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Predicting the structure of turtle assemblages along a megatransect in West Africa

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RUNNING HEAD: Turtle communities along a megatransect

Understanding large- and small-scale patterns as well as the determinants of species richness is central for the study of evolutionary mechanisms. The extent to which species richness in local communities is related to larger scale processes is a pre-eminent topic in ecological and evolutionary research. To investigate how local and regional species richness are related, we sampled freshwater turtle assemblages in seven localities to represent the variation in ecological conditions along a 90km South-North megatransect in Benin, West Africa. In each locality, all turtles captured were identified and measured, and microhabitat classified in which individual turtles were observed. Based on these data we used community diversity metrics to compare turtle assemblages. Spatial autocorrelation did not affect our data. For all localities pooled, only two species (*Pelusios castaneus* and *Pelomedusa olivacea*) were the most common, and one species (*Trionyx triunguis*) the rarest. Analyses of the commonest and more numerous species showed that the abundance of *P. castaneus* declined with an increase in latitude and longitude, but the opposite was true for *P. olivacea*. We showed that various microhabitat characteristics were significantly correlated with the abundance of the two common species. We found significant but variable South-North gradients in microhabitat use for different turtle species. Our results highlight the importance of studying interactions between local environments, the ecological requirements of each species, and their synecological relationships.

ADDITIONAL KEYWORDS: community structure, latitudinal gradients, species diversity metrics, microhabitats, spatial effects, Testudines.

INTRODUCTION

Understanding the large- and small-scale patterns and determinants of species richness is central for the study of the evolutionary mechanisms, for instance the historical morphological differentiation as a niche partitioning pattern and its influences on speciation (e.g., Futuyma 2006). Richness patterns of terrestrial and freshwater species are inversely related to latitude (Willig & Lyons 1998; Chown & Gaston 2000; Mora & Robertson 2005). This pattern has been documented for numerous taxonomic groups (ranging from protists to primates) for data across regional and global scales (Adams 2009). Species richness is presumed to be a consequence of systematic spatial variation in the balance of speciation versus extinction and immigration versus emigration of species (Adams 2009). A large number of different reasons have been suggested to explain the latitudinal variation in species numbers (Rapoport 1982; Adams 2009). One factor, the relationship between the number of species in an area and ambient available ('usable') environmental energy, is considered to be important in modulating any effect of the physical structure of the Earth in determining species richness gradients (e.g. He & Legendre 1996). However, other mechanisms, for instance interspecific competition and niche resource partitioning, have been considered among the prominent forces determining community structure and species richness at local scales (Connell 1980, 1983; Barbault 1991). Consequently, various statistical tools have been used to uncover community assembly rules and thus identify eventual non-random patterns in community structure (e.g. see Gotelli & Graves 1996; Luiselli 2008a; Ulrich & Gotelli 2010; Gotelli & Urlich 2012).

Whereas freshwater turtle communities have been well studied by in numerous bioregions worldwide (e.g. see Luiselli 2008a; Stephens & Wiens 2009), sub-Saharan freshwater turtle communities have been somewhat neglected (Luiselli 2008b) despite their high species richness throughout the entire region (Branch 2008; Bombi *et al*. 2011). The only published studies have been descriptive (e.g., Akani *et al*. 2018) or confined to a relatively well defined geographic area (e.g. Niger Delta, see Luiselli *et al*. 2004, 2006).

To understand global variation in biodiversity, we need not only explore the importance of differences in patterns observed at local and at regional scales, but also determine how diversity at one scale might relate to that at another (Yanoviak 2001; Poisot *et al*. 2010; Rasche *et al*. 2011). Finding the correct scale for explaining a given phenomenon is a challenge (Cooper *et al*. 2007; Tucker 2009; Barley & Meeuwig 2017). Selecting too large a scale (i.e., large grain sizes) may result in too much variation in measured variables (i.e., induce chaos), whereas too fine a scale may lose sight of existing patterns (for instance, there might be apparent population declines because a subgroup of monitored individuals may be affected by an intervening perturbation event that has no effect at the population level). Thus, empirical studies that are larger than local scales but smaller than the regional/global, are useful to better understand patterns of how biodiversity is organised. In this regard, a promising option is the use of mega-transects, i.e. much-larger-than-usual (few hundreds up to few thousands meters long) transects joining several study sites from a given region, to explore more general patterns but still resulting from a local scale (Huber and Chao, 2019). Though promising, these mega-transects have been rarely used by community ecologists in tropical and in temperate contexts (but see Luiselli *et al*. 2008; Huber & Chao 2019).

In this paper, we examine diversity patterns and local community structure of turtle assemblages along a South-North oriented mega-transect in Benin (West Africa). We test whether large-scale spatial effects predict the structure of animal communities at the local scale by recording the presence and local abundance of freshwater turtles in seven randomly selected sites along the mega-transect. Using numbers of observed individuals and various diversity metrics, we describe local community structure. We also examine microhabitat selection by sympatric species, as well overall latitudinal gradients. Our results are useful in understanding the “rules” governing the assembly of local communities (Caley & Schluter, 1997) and how these relate to processes acting at larger spatial scales.

MATERIALS AND METHODS

The taxonomy of African turtles has been undergoing considerable revisions during the last decade (e.g. Branch 2008). For practical reasons, we follow the recognized taxonomic names given in Turtle Taxonomy Working Group (2017).

STUDY LOCATIONS

We studied turtle communities in seven discrete sites in Benin during the wet season (May-June) from 2010 until 2012. All sites were found in riverine freshwater habitats, selected to represent the range of ecological conditions found from the south to the north of the country (Figure 1): 1) Cotonou (decimal coordinate system: 6.479947 N, 2.392178 E); 2) Ouémé (6.635108 N, 2.455157 E); 3) Adjohoun: 6.697428 N, 2.437219 E; 4) 6.762794 N, 2.427668 E; 5) Djigbé (6.830605 N, 2.378119 E); 6) 6.956216 N, 2.325714 E; 7) Za-Kpota (7.220734 N, 2.094006 E). The linear distance from the southernmost to the northernmost site was 90 km.

Benin is characterised by a wide range of ecosystems, related to differences in climate and topography. All study sites were within the Guineo-Congolian vegetation zone. General characteristics of each sites, according to Corine landcover and rainfall, are given in Table S1. In all sites, we surveyed the main river tracts; these differed locally in terms of current speed, riverbed characteristics and vegetation (both in the banks and in the water) (see below).

