



Anuran diversity of cultivated wetlands in Rwanda: melting pot of generalists?

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Abstract. Since 2009 we surveyed anuran communities of two cultivated valley-bottom wetlands (“marais”) at approximately 1,600 m a.s.l. (Rugeramigozi and Butare wetland, Rwanda) to determine species richness and composition after decades of crop production. For the assessment of species presence and abundance, we used standardised bioacoustic recordings of male anurans advertising in a given microhabitat type complemented with visual species detection and identification. We hypothesize that present-day anuran communities in cultivated marais do not reflect the historical association to gallery forests, but represent assemblages of disturbance-tolerant species, i.e. a melting pot of habitat generalists. In fact, microhabitat diversity and species composition were similar at the two study sites and the 13 species detected in the Rugeramigozi wetland were also present among the 17 species detected in the Butare wetland. With the exception of two ubiquitous species, none of the species showed a forest-association. Species richness of cultivated valley-bottom wetlands is about a third of total richness in Rwanda and outnumbered that of natural habitats about twofold. We conclude that high species richness and homogeneous species composition is the result of the specific landscape configuration of wetland belts connected over hundreds of kilometres allowing for uninterrupted dispersal along these corridors. Therefore, all species capable of exploiting these habitats could reach any point of the wetland network, i.e. similar-structured cultivated wetlands represent a melting pot of mainly generalist species.

Key words. Amphibia, Anura, bioacoustic and visual species detection, advertisement call activity, cultivated wetlands, microhabitat diversity, Afrotropics.

Introduction

High primary production and strong selection pressures on local organisms tend to produce a rich biodiversity in wetlands (GIBBS 2000, MELI et al. 2014, TOSZOGYOVA & STORCH 2019). Amphibia are among the key groups contributing to total diversity of wetland and providing important ecosystem services (BABBIT 2005, GIBBONS et al. 2006, HOCKING & BABBIT 2014). The worldwide degradation of natural wetlands due to human land use has had significant influence on the community composition and population size of amphibians inhabiting affected wetlands (e.g., CUSHMAN 2006, MACHADO & MALTCHIK 2010, HOF et al. 2011, NAITO et al. 2012, LOPEZ et al. 2015, BEHN et al. 2018, DUPLER et al. 2019). Some species decline or become locally extinct in response to agricultural use of natural wetlands, other benefit from land use change (e.g., GIBBS et al. 2005, NAITO et al. 2012, KROSS & RICHTER 2016, RIBEIRO et al. 2017a, b).

In Sub-Saharan Africa, human population growth and corresponding demand for food security has led to intensive agricultural use in most natural wetlands (e.g., SCOONES 1991, REBELO et al. 2010, RIVERS-MOORE & COWDEN 2012, RUSSEL & DOWNS 2012, BEHN et al. 2018). The Albertine Rift region in East Africa comprising numerous and extensive wetlands and lakes is no exception from the rule. Its vertebrate diversity is one of the richest of the continent (PLUMPTRE et al. 2007). For example, Rwanda as part of the Albertine Rift harbours 53 anuran and one caecilian species according to FROST (2019), but evidence for the actual presence of nine anuran species tentatively listed for Rwanda is missing (DEHLING & SINSCH, unpublished observations). Many of these species inhabit the swamps at the valley bottoms (“marais”, 1,000–1,700 m a.s.l.) that form continuous wetlands between the thousands of hills (DEUSE 1963, CAMBREZY 1981, FISCHER & HINKEL 1992). At this altitudinal range, submontane forest has proba-

bly bordered valley-bottom wetlands during most of the Holocene (JOLLY et al. 1997, POULSEN et al. 2005). There is evidence for widespread forest clearance beginning about 1,000 years before present, probably because of human land use (JOLLY et al. 1997, RYAN et al. 2017). In the 1950s, most remnants of gallery forest near the wetlands had already disappeared in Rwanda (LAURENT 1956). Clearance of gallery forest has not been the only human impact on the valley-bottom wetlands; intensive agricultural use for at least a century has replaced the originally extensive papyrus swamps (FISCHER et al. 2011, SINSCH et al. 2011, 2012, DEHLING & SINSCH 2013a, 2013b, GoR 2017). Production of mainly rice among other crops, and of fish in artificial ponds represent the main human activities in wetlands, whereas fabrication of bricks for housing is restricted to the peripheral zones (NABAHUNGU & VISSER 2011, MBABAZI 2011, KARAME et al. 2017, NSENGIMANA et al. 2017, UWIMANA et al. 2018).

The consequences of wetland degradation for the structure of local anuran communities are not well understood because there are no natural valley-bottom wetlands with

gallery forest at similar elevations left to compare (SINSCH et al. 2012). The only remaining forest-associated natural wetlands in Rwanda are restricted to approximately 1,300 m a.s.l. in Akagera National Park or to above 2,000 m with amphibian communities dominated by high montane forest species, that are rarely present in lower elevations (POYNTON et al. 2007, SINSCH et al. 2011, MALONZA & VEITH 2012, VAN DER HOEK et al. 2019, DEHLING & SINSCH 2019). In this study, we survey anuran communities of two valley-bottom wetlands at approximately 1,600 m a.s.l. (Rugeramigozi wetland, Muhanga district; Butare wetland, Huye district; Fig. 1) to determine species richness and composition after decades of crop production. For the assessment of species presence and abundance, we chose the bioacoustic approach, i.e. standardised recordings of male anurans advertising in a given microhabitat type complemented with visual species detection and identification. This approach has been successfully applied for diversity assessments in afro-tropical wetlands (SINSCH et al. 2011, 2012, DEHLING & SINSCH 2013a, MINDJE et al. 2020). To overcome the absence of baseline studies in valley-bottom

