Lizard community structure and spatial resource use along a forest-savannah-urban habitat gradient in the Dahomey Gap (West Africa)

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Abstract

Studies of animal communities along habitat gradients are useful in understanding the ecologicsl factors affecting species diversity and richness. Almost no investigations have been carried out on the community structure of vertebrate groups along habitat gradients modified by humans in historical or prehistoric times. Here, we analyze the community structures of lizards in suburban Lomé (Togo) and compare these with nearby savannah and forest sites using various statistical methods. We recorded a total of 25 lizard species in all sites. There was a heavy reduction in species richness from forest (18 taxa) to savannah (13) to suburbs (9); 24% of the species occurred in all habitat types, 40% solely in forest, and only two were found exclusively in suburban habitats. Suburban habitat types were relatively homogeneous in the number of observed species (maximum number of taxa per habitat = 6). There were significant interspecific differences in substratum type preferences and vertical spatial niche among species, but no evidence of nonrandom niche partitioning. There was a nonrandom "clustered" distribution of the various species along the available resource categories, indicating that species-specific preferences instead of community-driven mechanisms are more likely to explain the observed patterns. We conclude that lizard communities in tropical cities are (i) less species-rich than in the surrounding more natural habitats, (ii) usually clustered into specific habitat/substratum types (often artificial ones), and (iii) not assembled through competitive interactions.

Keywords Sauria · Togo · Niche partitioning · Habitat use · Community ecology · Ecological gradients

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Introduction

Studies of habitat gradients can inform community ecology theory because the environmental continuum may be a useful axis to understand how attributes of individuals generate structure at the community level (e.g. see Wellborn et al. 1996; Fu et al. 2007; Pillsbury and Miller 2008; Batteman et al. 2010; Ramírez-Bautista and Cruz-Elizalde 2013; Cruz-Elizalde et al. 2016; Khatiwada et al. 2019). Community structure across a given gradient may be determined by a number of factors that limit the potential breadth of species distributions. For instance, physical factors may affect the potential breadth of species distributions (e.g. proximate ecophysiological performances; see Barbault and Stearns 1991; or habitat characteristics, e.g. Avila et al. 2017). Also, biotic effects mediated by ecological interactions, such as predation (Nurminen et al. 2018; Freestone et al. 2020) and interspecific competition (Pianka 1986; Salinas-Ramos et al. 2020; Powell et al. 2021), as well as by landsdcape modifications at both the medium and small spatial scales (e.g.

Berriozabal-Islas et al. 2018), may be important. These studies can be even more informative when the habitat gradient also includes deforested areas or urban zones (Cruz-Elizalde et al. 2014, 2016). Traditional, site-specific agroecosystems and grazing may heavily affect the community structure and species richness of animals (e.g. Lara-Tufiño et al. 2019) where crop area and management intensity are important factors (Badillo-Saldaña et al. 2020).

Most community structure studies along tropical habitat gradients have concentrated on habitats that have been modified by humans during recent times, for instance burnt versus non-burnt areas (Akani et al. 2018; Costa et al. 2020) or forest-plantation mosaics (Palmeirim et al. 2017; Supsup et al. 2020). However, few investigations have been carried out on the community structure of any vertebrate group across habitat gradients modified by humans in historical or prehistoric times. These types of studies may be important to better understand long-term effects of habitat characteristics on community dynamics. The Dahomey Gap in West Africa offers an excellent setting for such studies as it is: (i) a human-derived vegetation region that was created in historical times and (ii) is a savannah-like vegetation zone interspersed by patches of moist tropical forest. This human-derived vegetation zone extends all the way to the Gulf of Guinea coast in Benin, Togo, and Ghana, and separates the forest zone that covers much of the south of the region into two separate forest regions (the Upper Guinean forests and the Lower Guinean forests; Demenou et al. 2018). Although some researchers consider that the Dahomey Gap was created by deforestation during the late Holocene, others suggest this is a natural transitional vegetation zone between forest and savannah (see Demenou et al. 2018 for a discussion). Presently, the Dahomey Gap also includes myriad urban centres, with Accra (capital of Ghana), Lomé (capital of Togo) and Cotonou/Porto Novo (Benin) being the largest.

In this study, we analyze the community composition of sympatric lizards along a habitat gradient (defined as the gradual succession of three clearly different vegetation zones, forest-savannah-suburbs [hereby FSS]) in south-western Togo, inside the Dahomey Gap. We focus (i) on the taxonomical composition and species richness of lizards within each habitat type, and (ii) on their resource partitioning patterns along the spatial niche axis regarding the suburban habitat. We selected the suburban habitat for a more detailed resource partitioning study because this is the simplest habitat type in the Dahomey Gap in terms of number of sympatric species, thus allowing a simpler quantitative assessment and better understanding of community dynamics.

We examine the following key questions:

Are there any species richness differences among lizard assemblages inhabiting the various habitats in the FSS gradient? This question is relevant because there is empirical evidence for tropical forest communities, not only of lizards, being more species-rich than savannahs or deforested areas (Estrada et al. 1993; Addai and Baidoo 2013; Yeo et al. 2017), with no quantitative data available for the Dahomey Gap region.

If so, are the inter-habitat differences in species richness due to recent ecological factors (i.e. recent events of local deforestation) or to broad historical/biogeographical events at the West African scale? This question is important because the Dahomey Gap is considered an anthropogenic vegetation zone that originated thousands year ago (Iloh et al. 2017; Demenou et al. 2018; Leaché et al. 2020). Thus, more factors than just local factors may influence the observed community structure.