Predominant vegetation in the study region was Guinea savannah grasslands with scattered patches of riparian forest (around 50 m width) along the banks of meandering rivers. Soils varied from muddy, clayey to sandy. Composition and structure of the riparian vegetation was influenced by the extent, duration, timing and frequency of flooding (O’Connor 2001); southernmost sites were generally moister and richer than the more northerly sites (Ceperley *et al*., 2010). Tree density varied between sites. The most common tree species were: *Pterocarpus santalinoides, Cola laurifolia, Vitex madiensis, Mitragyna inermis, Eugenia kerstingii, Parinari curatellifolia,* *Diospyros mespiliformis, V. simplicifolia, Margaritaria discoidea*, and *Ficus capreaeifolia*. Average tree height (all sites pooled) was 17.5 ± 14.3 m.

FIELD PROTOCOLS

In each site, we surveyed an area of about 3000 m^2 (shape depending on the configuration of the water-bodies) for a total of 10 field days during the wet season (April to September). Turtles were caught by hand and with fishing traps. Fishing traps were baited funnel traps, made of non-stretch fine mesh of 2.5cm. We used this mesh size to avoid the legs of the turtles becoming entangled. The top of the traps remained above water, to allow captured turtles to surface for air. None of the captured turtles died during the field study. We used fish pieces as bait. The same number of traps (n = 30) were deployed at each site during each day. We placed ten traps in each of the three aquatic vegetation categories (see below) in each site, and then recorded current speed and bank vegetation data (see below for the various categories) for each of the points where traps were placed.

Field surveys started at 07:00 h and ended at 18:30; traps were examined twice a day: around 07:00 h and around 18:00 h. We also examined individuals taken by local fishers or on sale in nearby markets. We considered only turtles found in riverine markets , and those caught by local fishermen that we knew originated within our study sites. These turtles were considered for the microhabitat analyses, only for the diversity metrics.

All turtles were identified to species, sexed, and marked by carapace scute notching. We measured turtle size using the curved carapace length and plastron length (morphometric data were not analysed in this paper as they were not directly relevant to the aim of this research). All animals were released unharmed at the point of capture.

Since previous studies on freshwater turtles in general have shown that presence/absence and population abundance of species are related to bank vegetation, aquatic vegetation and current speed (e.g. Ficetola *et al*. 2004; Wyneken *et al*. 2008; Vignoli *et al*. 2015), we classified the microhabitat in which we observed turtles (apart from those recorded in markets) according to three independent variables (Figure 2):

(a) Speed of water current (three categories: 0 = no current; 1 = moderate current; 2 = high current). Current speed was evaluated by eye within a 10 m radius around the sighting point of each individual turtle.

(b) Bank vegetation was recorded along the bank of the water body where each individual turtle was sighted: 0 = no bank vegetation (NBV); 1 = moderate bank vegetation (MBV); 2 = high bank vegetation (HBV). NBV was assigned when the banks were bare or only with herbaceous vegetation; MBV was assigned when there were reeds and bushes but no trees (no gallery forest). HBV was when the bank vegetation consisted of a strip of gallery forest.

(c) Aquatic vegetation was classified as: 0 = no aquatic vegetation (NAV); 1 = moderate aquatic vegetation (MAV); 2 = high aquatic vegetation (HAV). NAV was assigned when there was less than 10% of the water surface covered by aquatic plants; MAV was when the water surface was covered by 11-30% by aquatic plants, and HAV was when aquatic vegetation covered more than 30% of the water surface. The % aquatic vegetation cover was evaluated by eye within a radius of 10 m around the site of sighting of each individual turtle.

We also used Google Earth to measure the river width within all study sites.

STATISTICAL ANALYSES

Diversity metrics analyses.

We evaluated whether our sampling effort captured the true species richness and diversity within each study site by (i) building a rarefaction curve for species discoveries at each site (and generating the 95% confidence intervals of the estimate after 9,999 bootstraps), and (ii) by Chao-1 index. The Chao-1 index calculates the theoretical number of species at each study site that can be expected on the basis of the sampling regime. The formula of the unbiased Chao-1 estimate is as follows:

$$\text{Chao1} = \text{Species richness} + F1\,(F1 - 1) / [2\,(F2 + 1)]$$

where F1 is the number of singleton species and F2 is the number of doubleton species at each study area.

We used univariate metrics of community diversity for each site (Magurran, 1988):

(a) Species richness, i.e. the total number of species recorded into each study area;

(b) Dominance:

$$D = \frac{\sum_i n_i(n_i - 1)}{n(n-1)}$$

where n_i is the number of individuals of the taxon i and n is the total number of turtles that were recorded at each study area;

(c) Simpson index (S): $S = 1 - D$.

(d) Shannon entropy index (Shannon & Weaver, 1963):

$$H = -\sum_i \frac{n_i}{n} \ln \frac{n_i}{n}$$

where n_i is the number of individuals of each species in each habitat type and n is the total number of turtles that were recorded in each study area.

(e) Evenness, calculated by Buzan and Gibson's formula:

$$e = H'/\log S$$

with H' representing Shannon's index, and S the total number of turtle species observed in each study area (Magurran 1988).

To statistically compare the various sites in terms of turtle community diversity metrics, we performed a bootstrap analysis by generating upper and lower confidence intervals of all abovementioned indices, with 9,999 random samples, each with the same total number of individuals as in each original sample generated (Harper 1999).

To determine whether the linear distance between pairs of sites can affect the species' assemblage heterogeneity across sites, for each diversity index and for each given pair of sites we first subtracted the value of site "a" by the value of site "b". Then, we correlated (using the Pearson's correlation coefficient) these subtraction values with the linear distance between the given pairs of sites. If the test was statistically significant, we would conclude that the linear distance between sites influence the difference in community metrics between sites.

Micro-habitat selection analyses

The variables used for the description of microhabitat characteristics were not significantly collinear at Spearman's rank correlation coefficient (in all cases, $P > 0.05$), and thus were retained for further statistical analyses. Also, because river width was not correlated with latitude ($r = 0.311$, $P > 0.05$), we also considered river width in the analyses. The frequencies of occurrence of the various species by the various categories in each of the three microhabitat variables were analyzed by contingency tables χ^2 tests. In order to analyse the data in more depth, we used Generalized Linear Models (GLM, Hosmer & Lemeshow 2000) to quantify (1) the effects of spatial components on the abundance of the various turtle species at each site and (2) the effects of spatial components on the diversity metrics (Simpson, Shannon, Evenness and Dominance) among the study sites. In these models, abundance per site was defined as the number of individuals observed for each species at each of the three microhabitat variables at each study site; the sampling units were the seven study sites. To test for possible spatial effects, we used the third-degree polynomial equation of latitude (Y) and longitude (X) of each site as follows (Carrete *et al*. 2007):

$$b1x + b2y + b3x^2 + b4xy + b5y^2 + b6x^3 + b7x^2y + b8xy^2 + b9y^3$$

This cubic trend surface ensures that (i) linear gradient patterns were calculated, and that (ii) more complex features (i.e. patches or gaps, which require quadratic and cubic terms to be fit) were also extracted (Legendre & Legendre 1998).

