Community Characteristics of Sympatric Freshwater Turtles From Savannah Waterbodies in Ghana

Suleman B. Gbewaa
KNUST: Kwame Nkrumah University of Science and Technology
S. Kobby Oppong
KNUST: Kwame Nkrumah University of Science and Technology
Brian D. Horne
Wildlife Conservation Society
Paul Tehoda
KNUST: Kwame Nkrumah University of Science and Technology
Fabio Petrozzi
Rivers State University of Science and Technology
Daniele Dendi
Rivers State University of Science and Technology
Godfrey C. Akani
Rivers State University of Science and Technology
Massimiliano Di Vittorio
Rivers State University of Science and Technology
Stephanie N. Ajong
Lagos State University
Nic Pacini
University of Calabria: Universita della Calabria
Julia E. Fa
Manchester Metropolitan University
Luca Luiselli (l.luiselli@ideccngo.org)
Rivers State University of Science and Technology https://orcid.org/0000-0001-6878-2916

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Abstract

Despite increasing pressures on freshwater resources worldwide, and the threatened status of most freshwater turtles, there is still limited knowledge of habitat use and niche partitioning in Afrotropical freshwater turtle communities. In this study, we describe habitat associations, community diversity, and temporal patterns of occurrence of freshwater turtle species in the Dahomey Gap ecoregion of Ghana (West Africa). We gathered data from 13 sites in central Ghana and along the Sene Arm of Lake Volta in the Digya National Park (Bono East Region). We employed opportunistic short-term surveys (at seven sites) together with longer-term (six-months duration) standardized evaluations of turtle presence and numbers in different habitats (at six sites). In addition, we interviewed fishers in the Lake Volta area to explore their perception about turtle abundance trends. Overall, 210 turtle individuals belonging to four species (*Trionyx triunguis, Cyclanorbis senegalensis, Pelomedusa* sp. and *Pelusios castaneus*) were recorded; for 139 individuals the precise capture sites and habitat type were recorded, whereas 71 individuals were observed in market places and were not considered in our analyses. We observed three sympatric species at the local scale of the various study sites. In each site, the dominant species was either *C. senegalensis* or *Pelomedusa* sp. However, *Pelomedusa* sp. was the most abundant species in temporary waterbodies whereas *C. senegalensis* was more numerous in permanent ones. A Multiple Correspondence Analysis visualized that, in permanent waterbodies all species were associated with similar physical habitat variables. *C. senegalensis* and *T. triunguis* were more abundant in localities containing woody emergent vegetation and inorganic substrate. In a Canonical Correspondence Analysis, we show that the density of herbaceous emergent vegetation was more important for *P. castaneus* than for *C. senegalensis*. Interviews with local people suggested that freshwater turtles do not have any special marketing interest for them, but that overfishing may have considerably affected the population density of these semiaquatic reptiles. Overall, Comparisons of diversity metrics between our study areas and previous literature revealed that turtle community composition was substantially the same, both qualitatively and quantitatively, all throughout the savannahs of West Africa.

Introduction

Freshwater turtles depend on aquatic and terrestrial habitats for different parts of their life cycle e.g., predator avoidance, feeding, courtship and mating, basking and nesting activities (Ficetola et al. 2004; Steen and Gibbs 2004). A complex network and interplay of biotic and abiotic factors control the structure of turtle communities (e.g., Bodie et al. 2000; Aresco 2009; Kessler et al. 2020; Luiselli et al. 2020). Even within a single river continuum a number of different turtle species may co-occur, each species selecting habitat features that best fit their life strategies (Lindeman 1999). Consequently, turtle species may show affinity for certain aquatic environmental conditions such as water level, water quality, flow characteristics, substrate type and vegetation, but also choose bank features for basking and nesting (Ficetola et al. 2004; Vignoli et al. 2015; Luiselli et al. 2020). A turtle community is also influenced by the characteristics of terrestrial habitats surrounding the water bodies (Marchand and Litvaitis 2004; Luiselli et al. 2020), often resulting from interspecific competition as highlighted in both temperate and tropical environments (e.g., Cadi and Joly 2003, 2004; Luiselli 2008; Petrozzi et al. 2021).

Previous freshwater turtle research in West Africa focused on taxonomy and distribution of species (e.g., Hoogmoed 1980; Bour and Maran 2003; Bombi et al. 2011; Segniagbeto et al. 2014 and references therein). More recently, much effort has been placed on the analysis of aspects of turtle community ecology that relate to habitat characteristics, including the effects of habitat pollution and degradation (e.g., Luiselli et al. 2000, 2004) and on the niche partitioning patterns and interspecific competition in rainforests areas (e.g., Luiselli et al. 2006a, 2006b; Petrozzi et al. 2021). Conversely, only one turtle community ecology study is available from the waterbodies of the Dahomey Gap (Luiselli et al. 2020). The Dahomey Gap is a region of Ghana, Togo and Benin where the forest-savanna mosaic extends to the coast, and separates the Upper Guinean forests (from Guinea to Western Ghana) from the Lower Guinean forests (Nigeria and Cameroon) (Weber 2001). This is one of the prominent ecological regions in West Africa because, being an abrupt savannah-like interruption to the forest blocks, it caused separation and genetical divergence in many organisms, thus producing high rates of speciation (Dinerstein et al. 2017). Despite its above-mentioned ecological relevance, there is so far only one research study published on the Dahomey Gap turtle communities (Luiselli et al. 2020), whereas no studies are available for the other countries within the savannah biome within the West African region.

In this study, we evaluated some aspects of community ecology, including diversity metrics, temporal trapping success and physical habitat characteristics of turtles in distinct sites in Guinean savannah waterbodies in Ghana. We also undertook interviews of fishers from a few villages in the Volta Lake area. Overall, the data presented in this study were opportunistically collected or recorded during a relatively short time period, and as a consequence sample sizes are relatively low. Given that there are no available data on the freshwater turtle community ecology present in Ghana, and that turtles are facing an unprecedented global risk of extinction (Stanford et al. 2020), the information presented herein is however of considerable scientific interest.

More specifically, we answer to the following key questions:

(1) How many species do occur sympatrically along a suite of distinct localities in the savannahs of Ghana?

(2) What are the main habitat features preferred by each turtle species in the community?

(3) Are the turtle communities of the various sites relatively similar across the whole Dahomey Gap biome, or are there remarkable site-specific variations?

