our surveys uncovered a total number of species (n = 20) that is higher compared to the species richness as that earlier reported and / or confirmed in the area (n = 15) by Amori et al. (2016), although the field effort during the present study was relatively limited. This discreparcy would be explained by the suboptimal knowledge about rodents and their distribution in this part of Africa, including a relatively low number of available vouchers in museum collections worldwide. Indeed, Amori et al. (2016) based their checklist essentially on museum vouchers, whereas no surveys explicitly focused on rodents were carried out in Togo either by them or by any other scientific team at the time of their article.

Among the species that have been caught by us but not reported by Amori et al. (2016), we can mention *Dendromus melanotis* and *Aethomys stannarius*. These species are even well known to the inhabitants of the surveyed villages that call them respectively, in Kotokoli language, Kople and Adjodji. *Dendromus melanotis* is a typical plantation species, that frequently occurs in banana plants in farmlands and in sweet potatoe fields, as well as in holes in trees, in fissures, cracks and trunks of trees in gallery forest, and orange trees (Happold 2016). However, in Cameroon this species has been recorded in grassy areas (Rosevear 1969), similarly to our study. *Aethomys stannarius* was never recorded in Togo before, but in the Guinea savannah of northern Nigeria where the general habitats is nearly identical to that of the study area and that is in continuity from the habitat type point of view. Previous studies indicated that grassland, woodland savanna, bush, cultivated areas and forest edges where there is moderate to dense cover are the primary habitats for this species (Happold 2016). Interestingly, some of the species cited by Amori et al. (2016) for the study area were not recorded during the present study. It is likely that these species escaped our sampling due to their elusive habits and of the fairly short time in which our research was carried out, and perhaps also because of a seasonality in their rhythms of activity not coinciding with our period of field research. However, the case of *Mastomys natalensis*, that should have been present in the study area (Amori et al. 2016) but neither observed by us nor apparently known to local populations, is noteworthy. In fact, *Mastomys natalensis* is a potential reservoir for the Lassa virus (Houéménou et al., 2019), and its presence in the area should have not been passed unknown if really present.

Overall, our study revealed a remarkable diversity of rodent species at FMNP. This evidence could be explained by the substantial variability of habitats found in this area, from gallery forests, open forests, wooded savannas, grassy savannas, artificial teak plantations and suburbs. Also, the presence of the rangers and the forest checkpoint in Bounako would play a strong dissuasive role in the exploitation of wild animals in general and the destruction of micro-habitats. This site deserves special attention of the authorities in charge of park management not only because of its rich biodiversity, but also because of the presence of several rodents that are potentially reservoirs of dangerous viruses for human health. It would indeed constitute one of the key areas in the possible establishment of ecological monitoring and epidemiological monitoring protocols for the park.

Are there any differences in the assemblage characteristics and community metrics of rodents in the different habitat types?

Our data revealed a clear habitat gradient effect in the community metrics: evenness, Shannon's diversity, Chao-1 and species richness increased from suburbs to gallery forest, whereas the dominance index showed an opposite pattern. Although these patterns were hypothesized a priori, as far as we are concerned it is the first time that they have been demonstrated on small mammalian communities of habitat gradients of the Dahomey Gap. A virtually identical pattern has been highlighted in lizard communities along the suburb-savannah-forest gradient of the Dahomey Gap (Luiselli et al. 2022), and it is therefore plausible that it is repeated almost constantly with other vertebrate and invertebrate taxa. Indeed, rodent species composition was significantly correlated with grass height, tree density, and ground cover in another South African savannah area (Delcros et al. 2015). The higher rodent species richness in gallery forest than all other habitats surveyed in FMNP conforms to what is expected, since it is well known how much higher the species richness of tropical forests was than any other terrestrial ecosystem in the world. (e.g. see Ashton 1989). Moreover, gallery forest is clearly the most heterogeneous habitat type in FMNP in terms of plant diversity, microniche availability and structural features, and species richness is also correlated with habitat heterogeneity in mammals (Kerr and Packer 1997) and other animals (Báldi 2008; St Pierre et al. 2014).

In contrast with our results, a study on rodents from arid savannahs in Senegal revealed that diversity and abundance of species was higher in anthropized than in natural habitats (Konečný et al. 2010). In addition, a study on medium and large mammals in the Dahomey Gap highlighted the existence of effects (i) species-area and (ii) of the position of the forest patches themselves (relative to human settlements and rivers) with regard to the species diversity and community metrics of fragmented forests (Segniagbeto et al. 2022). Our data cannot evaluate whether effect (i) does apply to rodents too. However, the effect (ii), i.e. a depression of both the specific diversity/richness and on the community evenness with increasing proximity to human settlements and increasing distance from watercourses, was also confirmed by the present study. In fact, gallery forests, which grow right along waterways, were found to be the richest habitats of small mammal species.

Are the rodent assemblages non-randomly structured?

We found a mean number of sympatric species in the FMNP savannahs (7.6) that is remarkably similar to that (6.33±3.8) reported by Amori et al. (2021) for West African savannahs in general, with the highest number observed by us (14) nearly identical to that (15) observed by Amori et al. (2021). These similarities suggest that the West African savannah habitats are homogeneous in terms of available resource and productivity, showing consistently similar rodent communities throughout the whole region/vegetation zone. Interestingly, the same "generalized" homogeneity in the number of sympatric species was also observed in West African savannah turtles (Luiselli et al. 2020; Gbewaa et al. 2021).

