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Anthropogenic Effects on Amphibian Diversity and Habitat Similarity in the Yoko Forest Reserve, Democratic Republic of the Congo

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Abstract: Anthropogenic disturbance of natural environments has negative impacts on biodiversity. Amphibians are especially sensitive to deforestation, and there is a high rate of this phenomenon in the Democratic Republic of the Congo. We studied the effects of this modification of forest ecosystems on the diversity of amphibians in the Yoko Forest Reserve. During twenty-four field sampling campaigns organized over a period of twelve months, amphibians were collected from nocturnal surveys supported by three techniques: visual spotting using a headlamp, systematic searching of habitats and acoustic hearing of vocalizations. Twelve sampling sites were chosen, and three habitats were explored at each site. Of these three habitats, one is the undisturbed habitat (primary forest), and two are disturbed habitats (fallow and field). Amphibian abundance, species richness, diversity, evenness and density were compared between these two types of habitat. A total of 4443 amphibians in 10 families, 17 genera and 33 species were recorded throughout the study area. Abundance, species richness and relative density were significantly higher in non-disturbed habitats than in disturbed habitats. On the other hand, primary forest is less diverse than fallow, but not significantly. It is, however, significantly more diverse than the field. The undisturbed habitat is also characterized by lower evenness than the disturbed habitats, with which it shares low similarities. The species *Amnirana albolabris*, *Phrynobatrachus auritus*, *Leptopelis notatus*, *Leptopelis millsoni*, *Xenopus pygmaeus*, *Hyperolius platyceps*, *Leptopelis calcaratus*, *Leptopelis christyi*, *Leptopelis ocellatus*, *Arthroleptis tuberosus*, *Ptychadena perreti*, *Amietia nutti*, *Arthroleptis variabilis*, *Cardioglossa leucomystax*, *Phrynobatrachus perpalmatus* and *Chiromantis rufescens* were recognized, in order of importance, as primary forest indicators according to the results of this study. All these differences between the two habitat statuses (undisturbed and disturbed) confirm the negative effects of natural habitat alteration on forest amphibians.

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1. Introduction

Fragmented landscapes have an impact on amphibians [1], affecting not only species numbers and distribution but also connectivity between populations [2–5]. The local matrix could be hostile to forest amphibians and limits their dispersal to isolated fragments. This disadvantage is linked to the species' ecology, which thus makes them vulnerable to natural habitat disturbance [6,7].

Amphibians are key components in ecosystem processes [8–10]. Yet habitat modification and loss are the main causes of their extinction [11–15], which is occurring at an accelerating rate in several regions of the world [13,16]. The disturbance of forest habitats currently observed in Central Africa [17] is accompanied by a considerable impact on landscape structure [18]. This could also be the case for forest areas in the Democratic Republic of the Congo (DRC), particularly those in and around Kisangani [19], which are currently threatened by slash-and-burn agriculture and timber exploitation [20–24]. To better understand species–landscape relationships, it is essential to increase data collection across various faunal groups. It is in this context that the present study was carried out on amphibians in the Yoko Forest Reserve (YFRE), one of the forest blocks still more or less intact in the vicinity of Kisangani, despite the anthropic pressure to which the area's forest ecosystems are subject. Apart from the preliminary survey carried out at four stations in the DRC [25], studies of the anthropogenic effects on amphibians are still in their infancy in and around Kisangani. Thus, the present analysis draws on studies carried out on rodents in the Masako Forest Reserve, located northeast of the city of Kisangani [26–28] to understand the effects of natural habitat modification on the fauna in the Kisangani region. It compares amphibian diversity in three habitats: field, fallow and primary forest, the latter serving as a control habitat for understanding the anthropogenic effects on amphibians in the YFRE.

This study verifies the following hypotheses: (i) Given that habitat disturbance affects amphibians in various regions of the world [7,29–33], the anthropogenic activities in the YFRE could have an impact on the distribution of abundances and species richness between the habitats created. (ii) Considering the available results on amphibian diversity in the context of anthropogenic effects [10,25,34–38], abundance, species richness, diversity, evenness and relative density could be significantly higher in the primary forest from its stable ecological conditions than in the other two habitats, and higher in the fallow than in the field. (iii) Based on their supposedly different faunas, primary forest, fallow and field would show low similarities to each other. (iv) As documented at four sites in the DRC [25], of all the families represented in the YFRE, the Hyperoliidae family may contain the highest number of amphibians in the primary forest, while the Ptychadenidae and Dicroglossidae families are expected to provide higher abundances in field and fallow, respectively, based on the habitat conditions and ecological requirements of the species. (v) As anthropogenic effects in the YFRE remain localized, and as demonstrated by previous studies [36,39,40], it is possible that all the species present in the study area are of forest affinity and that none are indicative of disturbed environments despite the affinities that might be found there.

This study aimed to examine the response of amphibians to habitat conditions while assessing their roles as indicators of natural habitat disturbance in the YFRE. Specifically, this research tries to (i) understand the influence of habitat conditions on the distribution of amphibian abundance and species richness, (ii) compare these habitats from their faunas, (iii) determine the rate of similarity between these habitats, (iv) identify the most abundant family in each habitat type and (v) determine which species can be considered as indicators of levels of disturbance in forest habitats to define conservation strategies.

2. Materials and Methods

The YFRE is located near the equator, between 0°15′ and 0°20′ N and 25°14′ and 25°20′ E [41], on the road connecting Kisangani with Ubundu, in the Tshopo Province. It is characterized by an average annual temperature of 25 °C, an average annual rainfall of 1750 mm and by the absence of dry months [42]. Throughout the Kisangani region, rainfall throughout the year is interrupted by two sub-dry seasons. The long rainy season runs from September to December, and the short rainy season covers the months from March to June. On the other hand, the long sub-dry season extends through January and February, and the short sub-dry season covers July and August [43,44]. The hydrographic network is dominated by rivers, the most important of which are the Yoko and Biaro streams. They receive water from numerous small streams before discharging into the Congo River. The Yoko stream, which gave the studied reserve its name, flows from west to east, dividing the study zone into two blocks, north and south. Within each block, six sites were identified (Figure 1).