Firstly, to test the pure effect of spatial components on turtles abundances, a stepwise forward regression procedure with the nine terms of the third-degree polynomial equation of the latitude and longitude as predictor variables and abundances of species as the dependent variable was used to test the statistical significance of each variable in turn, and variables were excluded when they did not correlate significantly with the dependent variable (Wald test $P > 0.05$). This analysis was carried out in order to remove the non-significant spatial terms (Legendre & Legendre 1998). The significant variables were subsequently computed using the best subset procedure. In this analysis, the abundances (number of individuals) were used as dependent variable, the spatial components and the microhabitat categories as predictors.

Spatial auto-correlation could bias model parameter estimation, especially when making ecological inference (Legendre & Legendre 1998). In order to test for the presence of spatial autocorrelation, firstly we make a preliminary forward stepwise regression forcing the significant spatial terms of the previous analysis (pure spatial effects) with the microhabitat categories as predictor variables and abundances of species as the dependent variable. Secondly, the eventually significant spatial terms ($P < 0.05$) were retained and included in each model to test if they accounted for a significant change in the model significance and deviance.

We standardized all variables, also for the diversity indices model, to remove the effect of differences in the original scale of measurement. The standardization of values contains options to standardize all values of the selected variables used in the model. All values of selected variables are replaced by standardized values, which were computed, using Statistica 6.0 software (www.statsoft.com), as follows:

Standardized score = (raw score – mean) /Standard Deviation

In all GLM models, the log link function and a Poisson distribution of error were used (McCullagh & Nelder, 1989).

We used Spearman's rank correlation analyses to analyse the correlation between latitude of each study site and (arcsin)percentage of individuals of each turtle species found in each microhabitat category in the seven sites. Alpha was set at 5%. We used the PAST 3.0 software for all the statistical analyses concerning the diversity metrics, and the Statistica 6.0 software (www.statsoft.com) for all the other statistical analyses.

RESULTS

OVERALL PATTERNS

A summary of the data collected on turtle species by study sites is given in Table 1. A total of 630 turtles were observed belonging to five species, three Pelomedusidae (genera *Pelomedusa* and *Pelusios*) and two Trionychidae (genera *Cyclanorbis* and *Trionyx*). For all species we observed both adults and juveniles, thus suggesting reproduction in the populations.

For all localities pooled, *Pelusios castaneus* and *Pelomedusa olivacea* accounted for most of the observed individuals (Figure S1). In terms of number of individuals, the rarest species was *Trionyx triunguis*, which accounted for 0.8% of the total observed sample. However, in terms of number of localities present, *Pelusios niger* was the rarest species (observed in 1/7 sampled localities) followed by *Trionyx triunguis* (2/7 sampled localities) (Table 1). Both *Pelusios castaneus* and *Pelomedusa olivacea* were observed in 100% of the sampled sites and occurred in sympatry also in the same microhabitats.

Overall, a rarefaction curve showed that the plateau phase was clearly reached in our sampling, and that no additional species would be expected in our sampled areas (Figure 3). Also, Chao-1 estimates confirmed that the overall turtle diversity was captured by our surveys (Table 2). In addition, we observed a reduction in evenness and an increase in dominance from South to North (Table 2).

No values of the difference of diversity indices between pairs of sites were significantly correlated to the linear distance between them (in all cases, at least $P > 0.250$), thus showing that linear distance cannot be used as a proxy of species heterogeneity across sites.

The raw dataset for the number of turtle individuals observed in the different microhabitat types (as described by current speed, aquatic vegetation and bank vegetation) is given in Table S2. The results obtained from our GLM models are summarized in Table 3 and are briefly explained below.

PURE SPATIAL EFFECTS

For *Pelusios castaneus*, our model showed that the abundance of this species declined with an increase in latitude (Table 3). For *Pelomedusa olivacea* abundance, there was positive effect of the interaction longitude × latitude (Table 3), that is: the abundance of this species increased with increases in latitude (towards North) and in longitude (towards East). Abundance of *Cyclanorbis senegalensis* was negatively affected by the interaction of latitude × longitude, that is: its abundance increased towards North but declined towards East. *Pelusios niger* and *Trionyx triunguis* could not be modelled due to the low number of sites where the species were recorded (1/7 and 2/7 respectively). The latitude effect was not due to the river width, as (1) these two variables were not autocorrelated (see above), and (2) the river width did not influence any of the species presence/absence and abundance (in all cases, at least $P > 0.05$).

SPATIAL AUTOCORRELATION

In the forward stepwise regression (testing any eventual spatial auto-correlation), none of the spatial terms forced with the microhabitat predictors were significant ($p>0.05$ for all models, in details: *Pelusios castaneus* Y: $P=0.633$; *Pelomedusa olivacea* XY: $P= 0.157$; *Cyclanorbis senegalensis* XY: $P= 0.103$) and none of the spatial terms accounted for any significant change in model deviance. Thus, no spatial autocorrelation was found for each of the analyzed species.

MICROHABITAT EFFECTS

Our model showed that the abundance of *Pelusios castaneus* increased significantly with an increase of MBV and HBV (Table 3), showing that the presence of this species was positively related to at least partial vegetation cover along the banks without high current speed.

The probability of an increased abundance of *Pelomedusa olivacea* was positively associated with no current and negatively associated with HBV (Table 3), showing that the presence of this species could be negatively related to the bank vegetation cover whereas it is favoured by the riverine spots empty of, or with scarce, aquatic vegetation.

Finally, the abundance of *Cyclanorbis senegalensis* was positively influenced by HBV. We were not able to model *Pelusios niger* and *Trionyx triunguis* due to too low number of sites where they were found (see above).

Contingency tables χ^2 tests revealed uneven distribution of the frequencies of individuals of the various species by microhabitat categories (all sites being pooled): *Pelusios niger* showed a significant preference for HBV and HAV ($P < 0.01$ both cases); *Pelusios castaneus* significantly avoided high current, NBV and NAV ($P < 0.01$ in all cases); *Pelomedusa olivacea* significantly avoided high current and HBV (at least $P < 0.05$), and *Cyclanorbis senegalensis* significantly avoided high current, NBV and NAV (at least $P < 0.05$ in all cases).

DIVERSITY EFFECTS

Our GLM models uncovered a positive effect of latitude and longitude, and a negative effect of the interaction longitude × latitude on the abundance of turtles (after pooling data from all species) (Table 4).

Results for the Dominance index indicated that there was a complex effect of spatial components, with values mildly (albeit significantly) increasing with an increase in latitude and longitude (Table 4). The "mild" increase is seen in Table 4 because the estimates of x^2 and y^2 were negative. Simpson and Shannon indices indicated a negative effect of longitude and a mild positive effect of the interaction between latitude and longitude, as shown by the fact that x^2 estimate had a positive sign (Table 4). There was a moderate (but statistically significant) negative effect of the latitude, as demonstrated by the Evenness index (Table 4).

