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Spatio-temporal distribution of five species of West African leaf-litter frogs

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Abstract. The spatio-temporal distribution of five leaf-litter frog species, *Phrynobatrachus ghanensis*, *P. phyllophilus*, *P. liberiensis*, *P. latifrons* and *P. tokba* was studied in Banco National Park (BNP), Ivory Coast. Frogs were sampled in a standardized way along ten transects, representing all major habitat types of the park. With acoustic and visual methods we recorded a total of 394 *P. ghanensis*, 303 *P. phyllophilus*, 510 *P. liberiensis*, 1704 *P. latifrons* and 225 *P. tokba*. The five leaf-litter frogs were widespread along the BNP transects, but showed clear differences concerning their habitat preferences. Only *P. latifrons* preferred more open habitats. All other species dominated in forested parts of BNP. All *Phrynobatrachus* species could be recorded throughout all seasons. The number of encountered specimens per species seemed to differ between seasons, however not statistically significant. Some species were not recorded during all seasons at all sites, however. Presence or absence of a particular leaf-litter frog largely depended on habitat preferences, underlining the suitability of these species as indicators for habitat changes.

Key words. Anura, anthropogenic disturbance, habitat selection, Ivory Coast, Phrynobatrachidae, *Phrynobatrachus*, rainforest.

Introduction

Whereas forests in western Ivory Coast and in Ghana have been studied with regard to the influence of human activities on anuran assemblages (Ernst & Rödel 2005, 2006, 2008, Ernst et al. 2006, Hillers et al. 2008, Ofori-Boateng et al. 2012, Adum et al. 2013), comparative studies are lacking for the rainforest remnants in-between these regions, namely eastern Ivory Coast. This is unfortunate as: (i) these forests may comprise equal, but yet unrecognized biological diversity, as recent species descriptions are indicating (e.g. *Astylosternus laticephalus*, *Morerella cyanophthalma*, Rödel et al. 2009, 2012); (ii) the western Ivorian studies illustrated that anuran assemblages are valuable model systems to detect and monitor environmental change in rainforests, however, (iii) human activities may act differently on anuran assemblage composition in different forest types (Ofori-Boateng et al. 2012); and (iv) the eastern Ivorian forests are among the most threatened rainforests in Africa (Norris et al. 2010, Mayaux et al. 2013).

They are mainly threatened by human encroachment, poaching, logging, as well as shifting agriculture (Zadou et al. 2011). One of the last eastern Ivorian forests, the Banco National Park, founded already in 1953, is situated in the middle of Abidjan, the largest city of Ivory Coast. Overall, this park is facing land losses due to human encroachment, road expansions, urbanization in general and pollution in particular.

Preliminary field surveys suggest that the rapid disruption of the eastern Ivorian forests imperils the local biodiversity (Lachenaud 2006, Bitty et al. 2013) including amphibians (Assemian et al. 2006). To assess the effects of forest degradation in these forests we chose leaf-litter amphibians. They have been shown to be especially appropriate for investigations concerning factors that influence community structure (Gascon 1986), since they comprise a significant proportion of the amphibian fauna at any given site (Allmon 1991) and because standardized methods exist for estimating their species richness and abundance (Heyer et al. 1994, Rödel & Ernst 2004). Previous research (Ernst & Rödel 2005, 2006, Hillers et al. 2008, Ofori-Boateng et al. 2012) has shown that leaf-litter frogs in general and particularly members of the genus *Phrynobatrachus* Günther, 1862 are well suited to study forest degradation effects in West Africa.

In Banco National Park, five species of this genus are known (Assemian et al. 2006): *P. ghanensis* Schiøtz, 1964, *P. latifrons* Ahl, 1924, *P. liberiensis* Barbour & Loveridge, 1927, *P. phyllophilus* Rödel & Ernst, 2002 and *P. tokba* (Chabanaud, 1921) (Fig. 1). As these frogs are easily assessed with standardized methods, they are also particularly suited for the long-term monitoring of population changes (Adum et al. 2013). However, in order to use these frogs for future studies on habitat degradation and population changes, their population status, their current distribution within the park, their activity periods and their habitat preferences need to be known.

Our study thus had two main goals: (1) to document the spatio-temporal distribution of the five *Phrynobatrachus* species in Banco National Park, in order to understand their relatedness to forest type and status (ecological preferences); and (2) to collect year round abundance data (temporal distribution) as a baseline for future monitoring of the forest's development, in particular with regard to the increasing human impact in this area.

