Diversity assessment of anurans in the Mugesera wetland (eastern Rwanda): impact of habitat disturbance and partial recovery

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Abstract. The Mugesera wetland, one of the key wetlands of Rwanda, has been subjected to substantial habitat alteration during the past decades. We studied the resulting impact on the anuran diversity, carrying out bioacoustic and visual surveys in six microhabitat types near Gashora for eight nights (three replicate surveys each) during the rainy season of 2018. The diel calling activity of anurans varied significantly between species and microhabitats. We detected twelve anuran species: *Afrixalus quadrivittatus, Amietia nutti, Hyperolius cinnamomeoventris, H. kivuensis, H. rwandae, H. viridiflavus, Kassina senegalensis, Phrynobatrachus kakamikro, P. natalensis, Ptychadena nilotica, Sclerophrys regularis*, and *Xenopus victorianus*. Except for the habitat specialist *H. cinnamomeoventris* all species are generalists, occupying all available microhabitat types independent of former or present degrees of disturbance. Partial regeneration of the natural vegetation (papyrus reed community) following massive human disturbance in the Mugesera wetland did not shift the species composition of local anurans towards that of a primary swamp community. Variation of local alpha-diversity followed closely the predictions of the Intermediate Disturbance Hypothesis. Hence, the Mugesera wetland currently constitutes a secondary papyrus swamp with an amphibian community indistinguishable from that of cultivated swamps.

Key words. Amphibia, Anura, bioacoustic, advertisement call activity, impact, degradation, wetlands renaturation, season, hour of the day, microhabitats.

Introduction

Amphibian populations are declining worldwide mostly due to complex interactions of pathogens, global climate change, overexploitation, and habitat alteration (Stuart et al. 2004, Hof et al. 2011). One of the key issues of global Amphibian conservation is therefore the identification of diversity hotspots (Myers et al. 2000, Vences & Köhler 2008, Perera et al. 2018). In Africa, the Albertine Rift region is one of the richest in vertebrate species diversity including amphibians and therefore a priority area for conservation (Plumptre et al. 2007). Rwanda forms part of the Albertine Rift region, harbouring a significant fraction of its biological diversity (Pomeroy 1993, Kanyamibwa 1998, Akinyemi 2017). Rwanda hosts 53 anuran and one caecilian species (Frost 2019), and six of them (five species of the *Hyperolius castaneus* group and *Boulengerula fischeri*) are currently considered endemic to the Albertine Rift (Nussbaum & Hinkel 1994; Dehling & Sinsch 2019). However, the Rift endemic *Callixalus pictus* Laurent, 1950 has not been collected for decades in Rwanda (Laurent 1950, Channing & Rödel 2019), illustrating the need for thorough surveys. Recent surveys yielded several species previously unknown to science (Dehling 2012, Channing et al. 2013, 2016). Reliable information on taxonomic delimitation of species and their geographical distributions is still absent for *Phrynobatrachus* and *Arthroleptis* and will probably further increase the known species richness of Rwanda. Identification of priority areas for amphibian conservation is additionally hampered by the fact that recent efforts to assess amphibian populations in Rwanda focused on a limited number of wetlands, most of which are intensively used for agriculture (Hölting et al. 2009, Roelke & Smith 2010, Sinsch et al. 2011, 2012, Dehling & Sinsch 2014, van der Hoek et al. 2019).

Afromontane wetlands provide a means of ecosystem services to humans mediated by a unique biological diversity not found elsewhere (Barbier et al. 1997, Rebelo et al. 2010). Amphibians are an important group within these ecosystems in that they reduce mosquito recruitment from ephemeral wetlands, and potentially control other pest species and predators of insect pollinators (Hocking & Babbitt 2014). Unfortunately, humans threaten the persistence of local amphibian populations of these wetlands by using fertilizers and pesticides for agriculture (Gardner 2001). In Rwanda, the increased demand for agricultural production has led to a policy of intensification of agriculture, e.g., by facilitating the growing of rice in key wetlands (Fischer et al. 2011, Nabahungu & Visser 2011, Nahayo et al. 2016, Karame et al. 2017). Impact on local amphibians is given little public regard in Rwanda due to local misconceptions and myths, and amphibian conservation draws as little attention as in many other countries (Ceríaco 2012).

In this study, we focused on the effects that human land use exerts on the anuran diversity of the Rweru-Mugesera Complex, an important RAMSAR site in Rwanda (Fischer et al. 2011). The specific study area within the Rweru-Mugesera Complex, the Mugesera wetland, is hydrologically part of the Nile Basin located on the southeastern plateau of Rwanda (Karame et al. 2017). It is subject to seasonal flooding and to simultaneous local crop and fish production, whereas some former agricultural areas are regenerating papyrus reed. Therefore, we found that amphibian-inhabited microhabitat types vary in their degrees of present and former disturbance through land use in the fringe area near Gashora, Rwanda. For the assessment of species presence and abundance in these microhabitat types, we chose the bioacoustic approach, i.e., standardised records of male anurans advertising in a given microhabitat complemented with visual species identification. This approach has been successfully applied to a diversity assessment in another Rwandan wetland near Huye (Sinsch et al. 2012). Aims of this study are: (1) to establish the presence and to assess the abundance of the local amphibian species inhabiting the Mugesera wetland, (2) to estimate the anuran diversity in six microhabitat types that represent a gradient of present human disturbance, (3) to compare the effect of former disturbance (baseline 2006) on present anuran diversity, and (4) to quantify statistically the effects of microhabitat, progress of the rainy period, and time of the day on the calling activity of local anurans.

