PUBLICATION INFORMATION

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1 **Predicting the structure of turtle assemblages along a megatransect in**

2 **West Africa**

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28   RUNNING HEAD: Turtle communities along a megatransect

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31   Understanding large- and small-scale patterns as well as the determinants of species richness is

32   central for the study of evolutionary mechanisms. The extent to which species richness in local

33   communities is related to larger scale processes is a pre-eminent topic in ecological and

34   evolutionary research. To investigate how local and regional species richness are related, we

35   sampled freshwater turtle assemblages in seven localities to represent the variation in ecological

36   conditions along a 90km South-North megatransect in Benin, West Africa. In each locality, all

37   turtles captured were identified and measured, and microhabitat classified in which individual

38   turtles were observed. Based on these data we used community diversity metrics to compare turtle

39   assemblages. Spatial autocorrelation did not affect our data. For all localities pooled, only two

40   species (*Pelusios castaneus* and *Pelomedusa olivacea*) were the most common, and one species

41   (*Trionyx triunguis*) the rarest. Analyses of the commonest and more numerous species showed that

42   the abundance of *P. castaneus* declined with an increase in latitude and longitude, but the opposite

43   was true for *P. olivacea*. We showed that various microhabitat characteristics were significantly

44   correlated with the abundance of the two common species. We found significant but variable South-

45   North gradients in microhabitat use for different turtle species. Our results highlight the importance

46   of studying interactions between local environments, the ecological requirements of each species,

47   and their synecological relationships.

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53 INTRODUCTION

54 Understanding the large- and small-scale patterns and determinants of species richness is central for

55 the study of the evolutionary mechanisms, for instance the historical morphological differentiation

56 as a niche partitioning pattern and its influences on speciation (e.g., Futuyma 2006). Richness

57 patterns of terrestrial and freshwater species are inversely related to latitude (Willig & Lyons 1998;

58 Chown & Gaston 2000; Mora & Robertson 2005). This pattern has been documented for numerous

59 taxonomic groups (ranging from protists to primates) for data across regional and global scales

60 (Adams 2009). Species richness is presumed to be a consequence of systematic spatial variation in

61 the balance of speciation versus extinction and immigration versus emigration of species (Adams

62 2009). A large number of different reasons have been suggested to explain the latitudinal variation

63 in species numbers (Rapoport 1982; Adams 2009). One factor, the relationship between the number

64 of species in an area and ambient available ('usable') environmental energy, is considered to be

65 important in modulating any effect of the physical structure of the Earth in determining species

66 richness gradients (e.g. He & Legendre 1996). However, other mechanisms, for instance

67 interspecific competition and niche resource partitioning, have been considered among the

68 prominent forces determining community structure and species richness at local scales (Connell

69 1980, 1983; Barbault 1991). Consequently, various statistical tools have been used to uncover

70 community assembly rules and thus identify eventual non-random patterns in community structure

71 (e.g. see Gotelli & Graves 1996; Luiselli 2008a; Ulrich & Gotelli 2010; Gotelli & Urlich 2012).

72 Whereas freshwater turtle communities have been well studied by in numerous bioregions

73 worldwide (e.g. see Luiselli 2008a; Stephens & Wiens 2009), sub-Saharan freshwater turtle

74 communities have been somewhat neglected (Luiselli 2008b) despite their high species richness

75 throughout the entire region (Branch 2008; Bombi *et al*. 2011). The only published studies have

76 been descriptive (e.g., Akani *et al*. 2018) or confined to a relatively well defined geographic area

77 (e.g. Niger Delta, see Luiselli *et al*. 2004, 2006).

78

79 To understand global variation in biodiversity, we need not only explore the importance of

80 differences in patterns observed at local and at regional scales, but also determine how diversity at

81 one scale might relate to that at another (Yanoviak 2001; Poisot *et al*. 2010; Rasche *et al*. 2011).

82 Finding the correct scale for explaining a given phenomenon is a challenge (Cooper *et al*. 2007;

83 Tucker 2009; Barley & Meeuwig 2017). Selecting too large a scale (i.e., large grain sizes) may

84 result in too much variation in measured variables (i.e., induce chaos), whereas too fine a scale may

85 lose sight of existing patterns (for instance, there might be apparent population declines because a

86 subgroup of monitored individuals may be affected by an intervening perturbation event that has no

87 effect at the population level). Thus, empirical studies that are larger than local scales but smaller

88 than the regional/global, are useful to better understand patterns of how biodiversity is organised. In

89 this regard, a promising option is the use of mega-transects, i.e. much-larger-than-usual (few

90 hundreds up to few thousands meters long) transects joining several study sites from a given region,

91 to explore more general patterns but still resulting from a local scale (Huber and Chao, 2019).

92 Though promising, these mega-transects have been rarely used by community ecologists in tropical

93 and in temperate contexts (but see Luiselli *et al*. 2008; Huber & Chao 2019).

94   In this paper, we examine diversity patterns and local community structure of turtle

95 assemblages along a South-North oriented mega-transect in Benin (West Africa). We test whether

96 large-scale spatial effects predict the structure of animal communities at the local scale by recording

97 the presence and local abundance of freshwater turtles in seven randomly selected sites along the

98 mega-transect. Using numbers of observed individuals and various diversity metrics, we describe

99 local community structure. We also examine microhabitat selection by sympatric species, as well

100 overall latitudinal gradients. Our results are useful in understanding the "rules" governing the

101 assembly of local communities (Caley & Schluter, 1997) and how these relate to processes acting at

102 larger spatial scales.