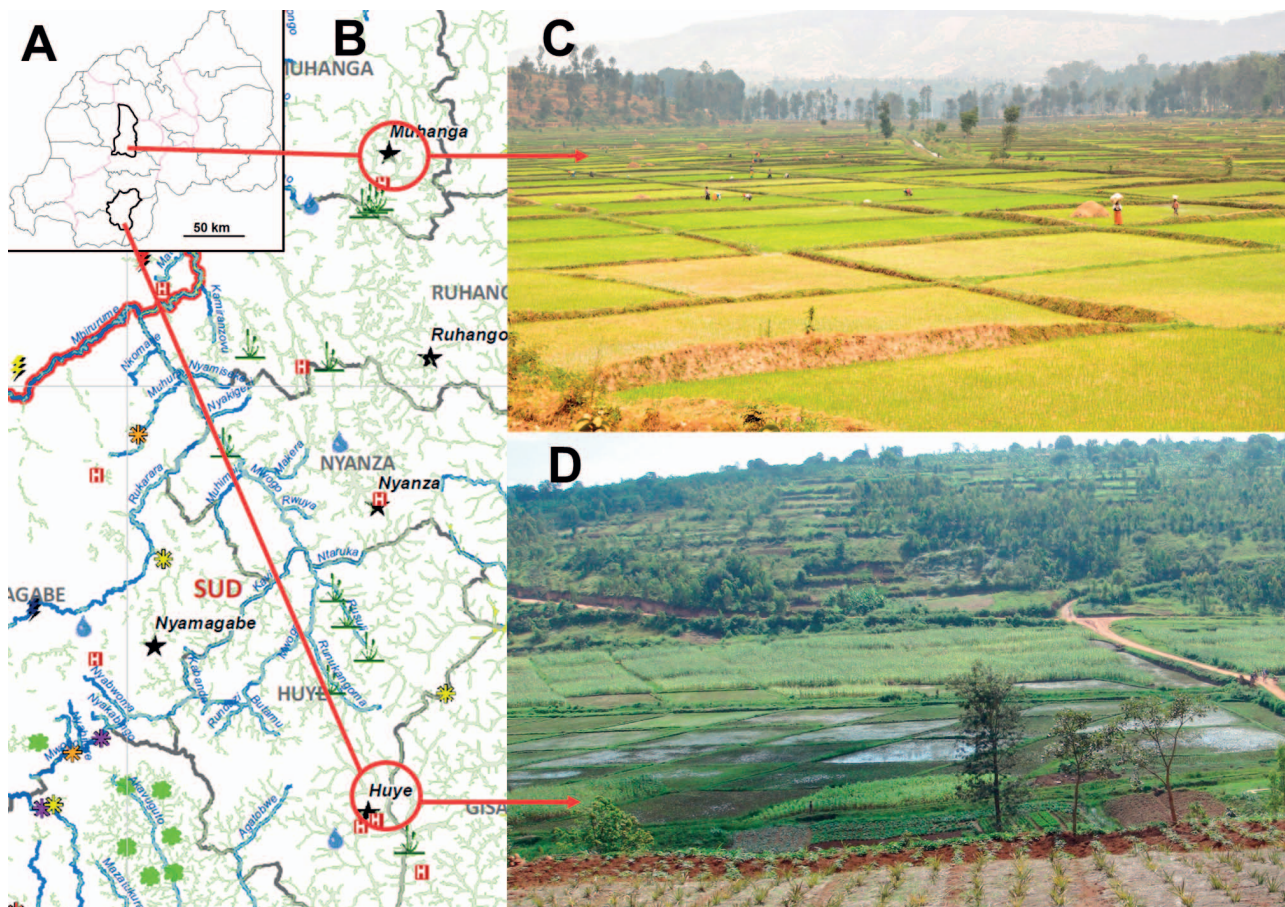


Figure 1. Cultivated wetlands in Rwanda. A) Districts of Rwanda, Muhanga and Huye districts are indicated by bold marginal line. B) Section of the REMA map (2008) showing the southern province. Symbols: major rivers (blue lines), wetlands (faint green areas), cities (black stars). Distance between the cities of Muhanga and Huye: 77 km. C) Intensive rice production in the Rugeramigozi wetland. D) Diverse crop production in the Butare wetland.

wetlands prior to degradation, we compiled species-presence data from literature on this altitudinal range in Rwanda to obtain a list of all amphibian species that may inhabit the available wetlands. We hypothesize that present-day anuran communities in cultivated valley-bottom wetlands do not reflect the historical gallery forest association, but represent assemblages of disturbance-tolerant species, i.e. a melting pot of habitat generalists. We predict: (1) Species richness and composition of cultivated-wetland communities are similar and related to the local microhabitat diversity; (2) species advertising in a given microhabitat type are the same in different wetlands; (3) average abundance of advertising species is similar in the same microhabitat type in different wetlands; and (4) acoustic abundance (= calling activity) varies among microhabitat types.