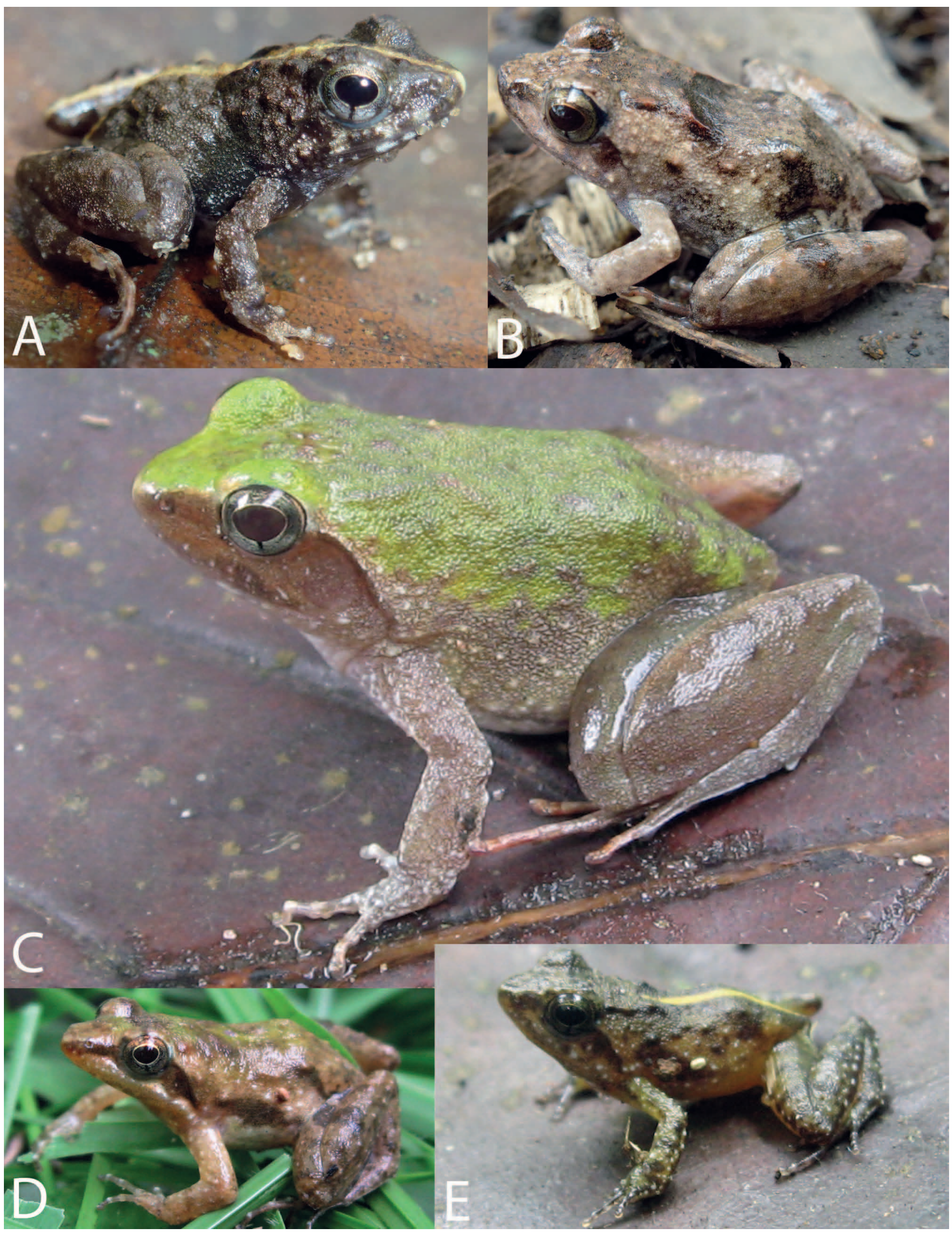

Figure 1. The five *Phrynobatrachus* species from the Banco National Park studied in the present paper. (A) *Phrynobatrachus ghanensis*; (B) *P. phyllophilus*; (C) *P. liberiensis*; (D) *P. latifrons*; (E) *P. tokba*.