Materials and methods
Study area

Species diversity and diel vocalisation activity of anurans were studied in the Mugesera wetland near Gashora, Bugesera District, Rwanda (2°12'34.1" N; 30°15'26.4" E, 1,330 m a.s.l.) from October to December, 2018 (Fig. 1). Average annual precipitation is 915 mm (832–1,000), minimum diel air temperature is about 16°C, and maximum temperatures may exceed 30°C in February and July-August (Prioul & Sirven 1981, GoR 2009, Karame et al. 2017). The study period fell within the rainy season, with up to 20 mm of daily rainfall and air temperatures of 17–22°C during the surveys (own measurements). The natural plant community is papyrus reed classified as *Cypero papyri-Dryopteridetum gongylodis* with *Cyperus papyrus* being dominant (Fischer et al. 2011). The wetland partly incorporates a widely undisturbed swamp area, and areas managed for fish and crop production and cattle grazing (GoR 2017, Karame et al. 2017). It has undergone considerable changes in land use during the past two decades. In 2006, extensive crop production dominated. In 2013, a dam was constructed, resulting in an artificial lake east of Gashora. In 2018, intensive crop and fish production characterised the area north of the road to Kibungo, whereas partial regeneration of the papyrus swamp has occurred south of the road dam (Fig. 1).

From the six microhabitat types, we chose eight sampling areas, representing a disturbance gradient from the regenerated papyrus swamp edge to the man-made dammed-up lake used for farming fish (Fig. 1). The sampling areas for surveying amphibians acoustically and visually were numbered from 1 to 6 in Figures 1 and 2. The edge of the papyrus swamp representing the most natural and most uniform microhabitat type was sampled at three sites
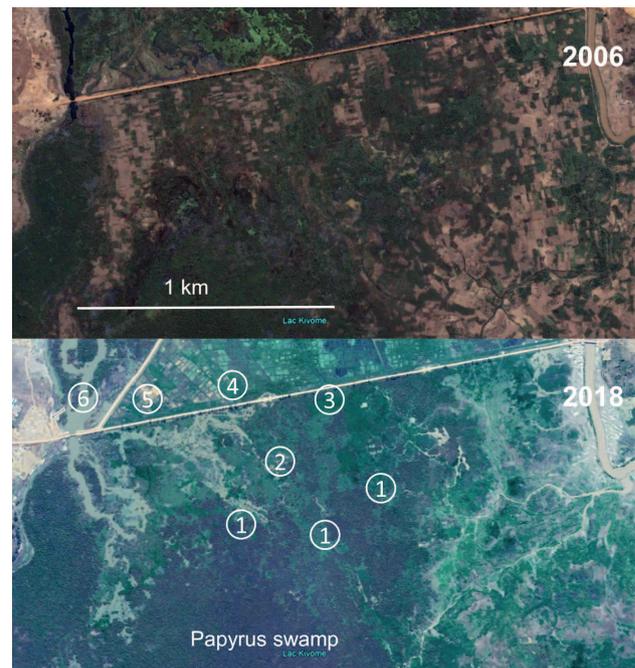

Figure 1. Aerial view of the study area during the dry season: Dark green areas = floating meadows of papyrus on the shore of Lac Kivome; small rectangles = fields, transversal brown line = road from Gashora to Kibungo. White circles with numbers = focus microhabitats for bioacoustic surveys (for details see Material & Methods). Photographs modified from Google Earth images taken on 15 July 2006 and 10 July 2018, respectively, i.e., during the dry season with low water level.

about 200 m distant from each other, and the remaining microhabitat types at one site each. The rationale for sampling the edge of the papyrus swamp three times was that it constituted the most frequent microhabitat type available at short walking distances and thus allowed to test for with-in-microhabitat type variation of species richness within the time available for a survey. All microhabitats included an open water surface area each, ranging from small (< 1 m²) to large (lake) depending on habitat type and seasonal water level fluctuations (Fig. 2).
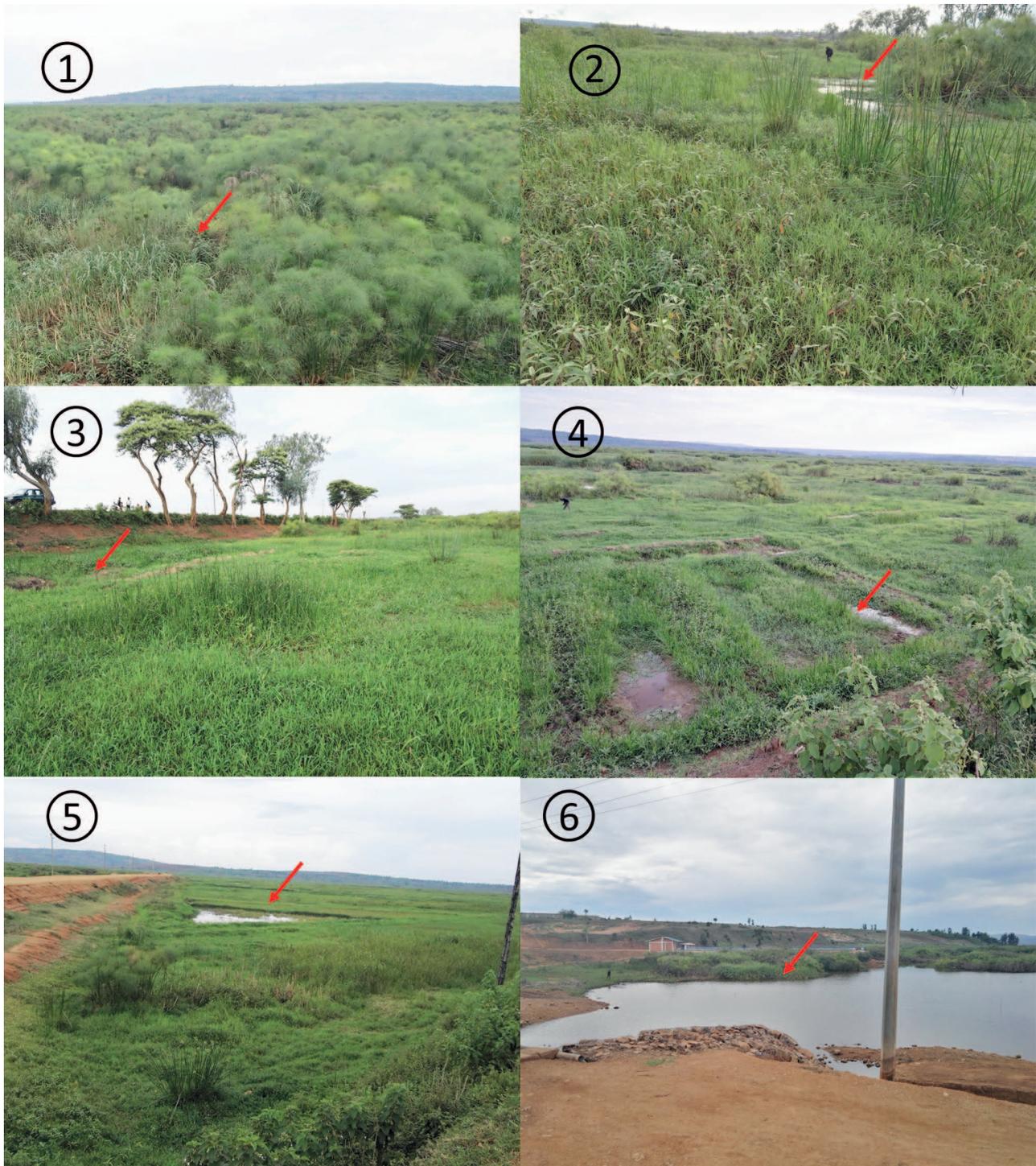