Materials and methods

Study areas

We studied species diversity and diel vocalization activity of the local anuran community in two Rwandan wetlands, which have been cultivated for intensive crop and fish production for decades (Fig. 1). The Rugeramigozi wetland (study period: October–December 2018) covers 1.8 km² in the Muhanga district of the southern province of Rwanda (2°07'4" S, 29°45'2" E, 1,650 m a.s.l., GoR 2017; Fig. 1B). The annual air temperature is 18.7°C on average, and total precipitation averages 1,207 mm (PRIOUL & SIRVEN 1981). Before official reclamation for rice agriculture in 1999–2000, this wetland was cultivated once a year in the dry season (from June to September) but nowadays, farmers in cooperatives practice rice agriculture in the wetland of Rugeramigozi throughout the year (NABAHUNGU & VISSER 2011). The study area referred to as Rugeramigozi wetland had a north–south extension of 0.60 km and an average width of 150–280 m. Located 77 km south of the Rugeramigozi wetland, we studied a wetland complex of interconnected swamps (Gaseke, Busenyi, Munota, Njabitare) near the town of Butare (study period: March 2009 to October 2012) in the Huye district of the southern province of Rwanda (2°35'54" S, 29°45'24" E, 1,645 m a.s.l.; Fig. 1C). The study area referred to as Butare wetland had a north–south extension of 4.45 km and an average width of 150–200 m (SINSCH et al. 2012). The annual air temperature is 19.1°C on average, and total precipitation averages 1,147 mm (PRIOUL & SIRVEN 1981).

We identified nine microhabitat types within the study areas (SINSCH et al. 2012) that anurans used for calling (Fig. 2): (A) partially flooded rice field, (B) dry crop (e.g. potato) field, (C) central ditch/stream, (D) irrigation channel with vegetation, (E) irrigation channel without vegetation, (F) occasionally flooded uncultivated meadow/swamp with low vegetation, (G) sedgy reed of > 1 m height on abandoned fields, (H) fish pond, (I) mud hole resulting from brick making. The remaining wetland area included buildings, brick-making plants, unpaved streets and other unsuitable habitats for amphibians.

Sampling, analysis and identification of anuran advertisement calls

At the Rugeramigozi wetland, we performed acoustic and complementary visual monitoring during eight days of the rainy season (October 29; November 11, 19, 27, and December 3, 14, 21, 28, 2018), each with three hourly replicate surveys of each microhabitat between 7 and 9 pm (early night hours). At the Butare wetland, acoustic and visual monitoring included 15 days mostly during the rainy period (March 3, 4, 5, 6, October 4, 5, 7, 8, 13, 16, 17, 2009, and September 6, 8, 10, 2010, October 9, 2012). March data were not included in the analyses to avoid a seasonal imbalance with the data collected in the Rugeramigozi wetland. Each monitoring day consisted of four hourly replicate microhabitat surveys between 7 and 10 pm. Visual surveys were non-invasive and species identification was based on external morphological features, whenever possible. If visual identification remained inconclusive (e.g. *Ptychadena* individuals), the specimen was collected for morphological species identification (DEHLING & SINSCH 2013a). Further voucher specimens of all species detected ($n = 10$ to $n = 114$) were collected for morphological and molecular analyses, and housed in the natural history museums of Bonn (ZFMK), Berlin (ZMB) and Stuttgart (SMNS) or in the local collection of the University of Koblenz-Landau.

A SONY PCM-D50 Linear PCM Recorder with stereo microphones, SONY Deutschland GmbH, Cologne was used to record the advertisement calls of reproductive anurans. In each microhabitat, a motionless position was adopted for ca. 2 min, so that the local anurans could recover from the disturbance caused by the approach. The recorder was turned on and slowly moved 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.

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 prepared using 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 recordings and published data (e.g., SINSCH et al. 2012, DEHLING & SINSCH 2013a). Acoustic identification was validated through comparison of external morphological features such as colour pattern, shape and size with keys for species determination (CHANNING & HOWELL 2006, DU PREEZ & CARRUTHERS 2009, DEHLING & SINSCH 2013b, CHANNING et al. 2016). The only species present and identified exclusively by the morphological approach was *Xenopus victorianus* because recording the underwater calls of *Xenopus* spp. (TOBIAS et al. 2011) was outside the scope of this study.

To distinguish anurans calling from the focus microhabitat and those in the vicinity, we used call amplitude as a criterion to estimate distance of the calling frog (SINSCH et al. 2012, MINDJE et al. 2020). Specimens were considered calling from the focus microhabitat, if calls were shown in bright colours in the sonograms and the ratio call amplitude/background noise was ≥ 2 in the corresponding os-

cillogram. In contrast, calls of specimens at least 20 m distant from the focus microhabitat were represented in pink colour in the sonograms and the amplitude of these calls was indistinguishable from that of the background noise in the corresponding oscillogram. We estimated the acoustic abundance of each species in a given microhabitat as the number of calling individuals per 2 min recording (MINDJE