Materials And Methods

Taxonomic note

The taxonomy of African turtles has been undergoing considerable revisions during the last decade (e.g., Branch 2008). For practical reasons, we follow the taxonomic nomenclature recognised by the Turtle Taxonomy Working Group (2017). In particular, for *Pelomedusa* we used the taxon attribute “sp.”, as the criteria that would warrant attribution to *P. olivacea*, *P. subrufa* or to *P. variabilis* are still being debated.

Study sites and protocol

Data presented herein is based on (i) short-term opportunistically collected data from distinct sites across Ghana (Fig. 1), and (ii) a longer-term (6-months-timespan) standardized field survey in the Lake Volta region (Fig. 2). Although there is some geographical variation, the climate in all study sites is tropical, with a dry season from October to April and a wet season from May to September. In all study areas, especially in Lake Volta, inland fisheries are well-established (Braimah, 1992). Capture fisheries in inland waters have impacted aquatic biodiversity, including turtles (Braimah, 1992).

Short term surveys.—Overall, seven distinct study areas were surveyed for short-term, six in the south-central part of Ghana (Akuapim South, Akuapim North, Akenkenso, Amansie East, Amansuri wetlands, Tano River) and one in the Lovi River, Mole National Park in the north of the country (Fig. 1). In Akuapim South, Akuapim North, Akenkenso, and Amansie East the field surveys were carried out during February-March and November-December 2003 as part of a larger project on tortoises throughout West Africa (Luiselli, 2006; Luiselli et al., 2008). In Amansuri wetlands, Tano River the surveys were carried out during 2017 and 2018, and in Mole National park also in 2011–2012 and 2017–2018. At two localities (Akenkensio and Amansie East) we surveyed temporary ponds and seasonal waterbodies, whereas in all other sites we surveyed permanent waterbodies (Table 1).

Table 1
Synopsis of the number of captured turtles during short-term surveys at various distinct study areas in Ghana. The number of individuals captured by traps/directly sighted in the wild or observed in the hands of local persons are given in parenthesis. Symbol for the data entries: 6 (4,2) = 6 individuals captured in total, with 4 of them by traps/directly sighted in the wild and 2 of them in the hands of local persons).

Site	**Surveyed habitat**	***Pelomedusa* sp.**	***P. castaneus***	***C. senegalensis***	***T. triunguis***	**TOTAL**
Akuapim S	Permanent river	0	6 (4,2)	6 (5,1)	2 (1,1)	14 (10,4)
Akuapim N	Permanent river	0	4 (4,0)	9 (9,0)	3 (3,0)	16 (16,0)
Akenkenso	Seasonal Ponds	21 (21,0)	2 (2,0)	5 (5,0)	0	28 (28,0)
Amansie East	Seasonal Ponds	19 (14,5)	4 (2,2)	7 (3,4)	0	30 (19,11)
Amansuri wetlands	Permanent swamp forest with *Raphia vinifera* and *Cyrtosperma senegalense*	0	7 (7,0)	8 (4,4)	5 (2,3)	20 (13,7)
Mole National Park	Permanent waterbody with rocky banks and substrate with perennial shrubs	0	0	7 (7,0)	0	7 (7,0)
Tano River	Permanent Forest pools	0	0	0	5 (5,0)	5 (5,0)
TOTAL		40 (35,5)	23 (19,4)	42 (33,9)	15 (11,4)	120 (98,22)

Field research at each site lasted 7–13 days. At each site, we caught turtles by hand nets and with traps. All turtles trapped/captured in the field were identified to species and sexed, measured for carapace and plastron length and then released unharmed in the capture site. Morphometric data are not presented in the present study but will be used for further studies on population structure by size of the various turtle species. Each trap, approximately 120 to 180 cm in length, had a hoop diameter of about 91 cm and fingered throats. In most cases, we placed the same number of traps (n = 30) at each site and each day. These traps, made of non-stretch fine (2.5 cm) mesh, were baited (with fish pieces). The fine mesh size avoided the legs of the turtles becoming entangled. The top of the traps remained above water to allow captured turtles to surface for air. All traps were inspected daily. No captured turtles died during our study. Fisher catches and any specimen on sale in local markets were also examined. The number of turtle individuals obtained by fishers versus those that were trapped, for each study site, is given in Table 1.

The capture sites of the various market specimens were obtained by interviews with the traders/fishers, but habitat data were not considered for the analyses for specimens that were not directly captured by us or observed when just catched by local people.
Thus, we excluded from the analyses all the turtle individuals (n = 71) that were observed in markets and were not attributable to any specific locality with precision.

Longer term surveys.— We also surveyed another six distinct localities using standardized trapping between January and June 2017, along a 20-km stretch of the Sene Arm of Lake Volta, in the Digya National Park (Fig. 2). This National Park is the oldest protected area in Ghana and second largest in the country, covering an area of 3,743km^2. It is bordered to the North, East and South by Lake Volta and drains up to 70% of the total landmass of Ghana. In each of these six localities, we set 10 locally constructed hoop traps (Fig. 3A) at each sampling site and we monitored them for a month before switching onto a different river stretch. Traps were permanently set at each trap station for an entire month, and checked daily. Traps were visited and rebaited daily with canned sardine for the first month, and with fresh fish for all subsequent months. All captured turtles were handled and measured as reported above.

Dominant bank vegetation along the shoreline was recorded by eye for each trap station and categorized into: (i) herbaceous vegetation, (ii) shrubs, and (iii) trees. Common herbaceous vegetation included *Vossia cuspidata* and *Polygonum senegalense*. The common shrub among the shoreline was *Mimosa pigra* while mahogany (*Khaya* spp.) and ebony (*Diospyros mespiliformis*) were common woody emergents recorded in the study area. Following Riedle et al. (2016), the percentage emergent vegetation cover of aquatic habitats was estimated within a 25 m radius circular plot around each trap site and categorised into three classes: absent (> 90% of the water surrounding the trap site was free of emergent vegetation at time of trapping), scarce (50–90% of the water surface free of emergent vegetation), and abundant (< 50% of the water surface free of emergent vegetation). The density of woody emergent vegetation was determined by estimating the number of woody plants within a 25 m radius surrounding each trap site. The estimated number of woody emergents was categorised into three classes; absent (< 25 emergent woody plants around the trap site at time of trapping), scarce (25–50 emergent woody plants), and abundant (> 50 emergent woody plants).