103

104   MATERIALS AND METHODS

105 The taxonomy of African turtles has been undergoing considerable revisions during the last decade

106 (e.g. Branch 2008). For practical reasons, we follow the recognized taxonomic names given in

107 Turtle Taxonomy Working Group (2017).

108

109   STUDY LOCATIONS

110 We studied turtle communities in seven discrete sites in Benin during the wet season (May-June)

111 from 2010 until 2012. All sites were found in riverine freshwater habitats, selected to represent the

112 range of ecological conditions found from the south to the north of the country (Figure 1): 1)

113 Cotonou (decimal coordinate system: 6.479947 N, 2.392178 E); 2) Ouémé (6.635108 N, 2.455157

114 E); 3) Adjohoun: 6.697428 N, 2.437219 E; 4) 6.762794 N, 2.427668 E; 5) Djigbé (6.830605 N,

115 2.378119 E); 6) 6.956216 N, 2.325714 E; 7) Za-Kpota (7.220734 N, 2.094006 E). The linear

116 distance from the southernmost to the northernmost site was 90 km.

117

118 Benin is characterised by a wide range of ecosystems, related to differences in climate and

119 topography. All study sites were within the Guineo-Congolian vegetation zone. General

120 characteristics of each sites, according to Corine landcover and rainfall, are given in Table S1. In all

121 sites, we surveyed the main river tracts; these differed locally in terms of current speed, riverbed

122 characteristics and vegetation (both in the banks and in the water) (see below).

123

124 Predominant vegetation in the study region was Guinea savannah grasslands with scattered patches

125 of riparian forest (around 50 m width) along the banks of meandering rivers. Soils varied from

126 muddy, clayey to sandy. Composition and structure of the riparian vegetation was influenced by the

127 extent, duration, timing and frequency of flooding (O'Connor 2001); southernmost sites were

128 generally moister and richer than the more northerly sites (Ceperley *et al*., 2010). Tree density

129 varied between sites. The most common tree species were: *Pterocarpus santalinoides, Cola*

130 *laurifolia, Vitex madiensis, Mitragyna inermis, Eugenia kerstingii, Parinari curatellifolia,*

131 *Diospyros mespiliformis, V. simplicifolia, Margaritaria discoidea*, and *Ficus capreaeifolia*.

132 Average tree height (all sites pooled) was 17.5 ± 14.3 m.

133

134   FIELD PROTOCOLS

135 In each site, we surveyed an area of about 3000 m^2 (shape depending on the configuration of the

136 water-bodies) for a total of 10 field days during the wet season (April to September). Turtles were

137 caught by hand and with fishing traps. Fishing traps were baited funnel traps, made of non-stretch

138 fine mesh of 2.5cm. We used this mesh size to avoid the legs of the turtles becoming entangled. The

139 top of the traps remained above water, to allow captured turtles to surface for air. None of the

140 captured turtles died during the field study. We used fish pieces as bait. The same number of traps

141 (n = 30) were deployed at each site during each day. We placed ten traps in each of the three aquatic

142 vegetation categories (see below) in each site, and then recorded current speed and bank vegetation

143 data (see below for the various categories) for each of the points where traps were placed.

144   Field surveys started at 07:00 h and ended at 18:30; traps were examined twice a day:

145 around 07:00 h and around 18:00 h. We also examined individuals taken by local fishers or on sale

146 in nearby markets. We considered only turtles found in riverine markets , and those caught by local

147 fishermen that we knew originated within our study sites. These turtles were considered for the

148 microhabitat analyses, only for the diversity metrics.

149   All turtles were identified to species, sexed, and marked by carapace scute notching. We

150 measured turtle size using the curved carapace length and plastron length (morphometric data were

151 not analysed in this paper as they were not directly relevant to the aim of this research). All animals

152 were released unharmed at the point of capture.

153

154   Since previous studies on freshwater turtles in general have shown that presence/absence

155 and population abundance of species are related to bank vegetation, aquatic vegetation and current

156 speed (e.g. Ficetola *et al*. 2004; Wyneken *et al*. 2008; Vignoli *et al*. 2015), we classified the

157 microhabitat in which we observed turtles (apart from those recorded in markets) according to three

158 independent variables (Figure 2):

159

160 (a) Speed of water current (three categories: 0 = no current; 1 = moderate current; 2 = high

161   current). Current speed was evaluated by eye within a 10 m radius around the sighting point

162   of each individual turtle.

163 (b) Bank vegetation was recorded along the bank of the water body where each individual turtle

164   was sighted: 0 = no bank vegetation (NBV); 1 = moderate bank vegetation (MBV); 2 = high

165   bank vegetation (HBV). NBV was assigned when the banks were bare or only with

166   herbaceous vegetation; MBV was assigned when there were reeds and bushes but no trees (no

167   gallery forest). HBV was when the bank vegetation consisted of a strip of gallery forest.

168 (c)   Aquatic vegetation was classified as: 0 = no aquatic vegetation (NAV); 1 = moderate aquatic

169   vegetation (MAV); 2 = high aquatic vegetation (HAV). NAV was assigned when there was

170   less than 10% of the water surface covered by aquatic plants; MAV was when the water

171   surface was covered by 11-30% by aquatic plants, and HAV was when aquatic vegetation

172   covered more than 30% of the water surface. The % aquatic vegetation cover was evaluated

173   by eye within a radius of 10 m around the site of sighting of each individual turtle.