Figure 2. Microhabitat types (numbers refer to the locations in Fig. 1). Red arrows mark the monitoring sites within each microhabitat. The road dam separating the northern and the southern study areas is visible in photograph 3, the dam separating the lake from the northern study area is visible on the left hand side in photograph 5. All photographs taken on 18 October 2018 by U. Sinsch.

For the purpose of this study, we define disturbance as the degree of absence of papyrus cover, the natural vegetation cover of the Mugesera wetland, following the removal of papyrus for gaining areas for agricultural use. We scaled the present degree of disturbance (DD_{2018}) of a microhabitat from 1 (near natural, i.e., with 90–100% papyrus cover) to 6 (completely transformed, 0–5% of papyrus cover), with subjective intergrades to describe non-extreme microhabitats. Aerial photos of the same region from 2006 served to estimate disturbance scores (DD_{2006}) relative to 12 years before our study. Focus microhabitats and their disturbance histories were (Fig. 2): (1) edge of the papyrus swamp (three replicate sites, $DD_{2018} = 1$, $DD_{2006} = 2$), (2) southern swamp between the edge of the papyrus swamp and the road dam ($DD_{2018} = 3$, $DD_{2006} = 5$), (3) swamp at road dam ($DD_{2018} = 4$, $DD_{2006} = 4$), (4) northern semi-cultivated swamp ($DD_{2018} = 4$, $DD_{2006} = 3$), (5) shallow fishpond with banking vegetation ($DD_{2018} = 5$, $DD_{2006} = 3$), and (6) dammed-up deep lake with little to no vegetation on the steep banks ($DD_{2018} = 6$, $DD_{2006} = 1$).

Sampling, analysis and identification of anuran advertisement calls

Bioacoustic sampling was conducted during eight survey nights during the rainy season, i.e., on 26, 27 and 28 October, 20, 21 and 22 November, and on 16 and 17 December. The soundscape of each microhabitat was recorded always in the same order at 7, 8, and 9 pm, i.e., during the first three hours of darkness after sunset. The data set per focus microhabitat comprised 24 standardised recordings each.

Advertisement calls were recorded with a Sony PCM–D50 Linear PCM Recorder with stereo microphones, Sony Deutschland GmbH, Cologne. In each microhabitat, a motionless position was adopted for ca. 2 min, so that the local anurans could recover from the disturbance caused by our approach. Then, the recorder was turned on and slowly moved by 360 ° around the body axis for another 2 min to cover the whole microhabitat (Sinsch et al. 2011, 2012). Local air temperature was measured at the end of the recording period. Where possible, representative individuals of calling frogs were collected in the focus microhabitat, kept for up to three hours in moist plastic containers, identified based on external morphological features such as colour pattern, shape and size as per published keys for species identification (Schiøtz 1999, Channing & Howell 2006, Du Preez & Carruthers 2009), and then released *in situ*. Stereo recordings were converted to mono at a sampling rate of 44.1 kHz and resolution of 16 bits, and subsequently, sonograms and oscillograms were created in Adobe Audition 1.0. Sonograms and frequency analyses were obtained applying Blackman–Harris Fast Fourier transformation with a FFT size of 1024 Hz. Call structure was characterized by measuring call duration [ms], pulses per call, pulse rate [Hz], pulse duration [ms], interpulse interval [ms], and dominant frequency [Hz] (Sinsch et al. 2012, Köhler et al. 2017). Linking advertisement calls to species

identification required comparing call features with previous records and published data (e.g., Sinsch et al. 2012, Dehling & Sinsch 2014). The only species observed and identified exclusively by its morphology was *Xenopus victorianus*, because recording the underwater calls of *Xenopus* spp. would have required a hydrophone that was not available for this study (Tobias et al. 2011).

Call records were also used to distinguish between anurans calling in the focus microhabitats from those in the more distant surroundings of the focus microhabitat. The criterion adopted to identify callers in the microhabitat was to consider exclusively advertisement calls that had call intensities (amplitude in oscillogram) at least twice as loud as the level of background noise. Such calls showed in bright colours in the sonograms. These species were also detected visually during recording, corroborating their actual presence in the focus microhabitat. Advertisement calls from specimens calling at distances of at least 20 m from the recording spot were often assignable to species based on the sonogram features. However, sonogram representation typically showed pink in colour, indicating intensities within the range of the background noise. We are aware that some species call louder (e.g., *Sclerophrys regularis*) than others (e.g., *Amietia nutti*) and the detection of additional species in the surroundings may be biased towards the more loudly calling species. Therefore, the list of species in the surroundings may not include all species actually present.

