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The anuran fauna in a protected West African rainforest and surrounding agricultural systems

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***Abstract.*—The conversion of tropical rain forests to agricultural systems is a major threat to tropical biodiversity. In West Africa, studies investigating the effects of this habitat conversion on biodiversity are scarce. In this study, we investigated which forest amphibians survive in the agroforestry systems surrounding West Africa's largest area of protected rainforest, the Taï National Park (TNP) in south-western Côte d'Ivoire. Species richness was assessed in different habitats types, i.e., a mosaic of coffee and cocoa plantations, rubber plantations, and rice fields, and compared to data from primary and degraded forests in TNP. The anuran assemblage composition differed considerably between forest and agroforestry systems, with the latter comprising only a small subset of generalist forest species and species which usually occur in highly degraded forest habitats or even savanna. Thus, the agroforestry systems in western Côte d'Ivoire seem to be unsuitable for the maintenance of the rich local and regional diversity of forest amphibians.**

Keywords. Agroforestry, amphibians, biodiversity, habitat conversion, Ivory Coast, Upper Guinea forest zone

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Introduction

While tropical rainforests may comprise about half of the world's biodiversity, they are shrinking at a very high rate. A comprehensive investigation on the African continent revealed that between 1990 and 2000, over 50 million ha of forest disappeared (FAO 2001, 2006). In West Africa, the situation is especially alarming as only 20% of the 1.5 million km^2 of forest present at the beginning of the 20th century persists to date (FAO 2006). The main driver of forest loss is logging and conversion into plantations (mainly oil palm, cocoa, coffee, and rubber), and other forms of agricultural land use.

Côte d'Ivoire is no exception to this trend of increasing forest loss. For example, Chatelain et al. (1996) revealed that in the most forested part of the country, the far south-west, 79% of forest had been lost in only 20 years. However, one large area of rainforest in that region prevailed: the Taï National Park (TNP). At about 536,000 ha, TNP represents more than 50% of the total area of protected West African rainforest (OIPR 2014), thus constituting the most important area of protected rainforest in the entirety of West Africa. However, the forests previously surrounding TNP, i.e., various forest fragments (Hillers et al. 2008) and classified forests (Alonso et al. 2005), are now almost completely logged or converted to small scale agricultural areas and industrial sized plantations (Rödel et al. 2021; all authors, pers. obs.).

The amphibian fauna of TNP and the surrounding classified and fragmented forests have been the focus of numerous taxonomic and ecological studies (Perret 1988; Rödel 1998; Rödel and Ernst 2000, 2001a,b, 2002a,b, 2004; Rödel et al. 2001, 2002a,b, 2003, 2004; Rödel and Branch 2002; Veith et al. 2004; Rudolf and Rödel 2005, 2007; Sandberger et al. 2010; Kpan et al. 2019, 2021). These studies have revealed that the amphibian communities show considerable differences between old growth and previously selectively logged forests (Ernst and Rödel 2005, 2006). Hillers et al. (2008) showed that these differences were more strongly associated with forest degradation rather than fragmentation. Ernst et al. (2006) and Ernst and Rödel (2008) observed that different frog groups react differently to logging, and emphasized that although species richness may remain similar between logged and pristine sites, functional

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diversity dramatically declines in altered West African rainforests. A recent study revealed that the recovery of amphibian assemblages in previously logged parts of TNP does occur, but it is very slow (Kpan et al. 2021). All these studies collectively highlight the sensitivity of forest amphibians to forest degradation, an observation that was also made in other West African forests (Ofori-Boateng et al. 2012; Adum et al. 2013).

However, we do not yet know to what extent West African forest amphibians might be able to persist in agroforestry systems. These artificial habitats now make up almost all the areas surrounding TNP, providing resources to local communities such as income, energy, shelter, and food (PNUE 2012). Studies from Asia have shown that agricultural areas, which comprise highly disturbed forests, may provide habitat for some amphibian species and thus could be a component for the maintenance of at least some part of the local biodiversity (Wanger et al. 2009; Faruk et al. 2013; Konopik et al. 2015). However, respective studies from West Africa are lacking so far.

This study aimed to determine the resistance of West African forest amphibians to the conversions of their original habitats to agricultural habitats. We examined anuran species richness and species turnover in three different habitats types, i.e., mosaic coffee and cocoa plantations, rubber plantations, and rice fields, and compared them to the primary and degraded forest in the TNP. We hypothesized that (a) species richness decreases, and (b) species turnover increases, with increasing disturbance between the habitat types.

Materials and Methods

Study area and study sites. Taï National Park is located in south-western Côte d'Ivoire, between the Cavally and Sassandra rivers, and the towns of Guiglo, Buyo, San Pedro, and Tabou. It extends from 05°08'N to 06°24'N latitude, and from 06°47'W to 07°25'W longitude (OIPR 2015). The climate of TNP is sub-equatorial with four seasons: a long rainy season from mid-March to July, a short dry season in August, a short rainy season from September to October, and a long dry season from November to mid-March. However, this regular seasonality has changed to some extent in recent years. The average annual rainfall is 1,800 mm, and ranges from 1,700 mm in the north to 2,200 mm in the south of the park (Chatelain et al. 2001). The average monthly temperature varies from 24–28 °C (Koné 2004). The relative air humidity is always high, ranging from 85% to 90% under the forest cover, and usually reaches 100% during the night (Bousquet 1978). The West African dry season wind, called Harmattan, is irregular and has little impact on the area, usually only extending over one to two weeks in December or January (Adou et al. 2005).