What are the main assembly rules of the studied lizard assemblages? Is interspecific competition for spatial niches an important determinant of the lizard community structure in the urban habitat? This question is relevant because it is easier to detect interspecific competition mechanisms in simple than in complex arenas, and thus a relatively simple natural scenario such as an urban ecosystem may help considerably our understanding on this issue.

To explore the three above-mentioned key questions, herein we analyze the general community characteristics with a special focus on (i) the community structure in the suburban area, (ii) the horizontal niche resource use, and (iii) the vertical niche resource use, and perform a simulations study to uncover the main reasons behind the observed patterns.

Materials and methods

Study areas and field protocol

To compare community composition of lizards across a gradient of habitat alteration (FSS), we used data from Segniagbeto et al. (2015) for forest and forest-derived savannah, supplemented by original opportunistic field observations (years 2013–2020). We compared these data with those we originally collected in the suburbs of Lomé (see below). The map of southern Togo, showing the various study areas, is given in Fig. 1. For forest, we considered the presence data of lizards for Missahohé, Agome Yo, Kpalimé and Agou, i.e. four hilly, adjacent sites situated near the border with Ghana in south-western Togo. These sites were characterized by a mosaic of mesophilic or semi-deciduous forests and savannahs where species such as *Berlinia grandiflora, Pseudospondias microcarpa*, *Uapaca guineensis*, *Khaya grandifoliola, Antiaris africana, Milicia excelsa, Triplochiton scleroxylon, Terminalia superba, Cola gigantea, Aubrevillea kerstingii,* and *Trilepisium madagascariensis* were especially dominant (Agbessi et al. 2021).
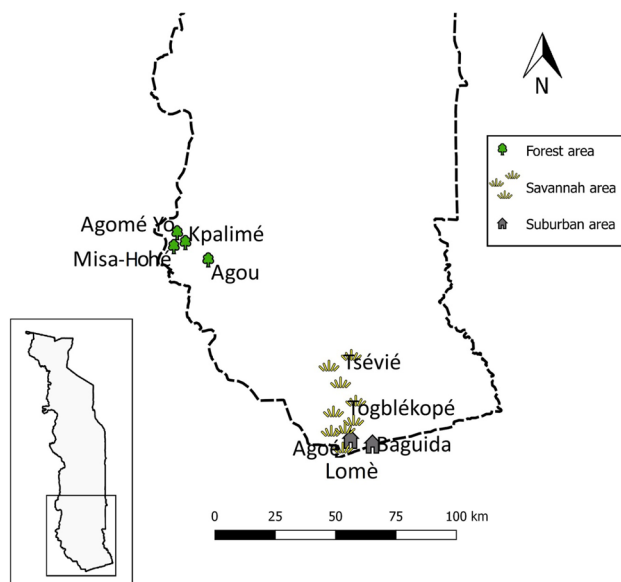
Fig. 1 Map of southern Togo, showing the various study areas

For forest-derived savannah, we considered the presence data of lizards at Tsévié, Tgblekope and Agoé, also situated in south-western Togo. The habitat in these sites was mostly grassland and shrubby savannah with common tree species being *Terminalia macroptera, Detarium microcarpum, Acacia polyacantha, Gardenia erubescens, T. laxiflora, Combretum glutinosum, Annona glauca, Pteleopsis suberosa, Strychnos spinosa, Securidaca longepedunculata* and *Sterculia setigera*.

The field study in the urban area was carried out in July–August 2013 and in July–August 2014 in a suburban area of Lomé (Baguida), the capital city of Togo, West Africa. Baguida is a residential area situated along the coast, at the western periphery of Lomé, nearby the city port and along the highway connecting Togo with Benin. Most green areas are small gardens and narrow strips of mainly ornamental plants along the coast and the touristic resorts. The climate of Togo is tropical, with a dry season from October to March, a wet season from April to September, but with a short period of relative short rains in August.

Suburban lizards were surveyed along random transects, by walking slowly by two–three researchers, passing through the Baguida landscapes, from about 0900-1200 h and 2000-2200 h, for a total of 21 field days in 2013 and 23 days in 2014. We did not undertake surveys during the middle of the day because lizards are relatively inactive due to the high ambient temperatures. We applied a Visual Encounter Survey (VES) in which we recorded any lizard observed at a distance from 10–150 cm. During the night, we used a flashlight (model Weltool T10) to examine the various substratum types and record lizards. For this analysis, we considered only the active above-ground individuals, so, we did

not consider those lizards (mainly *Agama agama*) that were observed while sleeping perched on walls, trees or other substrates (Amadi et al. 2020b, 2021).

Each observed lizard was identified to species and sex; however, *Hemidactylus angulatus* and *H. mabouia* were pooled due to their difficulty in indentifying the separate species in the field. We recorded habitat characteristics of each lizard along a horizontal and a vertical spatial axis (Rugiero et al. 2021). To evaluate the horizontal spatial resource use, we recorded the substratum in which each lizard was recorded (Rugiero et al. 2021). Lizard sightings were assigned to one of the following six substratum types depending on where they were perched at the time of sighting: 1) cement/asphalt, (2) grass, (3) trees/wood, (4) sand, (5) bushes, and (6) stone-piles. The availability of each substratum type was determined by eye by inspecting the relative area occupied by each habitat type in 1000 random spots of 5×5 m selected along the surveyed area. Horizontal spatial resource use, was determined as the height from the ground for each individual lizard at sighting. We defined five height categories: (a) on the ground (up to 10 cm height); (b) 11–50 cm height; (c) 51–100 cm height; (d) 101–150 cm height; (e) > 150 cm height.