Finally, we estimated the calling activity (= abundance) of each species in a given microhabitat as the number of calling individuals per 2 min of recording. Counts of advertisement calls per species confound call repetition rates (e.g., high in *Hyperolius viridiflavus*, low in *H. kivuensis*) with actual abundance. If few individuals per species call, it is possible to distinguish calls emitted by the same individual from those of conspecifics by comparing individual features such as dominant frequency (related to body size) and call amplitude (related to the distance of the caller from the microphone), among others. We were able to distinguish between up to five individual callers, but as some species advertise in choruses (e.g. *H. viridiflavus, H. rwandae*), we assigned choruses numerically to six individuals independent of the actual number of callers. The rationale for choosing this numerical value was that all choruses consisted at least of six individuals, whereas any higher number would not have been representative for all choruses.

Statistical analysis

Alpha- and beta-diversity values were computed using the statistical package EstimateS version 9.1.0 (Colwell & Elsensohn 2014). Alpha-diversity was quantified as species richness (local number of species) and as Shannon-Wiener Index (H'; local number and abundance of species). We used rarefaction analyses to obtain species accumulation curves. If species accumulation curves reached asymptotic values, our sampling effort was deemed suf-

Table 1. List of anuran species detected in the Mugesera wetland. The results of a previous inventory (Fischer et al. 2011) are also listed for reference. Note that taxonomic reassignments have led to several changes in the species names listed in Fischer et al. (2011).

Taxon	Detection method (this study, 2018)		Fischer et al. (2011)
	acoustic	visual	acoustic + visual
Bufonidae			
Sclerophrys regularis (Reuss, 1833)	+	–	+
Hyperoliidae			
Afrixalus quadrivittatus (Werner, 1908)	+	+	+
Hyperolius cinnamomeoventris Bocage, 1866	+	–	–
Hyperolius kivuensis Ahl, 1931	+	+	+
Hyperolius lateralis Laurent, 1940	–	–	+
Hyperolius rwandae Dehling et al., 2003	+	+	+
Hyperolius viridiflavus (Duméril & Bibron, 1841)	+	+	+
Kassina senegalensis (Duméril & Bibron, 1841)	+	+	+
Phrynobatrachidae			
Phrynobatrachus kakamikro Schick et al., 2010	+	–	+
Phrynobatrachus natalensis (Smith, 1849)	+	+	+
Pipidae			
Xenopus victorianus Ahl, 1924	–	+	+
Ptychadenidae			
Ptychadena anchietae (Bocage, 1868)	–	–	+
Ptychadena nilotica (Seetzen, 1855)	+	+	+
Ptychadena porosissima (Steindachner, 1867)	–	–	+
Pyxicephalidae			
Amietia nutti (Boulenger, 1896)	+	–	+

ficient to consider the number of observed species as being representative for the surveyed microhabitat type. To quantify the potential effect of changes in disturbance (CD = DD_{2018} - DD_{2006}), we tested for Spearman-rank correlations between CD and the alpha-diversity values. We chose the Bray-Curtis Dissimilarity Index to describe beta-diversity. We used ANCOVAs (Analysis of Covariance) to estimate the influences of microhabitat type, time of day (categorical fixed factors), and season, i.e., we related the date of record (continuous covariate) to the local numbers of species and individuals per species calling within a 2 minute-record. Analyses were run on raw data, because distributions did not deviate significantly from normality. To quantify the effect of season on the local number of species, we fitted a polynomial regression (2nd order) to data. Significance level was set at alpha = 0.05. All statistical procedures were performed using the program package Statgraphics Centurion version 18.1.01 (64-bit).

Results

We recorded the presence of twelve anuran species representative of six families in the Mugesera wetland (Table 1).

Seven species were detected bioacoustically and visually, four exclusively based on call records, and one exclusively visually (Table 1). With the exception of *Phrynobatrachus kakamikro*, which is classified as "data deficient", all these species are classified "least concern" in the red list of amphibians (IUCN 2019). Bioacoustic detection rates of species across 24 call records per microhabitat ranged from 90–100% in *Hyperolius kivuensis* and *H. viridiflavus* to less than 10% in *Amietia nutti, Ptychadena nilotica*, and *H. cinnamomeoventris*. We did not detect *H. lateralis, P. anchietae*, or *P. porosissima* that were reported from this wetland by Fischer et al. (2011), but found *H. cinnamomeoventris* as a new local record. *H. kivuensis* and *H. viridiflavus* called in all microhabitat types, whereas the remaining species used between one and four of the surveyed microhabitats (Table 2). *Sclerophrys regularis* was the only species that we never detected in any focus microhabitat, but these toads called from sites within the study area that were not surveyed. Overall, the number of additional species detected in the surroundings of the focus microhabitats was low, ranging from zero to four (Table 2). Note that the actual number of additional species might have been lowered by the limitations of the bioacoustic assessment method used (see Material & Methods).

Table 2. Presence (X) and detection rate (% presence in total number of call records) of anuran species in the six microhabitats surveyed in the Mugesera wetland (Figs 1, 2). We distinguish between species calling in the focus microhabitat (FM) and additional species calling only in the surrounding areas (SA). Microhabitats are ordered along the disturbance gradient, species alphabetically (for details see Material & Methods section). Species richness = number of species.