Taï National Park is the largest prevailing rainforest area in the Upper Guinea biodiversity hotspot (Myers et al. 2000; Bakarr et al. 2001). Botanically, TNP is part of the large Guinean-Congolese floristic region (Dupuy et al. 1999), and the flora of TNP comprises more than 1,350 species, of which 80 are endemic (Chatelain and Kadjo 2000). The Park includes approximately 145 mammal species, corresponding to 93% of the mammal fauna of the western Guinean forest zone (Riezebos et al. 1992), as well as 234 bird species (OIPR 2014), 60 fish species (Grell et al. 2013), 43 snake species (Rödel and Mahsberg 2000; Ernst and Rödel 2002), four turtles, two crocodiles, and 11 lizard species (MOR, unpub. data). So far 56 amphibian species have been recorded from TNP (Rödel and Ernst 2004; Ernst et al. 2006), two of which seem endemic; namely *Phrynobatrachus taiensis* (Phrynobatrachidae; Perret 1988), and *Hyperolius nienokouensis* (Hyperoliidae; Rödel 1998).

We surveyed the amphibians in different habitat types in five sectors of TNP: ADK/V6, Soubré, Taï, Djapadji, and Djouroutou (Fig. 1). These habitat types were either located inside TNP, along the park's periphery, or in agricultural systems surrounding TNP. The habitats inside TNP consisted of two types: (i) primary forests characterized by dense forests with a high, closed canopy, and (relatively) open undergrowth, and (ii) degraded forests with large canopy gaps and denser understory. The degraded forests were mainly encountered at the edge of the TNP, often in direct proximity to crops. All agricultural sites where in the periphery of the TNP, and consisted of a mosaic of coffee and cocoa plantations, rubber plantations, and rice fields, often in close

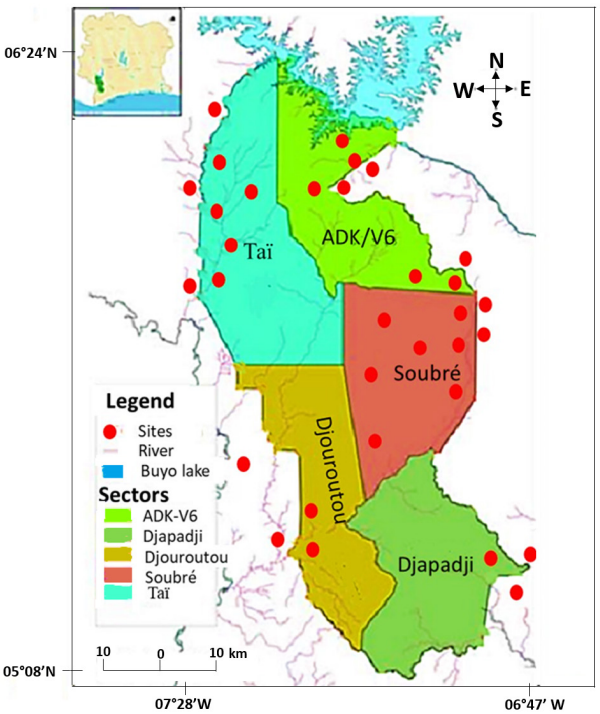

Fig. 1. Locations of the 32 study plots in the Taï National Park and surrounding agroforestry systems (see Appendix 1 for the plot list and habitat descriptions). Inset figure: position of Taï National Park in Côte d'Ivoire.