Statistical analyses

We compared lizard community compositions among the three FSS gradient qualitatively as there was not sufficient numerical data in Segniagbeto et al. (2015) to allow any statistical analysis. The differences in frequencies of observed lizards by species and by substratum type, as well as within species (i.e. males versus females versus juveniles) and by substratum type, were assessed by a contingency table χ^2 test. Pearson's correlation coefficient was used to analyze the correlation between substratum type availability (independent variable) and number of observed lizards by species (dependent variable). To minimize statistical biases due to too small a sample size, we did not analyze the data by contingency tables and correlations for those species with less than 30 sightings (Gotelli 2012).

To differentiate the various types of substrates in terms of their quantitative lizard community composition, we used a One-Way Analysis of Similarities (ANOSIM). ANOSIM is roughly analogous to an ANOVA in which the univariate response variable is replaced by a dissimilarity matrix, i.e. with distances that were converted to ranks (Clarke 1993). Significance was computed by permutation of group membership, with 9,999 replicates, and Bray–Curtis was used as distance measure. Sequential Bonferroni correction was used for post-hoc comparisons of pairwise ANOSIMs between all pairs of groups.

We calculated a Chao-1 index to predict the theoretical number of species that can be expected to use each

substratum type based on the sampling regime. In addition, the following univariate community diversity metrics were calculated for each substratum type: (i) Species richness (total number of species recorded at each site); (ii) Dominance (D); (iii) Simpson index (S) S = 1 − D; (iv) Shannon entropy index (H'; Shannon and Weaver 1963) and (v) Evenness (e), calculated by Buzan and Gibson's formula (Magurran 1988). For each diversity metric, we also generated upper and lower 95% confidence intervals by performing a bootstrap analysis with 9999 random samples, each with the same total number of individuals as in each original sample generated (Harper 1999).

Niche breadth (B) in resource use, for all the studied dimensions (horizontal, vertical, as well as arboreal versus terrestrial and subterranean) was assessed by the Simpson's (1949) index. To evaluate the "structure" (sensu Gotelli and Entsminger 2003) of the lizard community in terms of substratum use and height of perches, we first calculated the similarity species/population groups using Pianka's (1986) symmetric equation (with 0 indicating no similarity and 1 total similarity), and then performed a statistical simulation study. To assess whether the various observed overlap values between species/population group pairs occurred by chance, we randomized the original species utilization matrices by shuffling the original values among the resource states by using the randomization algorithms RA2 and RA3 (Lawlor 1980), with 30,000 random Monte Carlo permutations generated by Ecosim software. RA2 tests for structure in the generalist–specialist nature of the resource utilization matrix by conserving guild structure but destroying observed niche breadth (Gotelli and Graves 1996). RA3 tests for guild structure by conserving niche breadth for each species but destroying guild structure manifested by the zero structure of the resource utilization matrix (Gotelli and Graves 1996). If the observed overlaps were significantly lower than the randomized overlaps, there was evidence of community-wide niche partitioning of the analyzed niche dimensions (substratum type and perch height). If the observed overlaps were significantly higher than the randomized overlaps, there was evidence of community-wide convergent use of the niche dimensions (i.e. a "contagion" effect), whereas if observed and randomized overlaps did not differ significantly, the lizard community used the niche dimensions by chance, i.e. randomly. The substratum type availability (%) was added to the Ecosim software for running the analyses.

The pairwise similarity of each lizard species with the availability of each substratum type was assessed by non-metric multidimensional scaling (nMDS), using cosine as similarity measure between items in the item-item matrix (Harper 1999). A Principal Component Analysis (PCA) was used to displaying the various lizard species by substratum type in the multivariate space, retaining only factors with eigenvalues > 1 in the analysis (Harper 1999).

Results

General community characteristics

For all study sites pooled, we recorded a total of 25 lizard species, belonging to five different families (Table 1). Along the FSS gradient, we found a reduction in species richness, from 18 taxa in forest, 12 in savannah and up to 9 in the suburbs (Table 1). Six species (24% of the total) were found in all habitat types along the gradient, 10 (40%) species were found exclusively in forest, four (16%) only in savannah, two in both forest and savannah (8%), in both forest and suburbs, and only in suburban habitats. The exclusively suburban species were the geckos *Ptyodactylus ragazzi*, recently

Table 1 Comparison of species richness along the forest, forest-derived savannah, suburbs gradient in South-Western Togo. 1 = indicates presence of a given species in a given habitat type along the FSS gradient

Genus	Species	forest	savannah	urban
Scincidae				
Trachylepis	*affinis*	1	1	
Trachylepis	*albilabris*	1		
Trachylepis	*maculilabris*	1	1	1
Trachylepis	*perrotetii*	1	1	1
Trachylepis	*polytropis*	1		
Trachylepis	*quinquetaeniata*	1	1	1
Cophoscincopus	*simulans*	1		
Mochlus	*guineensis*	1		
Panaspis	*togoensis*	1		
Gekkonidae				
Hemidactylus	*albituberculatus*		1	
Hemidactylus	*angulatus*	1	1	1
Hemidactylus	*fasciatus*	1		
Hemidactylus	*kyaboensis*	1		
Hemidactylus	*mabouia*	1	1	1
Hemidactylus	*muriceus*	1		
Ptyodactylus	*ragazzi*			1
Tarentola	*ephippiata*			1
Agamidae				
Agama	*agama*	1	1	1
Agama	*sankaranica*		1	
Chamaeleonidae				
Chamaeleo	*gracilis*	1	1	
Chamaeleo	*necasi*	1		
Chamaeleo	*senegalensis*		1	1
Varanidae				
Varanus	*exanthematicus*		1	
Varanus	*niloticus*		1	
Varanus	*ornatus*	1		
TOTAL		**18**	**13**	**9**

introduced by merchants of charcoal and firewood from the northern regions of Togo (our unpublished observations), and *Tarentola ephippiata*. These two species are currently common in some areas of Lomé, such as in the Be-Kpotà sector of the main city centre.