Microhabitat type	(1) Papyrus edge		(2) Southern swamp		(3) Swamp road dam		(4) Northern swamp		(5) Fishpond		(6) Dammed-up lake	
Species	FM	SA	FM	SA	FM	SA	FM	SM	FM	SM	FM	SM
Afrixalus quadrivittatus			X (29%)		X (38%)				X (21%)			
Amietia nutti	X (3%)		X (8%)		X (25%)					X	X (4%)	
Hyperolius cinnamomeoventris									X (8%)			
Hyperolius kivuensis	X (33%)		X (88%)		X (92%)		X (75%)		X (96%)		X (29%)	
Hyperolius rwandae							X (38%)		X (38%)		X (21%)	
Hyperolius viridiflavus	X (8%)		X (58%)		X (38%)		X (21%)		X (54%)		X (100%)	
Kassina senegalensis		X	X (8%)			X	X (25%)		X (29%)			X
Phrynobatrachus kakamikro			X (17%)		X (21%)				X (4%)		X (4%)	
Phyrnobatrachus natalensis		X						X	X (13%)			
Ptychadena nilotica		X					X (4%)		X (4%)		X (4%)	
Sclerophrys regularis		X						X		X		
Xenopus victorianus									X (visual)			
Species richness	3		6		5		5		10		6	
Shannon-Index H'	0.80		1.33		1.24		1.32		1.56		0.77	

Amphibian diversity along a disturbance gradient

Alpha-diversity in terms of species richness and the Shannon-Wiener Index varied considerably between the focus microhabitats surveyed (Table 2). Species accumulation curves reached the asymptote at each microhabitat surveyed (Fig. 3). The three recording sites at the edge of the papyrus swamp yielded similar estimates of species richness (2–3 species; Fig. 3). This microhabitat type had the lowest species richness and the shallow fishpond with abundant bank vegetation had the highest with 10 species. The lowest Shannon-Wiener Indices were found at the papyrus edge and the dammed-up lake (H': 00.8 and 0.77, respectively), whereas the maximum value was recorded at the fishpond (H': 1.56) (Table 2). The Bray-Curtis Dissimilarity Matrix grouped the local anuran communities into three clusters (Fig. 4). The first cluster consisted of the three microhabitats south of the road dam, the second one comprised the two microhabitats north of the road dam,

and outgroup to all was the dammed-up lake that was spatially separated by an additional dam from all other microhabitats (Figs 2, 4).

Plotting local alpha-diversity against the present-day disturbance gradient yielded an inverted u-shaped graph (Fig. 5). The communities at the extremes of the gradient, the near-natural papyrus swamp and the artificial dammed-up lake, respectively, had low numbers of species and minimal Shannon-Wiener values. In contrast, moderately disturbed microhabitats had greater species richness and Shannon-Wiener values. There was a considerable change in the disturbance scores (CD) between 2006 and 2018, e.g., the score of the dammed-up lake habitat deteriorated from 1 to 6, whereas that of the southern swamp improved from 6 to 3. Still, we did neither detect significant Spearman's rank correlations between CD and species richness ($r_{Spearman}$ = 0.4030; P = 0.3675) nor between CD and Shannon Index ($r_{Spearman}$ = -0.2319; P = 0.6041).

Variation of diel calling activity as per season and microhabitat

The number of species detected within a 2 minute-record did not differ significantly between the three hours per survey day (1-factor ANCOVA: $F_{2,138}$ = 1.77, P = 0.1736), but was significantly influenced by the recording date, i.e., by the progressing of the rainy season (1-factor ANCOVA: $F_{1,138}$ = 7.75, P = 0.0062). When the temporal variation of species richness during the rainy season was fitted with a polynomial regression ($F_{2,191}$ = 13.08, P < 0.0001; R^2 = 12.2%) it demonstrates an increase in advertising species in December (Fig. 6). However, detectable species composition changed as well, from *H. kivuensis, H. rwan-*

dae, H. viridiflavus, K. senegalensis, A. quadrivittatus, P. nilotica, and *A. nutti* in October to additionally *P. kakamikro, P. natalensis* and *H. cinnamomeoventris* later in the rainy season. Only four species advertised throughout the whole study period: *H. kivuensis, H. viridiflavus, K. senegalensis,* and *A. nutti.*

At species level, we analysed the calling activity of four species that were recorded at least during 20 of the 192 surveys. Calling activity increased from 7 to 9 pm in *H. kivuensis* (2-factor ANCOVA: $F_{2,116}$ = 9.14, P = 0.0002), decreased in *H. rwandae* (2-factor ANCOVA: $F_{1,22}$ = 16.17, P = 0.0001) and *A. quadrivittatus* (2-factor ANCOVA: $F_{1,20}$ = 5.58, P = 0.0154), and remained unchanged in *H. viridiflavus* (2-factor ANCOVA: $F_{2,68}$ = 1.05, P = 0.3553) (Fig. 7). The average
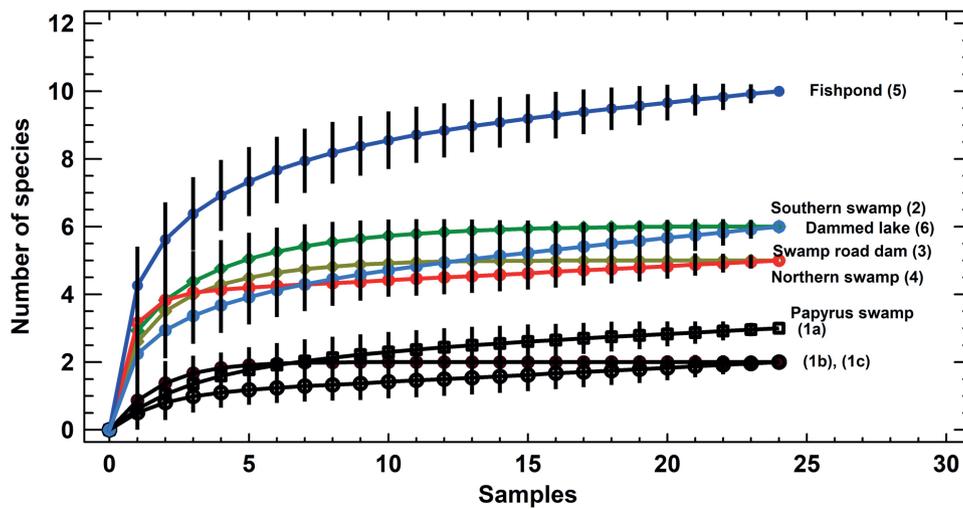