Shoreline and benthic substrate type was determined by collecting two samples from each site and by subjectively assessing the degree of roughness and the relative amount of plant matter by rolling it between two fingers (Riedle et al. 2016). Substrate samples were classified into: (i) organic (> 50% of woody debris, leaf litter and other plant matter) or (ii) inorganic (> 50% of stone, sand and clay) (Riedle et al. 2016).

Interview surveys.—Interviews were carried out in three fisherfolk communities in the Lake Volta area: Kpachaa (7°39'47.11"N, 0°18'11.39"W), Tatto (7°39'49.29"N, 0°16'39.99"W), and Donkorpe (7°42'26.84"N, 0°13'43.40"W). We first undertook a reconnaissance of the dominant community livelihoods to determine suitable respondents.

Selected focus groups, mainly fishermen, were met and discussions revolved around prevalence and expertise in turtle harvesting, as well as on local traditional trap designs.
Sixty questionnaires were administered to selected respondents, identified during the focus group discussion, who revealed having extensive knowledge of freshwater turtles. Questionnaires (Appendix I) sought to elicit information on perceived species richness, population status, spatial distribution and awareness of conservation threats to freshwater turtles. Sixty percent of the respondents were chosen from the Tatto community, which showed a higher percentage of experienced turtle hunters. Twenty percent of the respondents were from Kpachaa and Donkorpe. No underage youth was interviewed, and all interviewees were informed about the scope of our study. Questionnaires were administered at locations chosen by the respondent, most of them within households and/or by the riverside as fishers were cleaning their nets. Interview questions were translated into the language preferred by the respondent (largely Twi or Ewe), with each interview session lasting on average one hour.

Statistical 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 9999 bootstraps); and (ii) calculating Chao-1 index. This latter index represents the theoretical number of species that can be expected on the basis of the sampling regime. In addition, the following univariate community diversity metrics were calculated for each site: (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). The combined use of these indices is useful to understand comparatively which areas are ecologically in better condition for turtles, the conservation value of each site increasing with decreasing values of D and increasing values of S, H' and E (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).

Comparisons of mean univariate diversity metrics values between our study areas and another study in comparable habitats in Benin (Luiselli et al. 2020) were made by one-way Analysis of Variance (ANOVA). Observed-versus-expected χ^2 tests were used to compare the frequencies of turtles across the various types of substrate/habitats and in relation to the relative availability of each substratum/habitat type in the field (used as null model). Using monthly records as samples, we performed a Multiple Correspondence Analysis (MCA) on the occurrence of turtle species and individual habitat variables collected in the Lake Volta study area, using the package FactoMine R for windows 3.2.2 (R core Team 2015). For the site/species matrix, we used a Canonical Correspondence Analysis (Legendre and Legendre 1998) to assess species occurrence in relation to habitat variables.

All statistical analyses were performed in PAleontological STatistics (PAST Ver. 4.0). For all statistical tests, alpha was set at 5%, and normality and homoscedasticity of variables was assessed by Shapiro-Wilk W test (P > 0.05) prior to using any nonparametric analysis.

Results

Overall, including both short-term surveys and the Volta Lake standardized longer-term surveys, we recorded 210 turtle individuals belonging to four species; 139 were attributed to precise capture sites with habitat recorded, whereas 71 individuals were observed in market places, but their locality of capture remained ambiguously attributed. These latter individuals were therefore excluded from our analyses: 23 *Pelomedusa* sp., 20 *Pelusios castaneus*, 18 *Cyclanorbis senegalensis*, and 10 *Trionyx triunguis*.

Short-term surveys.—During these surveys we captured/examined 120 turtles with confirmed locality of capture, belonging to four species (Table 1): Pelomedusidae – *Pelomedusa* sp. (n = 40), *Pelusios castaneus* (n = 23); Trionychidae – *Cyclanorbis senegalensis* (n = 42), *Trionyx triunguis* (n = 15). Other two species potentially present in the area according to historical records, *Cyclanorbis elegans* and *Pelusios cupulatta*, were never observed. Overall, 18.3% of the recorded individuals (n = 120) were observed in the hands of local fishers, and the rest was captured by traps or directly observed in the wild. The percentage of individuals provided by local persons varied substantially across localities (range: 0-36.7%) and among species: it was 12.5% in *Pelomedusa* sp., 17.4% in *P. castaneus*, 21.4% in *C. senegalensis* and 26.7% in *T. triunguis*. Overall, the percentage of turtle individuals provided by locals was not significantly different between Trionychidae (22.8%, total n = 57) and Pelomedusidae (14.3%, n = 63) (χ^2 = 0.3, df = 1, P = 0.584).

Diversity profiles differed between sites (Figure 4a), with Akenkenso being characterized by a more simplified community composition than the other three sites. Saturation curves showed that species diversity was adequately sampled in five study sites except Tano River and Mole National Park; the latter two because of low sample sizes (Figure 4b). In all sites with adequate sample size, the total number of sympatric species was the same, i.e. 3 (Table 2). However, only one species was recorded in two sites with inadequate sample size (Table 1). *Pelomedusa* sp. was the most abundant species in the two sites where temporary waterbodies were surveyed, whereas *C. senegalensis* appeared to be the most common species in all sites with permanent waterbodies (Table 1). Interestingly, no *Pelomedusa* individual was ever caught in permanent waterbodies (Table 1).

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

	Akuapim S	Lower	Upper	Akuapim N	Lower	Upper	Akenkenso	Lower	Upper	Amansie East	Lower	Upper	Amans wetlan
Species richness	3	3	3	3	3	3	3	3	3	3	3	3	3
Individuals	14	14	14	16	16	16	28	28	28	30	30	30	20
Dominance	0.3878	0.3367	0.5612	0.4141	0.3359	0.6797	0.5995	0.4464	0.8036	0.4733	0.3689	0.6622	0.345
Simpson	0.6122	0.4388	0.6633	0.5859	0.3203	0.6641	0.4005	0.1964	0.5536	0.5267	0.3378	0.6311	0.655
Shannon	1.004	0.7589	1.093	0.9841	0.6019	1.095	0.7119	0.4087	0.9407	0.8975	0.6277	1.044	1.081
Evenness	0.9099	0.712	0.9948	0.8918	0.6085	0.9962	0.6793	0.5016	0.8539	0.8178	0.6244	0.9466	0.9821
Chao-1	3	3	3	3	3	3	3	3	3	3	3	3	3

Dominance index at our study areas did not differ from those observed in similar habitats in Benin (data in Luiselli et al., 2020): ANOVA F=2.172, P = 0.473; the same was true for Simpson index (F = 1.043, P = 0.955), Shannon index (F = 1.577, P = 0.387), and Evenness index (F = 1.77, P = 0.237).