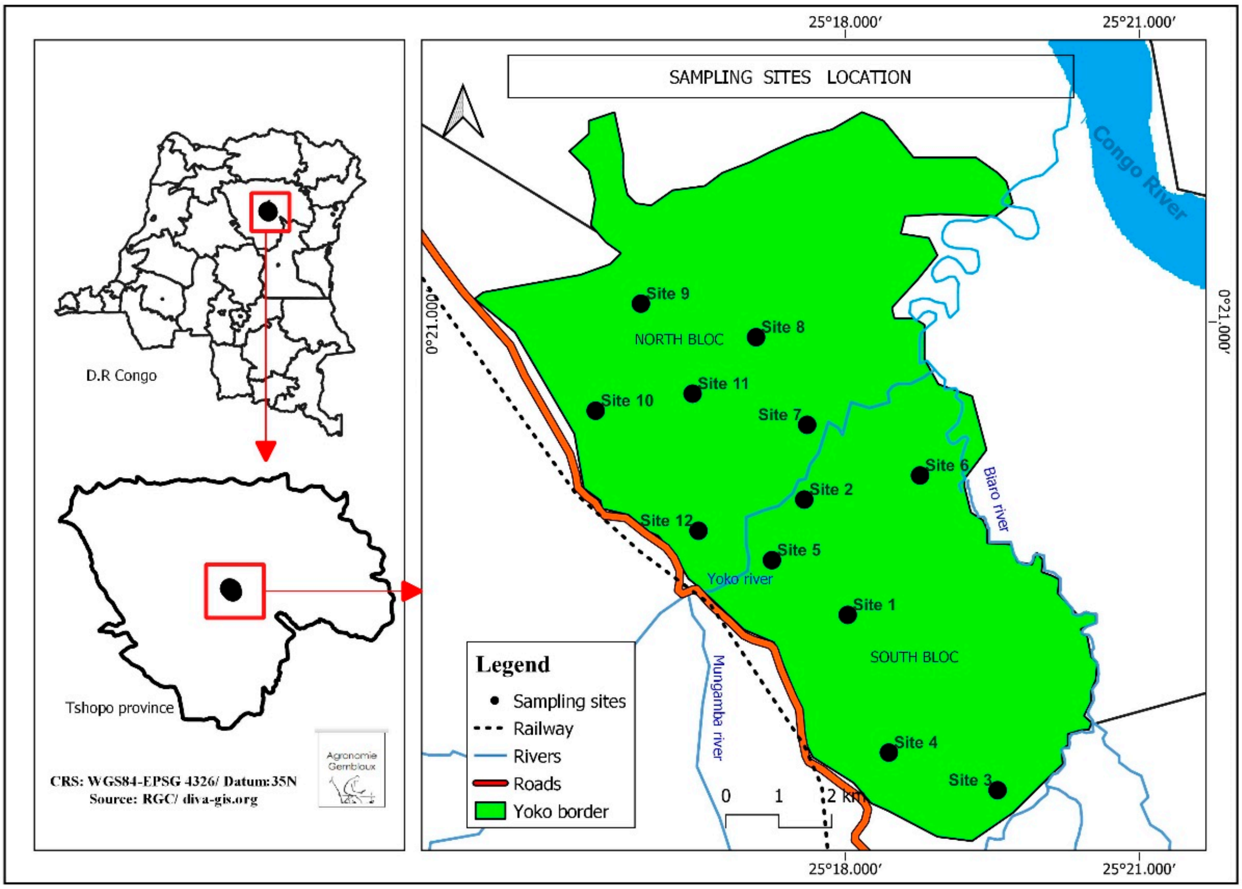

Figure 1. Location map of the sampling sites in the two blocks of the YFRE, Tshopo Province, DRC (data sources: RGC: https://www.rgc.cd, accessed on 14 October 2023).

According to their ecological characteristics relative to the degree of habitat disturbance as described in the literature [25,29,36,39,45], the exploited habitats in each site were categorized into undisturbed and disturbed. Thus, primary forest corresponds to the undisturbed stage, while field and fallow correspond to the disturbed stages, the former being more disturbed than the latter. Sampling was carried out in these three habitats, which characterize each of the twelve sites. However, the analyses did not focus on habitat categories (undisturbed and disturbed), but rather on the habitats themselves (primary forest, fallow and field).

Primary forest is dominated by *Trilepisium madagascariense* Dc. (Moraceae), *Uapaca guineensis* Mull. Arg., *Ricinodendron heudelotii* (Baillon) Pierre ex Heckel (Euphorbiaceae), *Vitex congolensis* De Wild. and Th. Dur. (Lamiaceae), *Milicia excelsa* (Welw.) C.C. Berg., *Scorodophloeus zenkeri* Harms, *Piptadeniastrum africanum* (Hooker f.) Brenan (Fabaceae), *Chrysophyllum pruniforme* Pierre ex Engler (Sapotaceae), *Cola griseiflora* De Wild., *C. acuminata* (P. Beauv.) Schott et Endl., *Sterculia tragacantha* Lindley (Malvaceae), *Anonidium mannii* (Oliver) Engler and Diels (Annonaceae), *Strombosia pustulata* Oliver (Strombosiaceae), *Panda oleosa* Pierre, *Microdesmis yafungana* J. Léonard (Pandaceae), *Turraeanthus africanus* (Welw.) Pellegr., *Carapa procera* DC, *Trichilia rubescens* Oliver, *T. gilgiana* Harms (Meliaceae), *Heisteria parviflora* Smith. (Olacaceae), *Aidia micrantha* (K. Schum.) F. White (Rubiaceae), *Mostuea batesii* Baker (Loganniaceae), *Rinorea* sp, *R. oblongifolia* (C.H. Wright) Marquand ex Chipp (Violaceae), *Campylospermum elongatum* (Oliver) Tieghem (Ochnaceae), *Afrostyrax lepidophyllum* Mildbr (Uaceae), *Megaphrynium macrostachyum* (Bentham) Milne-Redh, *Marantochloa mannii* (Bentham) Milne-Redh (Maranthaceae). Fallow is dominated by *Manniophyton fulvum* Mull. Arg., *Uapaca guinneensis* Mull. Arg., *Tetrorchidium didymostemon* (Baillon) Pax et Hoffm., *Macaranga monandra* Mull. Arg. (Euphorbiaceae), *Oncoba welwitschii* Oliver, *Barteria nigritiana* Hooker f. (Flacourtiaceae), *Zanthoxylum gilletii* (De Wild.) P.G Waterman (Rutaceae), *Triumfetta cordifolia* Guill., Perr. and A. Rich (Malvaceae), *Afromomum sangineum* K. Schum. (Zingiberaceae), *Pycnanthus angolensis* (Welw.) Exell (Myristicaceae), *Canarium schweinfurthii* Engler (Burseraceae), *Terminalia superba* Engler and Diels (Combretaceae), *Albizia gummifera* (J.f. Gmelin) C.A. SM (Fabaceae), *Pauridiantha callicarpoides* (Hiern) Bremek. (Rubiaceae), *Harungana madagascariensis* Lam. ex Poiret (Hypericaceae), *Ficus exasperata* Vahl., *F. mucuso* Welw. ex Ficalho and *Trilepisium madagascariense* DC. (Moraceae). The species *Oriza sativa* L., *Zea mays* L. (Poaceae), *Capsicum annuum* L., *Solanum melongena* L. (Solananceae), *Musa sp* (Musaceae), *Manihot esculenta* Crantz (Euphorbiaceae) and *Elaeis guineensis* Jacq (Arecaceae) are among the most dominant in the field. Orphaned primary forest species such as *Julbernardia seretii* (De Wild.) Troupin, *Pterocarpus soyauxii* Taub. (Fabaceae), *Pseudospondias microcarpa* (A. Rich.) Engler (Anacardiaceae), *Ricinodendron heudelotii* (Baillon) Pierre ex Heckel (Euphorbiaceae), *Schotia biquaertii* (De Wild), *Petersianthus macrophylla* (P. Beauv.) Liben (Lecythidaceae), *Khaya anthotheca* Dc. (Meliaceae), *Nesogordonia kabingaensis* (K. Schum.) Capuron (Malvaceae), *Margaritaria discoidea* (Baillon) and Webster (Phyllanthaceae) are also recorded in the field.

This study covered 4443 amphibians, all belonging to the Anura order and divided into 10 families, 17 genera and 33 species (Table 1).