Figure 3. Rarefaction analysis of anuran species richness based on 24 combined visual and bioacoustic surveys. Symbols represent frequency estimates, and the vertical bars the corresponding standard deviations.
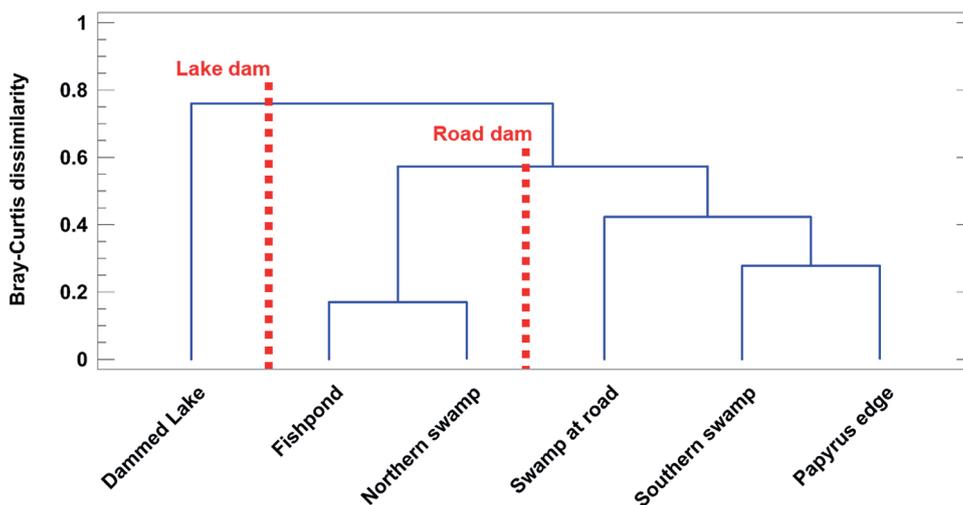

Figure 4. Cluster analysis (method: complete linkage) of Bray-Curtis dissimilarity scores between the anuran communities advertising in six focus microhabitats (for details see Table 2) of the Mugesera swamp. Red dotted lines indicate geographical barriers separating groups of microhabitats (see Fig. 1).

calling activity did not change significantly in any of these species between October and December (2-factor ANCOVA: P > 0.05). In contrast, variation of calling activity per microhabitat differed significantly in *H. kivuensis* (2-factor ANCOVA: $F_{5,116}$ = 8.98, P < 0.0001). The average number of calling individuals ranged from 3.7 ± 0.3 in the northern swamp and the fishpond to 1.4 ± 0.3 in the papyrus swamp and the dammed-up lake. In *H. viridiflavus*, between-habitat variation of calling activity was also significant (2-factor ANCOVA: $F_{5,68}$ = 7.88, P < 0.0001). At the dammed-up lake, we recorded exclusively choruses of many individuals, whereas only 2–3 individuals were found advertising in the record from the southern swamp near the road dam. The calling activities of *H. rwandae* and *A. quadrivittatus* did not differ significantly between the microhabitats used

(2-factor ANCOVA: Hr, $F_{1,22}$ = 0.91, P = 0.3545; Aq, $F_{1,20}$ = 0.69, P = 0.4189). However, *H. rwandae* called, with a few exceptions, in choruses of considerably more than five individuals, whereas most records of *A. quadrivittatus* included only one or two advertising individuals.

Discussion

Our study demonstrates that combined bioacoustic and visual surveys are a suitable tool for the diversity assessment of tropical anuran communities in grasslands (Hsu et al. 2006, Sinsch et al. 2012, Madalozzo et al. 2017). Puddle frogs, *Phrynobatrachus* spp., that usually stay hidden in the mud are easily detected by hearing and recording their
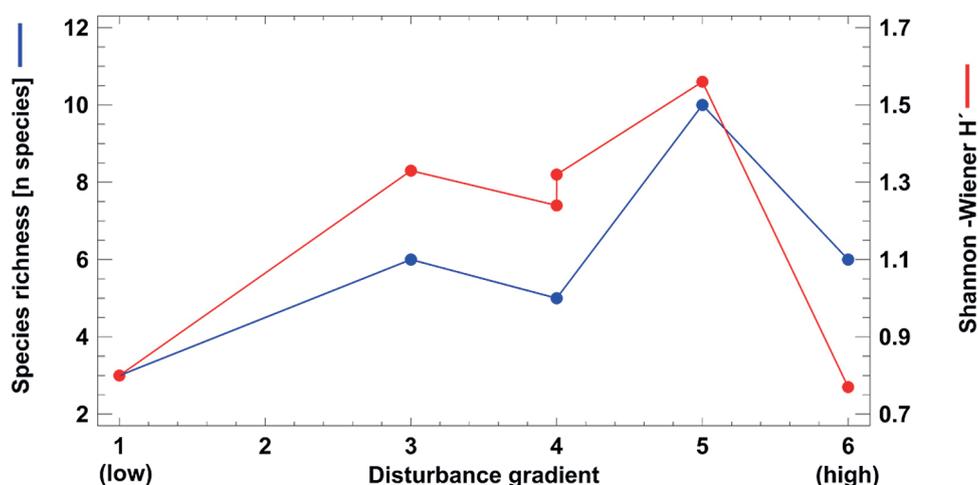