There were significant differences in the frequency of species by ecological niche (arboreal/climbers; arboreal-terrestrial; terrestrial; subterranean) across the FSS gradient (contingency table: $\chi^2 = 23.4$, df $= 6$, $P < 0.001$), although arboreal-terrestrial and arboreal/climbers were dominant in all habitat types (Fig. 2).

Community structure in the suburban area

In the suburban site, we observed a total of 611 individuals belonging to 6 lizard species. Three of the observed species were Scincidae: 2 individuals of *Trachylepis maculilabris*, 8 *Trachylepis perrotetii*, and 122 were *Trachylepis quinquetaeniata*. There was also one Agamidae (352 individuals of *Agama agama*), one Gekkonidae (126 individuals of *Hemidactylus* sp.), and one Chamaeleonidae (one individual of *Chamaeleo senegalensis*). Only three species were observed in sufficient number for statistical analysis to determine their niche patterns: *A. agama, T. quinquetaeniata* and *Hemidactylus* sp. The first two species were observed only during 0900–1200 h, whereas *Hemidactylus* sp. mainly during 2000–2200 h, with four individuals sighted in the morning sampling.

Based on the saturation curve of number of observed individuals against number of uncovered taxa, we concluded that species richness was adequately sampled within each habitat type (Online Supplementary Fig. S1). Habitat types were relatively homogeneous in terms of number of observed species, with the highest number (n = 6) being observed in bushes (Table 2). Chao-1 estimated that the maximum number expectable per habitat
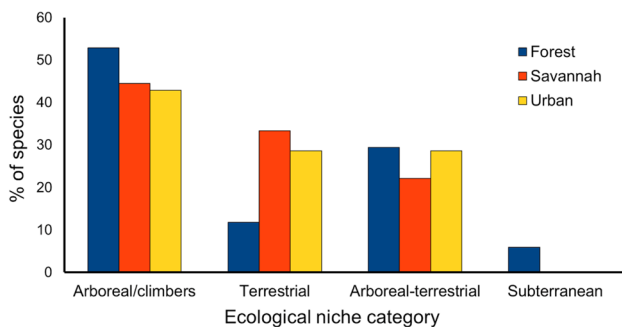

Fig. 2 Distribution frequency of species by ecological niche (arboreal/climbers; arboreal-terrestrial; terrestrial; subterranean) across the forest-savannah-suburbs gradient. Sample sizes: forest n = 19; forest-derived savannah n = 9; suburban area n = 7

type is 7 (Table 3). In terms of diversity metrics (calculated from the number of individuals by lizard species sighted on each substratum), the various substrates showed relatively similar values, with bushes and trees/wood being used by a slightly higher diversity of species and with a slightly higher evenness than the other substrates (Table 3). However, there were no statistically significant differences among substrates for any of the diversity metrics using ANOSIM (mean rank within substratum types = 29.46; mean rank between substratum types = 37.6; R = 0.05, at least $P > 0.155$ in all metrics).

Suburban lizards: horizontal niche resource use

The number of sighted individuals by (i) species, (ii) substratum type, and (iii) in relation to the relative availability of each substratum, are reported in Table 2. Contingency table analysis revealed that the three species used the various substrates in a significantly different way ($\chi^2 = 225.68$, df $= 5$, $P = 0.00001$), with *A. agama* being observed mainly in cement and grass, *T. quinquetaeniata* mainly in bushes and sand, and *H. angulatus* in cement and trees/wood. Within species, there were neither intersexual ($\chi^2 = 7.2$, df $= 5$, $P = 0.209$) nor adults versus juveniles ($\chi^2 = 8.6$, df $= 5$, $P = 0.111$) differences in *A. agama;* similarly, there were no significant intersexual differences in *T. quinquetaeniata* ($\chi^2 = 3.2$, df $= 5$, $P = 0.668$), with the number of juveniles being too small for any statistical analysis. Overall, cement (29.7% of the sightings) and grass (29.8%) were the substrates where lizards (all pooled species) were more frequently observed, followed by trees (12.7%), bushes (10.3%), sand (7.8%) and stonepiles (0.4%).

Substrates were used in relation to their relative availability by *A. agama*, but not by *T. quinquetaeniata* and *H. angulatus* (Table 4). A nMDS analysis, with cement and grass being placed along the Component 1 (positive values) and trees, bushes and stone piles along Component 2 (negative values), revealed that *T. quinquetaeniata* resulted positioned towards high positive values of Component 1 and negative values of Component 2, whereas *A. agama* at negative values of both Component 1 and 2, and *H. angulatus* at negative values for Component 2 but highly positive values for Component 2 (Fig. 3). In this analysis, Component 1 explained 77.02% of the whole variance and Component 2 explained 22.35%. The three species were also clearly spaced apart in the multidimensional space, with *A. agama* being very close to the habitat availability centroid, in a PCA diagram (Fig. 4). In both analyses, *Hemidactylus* sp. centroid was spaced far away from that of the other two species within the multidimensional space.