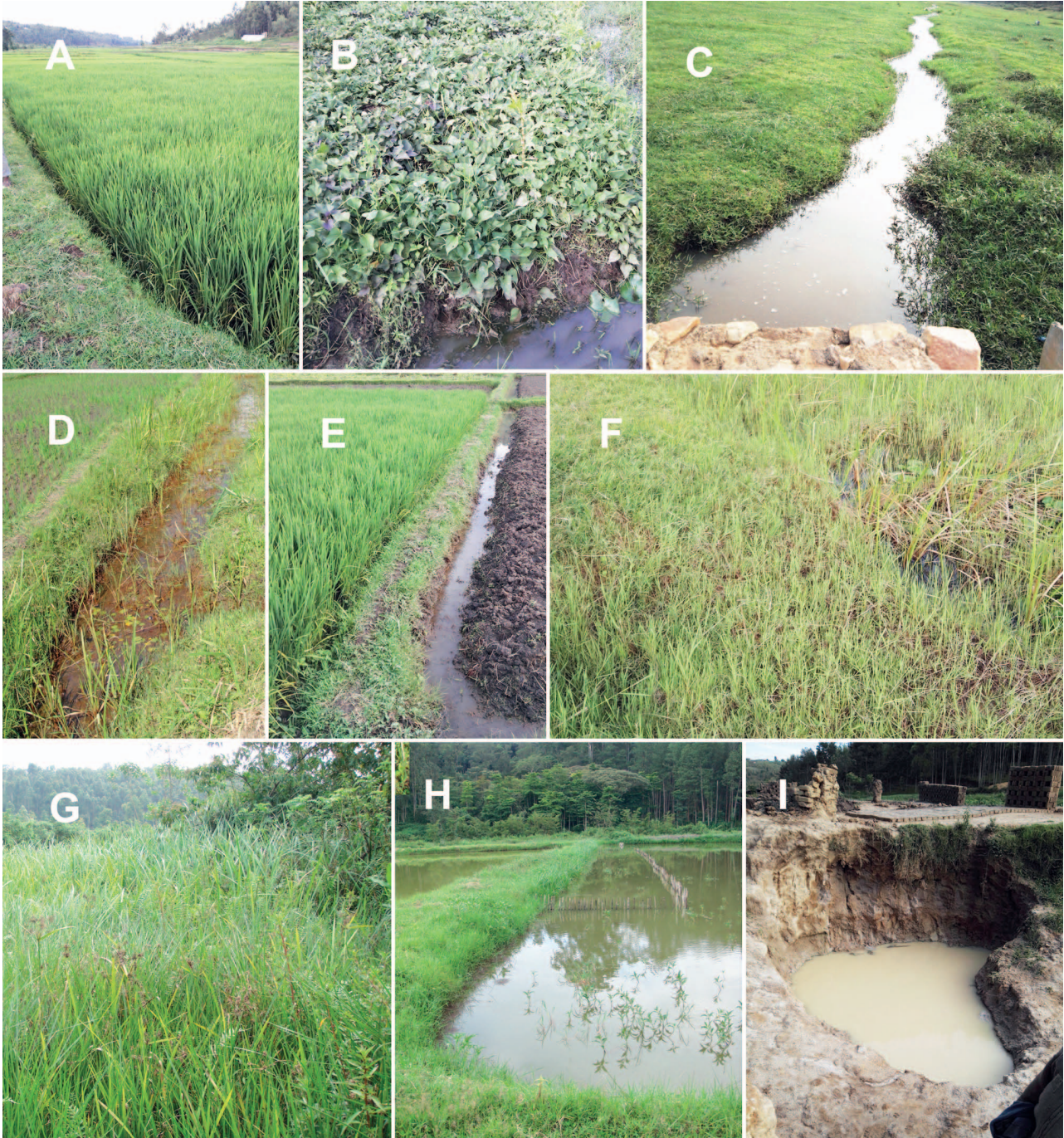


Figure 2. Microhabitat types in cultivated wetlands used by anurans for advertising. A) Partially flooded rice field, B) dry crop field, C) central ditch/stream, D) irrigation channel with vegetation, E) irrigation channel without vegetation, F) occasionally flooded uncultivated meadow/swamp, G) sedgy reed on abandoned field, H) fish pond, I) mud hole.

et al. 2020). 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 are calling, it is possible to distinguish calls given by the same individual from those of distinct 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 among up to five distinct callers, and assigned choruses of more than five callers numerically to six individuals independent of the actual number of callers. The rationale for choosing this numerical value was that all choruses consisted of at least six individuals, whereas any higher value would not have been representative for all choruses.

Literature compilation of species inhabiting the surveyed altitudinal range

In an attempt to compile a list of amphibian species, which are or were present in the valley-bottom wetlands in the altitudinal range of 1,000–1,700 m, we used available data bases (AMPHIBIAWEB 2019, FROST 2019, IUCN 2019) and retrieved all publications dealing with amphibians in Rwanda. These publications comprise the original descriptions of species collected in Rwanda and subsequent scientific surveys in this elevation belt (e.g., FISCHER & HINKEL 1992, HÖLTING 2008, FISCHER et al. 2011, SINSCH et al. 2012, DEHLING & SINSCH 2013b, CHANNING et al. 2016, DEHLING & SINSCH 2019; MINDJE et al. 2020). Our main source for information on present-day distribution of amphibians in Rwanda are unpublished surveys by J.M. DEHLING and U. SINSCH throughout Rwanda between 2009 and 2019. We assign the association of each species to three habitat categories: (1) open wetlands, (2) forest, and (3) forest edge, i.e. wetlands with gallery forest.

Statistical analysis

Alpha- and Beta-diversity measures were computed using the statistical package EstimateS version 9.1.0 (COLWELL & ELSENHOHN 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 for each wetland. If species accumulation curves reached asymptotic values, sampling effort was sufficient to consider the number of observed species representative for the wetland. We chose the Sørensen similarity index for presence/absence data of species and the Bray-Curtis similarity index using the acoustic abundance of species to describe beta-diversity. We used ANCOVAs (Analysis of Covariance) to estimate the influence of fixed factors “wetland” (Rugaramigozi or Butare), and “microhabitat type” (see list above) and of the continuous covariate “hour of recording” (7–9 pm) and “rainy period” (Oc-

tober 1 set to day 1 of the rainy season) on the local number of species and individuals per species calling within a 2 min recording. Analyses were run on raw data because distributions did not deviate significantly from normality. 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

Microhabitat and anuran diversity in cultivated wetlands

The two wetlands included eight of the nine studied microhabitat types each, in which local anurans called and reproduced (Table 1). The two wetlands shared seven microhabitat types (partially flooded rice field, dry crop field, central ditch, irrigation channel with vegetation, occasionally flooded uncultivated meadow with low vegetation, fish pond, mud hole) with relative proportions of the total area varying from year to year. Note that there were very few irrigation channels without vegetation in the Butare wetlands as well, but they were not studied and therefore, they are not included in the analysis of habitat diversity. Wetland localities with natural gallery forest were absent, but the Arboretum de Ruhande of the University of Rwanda at Huye represented a human-made forest created in 1934 (BOEDTS 2016, HÖLTING 2008). Crop production was more intensive in the Rugaramigozi wetland than in the Butare wetland, rice fields alone covered 34% of the study area. Therefore, abandoned or temporarily unused fields with re-establishment of the natural sedge reed cover were absent within the Rugaramigozi study area, but present in the Butare wetland (Fig. 2G).