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

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179   STATISTICAL ANALYSES

180 *Diversity metrics analyses.*

181 We evaluated whether our sampling effort captured the true species richness and diversity within

182 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 above-

207   mentioned indices, with 9,999 random samples, each with the same total number of individuals as

208   in each original sample generated (Harper 1999).

209

210   To determine whether the linear distance between pairs of sites can affect the species'

211   assemblage heterogeneity across sites, for each diversity index and for each given pair of sites we

212   first subtracted the value of site "a" by the value of site "b". Then, we correlated (using the

213   Pearson's correlation coefficient) these subtraction values with the linear distance between the

214   given pairs of sites. If the test was statistically significant, we would conclude that the linear

215   distance between sites influence the difference in community metrics between sites.

216

217   *Micro-habitat selection analyses*

218   The variables used for the description of microhabitat characteristics were not significantly collinear

219   at Spearman's rank correlation coefficient (in all cases, $P > 0.05$), and thus were retained for further

220   statistical analyses. Also, because river width was not correlated with latitude ($r = 0.311$, $P > 0.05$),

221   we also considered river width in the analyses. The frequencies of occurrence of the various species

222   by the various categories in each of the three microhabitat variables were analyzed by contingency

223   tables χ^2 tests.   In order to analyse the data in more depth, we used Generalized Linear Models

224   (GLM, Hosmer & Lemeshow 2000) to quantify (1) the effects of spatial components on the

225   abundance of the various turtle species at each site and (2) the effects of spatial components on the

226   diversity metrics (Simpson, Shannon, Evenness and Dominance) among the study sites. In these

227   models, abundance per site was defined as the number of individuals observed for each species at

228   each of the three microhabitat variables at each study site; the sampling units were the seven study

229   sites. To test for possible spatial effects, we used the third-degree polynomial equation of latitude

230   (Y) and longitude (X) of each site as follows (Carrete *et al*. 2007):

231

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

233

234   This cubic trend surface ensures that (i) linear gradient patterns were calculated, and that (ii)

235 more complex features (i.e. patches or gaps, which require quadratic and cubic terms to be fit) were

236 also extracted (Legendre & Legendre 1998).

237   Firstly, to test the pure effect of spatial components on turtles abundances, a stepwise

238 forward regression procedure with the nine terms of the third-degree polynomial equation of the

239 latitude and longitude as predictor variables and abundances of species as the dependent variable

240 was used to test the statistical significance of each variable in turn, and variables were excluded

241 when they did not correlate significantly with the dependent variable (Wald test $P > 0.05$). This

242 analysis was carried out in order to remove the non-significant spatial terms (Legendre & Legendre

243 1998). The significant variables were subsequently computed using the best subset procedure. In

244 this analysis, the abundances (number of individuals) were used as dependent variable, the spatial

245 components and the microhabitat categories as predictors.

246

247 Spatial auto-correlation could bias model parameter estimation, especially when making ecological

248 inference (Legendre & Legendre 1998). In order to test for the presence of spatial autocorrelation,

249 firstly we make a preliminary forward stepwise regression forcing the significant spatial terms of

250 the previous analysis (pure spatial effects) with the microhabitat categories as predictor variables

251 and abundances of species as the dependent variable. Secondly, the eventually significant spatial

252 terms ($P <0.05$) were retained and included in each model to test if they accounted for a significant

253 change in the model significance and deviance.

254

255 We standardized all variables, also for the diversity indices model, to remove the effect of

256 differences in the original scale of measurement. The standardization of values contains options to

257 standardize all values of the selected variables used in the model. All values of selected variables

258 are replaced by standardized values, which were computed, using Statistica 6.0 software

259 (www.statsoft.com), as follows:

260

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

262

263 In all GLM models, the log link function and a Poisson distribution of error were used

264 (McCullagh & Nelder, 1989).

265 We used Spearman's rank correlation analyses to analyse the correlation between latitude of

266 each study site and (arcsin)percentage of individuals of each turtle species found in each

267 microhabitat category in the seven sites. Alpha was set at 5%. We used the PAST 3.0 software for

268 all the statistical analyses concerning the diversity metrics, and the Statistica 6.0 software

269 (www.statsoft.com) for all the other statistical analyses.

270

271 RESULTS

272 OVERALL PATTERNS

273 A summary of the data collected on turtle species by study sites is given in Table 1. A total of 630

274 turtles were observed belonging to five species, three Pelomedusidae (genera *Pelomedusa* and

275 *Pelusios*) and two Trionychidae (genera *Cyclanorbis* and *Trionyx*). For all species we observed

276 both adults and juveniles, thus suggesting reproduction in the populations.

277 For all localities pooled, *Pelusios castaneus* and *Pelomedusa olivacea* accounted for most of

278 the observed individuals (Figure S1). In terms of number of individuals, the rarest species was

279 *Trionyx triunguis*, which accounted for 0.8% of the total observed sample. However, in terms of

280 number of localities present, *Pelusios niger* was the rarest species (observed in 1/7 sampled

281 localities) followed by *Trionyx triunguis* (2/7 sampled localities) (Table 1). Both *Pelusios castaneus*

282 and *Pelomedusa olivacea* were observed in 100% of the sampled sites and occurred in sympatry

283 also in the same microhabitats.

284   Overall, a rarefaction curve showed that the plateau phase was clearly reached in our

285   sampling, and that no additional species would be expected in our sampled areas (Figure 3). Also,

286   Chao-1 estimates confirmed that the overall turtle diversity was captured by our surveys (Table 2).

287   In addition, we observed a reduction in evenness and an increase in dominance from South to North

288   (Table 2).