Materials and methods

Study site

The Banco National Park (BNP; 5°21'–5°25' N; 4°01'–4°05' W) is a small (3,474 ha) rainforest remnant, located in the middle of Abidjan, the economic capital of Ivory Coast (Fig. 2). This relict of evergreen forest (Hall & Swaine 1981, Parren & de Graaf 1995) is a refuge for several forest dependent plant and animal species (Assemian et al. 2006, Bitty et al. 2013, Camara et al. 2009, 2012, Lauginie 2007), including some frog species described from this forest (Perret 1985, 1994 [*Aubria occidentalis* currently not regarded as valid], Rödel et al. 2009, 2012). The mean annual temperature in BNP is 26–27°C. The mean annual precipitation ranges from 1,600–2,500 mm. A longer major dry season extends from December to March, and is followed by the period of a major rainy season with highest precipitation in April to July. A minor dry season lasts from August to September while a minor rainy season ranges from October to November. Assemian et al. (2006) provide a summary of the climate, vegetation and particularly the anuran fauna of this park.

Sampling methods

Within a general amphibian monitoring program of the BNP (see Assemian et al. 2006) we searched for frogs along ten transects between March 2004 and February 2005 (T1–T10 in Fig. 2), thus covering the rainy and the dry seasons. Transects were chosen in order to cover the major habitat types including a disturbance gradient from natural to heavily degraded forest. Large parts of the park comprise almost (i) primary dry and (ii) swampy forests, on predominantly sandy soils. In addition BNP comprises various altered habitats: (iii) a fish farm on a forest clearing in the park's center, as well as (iv) areas impacted by illegal forest extraction, plantations and pollution at the park's edges. Coordinates as well as transect characteristics (including anthropogenic influence) are summarized in the appendix.

A transect was 600 m long, and frogs were searched one meter to the left and right of the path (surface covered per transect walk: 1,200 m^2). Each transect was examined 24 times, the visits evenly spread across the entire study period. Every transect walk lasted approximate 45 min. A detailed description of the collecting method and the general transect design is given by Rödel & Ernst (2004). Our searching techniques included acoustic and visual scanning of the terrain and investigation of potential hiding places. All frogs were captured, determined, sexed and measured. Snout–vent-lengths were taken with a dial caliper (accuracy ± 0.5 mm). A few vouchers per species were euthanized in a chlorobutanol solution and thereafter preserved in 70% ethanol. These frogs are deposited in the collection of the "Laboratoire d'Environnement et de Biologie Aquatique" at the Nangui Abrogoua University, Abidjan, and serve as the bases of a national reference collection.

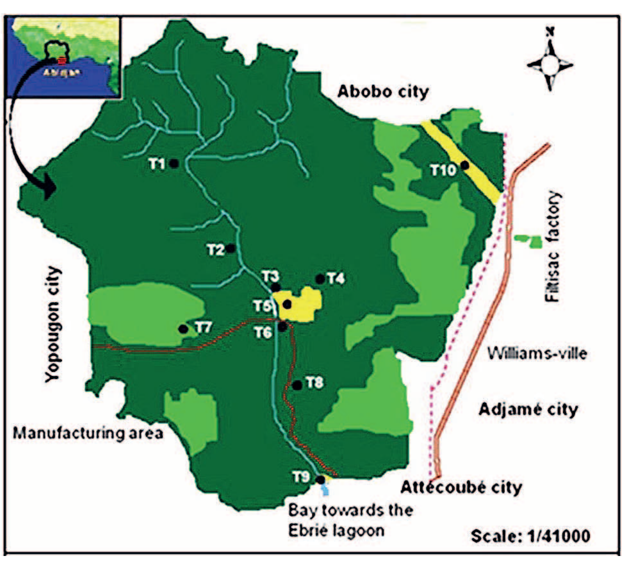

Figure 2. The position of transects in Banco National Park, Ivory Coast. Indicated are major forest types and position of the park in Ivory Coast (inlet in upper left corner); T1–T10: position of transects; dark green: closed canopy forest; light green: forest with clearings; yellow: logged, open areas; shown are as well the River Banco, dividing the park; solid lines: roads; stippled line: railway.

Statistical analyses

We calculated the relative species abundances per transect-hour, using the data of all 240 transect walks. Because species abundances were not normally distributed (Kolmogorov-Smirnov test), we used non-parametric tests for subsequent analyses. We used the Self Organizing Map (SOM) algorithm, SOM Toolbox version 6.1 for Matlab, according to Ibarra (2004) to arrange sampling sites (transects T1–T10) with respect to environmental parameters (river, brooks, ponds, swamps, canopy cover, as well as density of leaf-litter layer, grass, shrubs and trees; e.g. closed canopy and large number of big trees for instance indicating more natural forest than parts with canopy gaps and dense shrubs), the different months of the year and frog assemblages. According to Kohonen (2001), the SOM can be viewed as a non-linear generalization of a principal component analysis (PCA). We set up our SOM by placing neurons at the nodes of two dimensional lattices. The neurons become selectively tuned to various input patterns during the course of the competitive learning. The locations of the neurons tuned in this way become ordered and a meaningful coordinate system for the input features was created in the lattice. The SOM thus formed the required topographic map of the input patterns (Fig. 3). For more detailed information on the SOM methodology, see Ibarra (2004) and Kohonen (2001). Collected habitat parameters were: type of potential breeding sites (River Banco, brooks, ponds, swamps) and vegetation structure (canopy cover,

Table 1. Scheffé post-hoc test for pairwise comparisons of transect abundances of five leaf-litter frog species of the genus *Phrynobatrachus*.