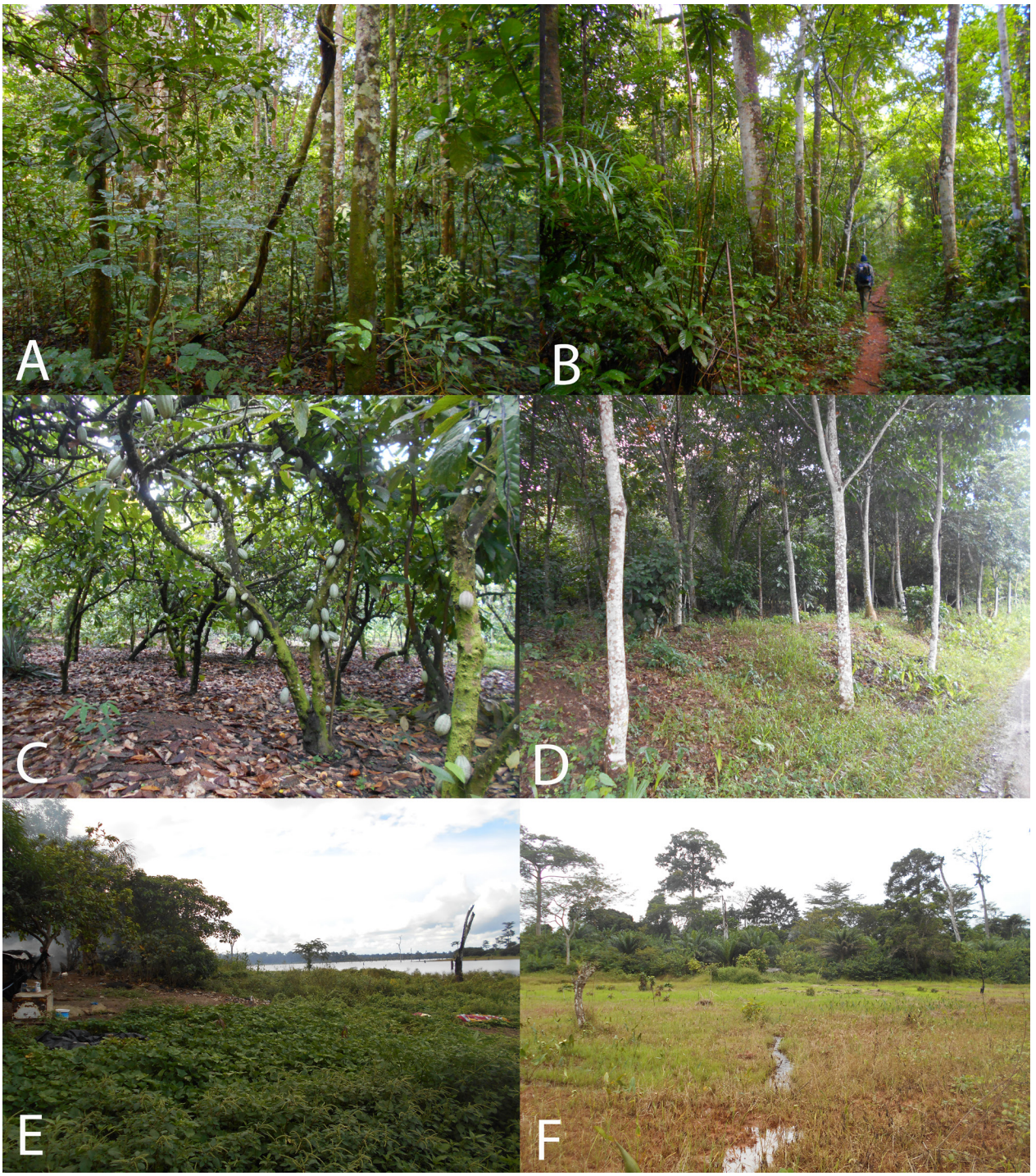

Fig. 2. The different habitats in and around Taï National Park which were surveyed for amphibians. **(A)** and **(B)** near primary forest; **(C)** cocoa plantation; **(D)** rubber plantation; **(E)** heavily degraded forest edge; **(F)** rice field.

proximity to villages (Fig. 2). Rice fields usually have no canopy and thus are not regarded as agroforestry habitats. However, in the West African forest zone (and elsewhere, compare Ndriantsoa et al. 2017), swamp forests are often cleared in order to establish rice fields (Rödel and Glos 2019). Therefore, we included rice fields here as well. The geographic positions of all study sites were recorded with a hand-held Garmin 60 CSx. A list of all sites, including a brief description of the habitats, is included in Appendix 1.

Sampling methods. The fieldwork was conducted from May to October 2018, thus covering the long and short rainy seasons, as well as the short period of reduced precipitation in August. A total of 32 plots of 100 x 50 m were established, 20 within the park and 12 in the agroforestry systems (Figs. 1–2). The sites in TNP comprised 14 plots in primary forest, and six in degraded forest. In the TNP periphery, three plots were established in coffee/cocoa plantations, two in rubber plantations, and seven in rice fields. Each plot was visited twice (total

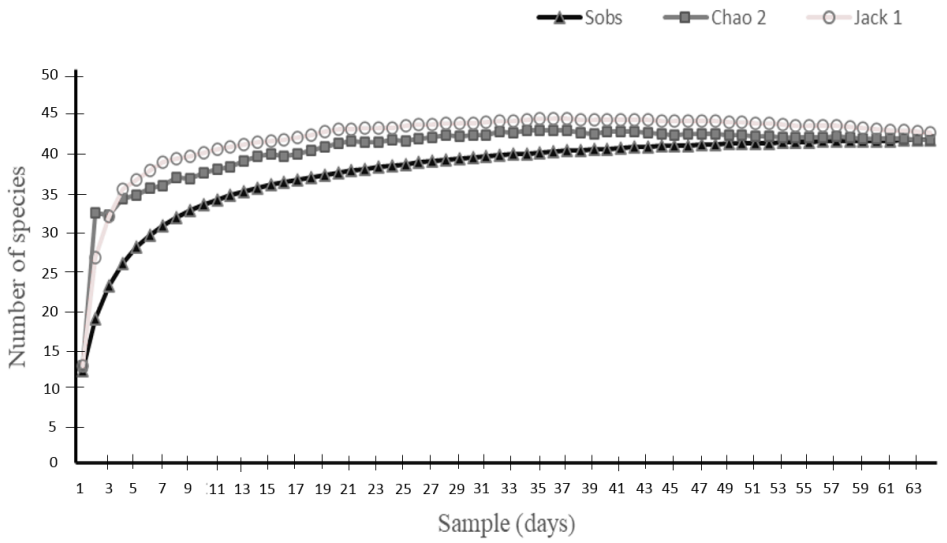

Fig. 3. Species accumulation curve (triangles) and estimated amphibian species richness (Chao 2, squares; and Jack-knife 1, circles) of the Taï National Park and surrounding agroforestry system. The mean values of 500 random runs of the daily species lists are given. A daily species list comprised the presence/absence records collected during seven hours of sampling (four hours during daylight, and three hours during night) on one plot by two people for a total of 14 person-hours.

64 days) with a consistent sampling intensity of 7 h/visit (four hours during daylight at 0700–1100 h, and three hours during night at 2000–2100 h GMT). Plots were always investigated by two people (for 14 person-hours per plot day), so the search effort represents a total of 896 person-hours of sampling. The average time between the two visits to a plot was three months (see Appendix 1).