Table 2 Raw data of the lizard sightings at the suburban area, divided by species and by substratum type, at Baguida (Lomé), Togo

substratum	% availability	A. agama males	A. agama females	A. agama juveniles	T. quinquetaeniata males	T. quinquetaeniata females	T. quinquetaeniata juveniles	T. maculilabris	T. perrotetii	Chamaeleo gracilis	Hemidactylus sp.
cement	46	26	48	40	0	4	0	2	0	0	54
grass	45	48	62	86	5	9	0	0	0	0	10
bushes	1,4	7	5	4	8	10	0	0	0	0	42
sand	7	4	6	5	13	17	0	0	0	0	0
trees/wood	0,5	2	1	0	17	23	7	0	2	1	12
stone piles	0,1	0	5	3	1	1	7	2	6	0	8
total	100	87	127	138	44	64	14				126

Suburban lizards: vertical (perch height) niche resource use

The raw data on the distribution of lizard sightings by vertical height from the ground are shown in Table 5. As for *A. agama*, males had much higher niche breadth (B = 4.46) than females (B = 2.41) and juveniles (B = 2.03). This difference was due to the fact that males (1) used more frequently perches at > 101 cm height (26.4% of observed individuals) than females (7.4%) or juveniles (2.9%), and (2) they were observed more frequently at 10–50 cm height, whereas females and juveniles mostly on ground (Fig. 5), Thus, males usually perched higher than females and juveniles and overall, the differences among the three groups of individuals were statistically significant (χ^2 test, $P < 0.001$). On the other hand, in *T. quinquetaeniata* the three groups of individuals did not differ significantly (χ^2 test, $P = 0.186$), with all of them being found essentially on ground (Fig. 6). However, also in this species males exhibited a wider niche breadth (B = 3.26) than females (B = 1.82) and juveniles (B = 1.56).

Suburban lizards: simulations studies

We also analyzed the collected data using null models Monte Carlo suimulations. The results of these simulations are presented below.

Horizontal niche resource use As for the substratum type use by lizards, the mean observed overlap between pairs of species was 0.625. The mean of the simulated overlaps with RA3 was 0.365 (variance of simulated indices = 0.0089; random seed = 1942475120), with P(observed ≤ expected) = 0.983 and P(observed ≥ expected) = 0.017. Using RA2, the mean of the simulated overlaps was 0.545 (variance of simulated indices = 0.0125; random seed = –523877646), with P(observed ≤ expected) = 0.753 and P(observed ≥ expected) = 0.247. Thus, RA3 differed significantly from RA2 in that it showed a non-random preference for same substratum types by the whole lizard community, whereas there was no preference according to the latter algorithm, with the substratum type selection being random.

Vertical niche resource use The mean observed overlap between pairs of species was 0.641. Using RA3, the mean of the simulated overlaps was 0.421 (variance of simulated indices = 0.00156; random seed = 956343435), with P(observed ≤ expected) = 0.999 and P(observed ≥ expected) = 0.001. With RA2, the mean of the simulated overlaps was 0.560 (variance of simulated indices = 0.00178; random seed = 1521330926), with P(observed ≤ expected) = 0.976

Table 3 Mean values of diversity metrics, with upper and lower 95% confidence intervals (CI), for the various substratum types surveyed in Baguida (Lomé), Togo. Values are calculated on the basis of the number of lizard individuals by species that were observed in each substratum type during the field surveys

	Species richness	Individuals	Dominance	Simpson	Shannon	Evenness	Chao-1
cement	3	178	0.547	0.453	0.713	0.68	3
Lower CI	3	178	0.3541	0.5472	0.9604	0.4867	3
Upper CI	6	178	0.4523	0.6454	1.162	0.8652	7
Grass	3	179	0.7591	0.2409	0.4851	0.5415	3
Lower CI	3	179	0.3556	0.5412	0.9555	0.4938	3
Upper CI	6	179	0.4588	0.6442	1.166	0.8845	7
trees/wood	3	76	0.4058	0.5942	0.9969	0.9033	3
Lower CI	3	76	0.3393	0.5083	0.8908	0.5555	3
Upper CI	5	76	0.4917	0.6586	1.196	0.9428	6
Sand	3	49	0.4969	0.5031	0.7982	0.7405	3
Lower CI	3	49	0.3294	0.4715	0.8477	0.5827	3
Upper CI	5	49	0.5277	0.6706	1.215	0.9612	6
Bushes	6	71	0.4767	0.5233	1.077	0.4891	6
Lower CI	3	71	0.3402	0.4983	0.8908	0.5569	3
Upper CI	5	71	0.5013	0.6594	1.182	0.9513	6
stone piles	3	25	0.3344	0.6656	1.097	0.9984	3
Lower CI	3	25	0.3184	0.3904	0.7038	0.5911	3
Upper CI	5	25	0.6096	0.6816	1.241	0.9784	6

and P(observed ≥ expected) = 0.024. In this case, both RA3 and RA2 gave consistent results, showing that there was a non-random preference for same height category by the whole lizard community.