289   No values of the difference of diversity indices between pairs of sites were significantly

290   correlated to the linear distance between them (in all cases, at least $P > 0.250$), thus showing that

291   linear distance cannot be used as a proxy of species heterogeneity across sites.

292   The raw dataset for the number of turtle individuals observed in the different microhabitat

293   types (as described by current speed, aquatic vegetation and bank vegetation) is given in Table S2.

294   The results obtained from our GLM models are summarized in Table 3 and are briefly explained

295   below.

296

297   PURE SPATIAL EFFECTS

298   For *Pelusios castaneus*, our model showed that the abundance of this species declined with an

299   increase in latitude (Table 3). For *Pelomedusa olivacea* abundance, there was positive effect of the

300   interaction longitude × latitude (Table 3), that is: the abundance of this species increased with

301   increases in latitude (towards North) and in longitude (towards East). Abundance of *Cyclanorbis*

302   *senegalensis* was negatively affected by the interaction of latitude × longitude, that is: its abundance

303   increased towards North but declined towards East. *Pelusios niger* and *Trionyx triunguis* could not

304   be modelled due to the low number of sites where the species were recorded (1/7 and 2/7

305   respectively). The latitude effect was not due to the river width, as (1) these two variables were not

306   autocorrelated (see above), and (2) the river width did not influence any of the species

307   presence/absence and abundance (in all cases, at least $P > 0.05$).

308

309   SPATIAL AUTOCORRELATION

310   In the forward stepwise regression (testing any eventual spatial auto-correlation), none of the spatial

311   terms forced with the microhabitat predictors were significant (p>0.05 for all models, in details:

312   *Pelusios castaneus* Y: P=0.633; *Pelomedusa olivacea* XY: P= 0.157; *Cyclanorbis senegalensis* XY:

313   P= 0.103) and none of the spatial terms accounted for any significant change in model deviance.

314   Thus, no spatial autocorrelation was found for each of the analyzed species.

315

316   MICROHABITAT EFFECTS

317   Our model showed that the abundance of *Pelusios castaneus* increased significantly with an

318   increase of MBV and HBV (Table 3), showing that the presence of this species was positively

319   related to at least partial vegetation cover along the banks without high current speed.

320   The probability of an increased abundance of *Pelomedusa olivacea* was positively

321   associated with no current and negatively associated with HBV (Table 3), showing that the presence

322   of this species could be negatively related to the bank vegetation cover whereas it is favoured by the

323   riverine spots empty of, or with scarce, aquatic vegetation.

324   Finally, the abundance of *Cyclanorbis senegalensis* was positively influenced by HBV. We

325   were not able to model *Pelusios niger* and *Trionyx triunguis* due to too low number of sites where

326   they were found (see above).

327   Contingency tables χ^2 tests revealed uneven distribution of the frequencies of individuals of

328   the various species by microhabitat categories (all sites being pooled): *Pelusios niger* showed a

329   significant preference for HBV and HAV (P < 0.01 both cases); *Pelusios castaneus* significantly

330   avoided high current, NBV and NAV (P < 0.01 in all cases); *Pelomedusa olivacea* significantly

331   avoided high current and HBV (at least P < 0.05), and *Cyclanorbis senegalensis* significantly

332   avoided high current, NBV and NAV (at least P < 0.05 in all cases).

333

334   DIVERSITY EFFECTS

335   Our GLM models uncovered a positive effect of latitude and longitude, and a negative effect of the

336   interaction longitude × latitude on the abundance of turtles (after pooling data from all species)

337   (Table 4).

338   Results for the Dominance index indicated that there was a complex effect of spatial

339   components, with values mildly (albeit significantly) increasing with an increase in latitude and

340   longitude (Table 4). The "mild" increase is seen in Table 4 because the estimates of x^2 and y^2 were

341   negative. Simpson and Shannon indices indicated a negative effect of longitude and a mild positive

342   effect of the interaction between latitude and longitude, as shown by the fact that x^2 estimate had a

343   positive sign (Table 4). There was a moderate (but statistically significant) negative effect of the

344   latitude, as demonstrated by the Evenness index (Table 4).

345

346   SOUTH-NORTH GRADIENT AND MICROHABITAT NICHE PARTITIONING

347   A statistically significant South-North gradient in microhabitat use of turtles was uncovered by

348   Spearman's rank correlation analyses for two species (*Pelusios castaneus* and *Cyclanorbis*

349   *senegalensis*) when current speed was considered, for one species when bank vegetation was

350   considered (*Cyclanorbis senegalensis*), and for one species (*Pelusios castaneus*) when aquatic

351   vegetation was taken into account (Table 5). The most striking differences along the latitudinal

352   gradient were observed between two Pelomedusidae species, viz. *Pelusios castaneus* and

353   *Pelomedusa olivacea* (Figure 4): northwards along the latitudinal gradient, the former species

354   appeared to be increasingly selecting spots with HBV (r = 0.72, P < 0.05) and HAV (r = 0.81, P <

355   0.05), whereas the latter species did not select spots with any particular type of bank vegetation (r =

356   -0.21, P = 0.655) and with no aquatic vegetation (r = -0.73, P = 0.05). In site 1, these two species

357   showed a similar preference for spots with moderate bank vegetation and moderate water vegetation

358   (Figure 4), thus being similar in terms of their microhabitat niche use. However, only in site 1 they

359 were sympatric with a third Pelomedusidae species (*Pelusios niger*), showing a statistically

360 significant preference for high bank vegetation spots ($\chi^2 = 13.44$, df = 2, P < 0.01) and for high

361 aquatic vegetation spots ($\chi^2 = 10.85$, df = 2, P < 0.01). Therefore, in site 1, *Pelusios niger* seems to

362 occupy the same microhabitat niche that *Pelusios castaneus* occupies northwards in sites where

363 *Pelusios niger* is not present.