Amphibians were located through visual and acoustical searches in all the different habitats of a plot (Heyer et al. 1994; Rödel and Ernst 2004). Individuals encountered were identified to the species level following the nomenclature of Frost (2020). It should be noted that *Arthroleptis* cf. *poecilonotus* (Fig. 4D) comprises a complex of species, which currently cannot be assigned with certainty to a valid name (compare Rödel and Bangoura 2004; Blackburn 2010; Blackburn et al. 2010; Channing and Rödel 2019). In TNP, two species occur in syntopy, and they are indistinguishable based on morphology and habitat preferences but discernible by their calls (Ernst and Rödel 2005). In this study, we treated them as a single taxon. Representatives of each species were collected, anesthetized in a chlorobutanol solution, and thereafter preserved in 70% ethanol. These voucher specimens were deposited in the collection of the Hydrobiology Unit of the Laboratory of Biology and Tropical Ecology at Jean Lorougnon Guédé University, Côte d'Ivoire.

Data analysis. As species detection probability seemed to differ among the species, and numbers of calling males could not be reliably counted on the plots, we used qualitative data for the assessments but not quantitative data. The estimated species richness, and thus the sampling efficiency, were calculated with the Jack-knife 1 and Chao 2 estimators using EstimateS software (Version 9.1.0; Colwell 2013). These two estimators are incidence based. The presence/absence data of the daily species lists (64 days of survey work) were used for all 41 species recorded in the entire study area, as well as for the different habitat types (see Table 1). To avoid order effects, 500 random runs of the daily species lists were conducted. In order to test for similarities or differences in amphibian species compositions in the investigated habitat types, the Jaccard's Similarity Index was calculated using the software PAST (Version 2.17c; Hammer et al. 2001).

In order to determine whether a particular species disappeared after habitat degradation, survived in the agroforestry systems, or even invaded such habitats, we classified each species in the following three categories (bearing in mind that the total numbers may deviate from the total number of recorded species as not all categories were known for all species, compare Table 1):

I. Habitat: F = species only occurring in closed forest; D = species occurring in degraded forest (may occur in closed forest, absent in open areas); O = species living in open areas (may occasionally be encountered in degraded forest); if a species could be observed in more than one category, it was assigned to the 'most open' habitat.

II. Micro-habitat of adults: f = fossorial; a = aquatic; l = leaf litter; t = arboreal.

III: Micro-habitat of tadpoles: d = direct developers and non-feeding non-hatching tadpoles, developing in leaf litter or in the soil; s = stagnant waters (ponds, puddles, tree holes); f = flowing water.

Results

Species richness and community composition. Overall, the surveys revealed 41 anuran species from 12 families

Table 1. Amphibian species recorded in the Taï National Park and surrounding agricultural areas, along with recorded and estimated species numbers per habitat type and general habitat preferences of adults and tadpoles (see Materials and Methods). Abbreviations: PF: primary forest; DF: degraded forest; CP: mosaic of coffee and cocoa plantations; RP: rubber plantation; RF: rice field; l: leaf litter; t: arboreal; a: aquatic; f: fossorial; F: closed forest; D: degraded forest; O: open habitat; ? : unclear as species identification was not possible; d: direct development and non-hatching/non-feeding tadpoles; s: tadpoles in stagnant water (ponds, puddles, tree holes); f: tadpoles in flowing water; *: comprises a species complex (see text); **: the two 'sub-species' occur in sympatry in TNP and may actually represent two valid species; ***: an undescribed species compare Jongsma et al. (2018).

	TNP habitat		Agricultural areas				
	PF	**DF**	**CP**	**RP**	**RF**		
Sample units (days)	28	12	6	4	14		
Search effort (person-h)	392	168	84	56	196		
Estimated species richness (Chao 2)	28.6 ± 2.1	23.8 ± 1.4	15.0 ± 1.6	7.9 ± 1.3	10.0 ± 0.1		
Estimated species richness (Jack-knife 1)	31.6 ± 1.7	26.3 ± 2.5	16.7 ± 1.8	9.0 ± 1.0	10.9 ± 0.9		
Number of species recorded	**27**	**23**	**14**	**7**	**10**		
Family and species	**PF**	**DF**	**CP**	**RP**	**RF**	**Habitat (adult)**	**Habitat (tadpole)**
Arthroleptidae							
Arthroleptis cf. *poecilonotus**	x	x	x	x		O, l	d
Astylosternus occidentalis	x					F, l	f
Cardioglossa occidentalis	x					F, l	f
Leptopelis occidentalis	x					F, t	s
Leptopelis spiritusnoctis		x			x	D, t	s
Leptopelis viridis	x					O, t	s
Bufonidae							
Sclerophrys maculata		x	x	x	x	O, l	s
Sclerophrys regularis		x	x	x		O, l	s
Sclerophrys togoensis	x					F, l	f
Dicroglossidae							
Hoplobatrachus occipitalis		x			x	O, a	s
Hemisotidae							
*Hemisus marmoratus**		x		x		O, f	s
Hyperoliidae							
Afrixalus dorsalis		x	x		x	O, t	s
Afrixalus nigeriensis	x					F, t	s
Hyperolius concolor		x	x		x	O, t	s
*Hyperolius f. fusciventris***					x	D, t	s
*Hyperolius f. lamtoensis***		x				D, t	s
Hyperolius guttulatus	x	x				O, t	s
*Hyperolius picturatus**	x	x	x			D, t	s
Hyperolius sylvaticus	x					F, t	s
Kassina sp.		x			x	?, t	s?
Conrauidae							
Conraua alleni	x					F, a	f
Pipidae							
Xenopus tropicalis	x					D, a	s
Phrynobatrachidae							
Phrynobatrachus alleni	x	x	x			F, i	s
Phrynobatrachus annulatus	x					F, l	?
*Phrynobatrachus calcaratus**	x	x	x			O, l	s
Phrynobatrachus fraterculus	x	x	x			D, l	?
*Phrynobatrachus gutturosus**	x	x				O, l	s
Phrynobatrachus latifrons		x	x	x	x	O, l/a	s
Phrynobatrachus liberiensis	x	x	x			F, l	f
Phrynobatrachus phyllophilus	x					F, l	s
Phrynobatrachus plicatus	x	x				F, l	s
Phrynobatrachus tokba	x					O, l	d