Amphibians were collected according to the method and techniques previously described [46], which deals with the diversity and endemism of amphibians in the YFRE. Two teams, each comprising four researchers, were hired to collect data simultaneously over a period of twelve months, i.e., one hundred and forty-four capture nights. The two teams worked simultaneously in the two blocks, visiting six sites in each block, for six days per mission for each team. Two missions were organized per month, so that each habitat in each site was sampled twice each month by one team during the twelve months of data collection. Thus, each site, through each of its habitats, was visited twenty-four times by four researchers, for a total of twenty-four effective capture nights per site. For the twelve sites, this would be equivalent to two hundred and eighty-eight effective capture nights. As both teams worked simultaneously, this reduced the number of trap nights to one hundred and forty-four for the whole study area, giving a sampling effort of 1152 person-nights.

Amphibian abundances are the numbers of individuals caught per habitat, family or species [47], while species richness corresponds to the number of species present in the habitats exploited [47,48]. Based on the data collected, we expect abundance and species richness to vary between sites across the habitats that characterize them. We also expect the values of these indices to be higher in primary forest than in the other two habitats, and also higher in the fallow than in the field. The Shannon–Wiener diversity index (Equation (1)) was used to assess amphibian diversity in each habitat. This ecological measure quantifies and compares diversity expressed in biologically interpretable units translating the effective number of species [48–50].

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \tag{1}$$

where H' is the Shannon index and p_i is the proportion of individuals of species i ($p_i = n_i/Nn_i$ equals the number of individuals of species i and N is the total number of individuals collected). Given that ecological conditions are stable in primary forest, we expect this habitat to be characterized by higher diversity than fallow and field. So, to assess how individuals are distributed between species within habitats, we used Pielou's evenness [51], the value of which is obtained by Relationship (2).

$$J = \frac{H'}{H_{max}} = \frac{H'}{\text{lnS}} \tag{2}$$

where J corresponds to Pielou's evenness, H' translates the Shannon–Wiener index or real diversity and H_{max} is the maximum diversity. Considering the conditions of variation of the results of this index, we expect to obtain a value close to 1 in the primary forest, in contrast to the values close to 0 expected in the fallow and in the field. Using Relationship (3) developed in [52], we calculated relative densities as the number of individuals per unit area to see whether or not amphibian numbers per hectare are the same in all the habitats characterizing our study area.

$$T(\%) = \frac{N}{(n \times t)} \times 100 \tag{3}$$

where T (%) is the relative density (the number of individuals per hectare), N is the number of individuals captured in the habitat, n is the number of collectors and t is the number of effective capture nights.

Using data from the three habitats with n_1, n_2 and n_3 elements, respectively, their respective averages a_1, a_2 and a_3 were calculated between the twelve capture sites for each habitat, the sites being taken as replicates. However, the data are not matched, as only new individuals were considered during capture and marked before release. Thus, the Kruskal–Wallis test was applied to examine whether there were significant differences between habitats about the calculated indices. This test was used because, apart from being independent, the samples did not follow the normal distribution. In fact, before performing the Kruskal–Wallis test, the Shapiro test was applied to check the normality of the data derived from the calculated parameters. All p-values were below 0.01. Whenever the Kruskal–Wallis test indicated significant differences, Dunn's test was applied to determine which habitats showed significant differences [53]. To examine whether or not amphibian faunas in exploited habitats are similar, we used two indices. The first is Sørensen's index (4), which is based on presence–absence [50], and the second is the so-called Bray–Curtis dissimilarity (5), which takes into account species abundances, placing much greater emphasis on double presences [50,54].

$$S_8 = \frac{2a}{2a + b + c} \tag{4}$$

where S_8 is Sørensen's similarity index, a is the number of species common to the habitats compared, and b and c correspond to the number of species present in only one of the two habitats.

$$D_{14} = \frac{\sum_{j=1}^{p} |y_{1j} - y_{2j}|}{\sum_{j=1}^{p} (y_{1j} + y_{2j})} = 1 - \frac{2W}{(A + B)} \tag{5}$$

where D_{14} is the Bray–Curtis dissimilarity (called *percentage difference*), and W is the sum of the minimum abundances of the different species (this minimum is defined as the abundance in the habitat where the species is rare). *A* and *B* are the sums of the abundances of all species in each of the two habitats considered. The choice of these two indices stems from the need to capture the impact of abundant species when comparing habitats. Since binary data are used to minimize this impact, the Bray–Curtis dissimilarity was used without any data transformation.

Table 1. Amphibian species recorded between December 2020 and November 2021 in three habitats in the YFRE (Democratic Republic of the Congo). N = abundance.

Family	Species	N
Arthroleptidae Mivart, 1869	*Arthroleptis variabilis* Matschie, 1893	17
	Arthroleptis tuberosus Anderson, 1905	28
	Leptopelis calcaratus Boulenger, 1906	30
	Leptopelis ocellatus Mocquard, 1902	60
	Leptopelis notatus Buchloz and Peters in Peters, 1875	263
	Leptopelis christyi Boulenger, 1912	283
	Leptopelis millsoni Boulenger, 1895	174
	Cardioglossa leucomystax Boulenger, 1903	48
Bufonidae Gray, 1825	*Sclerophrys gutturalis* Power, 1927	9
	Sclerophrys pusilla Mertens, 1937	78
	Sclerophrys gracilipes Boulenger, 1899	17
	Nectophryne batesii Boulenger, 1913	4
Dicroglossidae Anderson, 1871	*Hoplobatrachus occipitalis* Günther, 1858	7
Hyperoliidae Laurent, 1943	*Hylambates verrucosus* Boulenger, 1912	55
	Afrixalus quadrivittatus Werner, 1908	15
	Afrixalus osorioi Ferreira, 1906	39
	Afrixalus equatorialis Laurent, 1941	3
	Hyperolius ocellatus Günther, 1858	12
	Hyperolius platyceps Boulenger, 1900	147
	Hyperolius langi Noble, 1924	12
	Hyperolius parallelus Günther, 1858	7
	Hyperolius sp.	8
	Cryptothylax greshoffi Schilthuis, 1889	6
	Kassina maculosa Sternfeld, 1917	1
Phrynobatrachidae Laurent, 1941	*Phrynobatrachus auritus* Boulenger, 1900	694
	Phrynobatrachus perpalmatus Boulenger, 1898	16
Pipidae Gray, 1825	*Xenopus pygmaeus* Loumont, 1986	41
Ptychadenidae Dubois, 1987	*Ptychadena christyi* Boulenger, 1919	126
	Ptychadena perreti Guibe and Lamotte, 1958	86
	Ptychadena mascareniensis Duméril and Bibron, 1841	145
Pyxicephalidae Bonaparte, 1850	*Amietia nutti* Boulenger, 1896	26
Ranidae Rafinesque, 1814	*Amnirana albolabris* Hallowel, 1856	1857
Rhacophoridae Hoffman, 1932	*Chiromantis rufescens* Günther, 1869	129
10 families	**33 species**	**4443**

Of all the families present in the study area, we expect the Hyperoliidae to score highly in primary forest, compared with the Ptychadenidae and Dicroglossidae, which are expected to be very abundant in the field and fallow, respectively. To do this, we used bar plots showing the occurrences of individuals from each family in each habitat. Despite the degree of habitat disturbance, we expect the species present in the YFRE to be all forest species. Thus, indicator value indices (6) were used to determine this association of species with habitats. These indices are components that can be interpreted as probabilities [55,56] and are potentially unique for each species [57]. The indicator value index for each species i in each habitat group j is the product of the two components noted A_{ij} and B_{ij} [55,57]. The component A_{ij} is the ratio between the average number of individuals of species i in habitat group j and the sum of the average numbers of individuals of species i in all habitats. This conditional probability is called the specificity or positive predictive value of the species as an indicator of the habitat group. The component B_{ij} corresponds to the frequency of occurrence of species i in habitat group j. This second conditional probability is called the species' fidelity or sensitivity as an indicator of the habitat group exploited [50]:

$$IndVal_{ij} = A_{ij} \times B_{ij} \tag{6}$$

where $IndVal_{ij}$ is the indicator value for species i in habitat group j, A_{ij} is the measure of specificity and B_{ij} is the measure of fidelity. Thus:

$$A_{ij} = N\ individuals_{ij} / N\ individuals_{i};$$
$$B_{ij} = N\ habitats_{ij} / N\ habitats_{j}$$