Lake Volta surveys.—Despite the longer term of study, only a total of 19 individuals belonging to three species (7 *Trionyx triunguis*, 9 *Cyclanorbis senegalensis* and 3 *Pelusios castaneus*) were recorded. The small sample size of *P. castaneus* impeded us from any conclusion about its phonological seasonality. By contrast, trapping success of *T. triunguis* was highest in the wet season (Apr-Jun), with at least one individual of *C. senegalensis* captured in each survey month (Figure 5A). We found no preference for terrestrial substrates (Figure 5B) for *C. senegalensis* and *P. castaneus* (in both cases, P > 0.5 at χ^2 test), but *T. triunguis* clearly favoured organic substratum (P < 0.05 at χ^2 test). There was no clear difference among species in terms of dominant bank vegetation, although all individuals of *P. castaneus* (n = 3) selected sites with herbaceous bank vegetation (Figure 5C). *Trionyx triunguis* individuals differed significantly from the other species (P < 0.05 at χ^2 test) in terms of their choice of sites with more emergent aquatic vegetation (Figure 6A and 6B); this species preferred sites with abundant wood and herbaceous vegetation, whereas the two other species had no special preference for any type of aquatic vegetation. Results of the Canonical Correspondence Analysis indicated that *C. senegalensis* and *T. triunguis* were more similar in their choice of habitat than *P. castaneus* (Figure 7). *Cyclanorbis senegalensis* and *T. triunguis* presence was more defined by the density of woody emergent and substrates. Positive values for woody emergents was linked to the presence of *T. triunguis* but not for *C. senegalensis*. By contrast, the existence of *P. castaneus* was related to negative values in the measured habitat variables except for herbaceous vegetation, the latter positively correlated with increased density of this species.

Interview surveys.—All interviewees reported that freshwater turtles were object of frequent sightings by community members. There were, however, different opinions concerning the number of species observed. While the majority of respondents (63%) could only differentiate between hardshell and softshell turtles (respectively Pelomedusidae and Trionychidae), fewer were able to distinguish correctly 3 or 4 species also according to carapace colouration/morphology. Local reports suggested that turtle species richness was comprised between two (63% of the respondents), three (29%), four (1%) and five (2%) species.

Most interviewees reported to be indifferent about turtle meat consumption. As many as 91.2% of the interviewees reported that turtle harvesting was not a widespread practice among their community and 76% of them held the view that not all community members harvested or consumed turtles and/or turtle products. Only 20.3% considered that some traditional harvesting practices do exist at the community level and 71.2% of respondents suggested that no traditional/cultural practices regulate the harvesting of turtles species.

Interviewees (93%) perceive freshwater turtles to occur in high densities at the scale of their own communities. On average, they reported that a turtle trapper during peak season (dry season) could catch as many as 6-10 turtles in 15 trap-nights. According to 67.9% of the respondents, harvesting of turtles (in fishing nets) is more common in the dry season until the beginning of the wet season between December - May. This is generally attributed to the lower water level that enables the setting of locally made turtle/tilapia traps in backwaters of the inlets to the main river channel.

A total of 61% of the interviewees believed that freshwater turtle abundance had not changed significantly in the last twenty years; 32.2% suggested it could be declining, and 6.8% did not have an opinion. More specifically, 57% of the respondents claimed that softshell turtles are more common than hardshells. The majority of respondents (74.6%) downplayed the ecological significance of turtles, as well as the opinion that their presence could pose health risks such as transmission of diseases to humans (59.5% of respondents). A minority (35.6%) affirmed that there is a positive relationship between turtle abundance and fish numbers, but 27.1% suggested that it could be negative, with 37.3% not sure of any relationship. Most respondents (83%) believed there is currently no regulation (local or national) of freshwater turtles harvest.

Discussion

Overall, in most study areas the data presented in this study were opportunistically collected or recorded during a relatively short time period, and as a consequence sample sizes are relatively low. According to our saturation curve analysis and the Chao-1 estimate our study revealed that for sites where we could obtain an adequate sample size, turtle species richness was low (three taxa). This result mirrors data for waterbodies in the Guinean savannahs of Benin, where also three species (maximum 4) also occurred sympatrically (Luiselli et al., 2020). In the savannah waterbodies of both Benin and Ghana, the same pair of species (*C. senegalensis* and *P. castaneus*) occurred in every available habitat (Figure 8), together with either *Pelomedusa* sp. (in temporary waterbodies) or *T. triunguis* (in perennial waterbodies). Although always parapatric, it is unlikely that *Pelomedusa* sp. and *T. triunguis* partition their niche as they differ in body size (*T. triunguis* being much larger), morphology and ecology (Branch 2008). However, it also is possible that *T. triunguis* acts as a predator of the juveniles of *Pelomedusa* or that the juveniles of *T. triunguis* may compete with *Pelomedusa* adults as both species are fundamentally carnivorous (see Luiselli et al., 2011). Unfortunately, there are no data available to confirm these hypotheses.

Univariate diversity indices also were similar among our study areas in Ghana and those in Benin (Luiselli et al., 2020), thus showing that the community composition was substantially the same, both qualitatively and quantitatively, all throughout the Dahomey Gap savannahs of West Africa.

Despite the relatively long duration of our field study at the Volta Lake area, we caught a very low number of turtles compared to previous studies in the savannah of West Africa (Luiselli et al., 2020). This could have been determined by different population abundances across sites, but also by the choice of trapping method that can influence sampling success (Tesche and Hodges, 2015), and by the time of the year when trapping was carried out. The ideal period for catching freshwater turtles is, at our study area in Ghana, the dry season, as confirmed by our interviews in nearby villages. This may be linked to the reduction in water levels, which increases turtle density within aquatic habitats and thus the probability of their detection. In seasonal ponds seasonal aestivation during dry season may occur, thus lowering turtle numbers (Luiselli et al., 2000), but this was not the case in our study since the field research was conducted in a permanent water body. Trapping success differed slightly for the three species, suggesting that waterbody condition preferences may differ between species (see also Luiselli et al., 2000). While *T. triunguis* mostly occurs in large rivers, thus larger water volumes, *C. senegalensis* prefers smaller streams and seasonal ponds and marshes (Gramentz, 2008). Unfortunately, no other study analysed the seasonal variation of trapping success in African savannah turtles, and so comparisons with our data could not be done.