P. ghanensis	*P. phyllophilus*	*P. liberiensis*	*P. latifrons*	*P. tokba*
T1–T3 (p=0.033)	T3–T6 (p=0.046)	T1–T6 (p=0.011)	T5–T9 (p=0.001)	T2–T6 (p=0.003)
T1–T6 (p=0.021)	T3–T8 (p=0.002)	T2–T6 (p=0.022)	T5–T10 (p=0.001)	T3–T6 (p=0.013)
T2–T3 (p=0.019)	T6–T8 (p=0.018)	T3–T6 (p=0.002)	–	T6–T7 (p=0.046)
T2–T6 (p=0.008)	–	–	–	–
T3–T6 (p=0.043)	–	–	–	–
T3–T8 (p=0.011)	–	–	–	–
T6–T8 (p=0.005)	–	–	–	–

density of leaf-litter layer, grass, shrubs and trees). On each transect, we recorded the number of brooks and ponds, counted the number of shrubs and trees in one meter distance to either side of the transect, and measured the mean leaf-litter layer thickness (calculated from the number of leaf layers counted at five points across the transect). The canopy cover was estimated in percentage (accuracy ± 5%) and varied from 0 (grassland) to 100% (primary forest with closed canopy cover). These habitat data were included in an input matrix which is composed of data of species abundances for each sampling site (Fig. 3).

Results

Species' distributions across habitat types

During 240 transect walks we recorded 394 *P. ghanensis* (2 individuals per transect-hour, herafter abbreviated t-h), 303 *P. phyllophilus* (2 frogs/t-h), 510 *P. liberiensis* (3 frogs/t-h), 1,704 *P. latifrons* (10 frogs/t-h) and 225 *P. tokba* (1 frog/t-h). We recorded *P. ghanensis* on transects T1 (10 individuals), T2 (12), T3 (125), T6 (242) and T8 (5). We found *P. phyllophilus* on T3 (238 frogs), T6 (63) and T8 (2). *P. liberiensis* was encountered on T1 (158 frogs), T2 (146), T3 (182) and T6 (24) whereas *P. latifrons* was observed on T5 (1259 individuals), T9 (268) and T10 (177). *Phrynobatrachus tokba* was recorded on T1 (19), T2 (68), T3 (64), T6 (4), T7 (51) and T8 (19). All species significantly deviated from a uniform distribution across the different transects (Kruskal-Wallis test: *P. ghanensis* p = 0.001, *P. phyllophilus* p = 0.001, *P. liberiensis* p = 0.003, *P. latifrons* p = 0.001, and *P. tokba* p = 0.005). The results of the Scheffé post-hoc tests for pairwise comparisons are presented in Table 1.

We tested the occurrences of the five *Phrynobatrachus* species across transects with respect to environmental parameters (habitat types). The SOM classified the five *Phrynobatrachus* species in three major groups (Fig. 4). The first group was exclusively represented by *P. latifrons* (Fig. 4a), this species apparently preferring open habitats dominated by grass, ponds, swamps and the Banco river (Fig. 4b). The second group corresponded to both *P. ghanensis* and *P. phyllophilus*. These species were largely distributed in vegetation with dense canopy and abundant leaf-litter layer (Fig. 4b). *Phrynobatrachus tokba* in the third group was predominantly encountered under trees and shrubs with close canopy, thick leaf-litter layers, close to brooks, swamps and the Banco river (Fig. 4b). In contrast, only populations of *P. liberiensis* were ranked both in the second and the third group.