For A_{ij}, $N\ individuals_{ij}$ is the average number of individuals of species i in habitat group j, while $N\ individuals_{i}$ is the sum of the average numbers of individuals of species i in all habitats. A_{ij} is maximal when species i is present only in habitat group j. For B_{ij}, $N\ habitats_{ij}$ is the number of sampling sites in habitat j where species i is present, while $N\ habitats_{j}$ is the total number of sampling sites in habitat j. B_{ij} is maximal when species i is present in all sampling sites of habitat j. The indicator value is multiplied by 100 and expressed as a percentage. To complete the analysis of species–habitat association rates, network analysis was carried out [58]. This analysis enables us to understand the various interactions within the YFRE. Field data were processed in Excel 2016. All analyses were performed using R.4.3.1 software (through RStudio 2023.12.1 + 402) [59]. Abundance, species richness, the Shannon–Wiener diversity index and Pielou's evenness per habitat were calculated using the "diversityresult" function in the "BiodiversityR 2.15-3" package [60]. Amphibian density in habitats was estimated using Equation (3). The means and standard deviations presented in Table 2 were calculated using the "aggregate" function in "Stats". Boxplots showing variation in abundance and specific richness by habitat, barplots illustrating the occurrence of individuals from different families by habitat and barplots illustrating the relative frequency of each species in each habitat were produced using the "ggplot" function in the "ggplot2 3.4.3" package [61]. The relative frequencies of species by habitat were displayed using the "ggstats 0.7.0" package [62]. For boxplots, the two graphs were put together using the "ggarrance" function from the "ggpubr 0.6.0" package [63]. Dissimilarities between habitats (Sørensen and Bray–Curtis) were calculated using the "vegdist" function in the "Vegan 2.6.4" package [64], a function that always provides dissimilarity [65]. Normality tests were performed using the "Shapiro.test" function, while the Kruskal–Wallis test was performed using the "kruskal.test" function, both functions coming from the "Stats" package, a default package in R. Dunn's test, meanwhile, was applied using the "dunn_test" function from the "rstatix 0.7.2" package [66]. Indices of indicator values were calculated using the "indval" function in the "labdsv 2.1-0" package [67], retaining only those species with an adjusted p-value less than or equal to 0.05. Bonferoni's correction method was used to adjust p-values. Network analysis was performed using the "bipartite 2.18" package [68].

Table 2. Comparison of abundance (N), species richness (S), Shannon–Wiener diversity (H'), Pielou's evenness (J) and relative density (individuals/ha: T (%)) between habitats. The averages given are those of the parameters calculated for all twelve sites for each habitat. Superscript letters *a*, *b* and *c* symbolize Dunn's test results. Values bearing the same letters are not statistically different, while differences were obtained between values bearing different letters.

Index		Field	Fallow	Primary Forest	Tests
N	Total	43	442	3958	*K = 30.98* *p-value < 0.001*
	Average	3.58 ± 3.73^{c}	36.83 ± 22.27^{b}	$329.\ 83 \pm 40.62^{a}$	
S	Total	6	27	32	*K = 30.4* *p-value < 0.001*
	Average	1.5 ± 0.91^{c}	11.08 ± 4.08^{b}	20.08 ± 3.23^{a}	
H'	Total	1.168	2.701	2.083	*K = 24.18* *p-value < 0.001*
	Average	0.4 ± 0.36^{b}	2.02 ± 0.39^{a}	1.86 ± 0.37^{a}	
J	Total	0.652	0.82	0.601	*K = 14.94,* *p-value < 0.001*
	Average	0.72 ± 0.42^{a}	0.87 ± 0.06^{a}	0.62 ± 0.11^{b}	
T (%)	Total	3.73	38.37	343.58	*K = 30.98* *p-value < 0.001*
	Average	3.73 ± 3.88^{c}	38.37 ± 23.2^{b}	343.58 ± 42.31^{a}	

3. Results

Based on the ecological conditions caused by agriculture in the study area, amphibian abundance and specific richness vary between sites across the habitats that characterize them (field, fallow and primary forest). Figure 2 shows these variations, confirming the first hypothesis of this study according to which the anthropogenic activities in the YFRE could have an impact on the distribution of abundances and species richness between habitats.

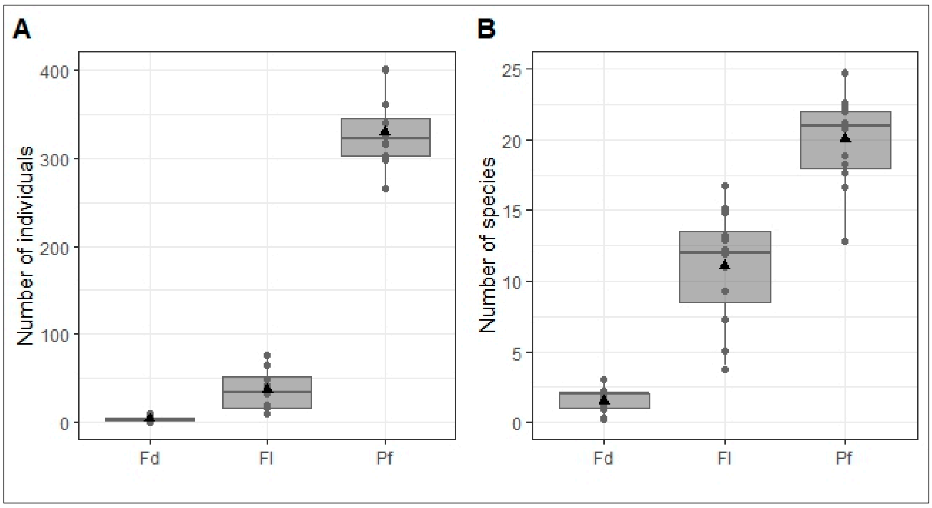

Figure 2. Distribution of amphibian abundance (**A**) and species richness (**B**) at twelve sites, each characterized by three habitats: field (Fd), fallow (Fl) and primary forest (Pf) in the YFRE. The abscissa represents the habitat, the ordinate number of individuals and the number of species, respectively. The points represent the values obtained per site, the triangles the mean values per habitat, and the vertical lines the standard deviations.

A total of 3958 (89.09%), 442 (9.94%) and 43 (0.97%) amphibians were collected in primary forest, fallow and field, respectively (Table 2), for a sampling effort of 1152 person-nights. Species richness was higher in primary forest (S = 32) than in fallow (S = 27) and field (S = 6). The same applies to density. The high diversity found in the fallow does not differ significantly from that obtained in the primary forest. Abundance, species richness and density were significantly higher in the primary forest than in the two disturbed habitats (fallow and field). On the other hand, its diversity was lower than that of the fallow, although significantly higher than that of the field. Primary forest has the lowest evenness of all habitats, and this is significant. These results partially confirm the second hypothesis of this study, according to which abundance, species richness, diversity, evenness and relative density could be significantly higher in the primary forest from its stable ecological conditions than in the other two habitats and higher in the fallow than in the field.