Table 1 (continued). Amphibian species recorded in the Taï National Park and surrounding agricultural areas, along with recorded and estimated species numbers per habitat type and general habitat preferences of adults and tadpoles (see Materials and Methods). Abbreviations: PF: primary forest; DF: degraded forest; CP: mosaic of coffee and cocoa plantations; RP: rubber plantation; RF: rice field; l: leaf litter; t: arboreal; a: aquatic; f: fossorial; F: closed forest; D: degraded forest; O: open habitat; ? : unclear as species identification was not possible; d: direct development and non-hatching/non-feeding tadpoles; s: tadpoles in stagnant water (ponds, puddles, tree holes); f: tadpoles in flowing water; *: comprises a species complex (see text); **: the two 'sub-species' occur in sympatry in TNP and may actually represent two valid species; ***: an undescribed species compare Jongsma et al. (2018).

Family and species	PF	DF	CP	RP	RF	Habitat (adult)	Habitat (tadpole)
Ptychadenidae							
Ptychadena cf. *aequiplicata**	x					F, l	s
Ptychadena bibroni	x					O, l	s
Ptychadena longirostris	x	x	x	x		D, l	s
*Ptychadena mascareniensis**		x	x	x	x	O, l	s
Ptychadena pumilio		x			x	O, l	s
Pyxicephalidae							
Aubria subsigillata	x					F, a	f
Rhacophoridae							
Chiromantis rufescens	x					D, t	s
Ranidae							
Amnirana aff. *albolabris****	x					D, l	f
*Amnirana galamensis**		x				O, l	s

and 17 genera (Table 1). Forests comprised more species (27 in primary, 23 in degraded forest) than agroforestry systems. Whereas 14 species were found in mixed coffee/cocoa plantations and 10 species in rice fields, only seven species were recorded in rubber plantations (Table 1). One-third of the species only occurred in forest (14 species, 34.1%), and 10 (24.4%) prevailed in degraded forests; however, the majority thrived well in open habitats (16, 39.0%). Only one species (2.4%) was fossorial, three (9.8%) were aquatic, 12 (29.3%) were arboreal, and the majority (23 species, 56.1%) occurred in the leaf litter. Three species had no free-living tadpole (4.9%), the tadpoles of seven species (17.1%) live in small rivers, and the majority (29, 70.7%) develop in stagnant waters of various sizes. A large proportion of frog species were only found in primary forest (15 species, 36.6%), but the remaining species either tolerated some habitat degradation, or only occurred in degraded habitats (13 species, 31.7%; Table 1). The primary forest records of two species known to usually occur in savanna habitats, *Leptopelis viridis* and *Ptychadena bibroni*, indicates that our 'primary forest' records also comprise 'guests' that do not normally live in that habitat.

Based on the daily species lists, the overall sampling efficiency for the entire study area was calculated (Fig. 3). The Jack-knife 1 estimator calculated 42.0 (SD: ± 1.0) amphibian species, and the Chao 2 estimator estimated 41.0 (SD: ± 0.1) species for the entire study area, which represent 97.6% and 100% of the 41 observed species, respectively. Therefore, we would not expect to find more species through an enhanced sampling effort. Concerning the different habitat types, the two estimators showed similar efficiencies in the respective habitats, with values ranging from 77.8% to 100% of the actual observed species counts. The lowest value was calculated by Jack-knife 1 for the rice fields, while the highest estimate was calculated by Chao 2 for rubber plantations (Table 1).

The results of the Jaccard's similarity of species assemblages between the five surveyed habitat types are presented in Table 2. The amphibian assemblages in degraded forest and the coffee and cocoa plantations were most similar with a value of 56.2%, followed by 42.9% similarity of amphibian assemblages in coffee/cocoa with those from rubber plantations. All other assemblages shared only a few species, e.g., the primary and secondary forest assemblages showed only 25.0% similarity. The lowest similarity was between primary forest and rubber plantations (6.3%).

Discussion

The results of this study revealed higher anuran species richness in forested habitats of Taï National Park (TNP) compared to the surrounding agroforestry systems.

Table 2. Jaccard's similarity of the anuran assemblages calculated with presence/absence data in pairwise comparisons between the five habitat types investigated in Taï National Park and the surrounding agroforestry systems. The values show the percentage of shared species between the two habitat types. The highest similarity in species composition was observed between degraded forest and coffee/cocoa plantations (in bold).