SOUTH-NORTH GRADIENT AND MICROHABITAT NICHE PARTITIONING

A statistically significant South-North gradient in microhabitat use of turtles was uncovered by Spearman's rank correlation analyses for two species (*Pelusios castaneus* and *Cyclanorbis senegalensis*) when current speed was considered, for one species when bank vegetation was considered (*Cyclanorbis senegalensis*), and for one species (*Pelusios castaneus*) when aquatic vegetation was taken into account (Table 5). The most striking differences along the latitudinal gradient were observed between two Pelomedusidae species, viz. *Pelusios castaneus* and *Pelomedusa olivacea* (Figure 4): northwards along the latitudinal gradient, the former species appeared to be increasingly selecting spots with HBV ($r = 0.72$, $P < 0.05$) and HAV ($r = 0.81$, $P < 0.05$), whereas the latter species did not select spots with any particular type of bank vegetation ($r = -0.21$, $P = 0.655$) and with no aquatic vegetation ($r = -0.73$, $P = 0.05$). In site 1, these two species showed a similar preference for spots with moderate bank vegetation and moderate water vegetation (Figure 4), thus being similar in terms of their microhabitat niche use. However, only in site 1 they were sympatric with a third Pelomedusidae species (*Pelusios niger*), showing a statistically significant preference for high bank vegetation spots ($\chi^2 = 13.44$, df = 2, $P < 0.01$) and for high aquatic vegetation spots ($\chi^2 = 10.85$, df = 2, $P < 0.01$). Therefore, in site 1, *Pelusios niger* seems to occupy the same microhabitat niche that *Pelusios castaneus* occupies northwards in sites where *Pelusios niger* is not present.

DISCUSSION

We revealed several intriguing spatial effects in the variation of diversity patterns and niche partitioning among sympatric turtle species in our latitudinal mega-transect. Some of these spatial effects were expected, but others were unforeseen, indicating the importance of the study of interaction between local characteristics of sites, ecological characteristics of the various species, and synecological relationships (for instance, interspecific competition).

Using the calculated community metrics, our independent sets of analyses (statistics on univariate diversity indices and GLM models) consistently showed a northwards almost linear decrease in species richness, Shannon, Simpson and Evenness indices, and an increase in Dominance values. These results confirm the known global patterns of decline of species richness from the Equator to more northern latitudes (e.g. Willig & Lyons 1998; Chown & Gaston 2000; Mora & Robertson 2005). This is despite the fact that we only covered a 90 km south-north latitudinal transect and all our study localities were within comparatively similar habitats. Turtle communities in our study were relatively species-poor (4-5 in total) with only two taxa (*Pelusios niger* and *Trionyx triunguis*) contributing to the higher species richness of the southernmost localities. *Pelusios niger* is a coastal terrapin inhabiting only the Gulf of Guinea region from Nigeria to Gabon, and in site 1 (in the surroundings of Cotonou) the species was in on its westernmost range limit (Luiselli et al., 2018) although a doubtful record exists for central Togo (see Segniagbeto et al., 2014). *Trionyx triunguis,* on the other hand, is a widespread species, but with a scattered distribution in West Africa where it is threatened with extinction (Segniagbeto et al., 2014). This species was also considered very rare from interviews with fishers, and therefore sold for a high price in markets (according to the interviewees, most of the individuals of this species are sold to Chinese expatriates, who like consuming these animals more than the natives do). Thus, apart from these rare/marginal species, the typical turtle community in Benin consisted of three species: *Pelomedusa olivacea, Pelusios castaneus* and *Cyclanorbis senegalensis*. The former two species were however the only two really abundant species of the study area, with well over 250 individuals observed per species.

Whereas species richness was certainly determined by global biogeographic patterns, other community metrics were more likely affected by local processes. Reduction of evenness and increases in dominance in natural communities clearly reflect habitat loss and alteration of the pristine environmental characteristics of a given site (Clark *et al*. 1998; Pitzalis *et al*. 2013; Zeng *et al*. 2014). Thus, along our mega-transect, the reduction of evenness and increase of dominance northwards would indicate that, even though the south is much more heavily urbanised, the geographical gradient in species diversity overruled any local effects of habitat alteration and human pressure.

The high dominance estimates were due to the prevalence of just two species (*Pelomedusa olivacea* and *Pelusios castaneus*) in nearly all our surveyed sites. These species were invariably the most abundant chelonian species in the country, as also seen in the adjacent Togo where habitat characteristics (Dahomey Gap savannah) were substantially similar (Segniagbeto et al., 2014). The same was also true for Nigeria, but with additional species (for instance *Pelusios niger*) that dominated the samples in other specific habitat types (rainforest and swamped forests; see Luiselli et al., 2004, 2006). Indeed, there was evidence of resource partitioning (possibly due at least in part to interspecific competition) among the three Pelomedusidae species in our seven study sites. In site 1, where three Pelomedusidae were sympatric, the far largest of the three (*Pelusios niger*) inhabited essentially well vegetated (both along the banks and in water) spots, confining the other two species to moderate and low vegetated spots, where it can be anticipated that the predation pressure by birds and terrestrial mammals (for instance, mongooses) is likely to be higher than in well vegetated places. On the other hand, going northwards, *Pelusios niger* was not present and was replaced in by *Pelusios castaneus*, that exhibit almost opposite habitat selection to *Pelomedusa olivacea*. Since *Pelusios castaneus* and *Pelomedusa olivacea* are nearly identical in body size and share very similar dietary habits in West Africa (Luiselli et al., 2004, 2011), they are likely to be competitors at the local scale, especially during the dry months when the food availability is low (Luiselli 2008a). Thus, their divergent habitat use may well be a mechanism of niche partitioning, that in turtle communities has been observed more frequently in freshwater than in terrestrial ecosystems (Luiselli 2008a). We are aware that our evidence of resource partitioning between these two species, although likely, remains correlational and therefore we cannot exclude the fact that species-specific eco-physiological characteristics may have played a role in the observed patterns. For instance, it is possible that hermoregulatory opportunities, whereby individuals of different species select habitats based upon thermal conditions, may in part contribute to the observed patterns (e.g. Gilbert & Miles 2019; Goiran et al. 2020). However, we doubt that this latter explanation is true because both species have a very wide distribution, encompassing regions with much wetter and much more arid climates than our surveyed sites, so it is unlikely that the observed habitat partitioning patterns can be explained by eco-physiological differences between species.

Overall, our study suggests that large-scale spatial effects, when considered on their own, can only partially predict the structure of the animal communities, given that the dominant forces in structuring communities are locally scaled: eco-physiological characteristics of the various species in the assemblage and, especially with regard to our case of study, their synecological interactions (for instance, interspecific competition). In addition, also additional predictors, such as local climate and topography, may play important roles in determining community structure (e.g. Gibson & Hulbert 1987; Guisan & Hofer 2003). Thus, extrapolating large-scale diversity models may be inadequate when the ecological contexts of the studies communities are poorly known. Moreover, our data shows that it is possible to highlight the importance of considering microhabitat data in diversity distribution analyses.