From the point of view of presence–absence occurrences, the primary forest shares only 26% similarity with the field, compared with 88% with the fallow (Table 3). Based on the abundance of amphibians in the habitats (Table 4), this similarity is 18% between primary forest and fallow, giving a dissimilarity of 82%. On the other hand, the similarity rate between primary forest and field is 1%, i.e., 99% dissimilarity. The fall in similarities between primary forest and fallow and between primary forest and field from the Sørensen index to the Bray–Curtis index shows the impact of the high abundance of individuals in the undisturbed habitat (primary forest) compared to the disturbed habitats (fallow and field). This confirms the third hypothesis of this study in terms of the specific composition between primary forest and fallow but invalidates the same hypothesis in terms of amphibian abundances, according to which primary forest, fallow and field would show low similarities to each other.

Table 3. Habitat similarities (based on Sørensen's index, S_8). Primary forest shares a high degree of similarity with fallow. On the other hand, the similarity is low between primary forest and field.

	Field	Fallow	Primary Forest
Field	1.00		
Fallow	0.36	1.00	
Primary forest	0.26	0.88	1.00

Table 4. Habitat similarities (based on Bray–Curtis dissimilarity, $1 - D_{14}$). Primary forest shares low similarities with the other two habitats (fallow and field).

	Field	Fallow	Primary Forest
Field	1.00		
Fallow	0.18	1.00	
Primary forest	0.01	0.18	1.00

The most abundance of amphibians collected in primary forests belongs to the Ranidae family, followed by Arthroleptidae, Phrynobatrachidae, Ptychadenidae and Hyperoliidae (Figure 3). Small numbers were provided by each of the other five families (Rhacophoridae, Pipidae, Bufonidae, Pyxicephalidae and Dicroglossidae). All these families except Pipidae and Pyxicephalidae are represented in the fallow but with almost the same abundance. These results invalidate the fourth hypothesis of this study, according to which, of all the families represented in the YFRE, the Hyperoliidae family may contain the highest number of amphibians in the primary forest, while the Ptychadenidae and Dicroglossidae families are expected to provide higher abundances in field and fallow, respectively. Ptychadenidae, Arthroleptidae and Bufonidae families are present in all habitats; Ranidae, Dicroglossidae, Phrynobatrachidae, Hyperoliidae and Rhacophoridae families live in primary forest and fallow. The Pipidae and Pyxicephalidae families are found only in the primary forest.

Based on the average numbers, frequencies and probabilities of species confirmed by the p-value were adjusted with the Bonferoni correction by multiplying by the number of tests rather than adjusting the significance level, typically 0.05 (Appendix A), *Amnirana albolabris*, *Phrynobatrachus auritus*, *Leptopelis notatus*, *Leptopelis millsoni*, *Xenopus pygmaeus*, *Hyperolius platyceps*, *Leptopelis calcaratus*, *Leptopelis christyi*, *Leptopelis ocellatus*, *Arthroleptis tuberosus*, *Ptychadena perreti*, *Amietia nutti*, *Arthroleptis variabilis*, *Cardioglossa leucomystax*, *Phrynobatrachus perpalmatus* and *Chiromantis rufescens* are, in order of importance, indicative of primary forest. No species is indicative of fallow or field. This means that the species exploiting these two habitats are forest species that adapt to their disturbance conditions. This trend is confirmed by the results of the network analyses (Figure 4a,b) and helps to confirm the fifth hypothesis of this study, according to which all the species present in the YFRE area are of forest affinity, and none are indicative of disturbed habitats despite the affinities that might be found. Two species, however, show particular behavior relating to an attachment to disturbed habitats. These are *Sclerophrys gutturalis* and *S. pusilla*, the former not being present in the undisturbed habitat (primary forest) and the latter being more abundant in the disturbed habitats (fallow and field) than in the undisturbed habitat (primary forest). However, the indicator values obtained in the fallow (*Sclerophrys gutturalis*: 22.2% with $p > 0.05$; *S. pusilla*: 46.1% with $p > 0.05$) and in the field (*Sclerophrys gutturalis*: 5.5% with $p > 0.05$; *S. pusilla*: 24.0% with $p > 0.05$) do not qualify these species as indicators of disturbed habitats.

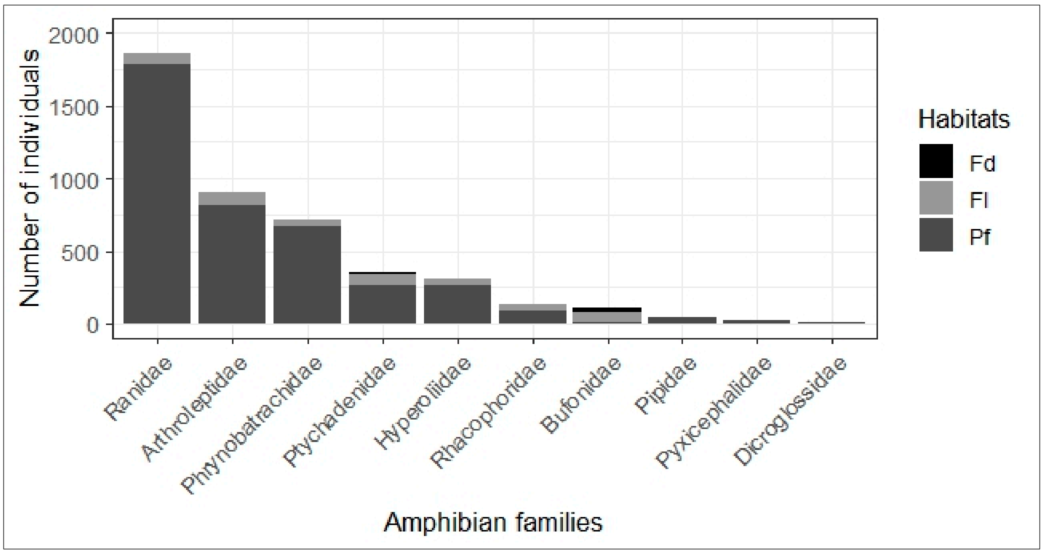

Figure 3. Amphibian abundance by family in logged habitats. The Ranidae, Arthroleptidae, Phrynobatrachidae, Ptychadenidae and Hyperoliidae families are, in descending order, most abundant in primary forest (Pf). On the other hand, Bufonidae family is most abundant in field (Fd) and fallow (Fl).