In our study, *C. senegalensis* and *T. triunguis* preferred inorganic substrate in benthic and terrestrial zones. Other turtles species are known to prefer organic substrates to aestivate and nesting (e.g., Marchand and Litvaitis, 2004); these substrates also provide comparatively better foraging opportunities (Marchand and Litvaitis, 2004). The preference of the two trionychid species for high densities of woody emergent vegetation may also be linked to prey availability. Turtles of the Trionychidae family are largely carnivorous and feed mainly on amphibians, snails and fishes (Akani et al., 2001; Luiselli et al., 2004; Gramentz, 2008), prey items that, at our study areas, are usually more abundant in spots characterized by high woody emergent density (our unpublished observations). The differences in habitat preferences between the two trionychids (*C. senegalensis* and *T. triunguis*) may also be due to resource partitioning to minimize interspecific competition (Pritchard, 2001; Luiselli, 2008; Akani et al., 2018). The same mechanism could be playing a role in the case of *Pelomedusa* sp. versus *P. castaneus*, given that these taxa are ecologically, morphologically and phylogenetically very similar. Despite their similarity, the latter two species differed remarkably in the number of trapped individuals during surveys in Ghana and Nigeria (Luiselli et al., 2000). In addition, signs of interspecific competition among sympatric populations of these two taxa were evidenced during field surveys carried out in the savannahs of Benin (Luiselli et al., 2020). Further investigations are needed to clarify interactions among these coexisting turtles.

Our study did not reveal the presence of the Critically Endangered *C. elegans*, possibly totally extirpated from Ghana and from the whole of West Africa (Luiselli et al., 2021). *Cyclanorbis elegans*, was historically known to occur in the Guinean savannah rivers of Ghana and one of the most threatened species in the world (Gramentz, 2008; Baker et al., 2015). This species has been recently rediscovered in South Sudan (Demaya et al., 2019a, 2019b), whereas no individual has been observed in Ghana (and in the rest of West Africa) since several decades (Stanford et al., 2018). Thus, our surveys were also important in order to confirm the likely extinction of West African populations of this Critically Endangered species (IUCN, 2020; Luiselli et al., 2021).*Trionyx triunguis* populations are threatened in West Africa (Segniagbeto et al., 2014; IUCN, 2020), and the fact that we captured 15 different individuals of this species, from four distinct localities, suggests that this species is still relatively widespread in Ghana. We recommend that Ghana may become a country of first choice for promoting the conservation and management of *T. triunguis* in the West African Region.

During our surveys in the Volta Lake area, we employed a considerable effort in terms of trap-days. However, as mentioned above, we captured a far lower number of turtle individuals than that obtained in similar habitats and in a even lower number of days in the adjacent Benin (Luiselli et al., 2020). This evidence would suggest that the turtle communities are heavily depleted in this part of Ghana. However, the results of our field surveys are in contrast with local ecological knowledge. Indeed, over 60% of the interviewees suggested that a good turtle density, especially Trionychidae, is still found at the study areas, while only ≈30% considered these animals to be in decline. The perceived abundance, together with the absence of strong interest in freshwater turtle hunting and consumption (even turtle eggs are not of special interest for local communities), may explain the lack of knowledge by local communities about the existence of harvest regulation at local or national level. Since most of the fishers reported no specific interest in catching turtles as their meat is of scarce marketing value, it is clear that freshwater turtles are just a bycatch of the fishing activities. This fact is also confirmed by that fishers were not generally concerned of the turtles as pests for their fish resource, thus showing that they should have no reasons for concentrating their hunting activities on turtles. Nonetheless, given the density of fishers in this part of Ghana, it is likely that, even if not specifically targeted, turtle populations may be so depleted that even their viability is not secure for the next decades. The rarest turtle of Africa (Baker et al., 2015), *C. elegans,* may have gone extinct locally because of this excess of fishing activities in its natural habitat. Also the West African endemic *Pelusios cupulatta* was not observed during our surveys, but it is possible that this was due to unsatisfying field effort at the single locality where this species may be present (Tano River). This species was fairly common in similar habitats in Cote d'Ivoire, where it occurs sympatrically with *P. castaneus* (Petrozzi et al., 2021).

It would be interesting to explore additional sites, in more remote areas, to see whether the pattern of turtle depletion that we observed at our study areas may be valid also more generally in the country. Based on the empirical observations of the present study we anticipate that turtle populations of Ghana are more depleted than those occurring in the neighbouring countries (for instance, Benin and Nigeria; see Luiselli et al., 2006b).

Declarations

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Author Contributions LL suggested the subject and the method of manuscript; SBG, SKO, PT, FP, DD, GCA, SNA, LL make the field study; SBG, MDV, LL, DD, NP analyzed the data; SBG, NP, BDH, JEF, LL prepared the first draft; all authors reviewed and approved the final draft.

Data Availability All data are presented in the paper.

Code Availability Not applicable.

Declarations

Ethics Approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication Not applicable.

Conflicts of Interest/Competing Interests The authors declare that they have no conflict of interest