Discussion

General community characteristics along the habitat gradient

Our study revealed that along the FSS gradient (i) there was a higher species richness in forest than in savannah and suburbs, and that (ii) the three communities were taxonomically distinct. Thus, there was a "forest-specific" assemblage of species (including e.g. *Varanus ornatus*) and less diverse

Table 4 Correlation values between substratum type availability and number of individuals observed in each substratum type at Baguida (Lomé), Togo. Raw data used for these analyses are in Table 2. Statistically significant P-values would indicate generalism in substratum type usage by lizards. Significance is in boldface

	Pearson's corr. Coeff. (R)	P
A. agama males	**0.915**	**< 0.01**
A. agama females	**0.979**	**< 0.0001**
A. agama juveniles	**0.896**	**0.0156**
T. quinquetaeniata males	–0.526	0.283
T.quinquetaeniata females	–0363	0.479
T. quinquetaeniata juveniles	sample too small	
Hemidactylus sp.	0.370	0.470

assemblages in savannahs (including e.g. *Varanus exanthematicus*) (Fig. 7) and suburbs, mostly characterized by ecological generalists with wide habitat tolerances. Both these diversity patterns were not unexpected (McKinney 2008). Concerning pattern (i), there is abundant available literature showing that lizard communities are significantly more species-rich in tropical forests than in more open or degraded environments due to higher environmental heterogeneity (Lewin et al. 2016), the same as generally observed in both vertebrates and invertebrates (e.g., Basset et al. 2008; Watling and Donnelly 2008; Ramírez-Bautista and
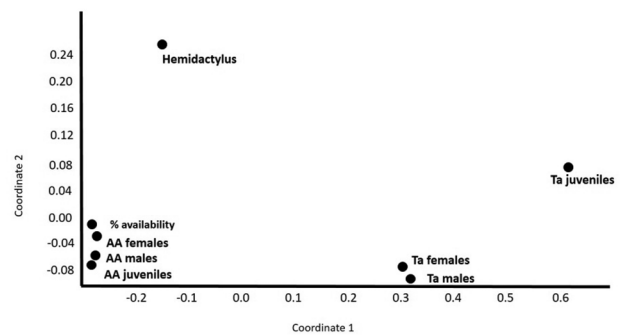

Fig. 3 Non-metric multidimensional scaling (with COSINE as similarity measure) representing suburban lizard species in relation to their substratum use and availability in the field. In this graphic, cement and grass are placed along the Component 1 (positive values) and trees, bushes and stone piles along Component 2 (negative values). Component 1 explained 77.02% of the whole variance and Component 2 explained 22.35%. Symbols: AA = *Agama agama*; Ta = *Trachylepis quinquetaeniata*
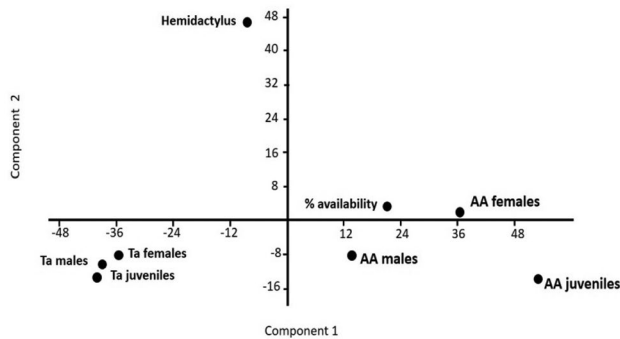
Fig. 4 Diagram of a Principal Component Analysis arranging suburban lizard species in relation to their similarities in substratum use and in relation to the overall substratum type availability in the field. Symbols: AA = *Agama agama*; Ta = *Trachylepis quinquetaeniata*
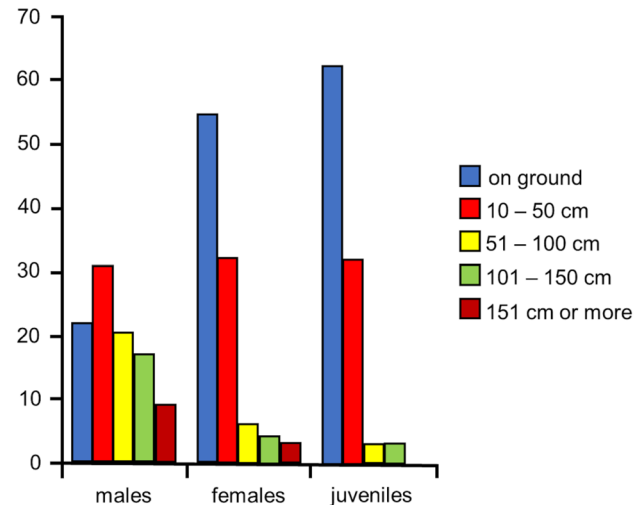

Fig. 5 Percentage of suburban *Agama agama* individuals observed at the various height categories from the soil. Sample sizes: males, n = 87; females, n = 127; juveniles, n = 138

Cruz-Elizalde 2013; Cruz-Elizalde et al. 2014, 2016). For instance, in the Philippines Supsup et al. (2020) found that higher amphibian and reptile species richness occurred in secondary forests than in mixed-use agricultural areas. Since habitat heterogeneity is an important predictor in explaining lizard richness in Africa (Lewin et al. 2016), it is likely that the multiple microniches available in the hilly forests of the Togo hills may explain the much higher species richness that we observed therein compared with savannah and suburban habitats of the same study region.

Concerning pattern (ii), the fact that we observed habitat-specific assemblages of lizards at our study area mirrors observations from Brazilian Cerrado lizard communities (Nogueira et al. 2009). In the Brazilian Cerrado, habitat-specialists with patchy distributions in the forest-savannah-plantation mosaics create habitat-structured lizard assemblages with faunal overlap between forest and savannah being limited and forested versus open areas acting as mutual barriers to lizard distribution (Nogueira et al. 2009). In our study case, the taxonomical composition of the savannah assemblage was similar as that of the suburban habitat (although in the savannah we also

observed *Agama sankaranica* and a few other species), thus suggesting that there is no clear barrier acting against lizard distribution between savannah and suburban areas in southern Togo.