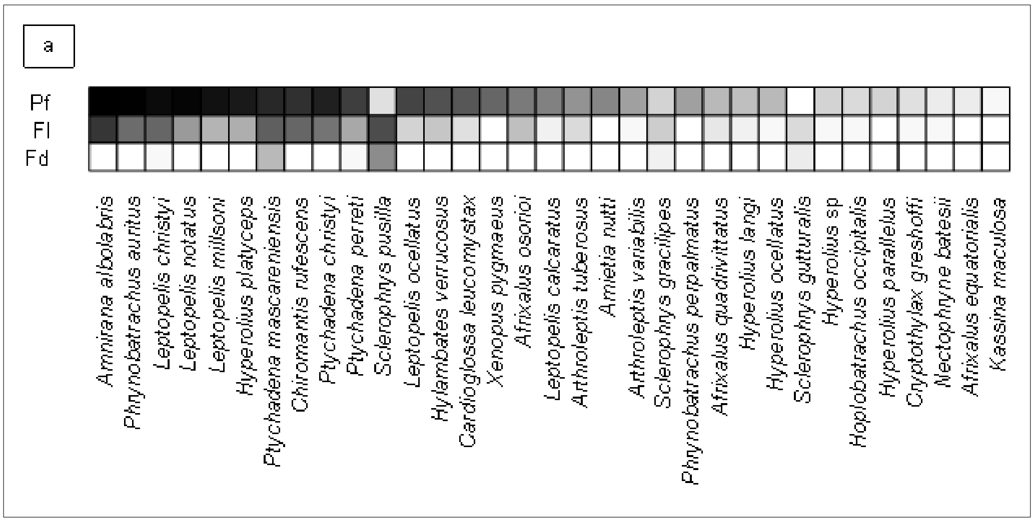

Figure 4. *Cont.*

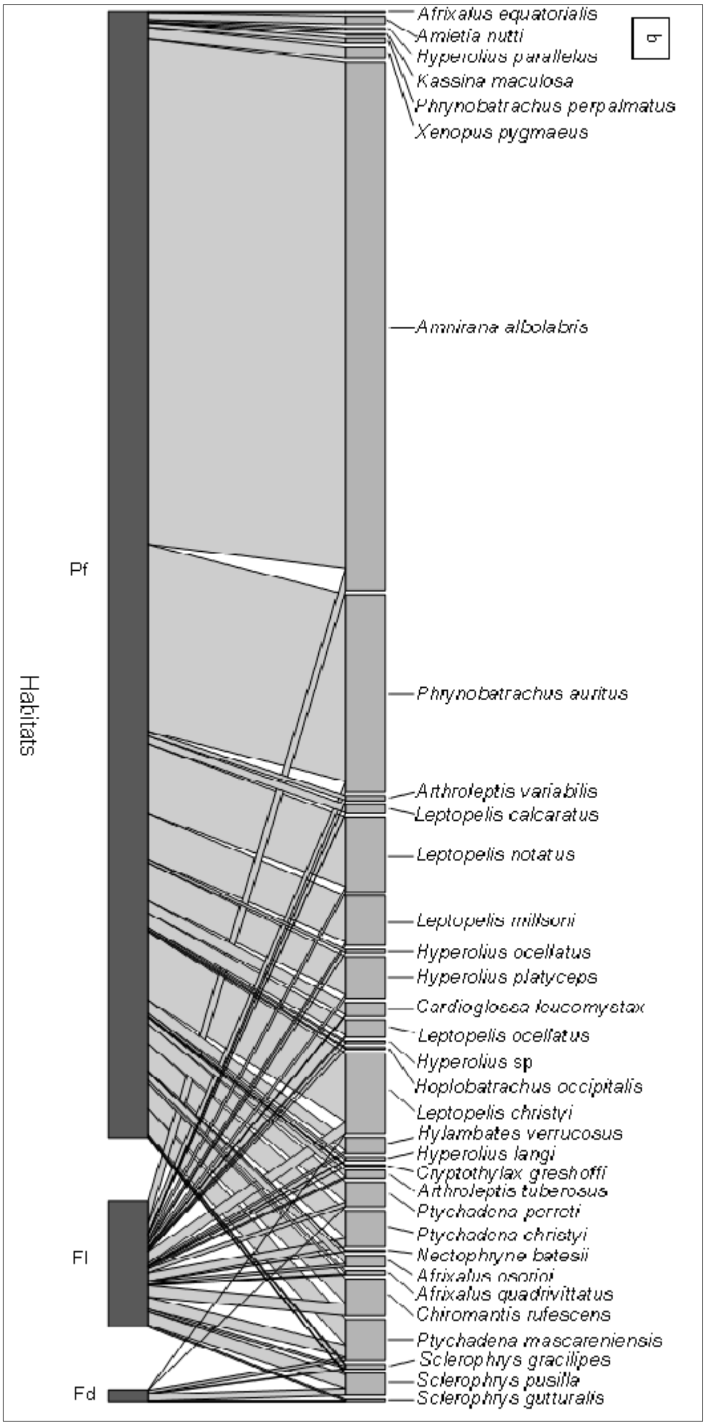

Figure 4. The network matrix (**a**) and its bipartite graph (**b**). The shading of the matrix entries indicates the number of observations. The sequence of species is shown in both network visualizations (line crossings).

4. Discussion

The presence of amphibians in exploited habitats can be seen as the result of the rate of habitat disturbance [31,69,70], which gives each habitat a particular status [25,71]. This modification affects the ecological and microclimatic factors of habitats, as well as the physiological conditions of amphibians. It generates adaptations in the latter, the degree of expression of which is specific to each species [34,36,72,73]. This study showed that the undisturbed habitat (primary forest) is richer in amphibians than the disturbed habitats (fallow and field). This result is confirmed by other studies carried out on amphibians [8,25,36,38].

The high abundance and species richness of amphibians in primary forests are thought to be linked to the high humidity, diversity of ecological niches, availability of food and canopy, all of which have positive effects on individual lifestyles [72,74]. Indeed, the diet of amphibians consists mainly of arthropods [10,75,76], of which *coleoptera* and *diptera* are very abundant in the litter of forest environments [77,78]. The primary forest within the YFRE combines all these conditions, making it favorable for amphibians.

Studies carried out have shown that, despite the colonization of disturbed habitats by amphibians, the species richness remains low in these habitats [6,13,25,34,39,69,70]. This low species richness of amphibians in disturbed habitats can be explained by the low biomass [79,80], responsible for the scarcity of prey for many species [81]. Added to this is the high degree of disturbance that characterizes these disturbed habitats [82]. The high diversity of amphibians in the fallow is thought to be the result of the habitat's high resilience to human activities [83–85] or its connectivity with the primary forest. As with rodents, the high diversity that characterizes fallow could be linked to the abundance of food resources that are specific to each of the species present [86]. These factors may be at the root of a better distribution of individuals between species within this habitat. In the context of this study, the high value of the diversity index in the fallow could also be the result of a better partition of species in this habitat than in the primary forest. The high diversity observed in the fallow contrasts with that observed in the field. Indeed, fallow is a vegetation state that tends towards the forest, unlike the field, which is a highly disturbed habitat. This creates the conditions necessary for forest species to survive in the fallow. Anthropogenic activities in the YFRE generally include slash-and-burn agriculture. The field is, therefore, a habitat where the original forest cover has been cut to make way for crops. On the other hand, fallow represents a habitat where agriculture has been stopped and forest dynamics have resumed through the establishment of woody forest species.

The low evenness in the primary forest could be the result of the high abundance in this habitat of the species *Amnirana albolabris* (n = 1778) and *Phrynobatrachus auritus* (n = 657), which together account for 61.5% of total species abundance in the primary forest, compared with 26.3% (n = 79 and 37) in the fallow and 0% in the field (n = 0 and 0). Figure 4 illustrates this situation.

One of the negative consequences of habitat disturbance is the modification of their conditions, which become favorable to predators because they favor the growth of their populations. For example, these habitats become very open, which increases the likelihood of amphibians being detected by their predators [30,87,88]. Habitat modification alters ecological processes, affects predator–prey relationships, and reduces amphibian density [30,89]. Beyond the consumption of arthropods and the cannibalism recognized in amphibians, the latter can also serve as prey for many other vertebrates [90]. As the abundance and density of amphibians are closely linked with those of their predators and prey, they maintain themselves in habitats through their trophic roles [10,91,92]. These trophic roles can influence the associations of amphibians with their habitats through the search for prey and shelter from predators.