364

365   DISCUSSION

366 We revealed several intriguing spatial effects in the variation of diversity patterns and niche

367 partitioning among sympatric turtle species in our latitudinal mega-transect. Some of these spatial

368 effects were expected, but others were unforeseen, indicating the importance of the study of

369 interaction between local characteristics of sites, ecological characteristics of the various species,

370 and synecological relationships (for instance, interspecific competition).

371   Using the calculated community metrics, our independent sets of analyses (statistics on

372 univariate diversity indices and GLM models) consistently showed a northwards almost linear

373 decrease in species richness, Shannon, Simpson and Evenness indices, and an increase in

374 Dominance values. These results confirm the known global patterns of decline of species richness

375 from the Equator to more northern latitudes (e.g. Willig & Lyons 1998; Chown & Gaston 2000;

376 Mora & Robertson 2005). This is despite the fact that we only covered a 90 km south-north

377 latitudinal transect and all our study localities were within comparatively similar habitats. Turtle

378 communities in our study were relatively species-poor (4-5 in total) with only two taxa (*Pelusios*

379 *niger* and *Trionyx triunguis*) contributing to the higher species richness of the southernmost

380 localities. *Pelusios niger* is a coastal terrapin inhabiting only the Gulf of Guinea region from

381 Nigeria to Gabon, and in site 1 (in the surroundings of Cotonou) the species was in on its

382 westernmost range limit (Luiselli et al., 2018) although a doubtful record exists for central Togo

383 (see Segniagbeto et al., 2014). *Trionyx triunguis,* on the other hand, is a widespread species, but

384 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

410 to moderate and low vegetated spots, where it can be anticipated that the predation pressure by birds

411 and terrestrial mammals (for instance, mongooses) is likely to be higher than in well vegetated

412 places. On the other hand, going northwards, *Pelusios niger* was not present and was replaced in by

413 *Pelusios castaneus*, that exhibit almost opposite habitat selection to *Pelomedusa olivacea*. Since

414 *Pelusios castaneus* and *Pelomedusa olivacea* are nearly identical in body size and share very similar

415 dietary habits in West Africa (Luiselli et al., 2004, 2011), they are likely to be competitors at the

416 local scale, especially during the dry months when the food availability is low (Luiselli 2008a).

417 Thus, their divergent habitat use may well be a mechanism of niche partitioning, that in turtle

418 communities has been observed more frequently in freshwater than in terrestrial ecosystems

419 (Luiselli 2008a). We are aware that our evidence of resource partitioning between these two

420 species, although likely, remains correlational and therefore we cannot exclude the fact that species-

421 specific eco-physiological characteristics may have played a role in the observed patterns. For

422 instance, it is possible that hermoregulatory opportunities, whereby individuals of different species

423 select habitats based upon thermal conditions, may in part contribute to the observed patterns (e.g.

424 Gilbert & Miles 2019; Goiran et al. 2020). However, we doubt that this latter explanation is true

425 because both species have a very wide distribution, encompassing regions with much wetter and

426 much more arid climates than our surveyed sites, so it is unlikely that the observed habitat

427 partitioning patterns can be explained by eco-physiological differences between species.

428 Overall, our study suggests that large-scale spatial effects, when considered on their own,

429 can only partially predict the structure of the animal communities, given that the dominant forces in

430 structuring communities are locally scaled: eco-physiological characteristics of the various species

431 in the assemblage and, especially with regard to our case of study, their synecological interactions

432 (for instance, interspecific competition). In addition, also additional predictors, such as local climate

433 and topography, may play important roles in determining community structure (e.g. Gibson &

434 Hulbert 1987; Guisan & Hofer 2003). Thus, extrapolating large-scale diversity models may be

435 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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577

578   **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

579

580

581   **Table 2**. Synthesis of the diversity measures (with upper and lower 95% confidence intervals

582   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

583

584

585 **Table 3**. Results of GLM, analyzing the effects of spatial components and microhabitat typologies

586 on species abundances. Only the significant effects are presented in this table. Y = latitude; X =

587 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

588

589

590 **Table 4**. Results of GLM, analyzing the effects of spatial components on abundances and on two

591 different diversity indices: Shannon index and Dominance index. Y = latitude; X = longitude.

592

	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

593

594 **Table 5**. Results of the Spearman's rank correlation analyses between latitude of each study site and (arcsin)percentage of individuals of each turtle

595 species that were found in each microhabitat category of the seven sites. Statistically significant correlations are given in boldface.

596

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

597

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*.