Habitat type	PF	DF	CP	RP	RF
Primary forest (PF)	-	25.00	21.22	6.25	13.33
Degraded forest (DF)	-	-	**56.22**	30.43	20.00
Coffee/cocoa plantation (CP)	-	-	-	42.85	25.00
Rubber plantation (RP)	-	-	-	-	16.67
Rice paddies (RF)	-	-	-	-	-

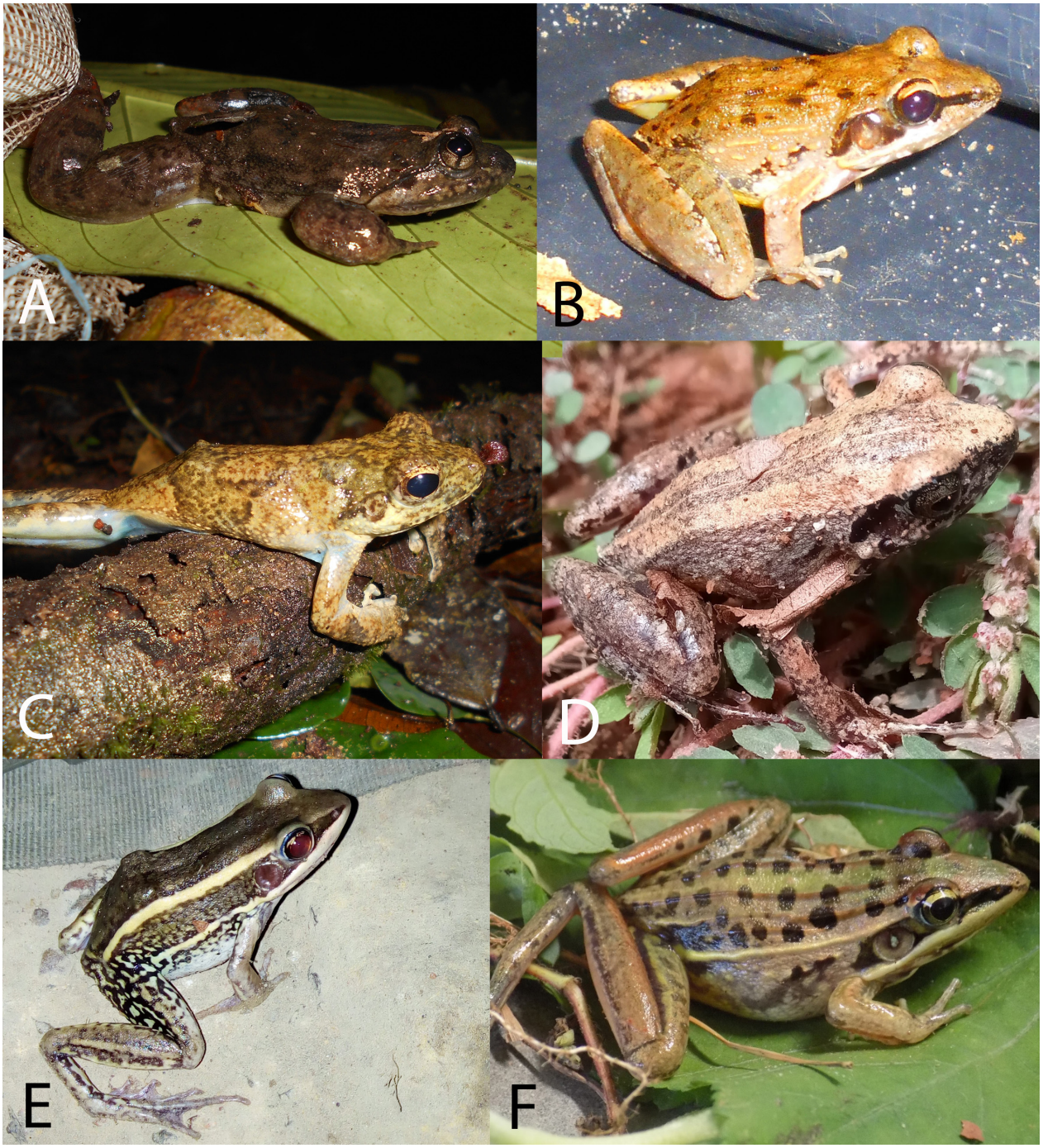

Fig. 4. Selected amphibian species from Taï National Park and surrounding agroforestry systems. **(A)** *Conraua alleni* inhabits rainforest streams. **(B)** *Ptychadena* cf. *aequiplicata* is a typical inhabitant of primary forest. **(C)** *Chiromantis rufescens* breeds in puddles along forest roads and stagnant ponds and puddles in the forest. **(D)** *Arthroleptis* cf. *poecilonotus* (a complex of at least two species) occurs in primary and degraded forest, and is particularly abundant in agroforestry systems. **(E)** *Amnirana galamensis* is a typical inhabitant of African savannas and was detected for the first time in the Taï area. **(F)** *Ptychadena mascareniensis* is a very abundant frog in rice fields.

Whereas 27 and 24 species were detected in old growth and degraded forests, respectively, only 14 species were found in mixed coffee/cocoa plantations, 10 in rice fields, and seven in rubber plantations. These observations are in agreement with a study from Southeast Asia. In Sulawesi, Wanger et al. (2010) observed a decrease in amphibian species richness along a land-use gradient from closed primary forest habitats to increasingly more open areas. In contrast, other studies revealed no significant effect of agricultural forest exploitation on amphibian species richness (Faruk et al. 2013; Konopik et al. 2015), with almost identical anuran species richness in forested sites and oil palm plantations in Malaysia. In fact, Ernst et al. (2006) also observed identical amphibian species

richness in old growth forest and previously selectively logged habitats of TNP. However, the species assemblage composition was found to change considerably with forest degradation (Ernst and Rödel 2005, 2006, 2008; Hillers et al. 2008; Kpan et al. 2021), and functional diversity was significantly lower in previously logged forests (Ernst et al. 2006).