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Table 1. Synthesis of the data collected on turtle species by locality in Benin.

	SITE 1	SITE 2	SITE 3	SITE 4	SITE 5	SITE 6	SITE 7
Pelusios niger	21	0	0	0	0	0	0
Pelusios castaneus	44	71	44	51	12	9	33
Pelomedusa olivacea	21	73	82	36	32	51	40
Cyclanorbis senegalensis	0	11	21	8	0	0	56
Trionyx triunguis	4	1	0	0	0	0	0

Table 2. Synthesis of the diversity measures (with upper and lower 95% confidence intervals calculated after 9999 bootstraps) for the data collected on turtle species by locality in Benin

	Species richness	Individuals	Dominance	Simpson	Shannon	Evenness	Chao-1
site1	4	90	0.3499	0.6501	1.167	0.8034	4
Lower	4	90	0.3067	0.577	1.032	0.7019	4
Upper	5	90	0.423	0.6931	1.258	0.8799	4
site2	4	156	0.4311	0.5689	0.933	0.6355	4
Lower	3	156	0.4006	0.5308	0.8438	0.5813	4
Upper	4	156	0.4692	0.5991	1.016	0.6907	4
site3	3	147	0.4212	0.5788	0.9646	0.8746	3
Lower	3	147	0.3784	0.5159	0.8685	0.7945	3
Upper	4	147	0.4841	0.6216	1.029	0.9332	3
site4	3	95	0.4389	0.5611	0.91	0.8281	3
Lower	3	95	0.3968	0.4968	0.789	0.7338	3
Upper	3	95	0.5023	0.6032	0.9934	0.9001	3
site5	2	44	0.6033	0.3967	0.586	0.8984	2
Lower	2	44	0.5165	0.2676	0.4382	0.7749	2
Upper	2	44	0.7324	0.4835	0.6765	0.9835	2
site6	2	60	0.745	0.255	0.4227	0.763	2
Lower	2	60	0.625	0.1244	0.2449	0.6388	2
Upper	3	60	0.8756	0.375	0.5623	0.8774	2
site7	3	129	0.35	0.65	1.074	0.9758	3
Lower	3	129	0.3353	0.6104	1.016	0.9211	3
Upper	3	129	0.3896	0.6647	1.096	0.9971	3

Table 3. Results of GLM, analyzing the effects of spatial components and microhabitat typologies on species abundances. Only the significant effects are presented in this table. Y = latitude; X = longitude.

Variables	Estimate	Standard error	Wald	P
Pelusios castaneus				
Spatial				
Intercept	0.055867	4746.863	0.000000	0.000000
Y	0.067192	12.371	0.000436	0.000011
Microhabitat				
Intercept	3.495156	0.069806	2506.994	0.000000
High current speed	-0.308178	0.078051	15.590	0.000079
No bank vegetation	-0.744146	0.092839	64.247	0.000000
Pelomedusa olivacea				
Spatial				
Intercept	3.849103	0.055867	4746.863	0.000000
XY	0.236329	0.067192	12.371	0.000436
Microhabitat				
Intercept		0.059037	4117.180	0.000000
High bank vegetation	-0.173336	0.054805	10.003	0.001563
No aquatic vegetation	0.390619	0.056001	48.653	0.000000
Cyclanorbis senegalensis				
Spatial				
Intercept	2.944080	0.123706	566.3917	0.000000
Y	0.726519	0.104126	48.6831	0.000000
Microhabitat				
Intercept	2.877759	0.134479	457.9303	0.000000
High current speed	0.909046	0.140107	42.0971	0.000000

Table 4. Results of GLM, analyzing the effects of spatial components on abundances and on two different diversity indices: Shannon index and Dominance index. Y = latitude; X = longitude.

	Estimate	Standard error	Wald	P
		abundance		
Intercept	0.000	0.04341	0.00000	1.000000
X	320.819	47.98205	44.70570	0.000000
Y	155.066	32.45264	22.83149	0.000002
XY	-110.328	13.64324	65.39394	0.000000
X2	-166.440	29.22114	32.44291	0.000000
		Dominance		
Intercept	0.000	0.02194	0.0000	1.000000
X	228.898	24.25326	89.0729	0.000000
Y	114.984	16.40369	49.1351	0.000000
XY	-48.909	6.89618	50.2982	0.000000
X2	-161.202	14.77027	119.1147	0.000000
Y2	-33.631	10.58621	10.0925	0.001489
		Simpson		
Intercept	0.000	0.08131	0.00000	1.000000
X	-339.782	89.88850	14.28866	0.000157
XY	77.286	25.55893	9.14366	0.002496
X2	230.051	54.74223	17.66058	0.000026
		Shannon		
Intercept	0.000	0.0952	0.00000	1.000000
X	-258.292	105.2681	6.02047	0.014141
XY	58.934	29.9320	3.87672	0.048960
X2	176.125	64.1084	7.54764	0.006009
		Evenness		
Intercept	0.000	0.1554	0.00000	1.000000
Y2	-233.907	74.9648	9.73582	0.001807

Table 5. Results of the Spearman's rank correlation analyses between latitude of each study site and (arcsin)percentage of individuals of each turtle species that were found in each microhabitat category of the seven sites. Statistically significant correlations are given in boldface.

Microhabitat variable	category	*Pelusios castaneus*	*Pelomedusa olivacea*	*Cyclanorbis senegalensis*
current speed	High	r = -0.11 P = 0.835	r = 0 P = 1	r = 0.8 P = 0.082
	Moderate	**r = 0.85 P = 0.016**	r = -0.11 P = 0.814	**r = -0.96 P = 0.03**
	No	**r = -0.83 P = 0.021**	r = -0.006 P = 0.989	**r = 0.946 P = 0.05**
bank vegetation	High	r = 0.72 P = 0.064	r = -0.203 P = 0.656	r = 0.69 P = 0.31
	Moderate	r = -0.72 P = 0.066	r = -0.522 P = 0.228	r = -0.90 P = 0.099
	No	r = -0.58 P = 0.17	r = 0.595 P = 0.158	**r = 0.98 P = 0.014**
aquatic vegetation	High	**r = 0.81 P = 0.028**	r = -0.73 P = 0.062	r = -0.28 P = 0.716
	Moderate	**r = -0.87 P = 0.01**	r = -0.32 P = 0.478	r = -0.42 P = 0.581
	No	r = -0.28 P = 0.548	r = 0.72 P = 0.068	r = 0.77 P = 0.231

CAPTIONS FOR THE FIGURES

Figure 1. Map of southern Benin, showing the seven study areas. For the geographic coordinates, see the text.