Figure 5. Effect of anthropogenic habitat disturbance on local amphibian diversity. Diversity is given as species richness (blue) and Shannon-Wiener H´ index (red). Each dot represents the anuran community of a focus microhabitat type (for details see text and Table 2).
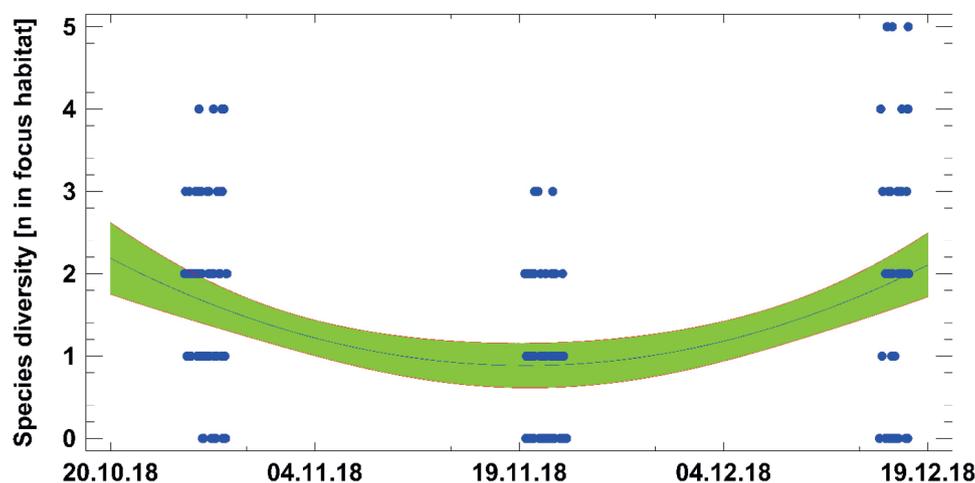

Figure 6. Seasonal variation of the number of species advertising simultaneously in the focus microhabitats. Each dot represents a single record per habitat. Dots are slightly jittered for visual distinction. Polynomial regression (n species = 887,561 - 70.55 × Date + 0.0014 × Date²) with corresponding 95% confidence interval (green area).

advertisement calls, even at relatively far distances. *Xenopus* spp., which call exclusively underwater, are detected by complementary visual observations. If temporal variation in calling activity is accounted for by replicates during several months of the rainy season, there is a good chance of registering almost all species present in the studied wetland. A similar study on the anuran community inhabiting the Huye wetland in Rwanda exemplifies the case (Sinsch et al. 2012). The initial data collection (2009–2010) included 15 bioacoustic and visual surveys, leading to the detection of 15 species. Follow-up surveys (2011–2018) yielded only two additional species (*Ptychadena uzungwensis*, *Sclerophrys kisoloensis*) that had been overlooked because they were present exclusively in a small section of the marais not visited before (Dehling pers. comm.).

Time of the day is an important factor influencing the calling activity in anuran communities (e.g., Bridges & Dorcas 2000, Oseen & Wassersug 2002, Hsu et al. 2006, Sinsch et al. 2012). Three replicate surveys during the early night hours offer a good chance not to miss a calling local species (Sinsch et al. 2012). Pronounced temporal variation of the acoustic community during the rainy season revealed that only a subset of local species starts calling and reproduction immediately after the onset of rains following the dry season. The need for a prolonged monitoring period is emphasized by the fact that *H. cinnamomeoventris* calls were restricted to the November survey, and those of *K. senegalensis*, *P. kakamikro*, and *P. natalensis* to December when heavy rainfalls occurred. It is not surprising that rainfall will stimulate anuran reproductive effort, leading to a pronounced change in the number of advertising spe-

cies in the rainy season (Oseen & Wassersug 2002, Hsu et al. 2006, Hirschfeld & Rödel 2011). In conclusion, we are confident that our survey strategy yielded a near-complete coverage of local anuran species in the Mugesera wetland.

Anuran species diversity in the Mugesera wetland

The present anuran diversity in the Mugesera wetland comprises 12 species, two less than encountered during a previous assessment by Fischer et al. (2011). Eleven species are represented in both inventories, all of them generalist species and common in heavily disturbed wetlands (Sinsch et al. 2012). Fischer et al. (2011) may have overlooked our only new local record, *H. cinnamomeoventris* due to the short seasonal activity period of these frogs in the Mugesera wetland. We failed to detect *H. lateralis*, which often co-occurs with *H. cinnamomeoventris*, but usually is restricted to near-natural reed habitats additionally including shrubs or trees. This type of habitat was not available in our study area, but in more distant parts of the Mugesera wetland where Fischer et al. (2011) recorded a single specimen (Dehling pers. comm.). We assume that the habitat specialist *H. lateralis* is not abundant in the area, possibly due to prolonged human disturbance. It may even have become locally extinct, because it is easily detected by its frequently repeated advertisement calls (Sinsch et al. 2012). We also failed to record *P. anchiatae* and *P. porosissima*, both of which are typically abundant in heavily disturbed habitats and absent from the pristine areas of Rwanda (Sinsch et al. 2012, Dehling & Sinsch
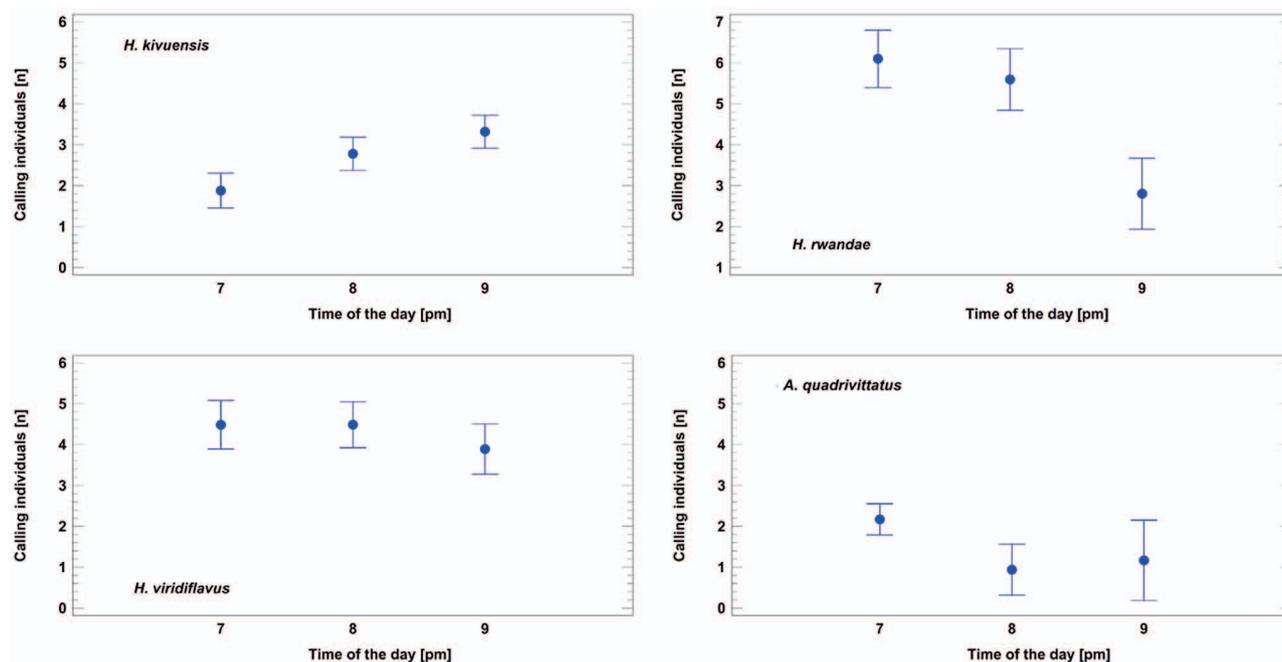