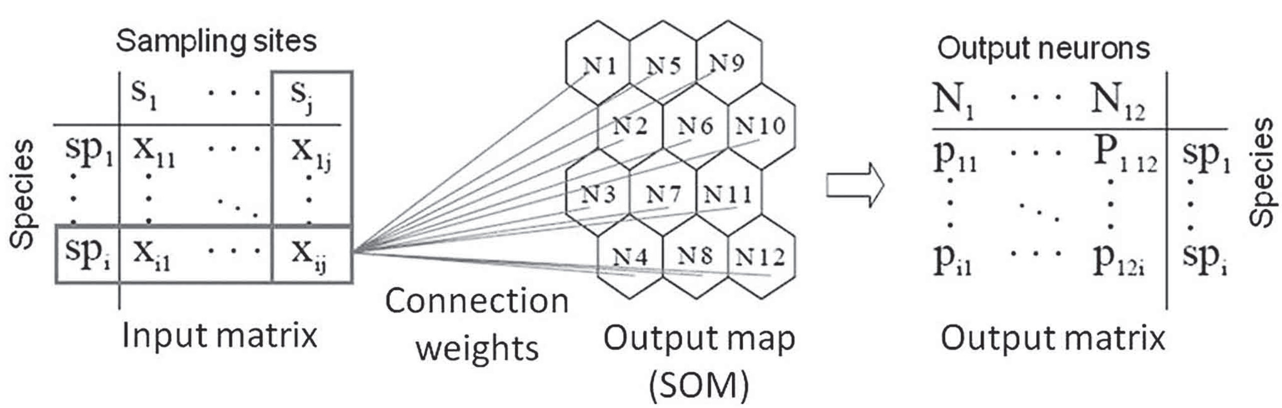

Figure 3. Self Organizing Map (SOM) according to Ibarra (2004). The input matrix is composed of data of species abundances (X_{ij}) for each sampling site (S_j). Once the connection weights are determined by the SOM (P_{ij}) in a minimal learning error, we obtain the map and output matrix.

Table 2. The population densities of the five *Phrynobatrachus* species across seasons. Calculations are based on 80 transect walks in the Longer Rainy Season (LRS) and Longer Dry Season (LDS), and 40 transect walks in the Minor Rainy Season (MRS) and Minor Dry Season (MDS). Transect-hour is abbreviated t-h.

Species	LRS (number of frogs; frogs/t-h)	LDS (number of frogs; frogs/t-h)	MRS (number of frogs; frogs/t-h)	MDS (number of frogs; frogs/t-h)
P. ghanensis	114; 2	129; 2	72; 2	79; 3
P. phyllophilus	140; 2	85; 1	29; 1	49; 2
P. liberiensis	175; 3	210; 4	68; 2	57; 2
P. latifrons	736; 12	451, 8	279; 9	238; 8
P. tokba	97; 2	15; 0	67; 2	46; 2

Seasonality

The species' distribution in across seasons was also investigated (Table 2; Fig. 5). We recorded 114 *P. ghanensis* (2 individuals/t-h/season) in the longer rainy season and 129 *P. ghanensis* (2 frogs/t-h/season) in the longer dry season (80 transect walks in each season). The abundances of this species in the minor rainy season was 72 (2 frogs/t-h/season) and in the minor dry season it was 79 (3 frogs/t-h/season; 40 transect walks in each season). Abundances of *P. phyllophilus* ranged from 140 (2 frogs/t-h/season, longer rainy season), 85 (1 frog/t-h/season, longer dry season), 29 (1 frog/t-h/season, minor rainy season) and 49 (2 frogs/t-h/season, minor dry season). In contrast in *P. liberiensis* we recorded 175 (3 frogs/t-h/season), 210 (4 frogs/t-h/season), 68 (2 frogs/t-h/season) and 57 (2 frogs/t-h/season), respectively in the longer rainy season, longer dry season, minor rainy season and minor dry season. During the respective seasons, the abundances of *P. latifrons* were 736 (12 frogs/t-h/season), 451 (8 frogs/t-h/season), 279 (9 frogs/t-h/season) and 238 individuals (8 frogs/t-h/season) while those observed in *P. tokba* were 97 (2 frogs/t-h/season), 15 (0 frog/t-h/season), 67 (2 frogs/t-h/season) and 46 frogs (2 frogs/t-h/season). Whereas the detectability between the species differed, the abundances within the five species showed no significant variation between seasons (Kruskal-Wallis test: $p \geq 0.675$).

Phrynobatrachus ghanensis was recorded in all seasons at sites T2, T3 and T6 but, not at sites T1 and T8 during the longer and minor dry seasons. *P. phyllophilus* was likewise detected at T3 and T6 in all seasons. At site T8 this species was encountered only during the longer rainy season. The preferred habitats of *P. tokba* in all seasons were T1, T2, T3, T7 and T8. The later species was detected at T6 only during the longer rainy season. In contrast we found *P. liberiensis* and *P. latifrons* in all seasons in their respective habitats (Fig. 5).