622   Fig. 1

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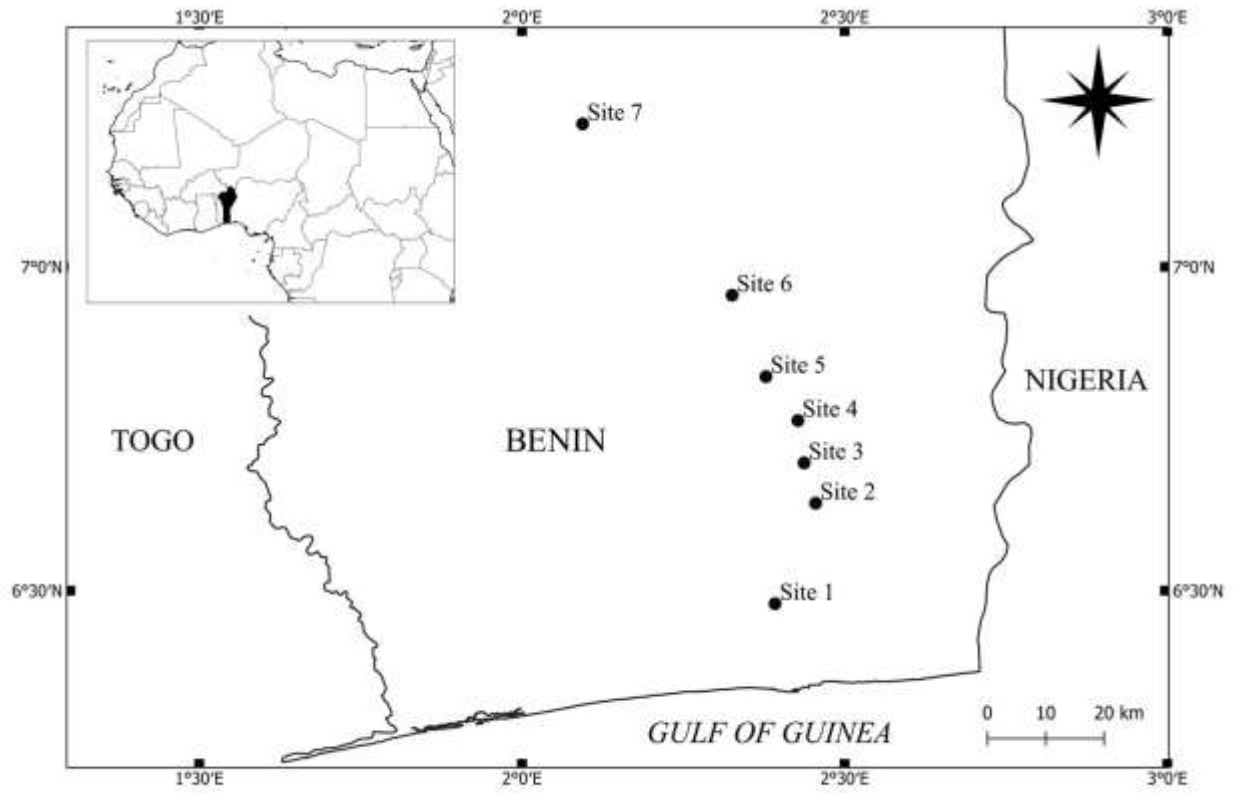
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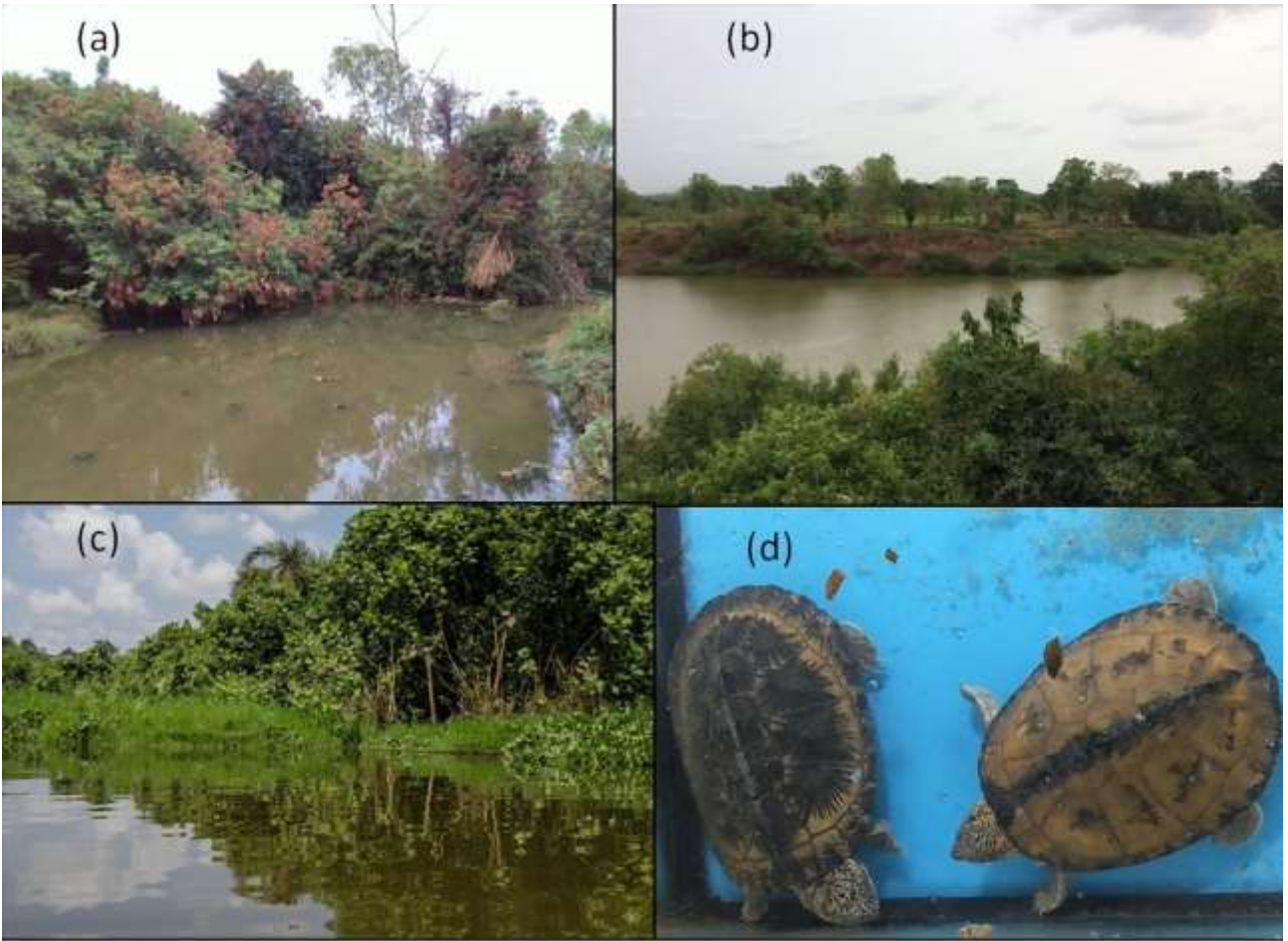639