The anuran diversity detected by complementary acoustic and visual surveys was 13 species in the Rugaramigozi wetland and 17 in the Butare wetland (Tables 1, 2). Species accumulation curves (Fig. 3A: rarefaction, B: jackknife estimates) run asymptotically to the empirically detected number of species demonstrating that the sampling was exhaustive (Fig. 3). All species inhabiting the Rugaramigozi wetland also occurred in the Butare wetland in which additionally *Hyperolius cinnamomeoventris*, *H. lateralis*, *Ptychadena uzunguensis* and *Sclerophrys kisoensis* were present.

Alpha- and beta-diversity variation between cultivated wetlands

Alpha-diversity of microhabitat types in terms of species richness varied considerably between two and 13 species (Table 2). The corresponding Shannon-Wiener estimates of alpha-diversity of local species that were detected calling at a given microhabitat ranged from 0.63 to 2.10 with an evenness of 0.70–0.87 (Table 2). The microhabitats harbouring more than 10 species included a variable proportion of reed vegetation with a height of 0.4–1.5 m.

Table 1. List of anuran species detected in the Rugeramigozi and Butare wetlands. * Species also reported for Butare by HÖLTING (2008).

Taxon	Rugeramigozi wetland (Muhanga)		Butare wetlands (Huye)	
	acoustic	visual	acoustic	visual
Bufonidae:				
<i>Sclerophrys kisoensis</i> (LOVERIDGE, 1932)	–	–	+	+*
<i>Sclerophrys regularis</i> (REUSS, 1833)	+	+	+	+*
Hyperoliidae:				
<i>Afrixalus quadrivittatus</i> (WERNER, 1908)	+	+	+	+*
<i>Hyperolius cf. cinnamomeiventris</i> BOCAGE, 1866	–	–	+	+
<i>Hyperolius kivuensis</i> AHL, 1931	+	+	+	+*
<i>Hyperolius lateralis</i> LAURENT, 1940	–	–	+	+
<i>Hyperolius rwandae</i> DEHLING et al., 2013	+	+	+	+
<i>Hyperolius viridiflavus</i> (DUMÉRIL & BIBRON, 1841)	+	+	+	+*
<i>Kassina senegalensis</i> (DUMÉRIL & BIBRON, 1841)	+	+	+	+*
Phrynobatrachidae:				
<i>Phrynobatrachus kakamikro</i> SCHICK et al., 2010	+	–	+	+
<i>Phrynobatrachus natalensis</i> (SMITH, 1849)	+	+	+	+*
Pipidae:				
<i>Xenopus victorianus</i> (AHL, 1924)	–	+	+	+
Ptychadenidae:				
<i>Ptychadena anchietae</i> (BOCAGE, 1868)	+	+	+	+
<i>Ptychadena nilotica</i> (SEETZEN, 1855)	–	+	+	+*
<i>Ptychadena porosissima</i> (STEINDACHNER, 1867)	–	+	+	+
<i>Ptychadena uzungwensis</i> (LOVERIDGE, 1932)	–	–	+	+
Pyxicephalidae:				
<i>Amietia nutti</i> (BOULENGER, 1896)	+	+	+	+*

Beta-diversity among most microhabitat types per wetland was low, as they shared a high number of species, often with similar abundances (Fig. 4). The exception from the rule was the mud hole microhabitat with steep shores and little to no shore vegetation. Mud holes shared the lowest number of species with most other microhabitats (Sørensen-Index: 0.250–0.375 in the Butare wetland, 0.286–0.545 in the Rugeramigozi wetland). Comparing the shared species among microhabitats across the two wetlands, species assemblages in each microhabitat type were mostly very similar independent of the specific wetland (Table 2).

Potential amphibian species inhabiting the surveyed altitudinal range

Data obtained from the literature and our own surveys yielded a list of 27 species known to occur in the elevation belt of 1,000–1,700 m a.s.l. (Table 3) in Rwanda. The Red list classification of these species is “Least Concern” for all but *Cardioglossa cyaneospila* (“Near Threatened”) and *Phrynobatrachus kakamikro* (“Data Deficient”) (IUCN 2019). Three species are assumed to inhabit exclusively forest habitats, three are associated with open wetlands with gallery forest, 19 live exclusively in open wetlands, and two are ubiquitous. With the exception of the ubiquitous *Sclerophrys*

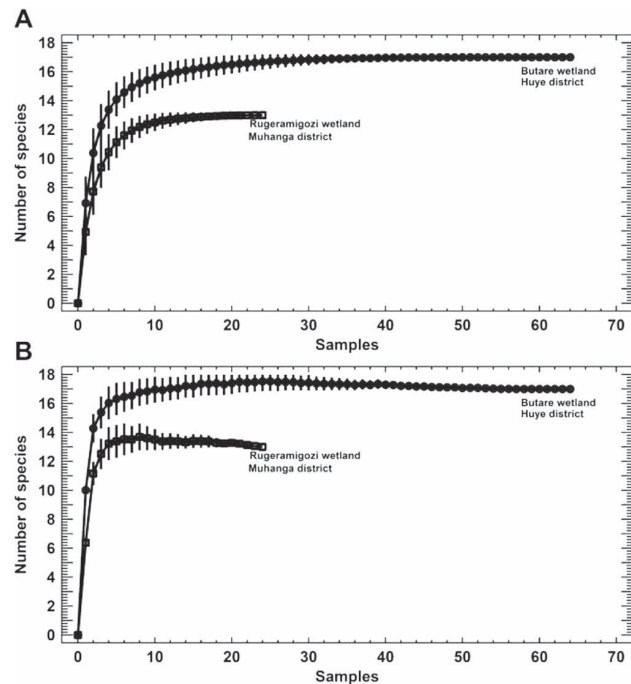


Figure 3. Anuran species accumulation curves based on combined visual and bioacoustic surveys in the studied wetlands. A) Rarefaction curves, B) Jackknife estimates. Symbols represent frequency estimates, and vertical bars corresponding standard deviations.