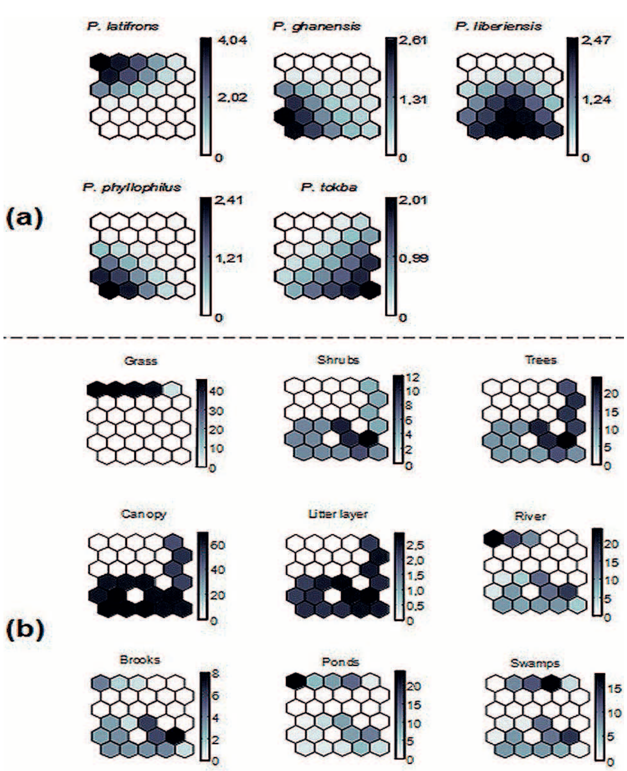

Figure 4. Distribution of the five species of *Phrynobatrachus* (a), and characterization of habitat types of the Banco National Park (b) based on the Self Organizing Map; black and/or dark polygons are representing areas where frog assemblages and environmental parameters were highly elevated whereas grayish and white polygons correspond to mean and very low gradient, respectively.

Discussion

We investigated the spatio-temporal distribution of *Phrynobatrachus ghanensis*, *P. latifrons*, *P. liberiensis*, *P. phyllophilus* and *P. tokba* across seasons and habitat types in BNP. The five West African leaf-litter frogs were widespread along the BNP transects, but showed clear differences concerning their habitat preferences. Only *P. latifrons* preferred more open habitats. All other species dominated in forested parts of BNP as it was illustrated by our Self Organizing Map which categorized the anuran assemblages in three distinct groups (Fig. 4a). According to Lamotte & Xavier (1981) and Rödel (2000) *P. latifrons* is a savannah specialist. In the forest zone it only maintains stable populations in disturbed forest or non-forest habitats and thus is a good indicator of forest degradation (Rödel & Branch 2002, Rödel & Agyei 2003, Adeba et al. 2010). *Phrynobatrachus ghanensis* and *P. phyllophilus* were more abundant on T3 and T6 than in any other areas in the park. Both of these sites are characterized by forest in near primary state, thus confirming Assemian et al. (2006) and Kouamé et al. (2008), who suggested that *P. ghanensis* and *P. phyllophilus* are restricted to primary forested parts. *Phrynobatrachus liberiensis* was abundant on T1, T2 and T3, the number of individuals for *P. tokba* was highest at T1, T2 and T7. Thus *P. liberiensis* seems to share the same habitats with *P. ghanensis* and *P. phyllophilus* on the one hand and with *P. tokba* on the other hand. However, *P. tokba* is not dependent on open water for reproduction and thus often occurs in drier parts of the forest (Rödel & Ernst 2002a, Rödel et al. 2005). It prefers dense undergrowth in forest areas, but survives as well in degraded forest, secondary growth and even dense tree savannah with very high grass (Lamotte 1966, Rödel 2003). We thus believe that the distribution of *P. liberiensis* in BNP actually is closer to those of *P. ghanensis* and *P. phyllophilus* than to *P. tokba*. *Phrynobatrachus liberiensis* is almost always occurring close to small creeks and brooks in swampy forest (Guibé & Lamotte 1963, Rödel 2003). This explains the high abundances of *P. liberiensis* on T1, T2 and T3. The predominance of *P. liberiensis*, the low abundances of *P. ghanensis* and the absence of *P. phyllophilus* at sites T1 and T2 clearly indicate that