Figure 2. Examples of habitat types as studied in the present paper: (a) site with no current speed (score = 0), high banks vegetation (score = 2) and no aquatic vegetation (score = 0); (b) site with high current speed (score = 2), moderate bank vegetation (score = 1) and no aquatic vegetation (score = 0); (c) site with moderate current speed (score = 1), high bank vegetation (score = 2) and high aquatic vegetation (score = 2); (d) two individuals (one male and one female) of *Pelusios niger* from study site 1 (Cotonou). This species was observed only in one of the surveyed sites, and is at its westernmost range tip in Benin

Figure 3. Rarefaction curve (and 95% confidence intervals generated after 9,999 bootstraps) for species discoveries in relation to sample size (graphic (a)) and scale diversity profiles (graphic (b)) for the various surveyed study areas for turtles in Benin. Bootstrapping were calculated using PAST 3.0 software.

Figure 4. Differences in microhabitat category use, along the South-North gradient, between *Pelomedusa olivacea* and *Pelusios castaneus*. The % of individuals are calculated, for each species, on the basis of the number of individuals occurring in each given category (no, moderate, high) of microhabitat (current speed, bank vegetation and aquatic vegetation) in relation to the total number of individuals of that species captured in each of the seven study sites. Symbols: P.cast. = *Pelusios castaneus*; Pe.oliv. = *Pelomedusa olivacea.*

Fig. 1

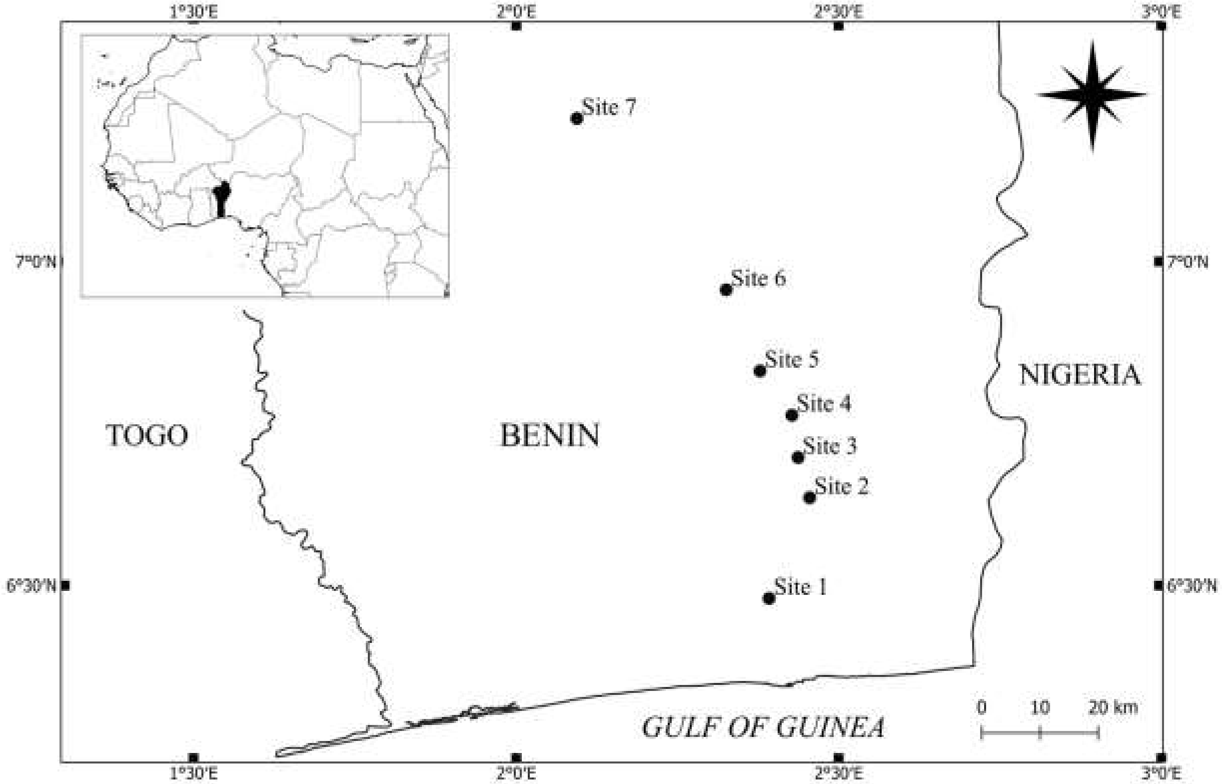

1°30'E
2°0'E
2°30'E
3°0'E
7°0'N
6°30'N
Site 7
Site 6
Site 5
Site 4
Site 3
Site 2
Site 1
TOGO
BENIN
NIGERIA
GULF OF GUINEA
0
10
20 km

Fig. 2.