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Table 2. Presence (X) and acoustic abundance (average number of calling males per 2 min recordings) of anuran species at the nine microhabitat types surveyed in the Rugeramigozi (R) and Butare (B) wetlands (Fig. 2). Species are listed alphabetically. Shannon and evenness index refer to the species calling at the focus microhabitat. Species richness = number of species.

Microhabitat type	rice field		dry crop field		central ditch		irrigation channel - vegetat.	irrigation channel + vegetat.		Uncultivated wet meadow		reed swamp	fish pond		Mud hole	
	R	B	R	B	R	B	R	B	R	B	R	B	R	B	R	B
<i>Afrizalus quadrivittatus</i>	-	X (1.0)	X (0.1)	X (0.4)	-	-	-	X (1.1)	X (0.9)	X (0.8)	X (1.0)	X (0.1)	X (0.5)	-	-	-
<i>Amietia nutti</i>	X (0.1)	-	X (0.1)	-	-	X (0.2)	-	-	X (0.6)	X	-	X (0.5)	-	X (0.1)	-	-
<i>Hyperolius cinnamomeiventris</i>	-	-	-	-	-	-	-	-	X (1.0)	-	X (0.6)	X (0.1)	-	-	-	-
<i>Hyperolius kivuensis</i>	X (0.9)	X (2.6)	X (1.4)	X (2.4)	X (0.3)	X (1.8)	X (0.1)	X (1.0)	X (2.8)	X (1.3)	X (3.1)	X (2.1)	X (1.0)	X (1.1)	X (0.7)	X (0.8)
<i>Hyperolius lateralis</i>	-	-	-	-	-	-	-	-	-	-	X (1.7)	X (2.1)	-	-	-	-
<i>Hyperolius rwandae</i>	-	-	X (0.3)	-	-	-	-	X (0.1)	X (0.3)	X (1.0)	X (1.3)	-	X (0.6)	-	-	-
<i>Hyperolius viridiflavus</i>	X (0.4)	X (3.7)	X (1.9)	X (3.7)	X (0.5)	X (3.0)	X (0.5)	X (2.3)	X (3.2)	X (3.5)	X (3.6)	X (3.2)	X (5.8)	X (2.4)	-	-
<i>Kassina senegalensis</i>	X (0.1)	X (3.3)	-	X (3.6)	-	X (2.6)	-	X (0.3)	X (3.0)	X (1.2)	X (2.5)	X (3.8)	X (0.5)	X (3.3)	X (0.9)	X (3.9)
<i>Phrynobatrachus kakamikro</i>	X (0.1)	X (2.5)	X (0.6)	X (0.6)	-	-	-	X (0.8)	X (1.4)	X (1.3)	X (1.0)	X (0.3)	X (0.3)	X (0.6)	-	-
<i>Phrynobatrachus natalensis</i>	X (0.1)	X (2.1)	-	X (0.3)	-	-	X (0.2)	-	X (1.6)	X (0.1)	X (0.4)	X (0.8)	-	-	X (0.2)	-
<i>Ptychadena anchietae</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X (0.1)	X (0.3)
<i>Ptychadena nilotica</i>	-	X (1.2)	-	-	-	-	-	X	X (0.5)	X	X (0.1)	-	X	-	-	-
<i>Ptychadena porosissima</i>	-	X (1.2)	-	-	-	-	-	X	X (0.3)	X	X (0.2)	-	X	X	-	-
<i>Ptychadena uzungwensis</i>	-	X (1.2)	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sclerophrys kisoensis</i>	-	-	-	-	-	-	-	-	-	-	X (1.3)	-	-	-	-	-
<i>Sclerophrys regularis</i>	-	X (1.4)	-	X (0.3)	-	-	X (0.7)	-	X (1.0)	-	-	X (2.0)	-	-	-	-
<i>Xenopus victorianus</i>	-	-	-	-	-	-	X	X	X	-	-	-	X	X	X	X
Species richness	6	10	6	7	2	4	5	9	13	10	12	10	9	7	5	4
Shannon-Index	1.26	2.10	1.28	1.52	0.63	1.17	1.15	1.47	1.98	1.67	2.03	1.81	1.15	1.26	1.08	1.06
Evenness	0.70	0.78	0.72	0.77	0.91	0.84	0.83	0.82	0.85	0.86	0.87	0.87	0.64	0.80	0.78	0.71

kisoensis and *Amietia nutti* (CHANNING & HOWELL 2006, CHANNING et al. 2016, IUCN 2019), none of the forest-only-associated species was detected in cultivated wetlands. Four out of the 19 open-land species (*Leptopelis bocagii*, *Hoplobatrachus occipitalis*, *Hyperolius parallelus* and *Xenopus vestitus*) were not detected in the Butare or Rugeramigozi wetlands. However, *L. bocagii* was detected in cultivated wetlands (not systematically surveyed) in the Huye and Rusizi districts (DEHLING & SINSCH, unpublished observations). *Hyperolius parallelus* and *X. vestitus* are com-

mon in cultivated valley-bottom wetlands near Lake Kivu, replacing their ecological equivalents *H. viridiflavus* and *X. victorianus* west of the Nyungwe Mountains (DEHLING & SINSCH 2019). *Hoplobatrachus occipitalis* is restricted to a small region in southern Rwanda (AmphibiaWeb 2019). Considering the geographical range limits of *H. occipitalis*, *H. parallelus* and *X. vestitus* to regions outside the Huye and Muhanga districts, only one of the potentially occurring open-land species (*L. bocagii*) was not detected in the studied cultivated wetlands.