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Figures

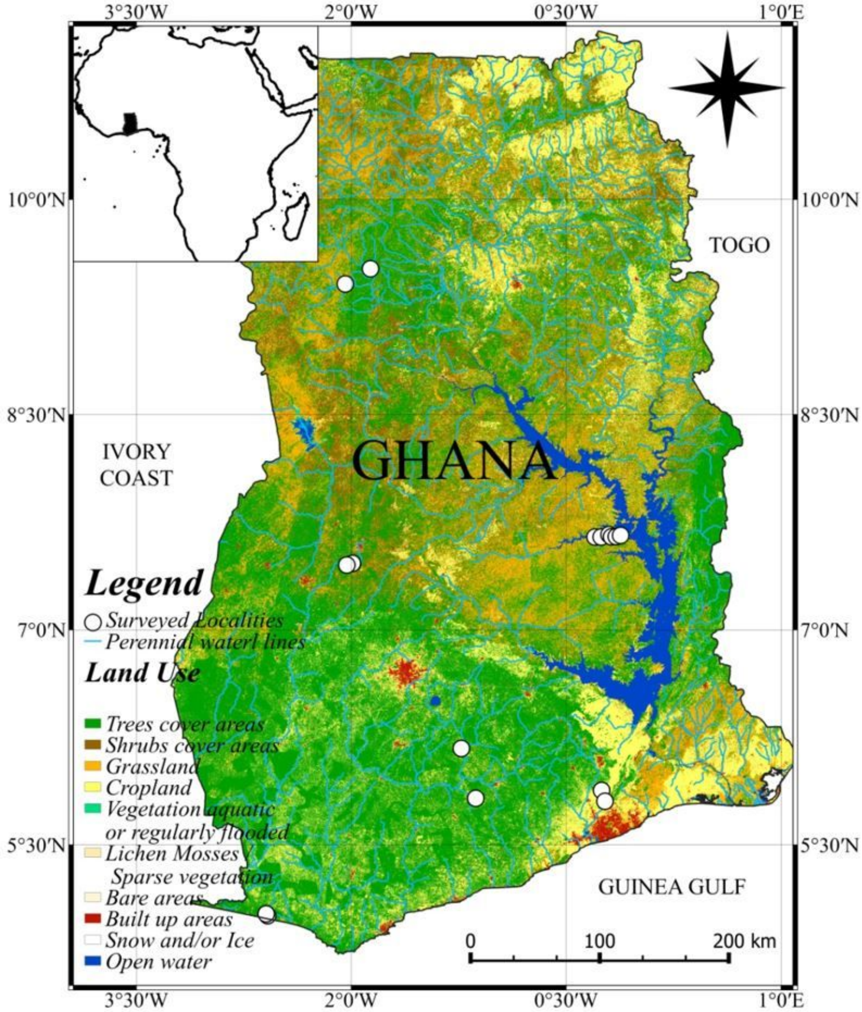

Figure 1

Map of Ghana, showing all the study areas. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

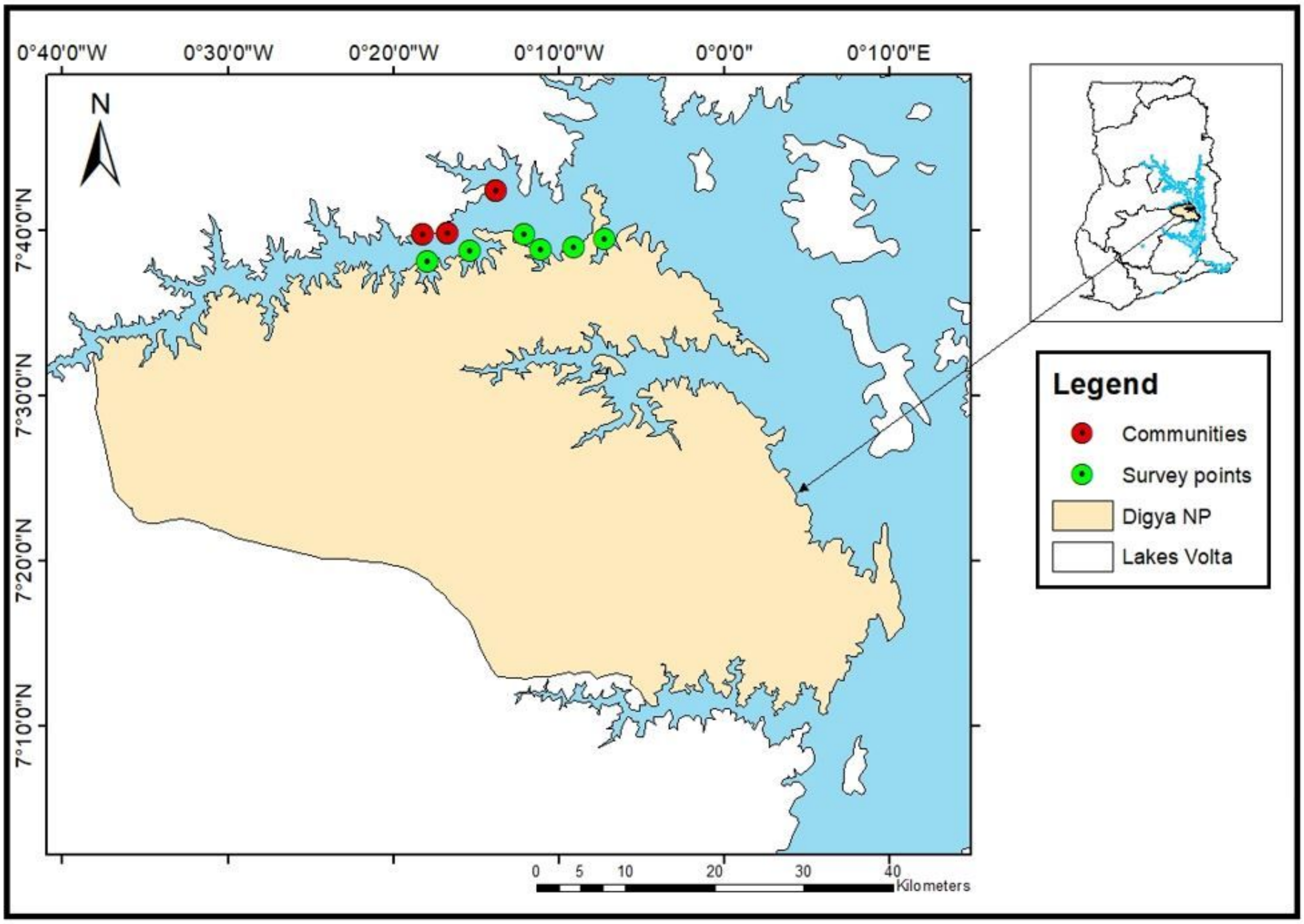

Figure 2

Map of the Lake Volta area, showing the Digya National Park and the sites used for trapping turtles (Survey points) and for the interviews with local persons (Communities). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 3

Types of traps used for capturing turtles at the survey stations in Ghana, and a typical habitat where turtles were captured in the Volta Lake area. (A) Setup of a hoop trap in an inlet along Sene Arm of the Volta Lake. (B) Local traps used for both fish and turtles by the fishers' communities. (C) Section of Sene Arm of the Volta Lake dominated by herbaceous emergent vegetation.