The species richness reduction from forest to urban areas may also be interpreted as an effect of habitat loss for forest-specialists (Turner 1996; Lea et al. 2003; Edwards et al. 2013; Decena et al. 2020). Indeed, studies from tropical Africa have revealed that forest loss (by slash-and-burn shifting cultivations or by direct tree cutting) at the local scale produced a considerable reduction in the species richness of lizards (Akani et al. 2018). In a Niger Delta area, the number of sympatric lizards was 9 in a unburnt forest patch, whereas it was just 2 in a nearby forest patch up to 12–16 months after fire (Akani et al. 2018). However, since the savannahs of southern Togo date back a few thousands years (see Salzmann and Hoelzmann 2005)), it is likely that

Table 5 Raw data of the lizard sightings, divided by species and by height from the ground, at Baguida (Lomé), Togo

| Species	Population category	on ground	10–50 cm	51–100 cm	101-150 cm	151 cm or more	Total
Agama agama	males	19	27	18	15	8	87
Agama agama	females	70	41	8	5	3	127
Agama agama	juveniles	86	44	4	4	0	138
Trachylepis quinquetaeniata	males	21	7	8	6	2	44
Trachylepis quinquetaeniata	females	44	15	3	1	1	64
Trachylepis quinquetaeniata	juveniles	11	2	1	0	0	14
Trachylepis maculilabris		2	0	0	0	0	2
Trachylepis perrotetii		7	1	0	0	0	8
Hemidactylus sp.		9	18	32	51	16	126
Chamaeleo gracilis		0	0	1	0	0	1
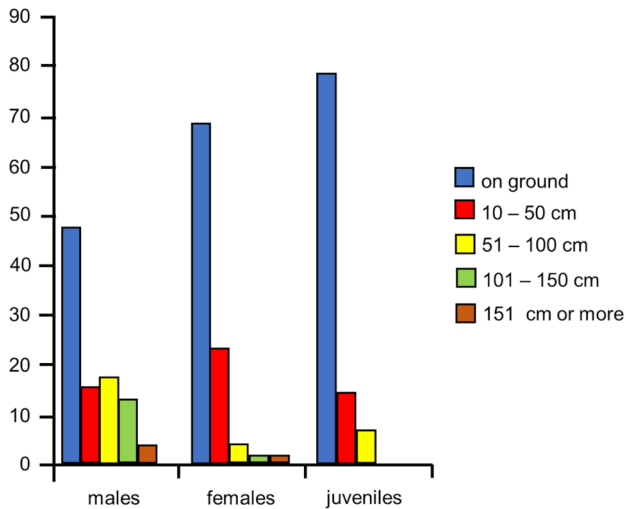
Fig. 6 Percentage of suburban *Trachylepis quinquetaeniata* individuals observed at the various height categories from the soil. Sample sizes: males, n = 44; females, n = 64; juveniles, n = 14

the lower species richness of savannah lizard assemblages was due more to broad historical events and geographical/climatological reasons (Salzmann and Hoelzmann 2005) than to local-scale recent habitat loss.

Suburban lizards: analysis of community structure and niche characteristics

Our data revealed that the various lizard species inhabiting suburban areas showed some interspecific differences in both substratum type preferences and vertical (perch height)

spatial niche. However, our null model simulation analysis did not uncover any nonrandom niche partitioning pattern, thus rejecting the hypothesis that these interspecific differences were due to a competitively assembled community structure (Gotelli and Graves 1996). Instead, we detected a nonrandom "clustered" distribution of the various species along a few of the available resource categories. Therefore, the main conclusion of our study is that species-specific preferences instead of community-driven mechanisms are more likely to explain the observed patterns at the study area. Thus, we found no support for the hypothesis that lizards, as they can increase net energy gain from careful thermoregulation and hence selection of appropriate basking substrates, can compete for, and exclude potential competitors from, optimum basking sites (e.g. Huey and Slatkin 1976). When interspecific competition cannot be advocated, the proximate external ecophysiological constraints are often considered the drivers of species-specific differences in niche characteristics (Barbault 1988; Barbault and Stearns 1991). In our case, thermal constraints pushing the selection of given substratum types for diurnal lizard basking (Huey and Slatkin 1976; Hailey 1982; Huey 1991) are unlikely to explain the observed patterns, as the study area has a tropical climate with ambient temperatures constantly ranging 27–32 °C all throughout the year (https://it.climate-data.org/ystem/togo/maritime-region/lome-764237/). Interspecific differences in substratum type and perch height uses due for foraging reasons are also unlikely as the various species have a relatively similar insectivorous diet: at the study area, the diet of *A. agama* consisted mainly of Coleoptera adults and Formicoidea (Akani et al. 2013) and that of *T.*