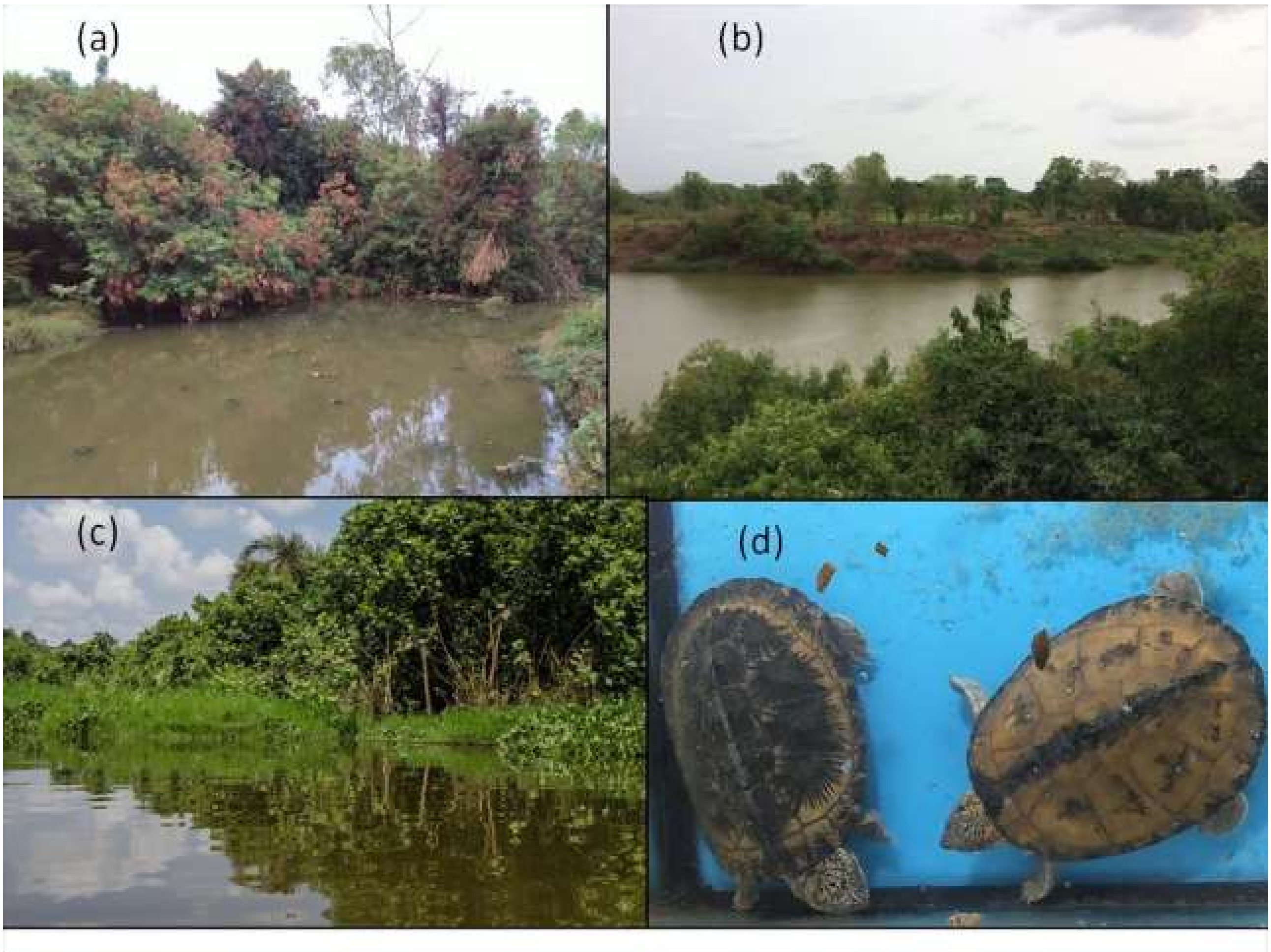


Fig. 3

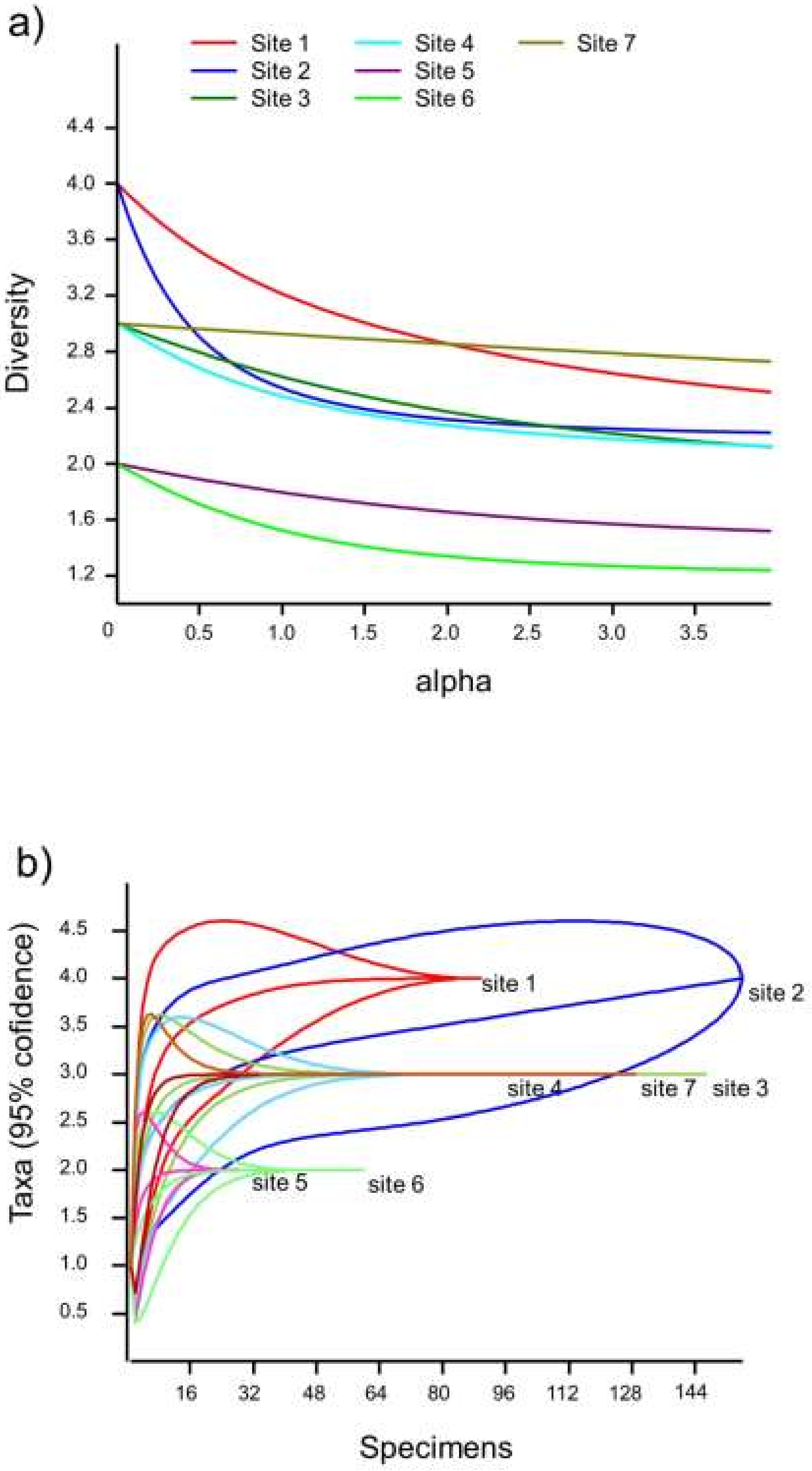
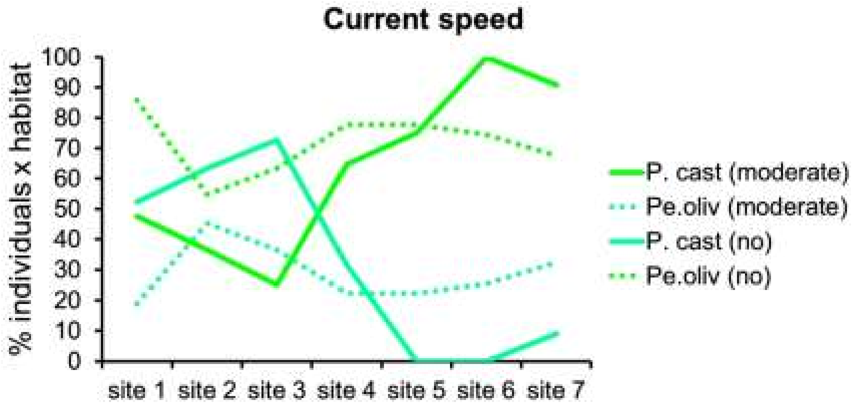
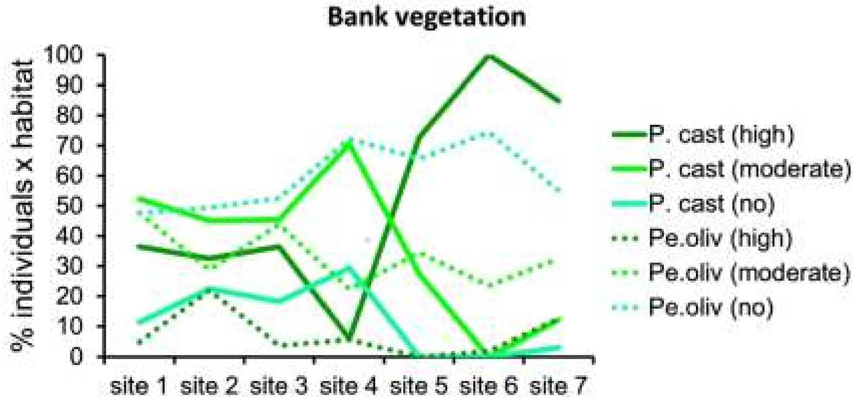
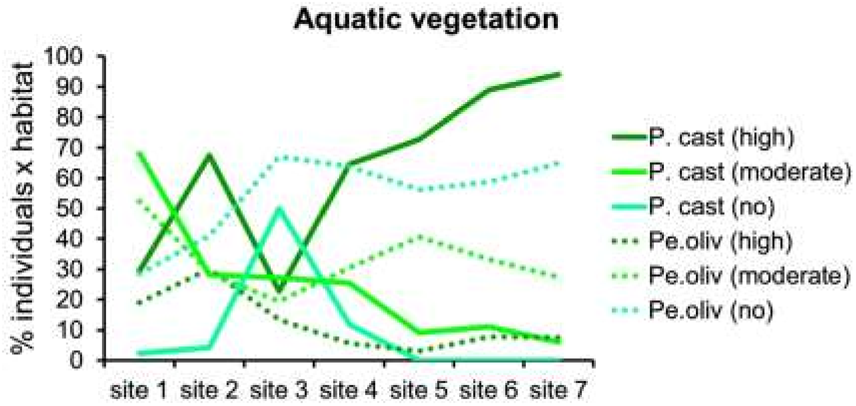