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642   *Fig. 2.*

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652   Fig. 3

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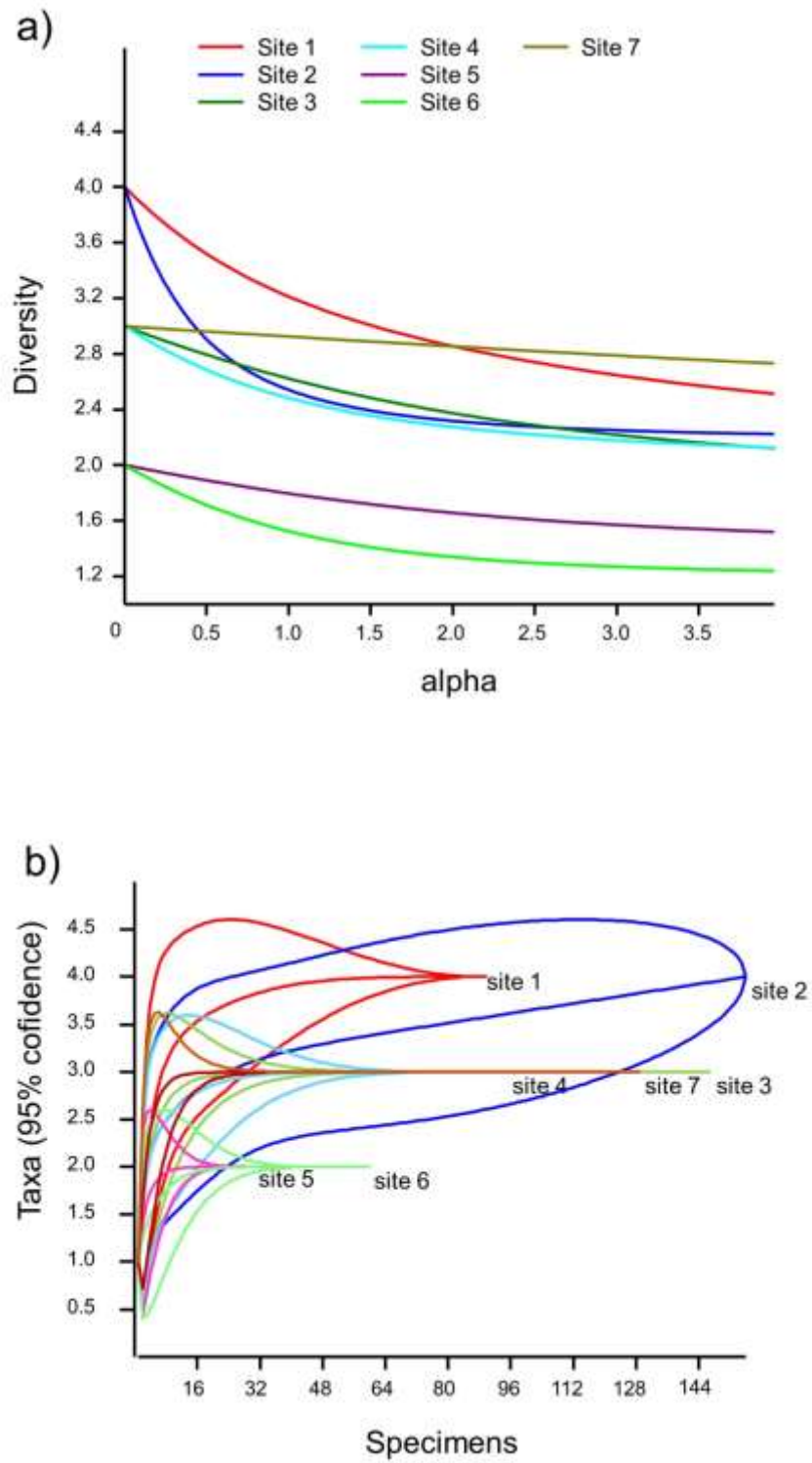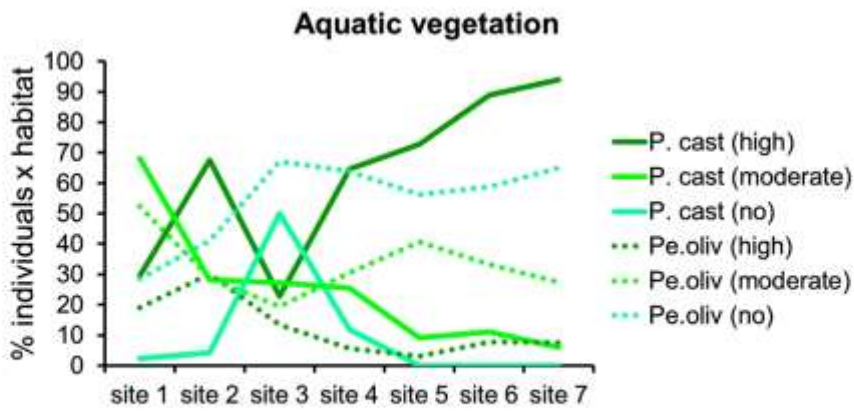658