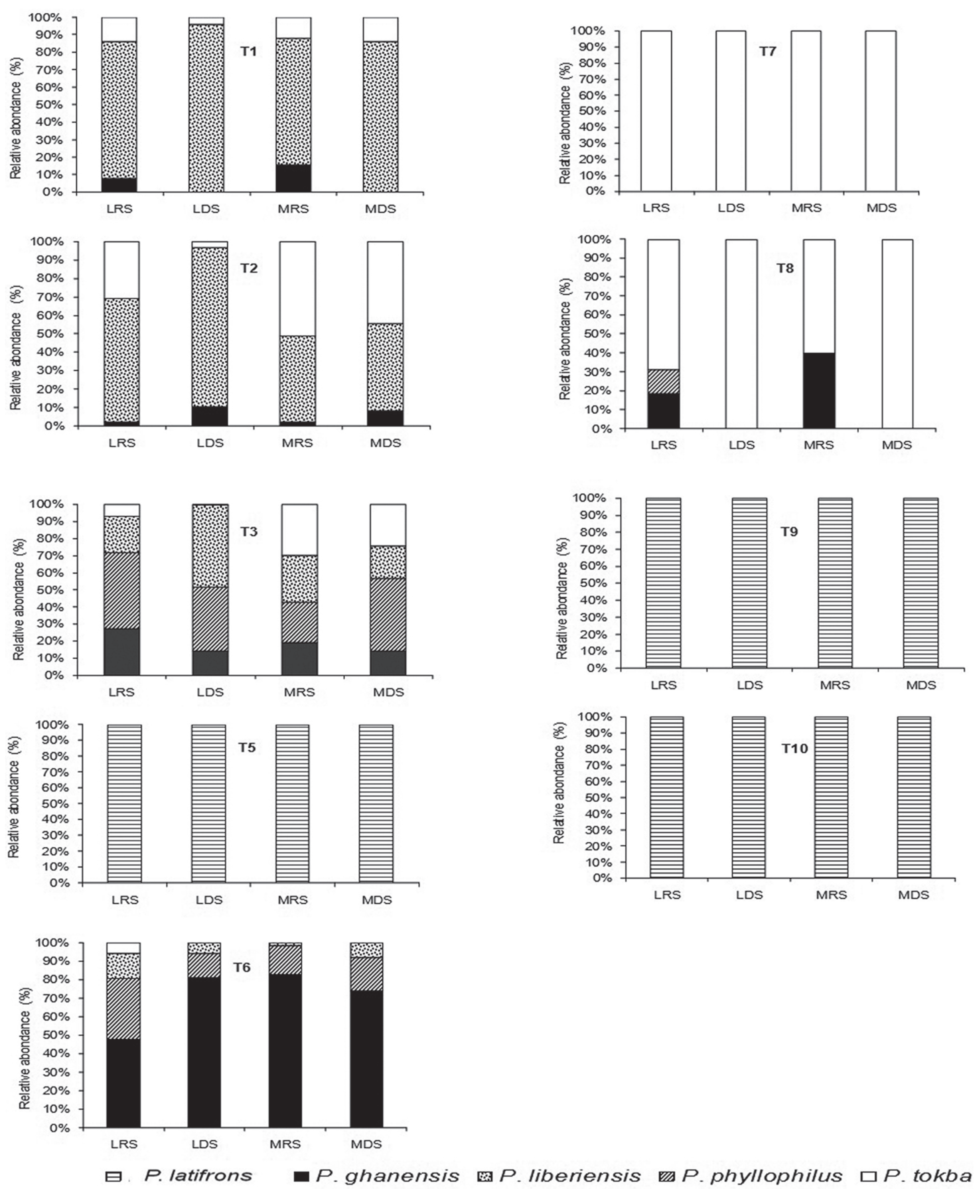

Figure 5. Distribution of the five *Phrynobatrachus* species from Banco National Park during all seasons in across the ten transects. LRS: Longer Rainy Season; LDS: Longer Dry Season; MRS: Minor Rainy Season; MDS: Minor Dry Season.

P. liberiensis is more adapted to aquatic areas of the forest than the other two species. This most likely is due to differing reproduction strategies of the species. *Phrynobatrachus liberiensis* reproduces in brooks in swampy forest areas (Rödel 2003), while *P. ghanensis* and *P. phyllophilus* reproduce in small stagnant puddles in forest (Schiøtz 1964, Rödel & Ernst 2002b). Among the five species, only *P. tokba* occurred at T7. This transect was characterized by dense, relatively dry forest (e.g. no open water). As explained above this species has an extraordinary reproductive biology, explaining this habitat choice. *Phrynobatrachus tokba* deposits clutches on leaves on the forest floor, partly hidden in wet leaf litter. The tadpoles are non-hatching and non-feeding and finish metamorphosis before hatching (Rödel & Ernst 2002a).