Figure 7. Diel variation of calling activity [number of calling individuals per 2 min] in species recorded during 21–117 surveys. Data are given as least square means and corresponding 95% confidence intervals.

2013). The low abundance of *P. nilotica* and the apparent absence of *P. anchiatae* and *P. porosissima* might be an effect of the expansion of areas with papyrus cover or due to imperfect bioacoustic detection. The calling behaviour of these *Ptychadena* spp. with their infrequent chorusing and low-amplitude calls is not suited to a standardised bioacoustic detection method with fixed periods of recording, but the few visual encounters with these conspicuous frogs are in agreement with supposing their low local abundance. Beyond doubt, *Ptychadena* spp. were considerably less abundant in the Mugesera wetland than in the marais of Huye, supporting the assumed effect of expanding papyrus swamp areas, which constitute unsuitable habitats for these frogs (Sinsch et al. 2012).

Actually, the anuran community of the Mugesera wetland near Gashora comprises mainly generalist species, indicating persistent effects of heavy human disturbance of this RAMSAR site. Exclusively the first record of a habitat specialist (*H. cinnamomeoventris*) and the low abundance of several generalist species (compared to the strongly altered Huye marais) may indicate on-going changes in species composition in response to the partial regeneration of the natural papyrus cover. A similar strong local site filter effect preventing the regeneration of natural communities was reported for secondary, but not for primary forests in Ivory Coast (Ernst & Rödel 2005). The partial regeneration of papyrus vegetation today induces the impression of a near-natural habitat, yet anuran species composition has not changed correspondingly and still resembles that of a heavily disturbed wetland.

The original composition of the native anuran community of undisturbed wetlands on the southeastern plateau of Rwanda remains a matter of speculation because humans have considerably affected all wetlands prior to the first scientific surveys (Clay & Lewis 1996, Olson & Berry 2003). The only species detected additionally in the Akagera wetland is *Leptopelis bocagii* (Fischer et al. 2011), a ground-dwelling frog of open savannah (Channing & Howell 2006). As this type of habitat has probably never been present in the Mugesera wetland it seems unlikely that this species has ever formed part of the native local community. The community structures of the remaining large wetland complexes Rugezi and Kamiranzovu at about 2,000 m a.s.l. in the north, which are still considered almost unaltered, do not provide indicators that could help to solve the riddle. The anuran species composition of this altitudinal belt differs substantially from that on the 1,300 m-plateau by including the montane species of the *H. castaneus* group, *Leptopelis* spp., and *S. kisoloensis* (Fischer et al. 2011, Roelke et al. 2011, Sinsch et al. 2011, Dehling & Sinsch 2019).

Effects of present and past human disturbance on the alpha-diversity of the surveyed microhabitats

Aerial views of the study area identify seasonal flooding and agricultural land use of varying intensity as the major factors impacting on microhabitat persistence. The unequal disturbance of the microhabitats surveyed led to a high beta-diversity of the Mugesera anuran community, reflecting the effects of the road dams as dispersal barriers (Fig. 5). The local alpha-diversity corresponded non-randomly to the present level of human disturbance in the focus microhabitats (Fig. 6), which is consistent with the predictions of the Intermediate Disturbance Hypothesis (Weithoff et al. 2001, Roxburgh et al. 2004, Bongers et al. 2009, Liu et al. 2019). As predicted, the extremes of the disturbance gradient (papyrus reed, dammed-up lake) produced the lowest Shannon indices, whereas intermediate disturbance levels as represented by the man-made fishpond with its large water surface and near-natural bank vegetation, resulted in the highest Shannon index. Tropical fishpond microhabitats are amongst the most heterogeneous sites, offering physical and acoustic niches for many species (Bertoluci & Rodrigues 2002, Vasconcelos & Rossa-Feres 2008). In contrast, the near-natural habitat (papyrus swamp) provides few physical niches for anurans, probably leading to a strong competition between local species and a subsequent reduction of diversity by out-competition. The estimated changes to the levels of disturbance exerted on the microhabitat types had no detectable effects on species diversity, supporting the proposed site filter effect (Ernst & Rödel 2005). Short-term regeneration/restoration has obviously no immediate effect on species composition. If human disturbance in the Mugesera wetland would come to a definite end, we hypothesize that species diversity would shrink to the euryoecious *Hyperolius* spp. and *A. nutti*. We do not expect that species of primary swamps would recolonise a regenerated Mugesera wetland because of the absence of suitable stepping-stone habitats.

In conclusion, the present study provides evidence that the species composition of local anurans does not change parallel to the partial regeneration of the natural papyrus vegetation following massive human disturbance in the Mugesera wetland. Generalist species that are common in cultivated wetlands continue to dominate all available microhabitat types independent of former or present degrees of disturbance. Variation of local alpha-diversity follows closely the predictions of the Intermediate Disturbance Hypothesis. Hence, the Mugesera wetland, once regarded as one of the key wetlands of Rwanda, is currently a secondary papyrus swamp habitat with an amphibian community indistinguishable from that of cultivated swamps.

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