Fig. 7 Some remarkable species observed at the study area in south-western Togo: (**a**) *Trachylepis perrotetii*, (**b**) *Trachylepis quinquetaeniata*, (**c**) *Varanus exanthematicus*, (**d**) *Varanus ornatus*
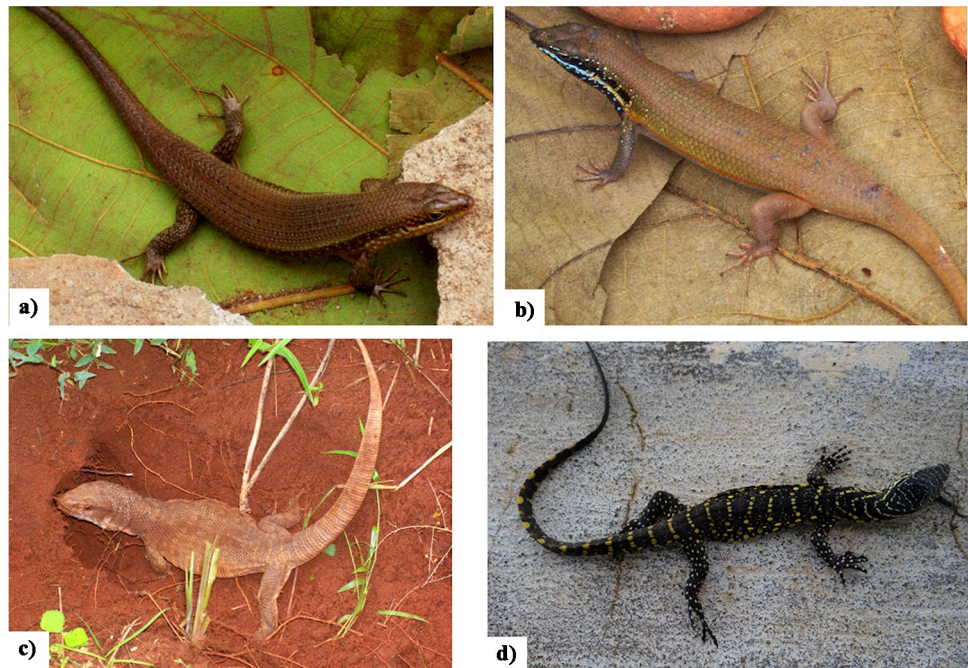
quinquetaeniata of Coleoptera adults and larvae, Lepidoptera adults and larvae and Formicidae (Dendi et al. 2019). For *Hemidactylus* sp. we do not have data for Lomé, but in another West African urban population (from Port Harcourt, Nigeria) the diet was composed mainly by Lepidoptera adults and Formicoidea (Amadi et al. 2020a). In this latter species, however, the use of cement and elevated heights are likely linked to the need to exploit artificially lighted spots for optimal foraging over the insects that are attracted by night around electric bulbs (Amadi et al. 2020a). The same strategy was also employed by *A. agama* in Nigeria (Amadi et al. 2021), but in Lomé we never observed any shifts from diurnal to nocturnal foraging activity in contrast with the Nigerian conspecifics (Amadi et al. 2020b, 2021), whereas dietary shifts have been observed in other tropical lizards from urban environments (Balakrishna et al. 2016). Thus, we suggest that antipredatory reasons may be behind the species-specific substratum type selection and the height of perches, given that predation risk is well known to be a crucial determinant of community structuring of tropical communities (e.g., Pianka 1973, 1986; Poulin et al. 2001; Olsson et al. 2005; Reyes-Olivares et al. 2020). We also noticed that the artificial substratum (cement) was predominantly used by both *A. agama* and *Hemidactylus* sp. In this regard, our data mirror other studies showing that lizards in urban areas use artificial substrates a large proportion of the time, and that these artificial substrates tend to be more uniformly available in urban environments than even optimal substrates for lizards in natural forest (Winchell et al. 2016; Amadi et al. 2020a, b).

Intraspecific differences in the two species for which we collected such data (*A. agama* and *T. quinquetaeniata*) were minor, but *A. agama* males tended to select higher perches than females and juveniles. This positive selection for elevated perches is likely related to the complex hierarchic structure of the *A. agama* groups, with dominant males often ystematic adult females from higher height (Anibaldi et al. 1998).

General considerations on lizard communities in tropical cities

Urbanization, involving the conversion of natural habitats into human-modified ecosystems, usually reduce both the diversity and the abundance of indigenous animal communities, leading in some cases to the extinction of some species or even facilitating the establishment of non-indigenous communities in cities and towns (Hamer and McDonnell 2010). Therefore, our general findings (i.e. a reduced species richness in the suburban habitat of the FSS gradient) are not surprising. However, Gekkonid species may be facilitated in urban areas for foraging by the presence of artificial lights at night, and this general pattern was also highlighted

in the present study. As mentioned above, our study also suggests that the lizard species used the available resources in a clustered way within the suburban habitat in Lomé. Whereas many studies analyzed reptile assemblages in secondary forests and altered habitats (e.g., Luja et al. 2008), the data available in the literature with regard to communities of lizards (or other reptiles) in tropical cities are relatively few and based on different methodologies from ours, and so comparisons with our study are not straightforward. However, in a snake community inhabiting a Brazilian city, Franca and Franca (2019) observed a clustered distribution for two species and dispersed distributions for eight species, and in a Indian city, Janiawati et al. (2016) demonstrated that the various reptilian species were clustered around water sources and vegetation cover patches. In fact, in urban fragments embedded in an "artificial matrix" hostile to the movement of individuals, most species tend to be concentrated into suitable microhabitats (and using clustered types of substratum) as extinction rates (stochastic or anthropogenic) are not compensated by colonization rates (Laurance et al. 2006a, b; Salomão et al. 2019).Thus, we may conclude that lizard communities in tropical urban areas are (i) less species-rich than in the surrounding more natural habitats, (ii) usually clustered into specific habitat/substratum types (often artificial ones), and (iii) not assembled through competitive interactions. Further studies should test the validity of these conclusions. In terms of conservation, to maintain the species richness of the Dahomey Gap habitat gradient, it is important to maintain the habitat heterogeneity presently available, and also enhance the number and the connectivity of forested patches that represent the main source of population diversity of lizards in the study region.

Declarations

Ethics approval not applicable.

Consent for publication All authors read and approved the final manuscript, and accepted to be co-authors in the published paper.

Conflicts interests The authors declare no competing interests.

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