Table 3. Actual presence of anuran species in three cultivated valley-bottom wetlands (this study, * FISCHER et al. 2011, MINDJE et al. 2020) and potential occurrence in the altitudinal range of 1,000–1,700 m a.s.l. in Rwanda. Potential occurrence is derived from literature surveys and unpublished observations by the authors (details in Material & Methods). + means presence, – absence.

Taxon	Habitat category	Cultivated wetlands			Literature compilation		
		Rugera-migozi	Butare	Mugesera*	Documented occurrence in habitat category		
		Open-land	Open-land	Open-land	Open-land	Open-land with gallery forest	Forest
Arthroleptidae:							
<i>Arthroleptis schubotzi</i> NIEDEN, 1911		–	–	–	–	–	+
<i>Cardioglossa cyaneospila</i> LAURENT, 1950		–	–	–	–	–	+
<i>Leptopelis bocagii</i> (GÜNTHER, 1865)		–	–	–	+	–	–
Bufonidae:							
<i>Sclerophrys kisoloensis</i> (LOVERIDGE, 1932)		–	+	–	+	+	+
<i>Sclerophrys regularis</i> (REUSS, 1833)		+	+	–	+	–	–
Dicroglossidae:							
<i>Hoplobatrachus occipitalis</i> (GÜNTHER, 1858)		–	–	–	+	–	–
Hyperoliidae:							
<i>Afrixalus quadrivittatus</i> (WERNER, 1908)		+	+	+	+	–	–
<i>Hyperolius cinnamomeoventris</i> BOCAGE, 1866		–	+	+	+	–	–
<i>Hyperolius kivuensis</i> AHL, 1931		+	+	+	+	–	–
<i>Hyperolius lateralis</i> LAURENT, 1940		–	+	+	+	–	–
<i>Hyperolius parallelus</i> GÜNTHER, 1858		–	–	–	+	–	–
<i>Hyperolius rwandae</i> Dehling et al., 2013		+	+	+	+	–	–
<i>Hyperolius viridiflavus</i> (DUMÉRIL & BIBRON, 1841)		+	+	+	+	–	–
<i>Kassina senegalensis</i> (DUMÉRIL & BIBRON, 1841)		+	+	+	+	–	–
<i>Phlyctimantis verrucosus</i> (BOULENGER, 1912)		–	–	–	–	+	–
Phrynobatrachidae:							
<i>Phrynobatrachus kakamikro</i> SCHICK et al., 2010		+	+	+	+	–	–
<i>Phrynobatrachus natalensis</i> (SMITH, 1849)		+	+	+	+	–	–
Pipidae:							
<i>Xenopus vestitus</i> LAURENT, 1972		–	–	–	+	–	–
<i>Xenopus victorianus</i> (AHL, 1924)		–	+	+	+	–	–
Ptychadenidae:							
<i>Ptychadena anchietae</i> (BOCAGE, 1868)		+	+	+	+	–	–
<i>Ptychadena chrysogaster</i> LAURENT, 1954		–	–	–	–	–	+
<i>Ptychadena nilotica</i> (SEETZEN, 1855)		–	+	+	+	–	–
<i>Ptychadena porosissima</i> (STEINDACHNER, 1867)		–	+	+	+	–	–
<i>Ptychadena uzungwensis</i> (LOVERIDGE, 1932)		–	+	–	+	–	–
Pyxicephalidae:							
<i>Amietia nutti</i> (BOULENGER, 1896)		+	+	+	+	+	+
Ranidae:							
<i>Amnirana albolabris</i> (HALLOWELL, 1856)		–	–	–	–	+	–
<i>Amnirana</i> cf. <i>galamensis</i> (DUMÉRIL & BIBRON, 1841)		–	–	–	–	+	–

Among- and within-species variation of microhabitat use

Microhabitat use of the anurans present in the two wetlands showed a generalist-specialist continuum (Table 2). *H. kivuensis* represented the generalist extreme being present in all microhabitat types, whereas *Ptychadena anchietae*, *P. uzungwensis* and *S. kisoloensis* were restricted to a single microhabitat type (Table 2).

The following account is ordered from generalist to specialist species according to the number microhabitat types used for calling. The underwater-calling *Xenopus victorianus* is not listed. We refrained from analysing acoustic abundance for the four *Ptychadena* spp. as well because these species form occasionally choruses, which were often silenced due to approach and therefore, recordings were not representative for acoustic abundance estimates.