The high similarity between primary forest and fallow (0.88), in terms of presence–absence occurrences, may be due to the connectivity between the two habitats, imposed by the shade of primary forest woody species. This facilitates amphibian mobility between the two habitats [34,64,74]. Using quantitative data, on the other hand, the Bray–Curtis index indicates a low similarity (0.18) between primary forest and fallow. This difference in results using presence–absence and quantitative data clearly indicates that the two habitats share most species but that the abundances of individuals per species between the two habitats are not at all close. In Masako Forest Reserve, a low similarity between these two habitats was found through rodents [27] using binary data. These differences in similarities between primary forest and fallow in Yoko and Masako Forest Reserves are thought to be a function of the ecological preferences of rodents, which differ profoundly from those of amphibians, and which may be associated with the indices used, but also with the ecological, microclimatic conditions of the habitats in the two Reserves.

According to the results of this study, the Ranidae family is most abundant in primary forests. These observations support previous findings [93] that reported the Ranidae species to be widely distributed in the forests and savannahs of eastern, central and western South Sahara in Africa. In contrast, the preliminary survey carried out previously [25] at four stations in the DRC showed that the Hyperoliidae family is more abundant in primary forests. In the YFRE, the Ranidae family is represented by a single species: *Amnirana albolabris*. Studies in other environments have shown that this species is largely confined to rainforest woodlands [94], where it inhabits cool, dark places near streams and springs [95]. As previously indicated [96], the high abundance of the species *Amnirana albolabris* in the primary forest within the YFRE may be justified by its distribution extending across sub-Saharan Africa and its ability to cross geographical barriers and forest refugia. The abundance of species in the Bufonidae family in disturbed habitats is justified by their tolerance of the conditions of these habitats [93,97], which confirms the observations made in the YFRE through three of the four species recorded.

Landscape quality is known to influence species distribution [4,5]. This makes it possible to estimate the importance of each habitat in the landscape [30,98] based on its vegetation, which conditions the presence of amphibians [13,70,99–101]. Examples include *Leptopelis notatus*, *Leptopelis calcaratus*, *Leptopelis millsoni*, *Leptopelis christyi*, *Leptopelis ocellatus* and *Amnirana albolabris*, which were frequently recorded on *Megaphrynium macrostachyum*, *Marantochloa mannii*, *Palisota ambigua* and *Palisota schweinfurthii*, some of the most dominant species of the herbaceous stratum in primary forest. The abundance of these plant species is positively correlated with that of the amphibians that use them [102].

Habitat conditions necessitate adaptations on amphibians [93,103,104] that allow us to distinguish between ubiquitous species, anthropophilous species and forest-dwelling species [105]. Silvicultural or primary forest specialist species are sensitive to the effects of forest change [32,106]. This may be the case for *Afrixalus equatorialis* (n = 3), *Amietia nutti* (n = 26), *Hyperolius parallelus* (n = 7), *Kassina maculosa* (n = 1), *Phrynobatrachus perpalmatus* (n = 16) and *Xenopus pygmaeus* (n = 41), which can be considered as primary forest specialists as they have only been found in this habitat. Only a few species are "anthropophilous" or affiliated with disturbed habitats [31]. These include *Sclerophrys kisoloensis* and *Hoplobatrachus occipitalis* [25]. On the other hand, previous studies [39] do not recognize any amphibian species attached to this type of habitat. Similarly, in the YFRE, *H. occipitalis* was more abundant in the undisturbed habitat (primary forest, n = 6) than in the disturbed habitats (fallow and field, n = 1 and 0, respectively). According to previous studies [85], generalist species can exploit both undisturbed and disturbed habitats. In addition to the six species found only in primary forest, 21 species were found in both primary forest and fallow, while the *Sclerophrys gutturalis* was found only in the field and in fallow. *Leptopelis christyi*, *Ptychadena mascareniensis*, *P. perreti*, *Sclerophrys gracilipes* and *Sclerophrys pusilla* were found in all habitats. Of the 26 species present concomitantly in primary forest and at least one other habitat, 25 are more abundant in primary forest, with the exception of *Sclerophrys pusilla*, which is more abundant in fallow and field than in primary forest (Figure 5). As mentioned above, the six species found only in primary forest are likely to be threatened by the loss or transformation of forest habitats. The 21 species found only in primary forest and fallow show adaptation to low levels of disturbance, while the five species found in all habitats show good adaptation to anthropogenic disturbance of forest habitats. The 21 species found in primary forest and fallow can be considered forest generalists. However, as shown in Figure 5, the abundance of species in primary forest indicates that these species are primarily forest dwellers. Only the three species of the Sclerophrys genus show a strong adaptation to the modification of forest habitats. These species could be affiliated with disturbed habitats, particularly *Sclerophrys gutturalis*, which was absent from the primary forest.

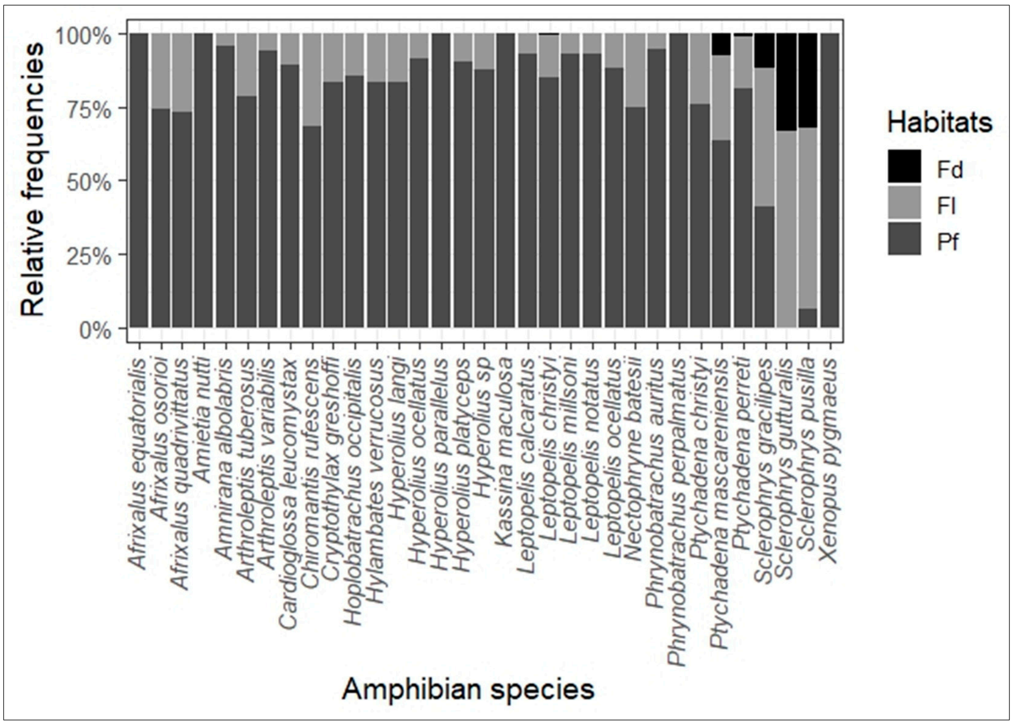

Figure 5. Relative frequencies of species in habitats within the YFRE. Each barplot represents the proportion of individuals of each species in each habitat.