Most of our null models revealed random community structure for rodents at FMNP, and none of the null models uncovered a significant resource partitioning pattern among the sympatric species in any of the studied habitats. Therefore, our results are in good agreement with those obtained by other studies using null model analyses of community structure of African small mammals (Amori and Luiselli 2011; Delcos et al. 2015). Our null model analyses also revealed that grassy savannahs and gallery forests are habitat types where species tend to congregate, possibly because food and shelter availability may be higher. We tentatively suggest that there may be higher resource availability for these two habitat types than for the other habitat types available in the study area, but we have no firm data to demonstrate this point. However, it is likely that seasonal variations in rainfall may influence remarkably the observed patterns. Clumping of species in particular habitat and / or resource types may occur, despite strong competition, because abundances of each species within these clumped habitat classes is low, relative to more dispersed habitat classes. This pattern was demonstrated for clumped distributions around particular body sizes (Holling 1992) and could not be totally ruled out in our study case. Although there is no evidence from our study that interspecific competition for the habitat niche is a prevalent assembling force in rodent communities from West African savannahs, the occurrence of food resource partitioning cannot be ruled out as it has been observed, using stable isotopes, in South Africa (Codron et al. 2015).

What are the main conservation implications of our study for the management of rodent populations in the Dahomey Gap savannahs?

As sampling only takes place on the periphery of the FMNP for relatively short periods and in the rainy season only, the list of small non-flying mammals presented at the end of this study is obviously not exhaustive. It would be desirable to increase the sampling effort while increasing the number of sampling sites and covering all seasons. Our surveys were unsuccessful in recording the enygmatic Togo mouse *Leimacomys buettneri*, a forest species that was never found since 1890, and that may be even extinct (Amori et al., 2016). This species was also clearly unknown to all the interviewees of our surveys. Therefore, we consider it unlikely that this species is present in the study area. For the next decade, field surveys should be continued by increasing the trapping effort and increasing the sampling sites in the FMNP, especially in the Bismarkburg area where *Leimacomys buettneri* was captured and described.

In conservation terms, all species identified in this study have an IUCN status of Least Concern (LC). However, at the local scale, human pressure including hunting and degradation of micro-habitats (especially in gallery forests and in wooded savannah) by agriculture and wildfires could make these species declining if nothing is done. Therefore it seems necessary that the communities living around the FMNP are involved in land management, with special control to deforestation phenomena at the local level, which certainly can negatively affect rodent populations on a local scale.

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Conflicts of interest

The authors declare no conflict of interest.

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SUPPLEMENTARY MATERIALS

Appendix 1: Form of the questionnaire used in this study for the face-to-face interviews

Nom de l'observateur :	Référence de la fiche :	Date de la pose des pièges :
Nom du site :	Altitude	Longitude
Nom du secteur :	N° de station	Nombre de pièges
Type de végétation Forêt dense Forêt claire Savane Prairie		Saison
Espèces végétales dominantes ou caractéristiques		

Date	Nombre de pièges	Nombre de pièges Déclenchés	Nombre de pièges Disparus	Nombre d'individus capturés

Numéro de la fiche : **sexe :** **Age :** **Profession :** **Lieu de résidence** :

Q1-Rencontrez-vous souvent des rongeurs dans votre localité ?	a-Oui b-Non
Q2-Quels sont les types de rongeurs que vous rencontrez ?	
Q3-Avez-vous une fois capturé les rongeurs ?	a-Oui b-Non
Q4-Pourquoi les capturez-vous ?	a-Pour les consommer b-Pour les vendre c-Autres
Q5-Par quels moyens vous les capturez ?	a-Piégeage b-Battue c-Empoisonnement c-autres

Q6-Quels sont les types de rongeurs que vous capturez	a- lors des battues? b-lors des piégeages ? c-Lors de l'empoisonnement ? d- lors des travaux champêtres ? e-Autres ?
Q7-Quels sont les meilleurs moments de capture ?	
Q8-Combien d'individus capturez-vous souvent en bonne saison ?	1-lors des battues ? a)1-5 b) 6-10 c)11-15 d>15 2-lors des piégeages ? a) 1-5 b)6-10 c)11-15 d>15 3-Lors de l'empoisonnement ? a) 1-5 b) 6-10 c) 11-15 d>15 4- lors des travaux champêtres ? a)1-5 b) 6-10 c)11-15 d>15
Q9-Combien d'individus capturez-vous souvent en mauvaise saison ?	1-lors des battues ? : a) Rien b)1-5 c) 6-10 d) 11-15 e) >15 2-lors des piégeages ? : a) Rien b) 1-5 c) 6-10 d) 11-15 e) >15 3-Lors de l'empoisonnement ? a) Rien b) 1-5 c) 6-10 d) 11-15 e) >15 4- lors des travaux champêtres ? a) Rien b)1-5 c) 6-10 d) 11-15 e) >15
Q10-Quels rongeurs capturez-vous fréquemment ?	
Q11-Quels rongeurs capturiez-vous avant et que vous ne capturez plus ?	

Appendix 2: List of predicted rodent species in and around the PNFM according to Amori et al. (2016)

Order	Family	Genus	Species
RODENTIA	HYSTRICIDAE	*Hystrix*	*Hystrix cristata*
	MURIDAE	*Gerbilliscus*	*Gerbilliscus kempi*
		Leimacomys	*Leimacomys buettneri*
		Lemniscomys	*Lemniscomys zebra*
		Mastomys	*Mastomys natalensis*
		Praomys	*Praomys daltoni*
			Praomys misonnei
		Uranomys	*Uranomys ruddi*
	NESOMYIDAE	*Cricetomys*	*Cricetomys gambianus*
	SCIURIDAE	*Funisciurus*	*Funisciurus leucogenys*
			Funisciurus pyrropus
			Funisciurus substriatus
		Heliosciurus	*Heliosciurus gambianus*
		Protoxerus	*Protoxerus stangeri*
		Xerus	*Xerus erythropus*