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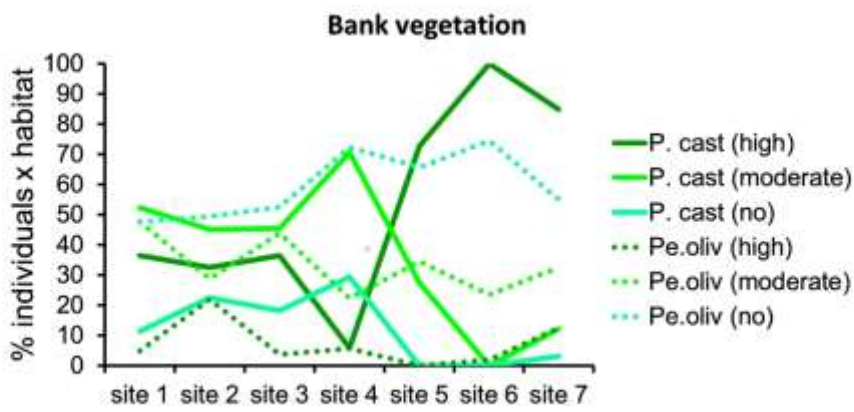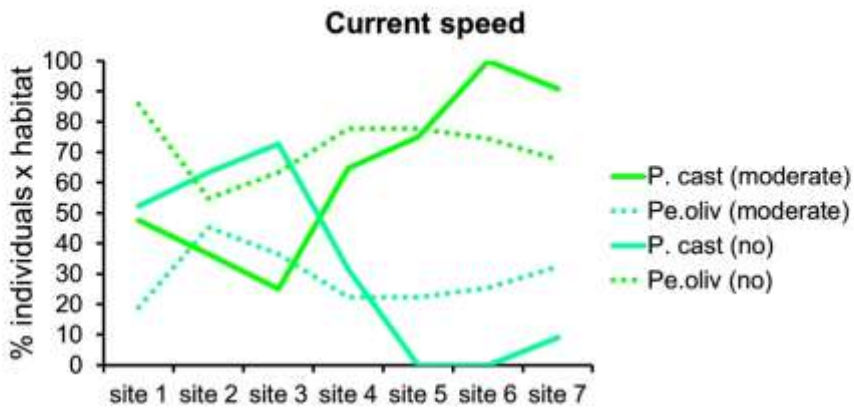
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671   Fig.4.

Current speed

Bank vegetation

Aquatic vegetation

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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

684

685   Table S2. Number of turtle individuals observed in the various microhabitat types (as described by

686   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

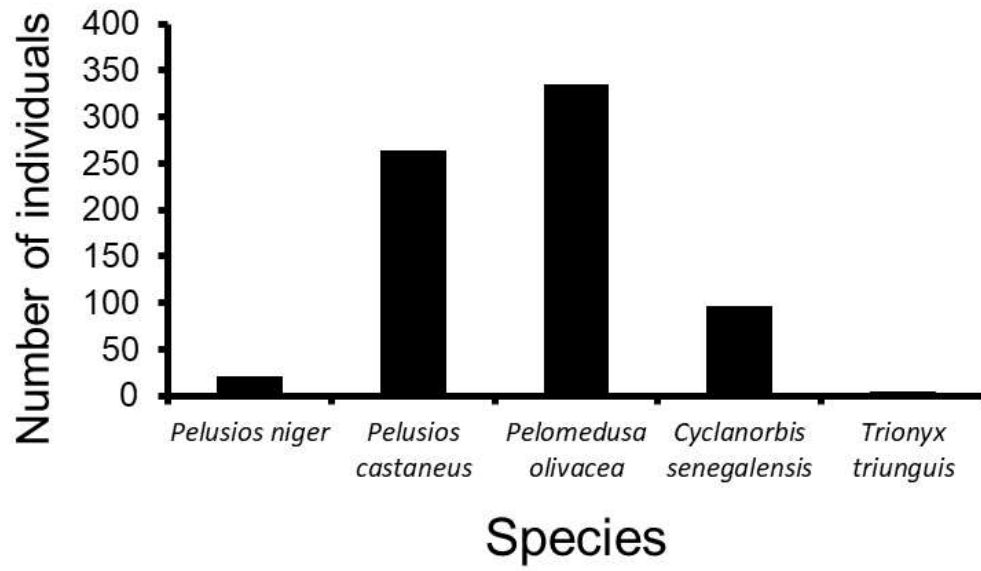|				
high bank vegetation	3	13	5	32
moderate bank vegetation	8	7	2	11
no bank vegetation	0	1	1	13
high aquatic vegetation	6	13	6	22
moderate aquatic vegetation	4	8	1	18
no aquatic vegetation	1	0	1	16
Trionyx triunguis				
high current	2	0		
moderate current	2	1		
no current	0	0		
high bank vegetation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

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

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