Based on amphibian adaptations to habitat conditions, some species have developed special diets [78,107]. Others are opportunistic predators [108–110] whose abundance in habitats depends on available prey [107,111]. This gives amphibians the power to adapt to ever-changing habitats [110,112]. This is the case for *Sclerophrys pusilla* and all other species of the Bufonidae family (with the exception of *Nectophryne batesii* in this study, Figure 5), whose abundance in disturbed habitats is thought to be due to the abundance and diversity of their prey within these habitats [110,113,114]. The same applies to *Ptychadena mascareniensis*, which is recognized as anthropophilic [105,115]. This is contrary to this study, which shows that this species is more abundant in primary forests than in disturbed habitats. Our observations of *Chiromantis rufescens* and *Hylambates verrucosus* in primary forest at YFRE support their previous classification as forest species [97]. Their presence in disturbed habitats could be an adaptation to maintain their populations in the face of current pressure on amphibians. The absence of *Sclerophrys gutturalis* in the primary forest deserves particular attention. As the species is not exotic in the study area, its local distribution and increase in numbers can be caused by deforestation and agriculture, reflecting changes in the diversity structure. Additional data are needed to ensure that this is not a sampling deficit.

Modification of natural habitats leads to changes in biodiversity at all levels [36]. These changes can be assessed based on the indicator amphibian species for each habitat, the number of which can be linked to the degree of disturbance associated with each species' ecology and sampling effort. The loss of forest ecosystems hurts terrestrial and aquatic biotopes, altering vegetation and water quality, respectively [7,116,117]. The reduction in forested areas has negative effects on amphibians [118]. These effects can extend to adjacent habitats [119]. The adaptation of species to a wide variety of habitats may be a strategy that enables them to maintain their populations [31,120,121] thanks to the movement of individuals provided by corridors [122].

5. Conclusions

Anthropogenic disturbance of natural environments negatively affects amphibians through their abundance and species richness, which are significantly higher in primary forests than in fallow and fields. The same applies to their density, which decreases as one moves from undisturbed to disturbed habitats. On the other hand, the undisturbed habitat is less diverse than the fallow, although not significantly so, but significantly more diverse than the field. Significantly, of all the harvested habitats, the undisturbed habitat had the lowest evenness, which is a situation that may be mainly associated with the high abundance of the species *Amnirana albolabris* in this habitat. The differences in abundance, diversity, specific richness and density between primary forest, fallow and field confirm the clear effects of natural habitat modification on amphibians, which are also evident in the low similarities between the two habitat statuses. Based on amphibian adaptations to the ecological conditions of the habitats, the Ranidae family presents a good proportion of amphibians in the undisturbed habitat, where it is followed by Arthroleptidae, Phrynobatrachidae, Ptychadenidae and Hyperoliidae. Also, the presence of *Amnirana albolabris*, *Phrynobatrachus auritus*, *Leptopelis notatus*, *Leptopelis millsoni*, *Xenopus pygmaeus*, *Hyperolius platyceps*, *Leptopelis calcaratus*, *Leptopelis christyi*, *Leptopelis ocellatus*, *Arthroleptis tuberosus*, *Ptychadena perreti*, *Amietia nutti*, *Arthroleptis variabilis*, *Cardioglossa leucomystax*, *Phrynobatrachus perpalmatus* and *Chiromantis rufescens*) indicates undisturbed habitat. All species are present in the primary forest, with the exception of *Sclerophrys gutturalis*. However, six species (*Afrixalus equatorialis*, *Amietia nutti*, *Hyperolius parallelus*, *Kassina maculosa*, *Phrynobatrachus perpalmatus* and *Xenopus pygmaeus*) have only been found in primary forest; they have the temperament of primary forest specialists.

The present study has shown the effects of modification of natural habitats on amphibians through the differences observed between undisturbed and disturbed habitats in terms of their abundance, species richness, diversity, evenness and density. The sensitivity of fauna species to habitat modification and the interactions between native vegetation and species calls for the definition of management plans to identify appropriate conservation strategies for sensitive and vulnerable groups such as amphibians. These strategies are based on the landscape approach to biodiversity conservation within fragmented ecosystems. The ecological conditions of Kisangani's forests are constantly changing, primarily due to shifting cultivation. Integrating this type of agriculture into environmental decision-making at local and national levels will ensure its control while guaranteeing the health of ecosystems, which is justified by the need to maintain biodiversity that is currently under threat. Additional analysis is required to compare this study and previous studies, which may be associated with the local characteristics of the study area. We recommend that the analysis of changes in amphibian diversity, for example, after deforestation, requires repeating the study as it becomes overgrown.

Author Contributions: Conceptualization, L.M., J.B. and L.I.; methodology, L.M., L.I., J.-C.M. and A.M.; validation, L.I. and J.B.; investigation, L.M. and A.M.; supervision, L.I. and J.-C.M.; data curation, L.M. and J.M.; formal analysis, L.M., J.M. and M.D.; writing-original draft preparation, L.M.; writing-review and editing, J.B., L.I., J.-C.M., M.D. and J.M.; visualization, L.M. and J.M.; project administration, J.B. and L.I.; funding acquisition, J.B. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement: This study was not subject to ethical review and approval as the field data collection methodology used the live capture of animals. Captured animals were marked and released. This allows the population to be re-sampled later without any bias using the same method, which avoids the destruction of the animals and facilitates the maintenance of ecological processes within the habitats.

Data Availability Statement: The data provided are confidential and available upon request from Loving Musubaho and Jan Bogaert.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Species affinities with exploited habitats. Indicator values (IndVal) expressed as percentages and frequencies are confirmed by their adjusted *p*-values less than or equal to the 0.05 threshold. A_{ij} = measure of specificity and B_{ij} = measure of fidelity.

Espèce	Habitat	A_{ij}	B_{ij}	$IndVal_{ij}$	*p*-Value	Frequency
Amnirana albolabris	Primary forest	0.9575	1.0000	95.7458	0.0001	23
Phrynobatrachus auritus	Primary forest	0.9467	1.0000	94.6686	0.0001	21
Leptopelis notatus	Primary forest	0.9316	1.0000	93.1559	0.0001	19
Leptopelis millsoni	Primary forest	0.9310	1.0000	93.1034	0.0001	19
Xenopus pygmaeus	Primary forest	1.0000	0.9167	91.6667	0.0001	11
Hyperolius platyceps	Primary forest	0.9048	1.0000	90.4762	0.0001	20
Leptopelis calcaratus	Primary forest	0.9333	0.9167	85.5556	0.0001	13
Leptopelis christyi	Primary forest	0.8516	1.0000	85.1590	0.0001	22
Leptopelis ocellatus	Primary forest	0.8833	0.8333	73.6111	0.0001	14
Arthroleptis tuberosus	Primary forest	0.7857	0.9167	72.0238	0.0001	17
Ptychadena perreti	Primary forest	0.8140	0.8333	67.8295	0.0007	17
Amietia nutti	Primary forest	1.0000	0.6667	66.6667	0.0002	08
Arthroleptis variabilis	Primary forest	0.9412	0.6667	62.7451	0.0003	09
Cardioglossa leucomystax	Primary forest	0.8958	0.6667	59.7222	0.0003	12
Phrynobatrachus perpalmatus	Primary forest	1.0000	0.5833	58.3333	0.0001	07
Chiromantis rufescens	Primary forest	0.6822	0.8333	56.8475	0.0019	16

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