Among the ten transects, we did not record any frogs at T4. This site is dryer than all other forested parts we investigated. The absence of amphibians in this zone could be explained by the combined effects of construction activities, the very low amount of leaf litter lying on the forest floor in particular (see Whitfield et al. 2014), and the relatively dry habitat, which may limit the survival of the very small study species. By effectively preserving moisture, thick leaf-litter layers may substantially contribute to a higher humidity (Urbina-Cardona et al. 2006). In addition at forest edges dryer and hotter conditions prevail (Murcia 1995, Harper et al. 2005).

We likewise recorded year round abundance data. Overall each of the five *Phrynobatrachus* species was recorded in all seasons, hence indicating that the frogs were also active during the longer and minor dry seasons. However, some species were not recorded during all seasons in the same sites. Whereas *P. latifrons* and *P. liberiensis* were found throughout all seasons at their sites, the other species showed differing activity across habitats and seasons (Fig. 5). *Phrynobatrachus latifrons* and *P. liberiensis* were found throughout the year at T5, T9, T10, and T1, T2, T3, T6, respectively. This can be explained by the persistence of year round water bodies. However, the used water bodies differed between sites and species. At T1, adults and juveniles of *P. liberiensis* were encountered only on the edges of the Banco river while frogs of this species lived in swamps at T2, T3 and T6. Even during the dry season *P. latifrons* males were heard calling at the fish farm (site T5), concealed between tufts of grass (T10) or from floating aquatic plants at the Banco river (T9). According to Rödel (2000), some *P. latifrons* migrate between different habitats between seasons. In Comoé National Park, he reported *P. latifrons* during the dry season from the river banks and near forest ponds. In the wet season they colonize stagnant, temporary savannah waters of differing size. Such migration does not seem to be necessary in the wetter BNP. In contrast *P. ghanensis*, *P. phyllophilus* and *P. tokba* occurred in different habitats during the different seasons in BNP. During less favorable periods (longer and minor dry seasons) adults and juveniles avoided dryer habitats and retreated into moister places (i.e. beneath moist leaf-litter layer, roots of trees and shrubs).

It has been shown that West African leaf-litter frogs react sensitively to comparatively minor forest degradation (Ernst & Rödel 2005, Ernst et al. 2006). The present study results add to this knowledge by confirming different, species specific, habitat preferences. In addition we show that these habitat preferences may differ between seasons. The results thus will be an important baseline for planning and conducting monitoring projects in the highly threatened and much neglected forests of south-eastern Ivory Coast. The leaf-litter frog species studied herein will be a very suitable group of organisms indicating the degradation status and habitat health of these forests. They can be monitored throughout the entire year with almost equal detectability. However, depending on the species, different seasonal habitat preferences have to be taken into account when interpreting respective monitoring data.

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Appendix

Geographic position and short description of study sites in Banco National Park

Transect #	Coordinates	Site description
T1	05°24'03"N/04°03'51"W	Dense and open forests, natural gaps, borders the Banco river, river's source in about 700 m distance, larger pond
T2	05°23'15"N/04°03'18"W	Large forest gap with a hill, swampy forest borders the Banco river
T3	05°23'12"N/04°03'09"W	Swampy forest, located about 50 m of the central clearing with a fish farm, close to the Banco river
T4	05°23'05"N/04°02'57"W	Closed canopy forest, low amount of leaf-litter lying on the forest floor, no open water, undulating terrain with many small hills, deeper valleys and buildings
T5	05°23'06"N/04°03'06"W	Central clearing with 16 artificial ponds, partly open, partly heavily vegetated and only with shallow water, temporary and perennial waters (the latter stocked with *Tilapia* fish), flowing creek crosses clearing and run along forest, surrounded by swampy forest, the Banco river and bamboo plots
T6	05°23'05"N/04°03'06"W	Very swampy part of the forest, partly inundated during the wet season, the water might be flowing
T7	05°22'56"N/04°03'30"W	Partly dense forest, partly more or less fragmented forest without open water, undulating terrain with a hill, massive amount of leaf-litter lying on the forest ground
T8	05°22'26"N/04°03'10"W	Located at the entry of the arboretum, open forest, swampy areas covered, bamboo areas
T9	05°21'41"N/04°02'32"W	Located at the main entry of the park, open zone covered by grass, heavily degraded and water polluted due to the "Fanico" launderers, people that use the river for religious rituals or car washing
T10	05°24'18"N/04°01'20"W	Heavily degraded forest with open canopy, three larger ponds that are polluted due to nearby mechanic quarters, corn, manioc and yam plantations