The impact of forest degradation on anuran assemblages was also evident in this study, which found the highest similarity between the degraded forest habitats in TNP and the coffee and cocoa plantations. Thus, the amphibians of the latter habitats clearly occupied altered environmental conditions, which were still 'forest-like' to some extent. That the presence of shade trees and suitable breeding habitats may substitute for forest to some degree was underscored by the presence of some species that typically occur in proper forest, i.e., *Phrynobatrachus alleni* and *Phrynobatrachus liberiensis*. However, other species recorded in those habitats, such as *Phrynobatrachus fraterculus* and *Hyperolius picturatus,* are typical inhabitants of farmbush, conforming with the degradation status of these plantations (Schiøtz 1967). Rice fields provided a home for various frog and toad species. However, all these anurans are either typical farmbush species or species that prefer even more open habitats, such as *Ptychadena* aff. *mascareniensis* (compare Ndriantosa et al. 2017; Rödel and Glos 2019). Lastly, the rubber plantations had a very reduced amphibian fauna, with the only species possibly reproducing there being *Arthroleptis* sp. and *Phrynobatrachus tokba*. That these direct developing frogs (Lamotte and Perret 1963; Barbault and Trefaut-Rodrigues 1979; Rödel and Ernst 2002a) can benefit from the degradation of forest has already been reported by Ernst and Rödel (2005). With the exception of rice fields, *Arthroleptis* species were found in all terrestrial ecosystems of the TNP area. Interestingly, *P. tokba* was recorded only from primary forest in this study, which is in sharp contradiction to previous research from TNP (e.g., Ernst et al. 2006; Kpan et al. 2021).

Based on our data, it is difficult to state whether the species suffering from forest degradation had particular life history traits, such as preferred micro-habitats or larval habitats (Table 1). This is partly due to the fact that some species were recorded exclusively in primary (e.g., *Leptopelis viridis* and *Ptychadena bibroni*) or degraded forest (*Amnirana galamensis*) which are known to usually occur in savanna habitats (Rödel 2000). These records may either indicate that our plot definition was not perfect (e.g., other neighboring habitat types with respective species) or these specimens were 'guests' and only encountered while migrating through the forested areas. For example, savanna amphibian communities in TNP are known to have become established on granite inselbergs within the forest (see Figs. 1.8 and 1.33 in Rödel et al. 2021), and these species may be rarely encountered in the forest between inselbergs (M.-O. Rödel, pers. obs. and unpub. data). However, the results of this study clearly show that the agroforestry systems in the TNP area could only provide habitat to a small subset of the regional species pool, namely some generalist forest amphibians and species that do not normally occur in forest ecosystems. Typical members of the latter group are species such as the three mentioned above, as well as *P.* aff. *mascarenisnsis* and *Phrynobatrachus latifrons*, which mostly occur in savanna habitats (Lamotte 1967; Rödel 2000).

In addition to the 56 species reported by Rödel and Ernst (2004) and Ernst et al. (2006), this study confirmed the presence of two additional species, *Conraua alleni* and *Amnirana galamensis*, thus raising the number of known amphibian species for the TNP area to 58. *Conraua alleni* (Fig. 4A) has been described from Liberia (Barbour and Loveridge 1927), and reported in Côte d'Ivoire to the south (Rödel and Branch 2002, Haute Dodo Classified Forest) and north of the TNP (Rödel 2003, Mont Sangbé National Park), as well as from Mount Nimba (Guibé and Lamotte 1958; Lamotte and Perret 1968; Kanga et al. 2021). This aquatic species prefers clear streams in forests (Rödel and Branch 2002; Rödel 2003; Rödel and Bangoura 2004). We also observed this species in permanent streams in primary forests with a closed canopy and open understory in the Soubré (05°28'49''N, 07°3'35''W) and Taï sectors (05°53'52''N, 07°23'57''W). In contrast, *A. galamensis* (Fig. 4E) is generally found in savanna habitats, survives successfully in modified habitats (Rödel 2000), and has even been reported from urban areas (Kouamé et al. 2015). This taxon is widespread in sub-Saharan Africa (Channing and Rödel 2019), but comprises several cryptic species (Jongsma et al. 2018). We found *A. galamensis* in a highly polluted area (06°14'12.7''N, 07°11'04.3''W) close to a village.

Although the estimators indicated that we could not expect to find many more species of the local amphibian assemblages, this seems unlikely. The overall species richness of our study was similar to that revealed in other nearby forest regions (see Rödel and Branch 2002). However, our species list here lacks a number of frogs which actually typically occur in swampy (e.g., *Phrynobatrachus villiersi, Kassina lamottei, Hyperolius zonatus*) or drier forest sites (*Phrynobatrachus guineensis*), along forest streams (*Leptopelis macrotis, Hyperolius chlorosteus, Amnirana occidentalis*), and even in more open sites within forest (*Phlyctimantis boulengeri*). Some of these species are only active through particular parts of the season and/or under certain climatic conditions, so it is possible that the number of visits per plot was not sufficient (i.e., rice fields) or well-suited (forested habitats) to detect them in this study (compare Veith et al. 2004). The latter is also indicated by the variations of our estimated sampling efficiency. These other species which we did not detect are generally very rare (*Sclerophrys taiensis*), are only active through very particular conditions (i.e., the largest

rains of the season: *Afrixalus vibekensis*), or need rare and hard-to-find micro-habitats (*Acanthixalus sonjae* in huge water-filled tree holes; compare the publications cited in the Introduction). However, the possibility that these species were missed in our study plots does not contradict our general conclusions. As almost all of the species which we could not detect are forest species or even forest specialists, the converse relationship between species richness and habitat degradation might actually be even larger than that documented in our study.