a)
Site 1
Site 2
Site 3
Site 4
Site 5
Site 6
Site 7
Diversity
4.4
4.0
3.6
3.2
2.8
2.4
2.0
1.6
1.2
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
alpha
b)
Taxa (95% cofidence)
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
site 1
site 2
site 4
site 7
site 3
site 5
site 6
16
32
48
64
80
96
112
128
144
Specimens

Fig.4.


Current speed
% individuals x habitat
100
90
80
70
60
50
40
30
20
10
0
site 1
site 2
site 3
site 4
site 5
site 6
site 7
P. cast (moderate)
Pe.oliv (moderate)
P. cast (no)
Pe.oliv (no)


Bank vegetation
% individuals x habitat
100
90
80
70
60
50
40
30
20
10
0
site 1
site 2
site 3
site 4
site 5
site 6
site 7
P. cast (high)
P. cast (moderate)
P. cast (no)
Pe.oliv (high)
Pe.oliv (moderate)
Pe.oliv (no)


Aquatic vegetation
% individuals x habitat
100
90
80
70
60
50
40
30
20
10
0
site 1
site 2
site 3
site 4
site 5
site 6
site 7
P. cast (high)
P. cast (moderate)
P. cast (no)
Pe.oliv (high)
Pe.oliv (moderate)
Pe.oliv (no)

Predicting the structure of turtle assemblages along a megatransect in West Africa

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ONLINE SUPPLEMENTAL MATERIALS

Table S1. Corine landcover characteristics and rainfall of the seven study sites in Benin.

Site	Land cover	rainfall	soil water holding (capacity, mm)	percentage tree cover (per km^2)
1	Savanna	1001 - 1500 mm per annum	10	47
2	Wetland/ floodplain	1001 - 1500 mm per annum	10	37
3	Savanna	1001 - 1500 mm per annum	10	37
4	Wetland/ floodplain	1001 - 1500 mm per annum	10	37
5	Savanna; Cropland and fallow with oil palms	1001 - 1500 mm per annum	30	51
6	Savanna	1001 - 1500 mm per annum	10	40
7	Wetland/ floodplain	1001 - 1500 mm per annum	10	54

Table S2. Number of turtle individuals observed in the various microhabitat types (as described by current speed, aquatic vegetation and bank vegetation) at the seven study sites in Benin.

	site 1	site 2	site 3	site 4	site 5	site 6	site 7
Pelusios niger							
high current	0						
moderate current	8						
no current	13						
high bank vegetation	18						
moderate bank vegetation	3						
no bank vegetation	0						
high water vegetation	16						
moderate water vegetation	5						
no water vegetation	0						
Pelusios castaneus							
high current	0	0	1	2	0	0	0
moderate current	21	26	11	33	11	9	30
no current	23	45	32	16	1	0	3
high bank vegetation	16	23	16	3	8	9	28
moderate bank vegetation	23	32	20	36	3	0	4
no bank vegetation	5	16	8	15	0	0	1
high water vegetation	13	48	10	33	8	8	31
moderate water vegetation	30	20	12	13	2	1	2
no water vegetation	1	3	22	6	1	0	0
Pelomedusa olivacea							
high current	0	0	0	0	0	0	0
moderate current	4	33	30	8	12	13	13
no current	18	40	52	28	20	38	27
high bank vegetation	1	16	3	2	0	1	5
moderate bank vegetation	10	21	36	8	11	12	13
no bank vegetation	10	36	43	26	21	38	22
high aquatic vegetation	4	22	11	2	1	4	3
moderate aquatic vegetation	11	21	16	11	13	17	11
no aquatic vegetation	6	30	55	23	18	30	26
Cyclanorbis senegalensis							
high current			1	0			4
moderate current		7	11	6			36
no current		4	9	2			16

high bank vegetation	3	13	5			32
moderate bank vegetation	8	7	2			11
no bank vegetation	0	1	1			13
high aquatic vegetation	6	13	6			22
moderate aquatic vegetation	4	8	1			18
no aquatic vegetation	1	0	1			16
Trionyx triunguis						
high current	2	0				
moderate current	2	1				
no current	0	0				
high bank vegetation	4	1				
moderate bank vegetation	0	0				
no bank vegetation	0	0				
high aquatic vegetation	4	1				
moderate aquatic vegetation	0	0				
no aquatic vegetation	0	0				

Figure S1. Total number of turtle individuals observed in Benin during the present study