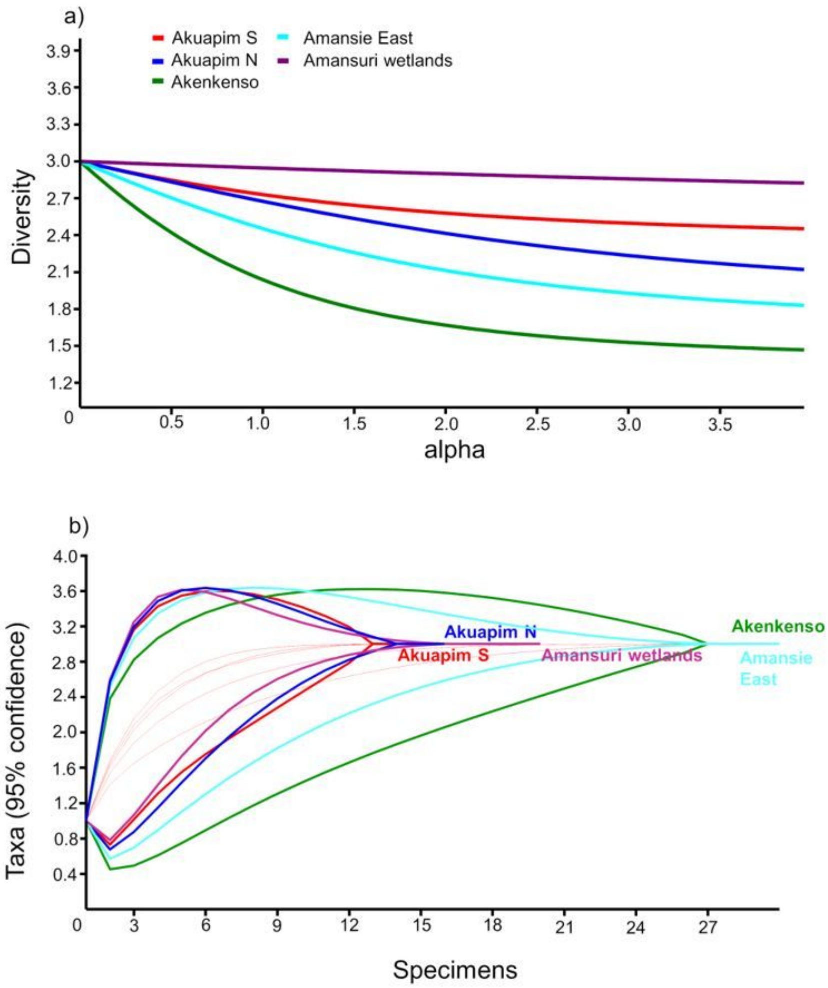

Figure 4

Diversity profiles (graphic a) and rarefaction curves (upper and lower lines representing the 95% confidence intervals generated after 9999 bootstraps) for species discoveries in relationship to sample size (graphic b) for the various opportunistically surveyed study areas for turtles in Ghana.

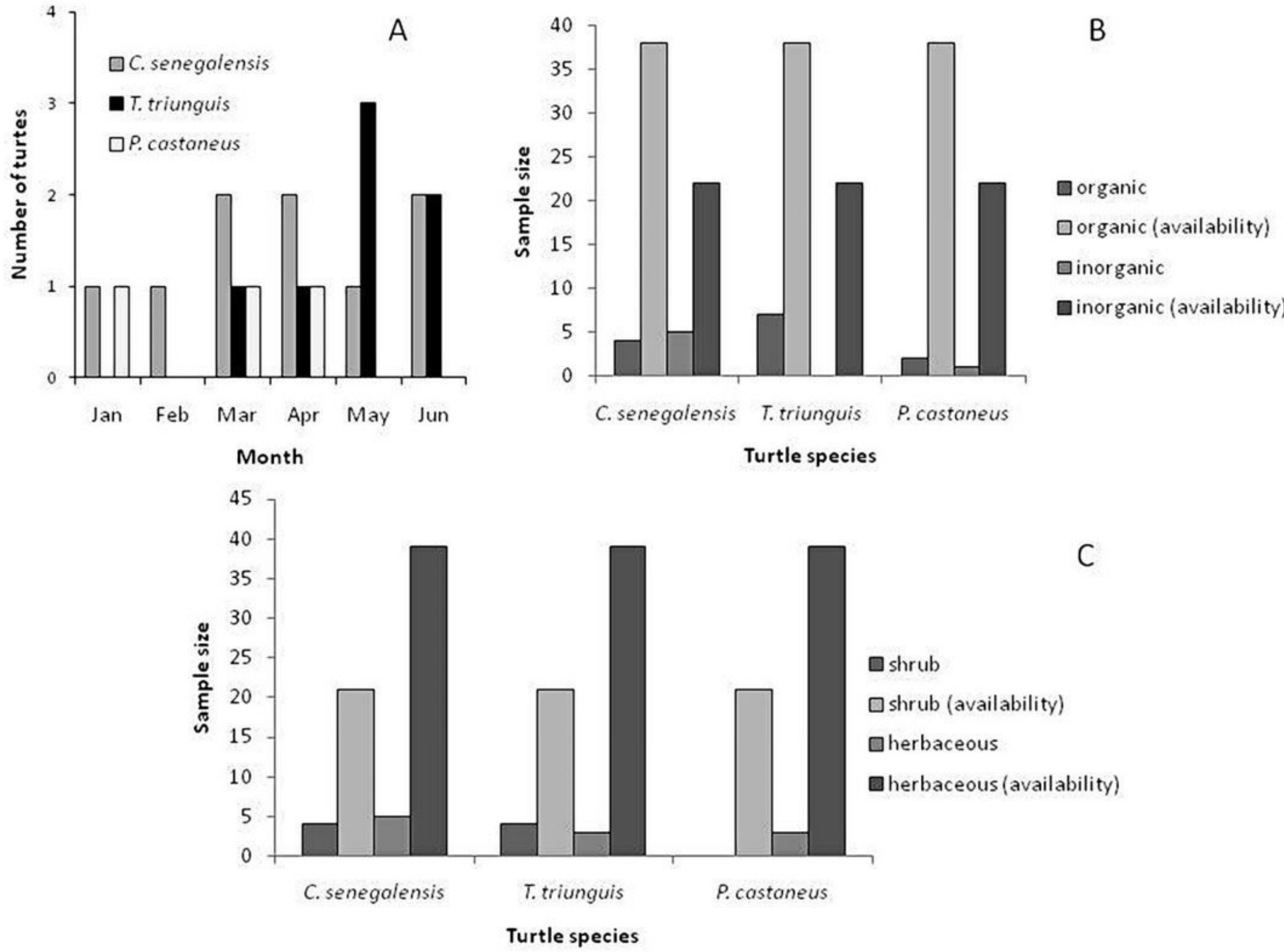

Figure 5

Temporal trapping success and habitat characteristics of the capture sites for freshwater turtles at Sene Arm of the Volta Lake, Ghana. (A) distribution of the captures by month. (B) distribution of the captures by type of aquatic substrate. (C) Type of dominant bank vegetation.