Conclusions

Our findings on the capacity (i.e., the very limited capacity) of agroforestry systems for the maintenance of anuran diversity has important implications for rainforest conservation in Côte d'Ivoire and the Upper Guinea forest zone. Our study showed that the conversion of forest to agroforestry systems significantly reduced species richness, in particular for the forest specialists. However, this study also showed that some of the more "forest-like" agroforestry systems, namely mixed coffee/cocoa plantations with shade trees, have some capacity to provide habitat for forest anuran communities, although largely pauperized. Several agroforestry systems established in the TNP area, e.g., vegetable gardens, oil palm and banana plantations, or mixed cultivations, have not been studied, so further research at such sites may improve our understanding of the potential for certain agroforestry systems in the maintenance of biodiversity. However, our study results, in combination with the results revealed by Ernst and Rödel (2005) and Kpan et al. (2021), show that the amphibian assemblages in formerly logged areas did not match those in old growth forest even 45 years after selective logging ceased. This clearly indicates that in order to conserve the huge diversity of specialist and range-restricted West African forest anurans, the remaining areas of pristine forests need to be maintained untouched.

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Appendix 1. List of sampled plots with their positions in the Taï area. For 'Sectors,' compare Fig. 1 and GPS position in WGS 84; 'Status' gives the habitat status; for 'Dates,' all survey dates are in 2018; and 'Habitats' gives short habitat descriptions and the habitat type of each plot (PF: primary forest; DF: degraded forest; CP: mosaic of coffee and cocoa plantations; RP: rubber plantation; RF: rice field).

Sector	Status	Dates	Latitude (N)	Longitude (W)	Habitats
ADK/V6	National Park	18 May, 20 August	06°11'45.3"	07°06'07.6"	Primary forest, stream (PF)
		19 May, 21 August	06°09'43"	07°17'59"	Primary forest (drier than others; i.e., no swamps) (PF)
		20 May, 22 August	06°06'22"	07°19'15"	Primary forest, stream (PF)
		21 May, 23 August	06°14'29"	07°13'32"	Degraded forest, lake (DF)
		22 May, 24 August	05°57'30"	06°55'50"	Primary forest (drier than others; i.e., no swamps) (PF)
	Agricultural system	12 May, 10 August	06°11'58.8"	07°04'39.6"	Rice field, river, grassland (RF)
		13 May, 10 August	06°12'44.4"	07°03'17.1"	Rice field, river, grassland (RF)
		14 May, 11 August	05°57'40"	06°55'36"	Cocoa/coffee plantation (CP)
Djapadji	National Park	12 June, 6 October	05°28'22.0"	06°55'06.8"	Primary forest (PF)
	Agricultural system	14 June, 9 October	05°29'06.2"	06°53'58.6"	Cocoa and rubber plantation (CP/RP)
		15 June, 10 October	05°10'06.2"	06°48'26.1"	Rice field, river, grassland (RF)
Djouroutou	National Park	20 June, 15 October	05°27'41.7"	07°13'03.3"	Primary forest, stream (PF)
		22 June, 16 October	05°32'10.0"	07°06'41.3"	Primary forest, stream (PF)
	Agricultural system	25 June, 20 October	05°23'28.8"	07°15'03.9"	Rice field, river, grassland (RF)
		26 June, 21 October	05°15'34.7"	07°19'18.3"	Rice field, river, grassland (RF)
Soubré	National Park	2 July, 28 September	05°50'48.5"	06°56'33.1"	Primary forest, stream (PF)
		1 July, 27 September	05°44'53.0"	06°56'52.0"	Primary forest, stream (PF)
		30 June, 26 September	05°38'52.0"	06°59'42.8"	Primary forest (drier than others; i.e., no swamps) (PF)
		29 June, 25 September	05°49'51.0"	06°56'32.0"	Primary forest (drier than others; i.e., no swamps) (PF)
		28 June, 24 September	05°53'41.0"	07°06'46.0"	Primary forest, stream (PF)
		27 June, 23 September	05°42'37.0"	06°58'30.0"	Primary forest, stream (PF)
		26 June, 22 September	05°36'04.9"	07°02'55.5"	Degraded forest, stream (DF)
	Agricultural system	28 May, 2 August	05°42'39.2"	06°53'14.1"	Cocoa/coffee plantation (CP)
		29 May, 3 August	05°36'45.1"	06°56'15.1"	Rubber plantation (RP)
Taï	National Park	4 June, 7 September	05°49'59.4"	07°20'32.7"	Degraded forest, buildings (DF)
		5 June, 9 September	05°50'04.7"	07°17'30.0"	Primary forest, stream (PF)
		6 June, 10 September	06°02'39.4"	07°24'46.1"	Primary forest, stream (PF)
		7 June, 11 September	06°03'40"	07°24'12"	Primary forest, stream (PF)
		8 June, 12 September	06°04'55.9"	07°27'12.6"	Primary forest (drier than others; i.e., no swamps) (PF)
	Agricultural system	21 June, 15 September	05°54'28.4"	07°25'43.4"	Rice field, river, grassland (RF)
		21 June, 28 September	05°52'32.23"	07°27'11.26"	Rice field, river, grassland (RF)
		15 June, 17 September	06°03'44.9"	07°25'46.8"	Cocoa/coffee plantation (CP)