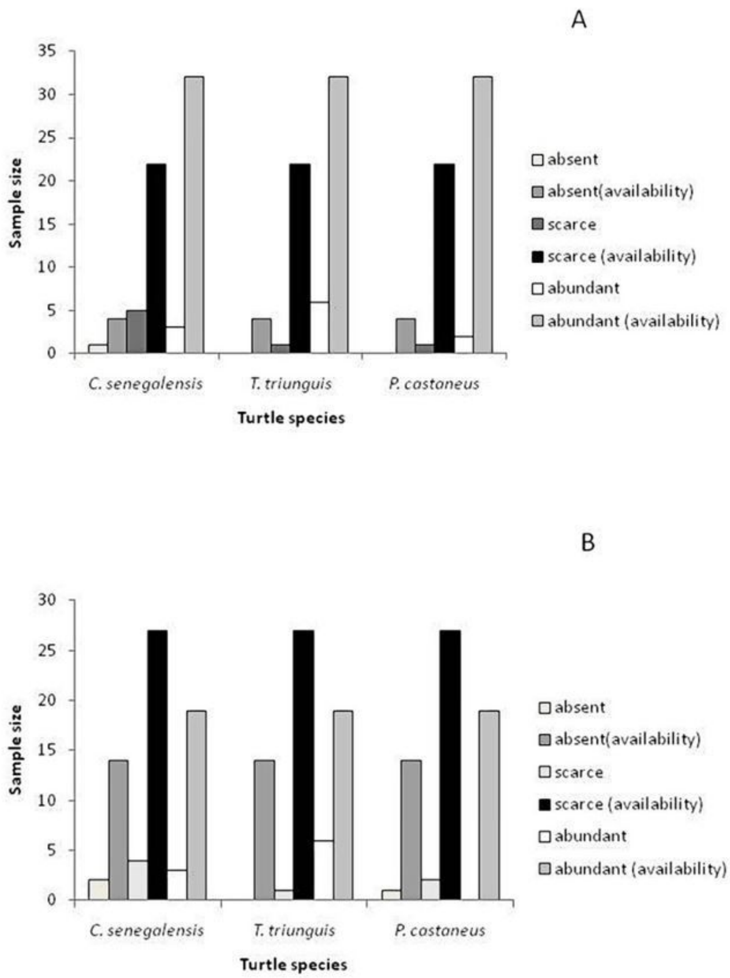

Figure 6

Aquatic vegetation characteristics of the capture sites for freshwater turtles at Sene Arm of the Volta Lake, Ghana. (A) emergent woody vegetation (absent, scarce or abundant); (B) emergent herbaceous vegetation (absent, scarce or abundant). For turtles, numbers would indicate the raw numbers of collected individuals.

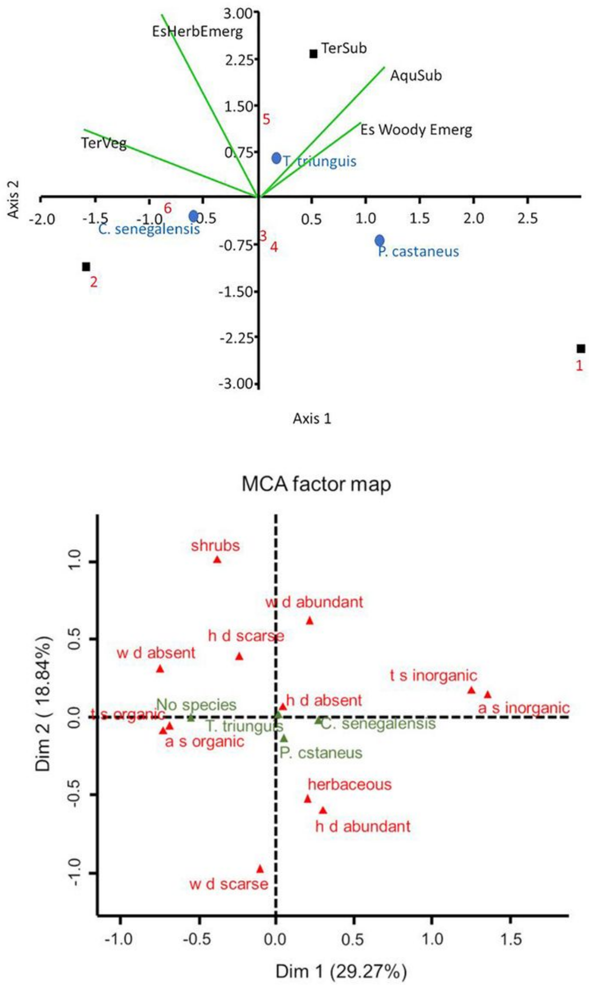

Figure 7

Freshwater turtles association with (i) sampling period and broad scale categories of habitat variables (graphic A), and (ii) with fine scale habitat variables in the Sene Arm of the Volta Lake (graphic B). Code: EsHerbEmerg= estimated herbaceous emergent, Es Woody Emerg= estimated woody emergent, TerSub= terrestrial substrate, AquSub= aquatic substrate, TerVeg= Terrestrial vegetation, 1-6 = January to June respectively. Symbols: H d= herbaceous density (absent, scarce or abundant), w d= woody emergent density (absent, scarce or abundant), a s= aquatic substrate type (organic or inorganic), t s= terrestrial substrate type (organic or inorganic).

Figure 8

Cyclanorbis senegalensis and its typical habitat in central Ghana. This is the most common turtle species along rivers and permanent waterbodies in this part of West Africa.

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