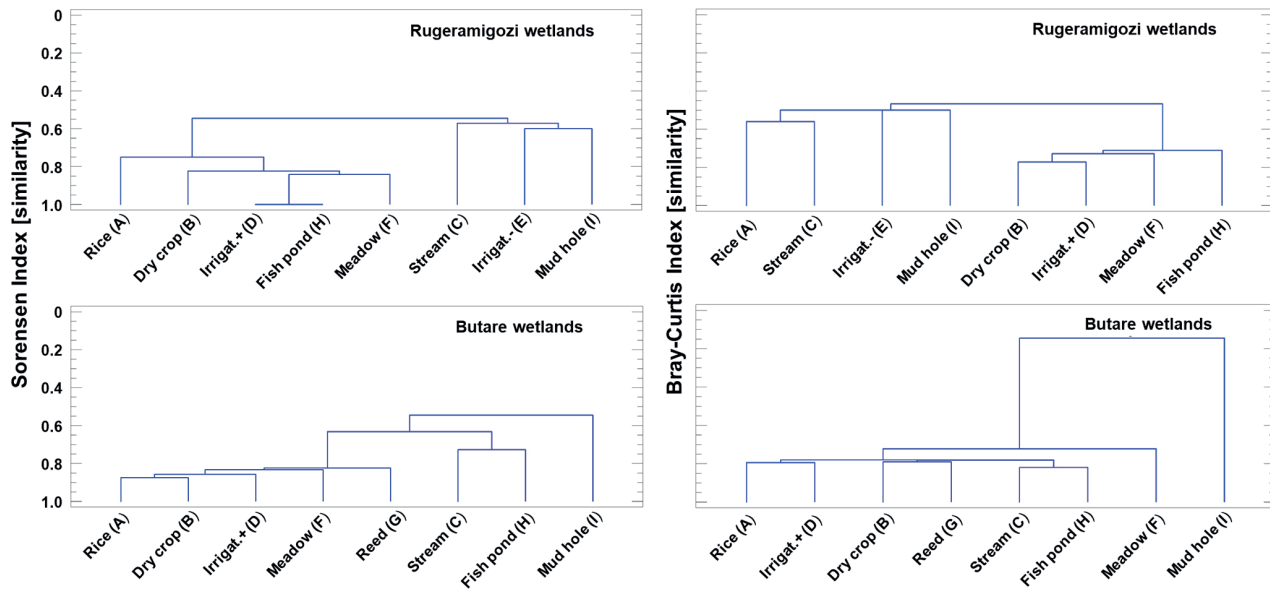


Figure 4. Beta-Diversity of the Rugeramigozi and Butare wetlands. (Left side) Sørensen similarity based on the presence of shared species, (right side) Bray-Curtis similarity based on the acoustic abundance of shared species. For abbreviations of microhabitats, see Material & methods and Figure 2.

Hyperolius kivuensis – Males used all nine microhabitat types for acoustic advertisement, usually calling from vegetation 0.2–0.6 m above the ground. Acoustic abundance increased from 7 to 9 pm (2-Factor ANCOVA; $F_{1,324} = 17.55$, $P < 0.0001$) and decreased from October to December (2-Factor ANCOVA; $F_{1,324} = 15.0$, $P = 0.0001$). Adjusted acoustic abundance did not differ significantly between the two wetlands (2-Factor ANCOVA; $F_{1,324} = 1.21$, $P = 0.2725$), but considerably among the microhabitats (2-Factor ANCOVA; $F_{8,324} = 5.97$, $P < 0.0001$). Central ditch and irrigation channel without shore vegetation harboured significantly less calling males than all other microhabitats (Fig. 5A).

Hyperolius viridiflavus – Males were detected in eight microhabitat types (absent in mud holes) calling from floating leaves upon water, moist ground and low vegetation, very often in choruses of more than five specimens. Adjusted acoustic abundance was independent from the hour of recording (2-Factor ANCOVA; $F_{1,287} = 0.06$, $P = 0.8045$) and the date within the rainy season (2-Factor ANCOVA; $F_{1,287} = 3.06$, $P = 0.0813$). Abundance did not differ signifi-

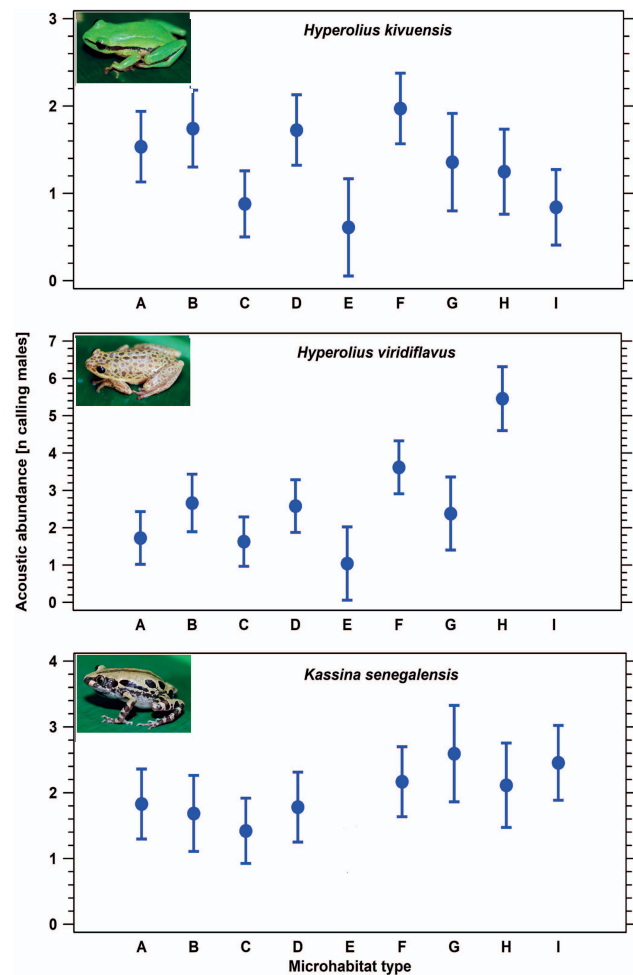


Figure 5. Acoustic abundance per microhabitat of the three most common anuran species. A) *Hyperolius kivuensis*, B) *Hyperolius viridiflavus*, C) *Kassina senegalensis*. Data are given as least square means (dots) and 95% Bonferroni confidence intervals (vertical bars) of a 2-Factor ANCOVA (wetland and microhabitat type as fixed factors, date and hour of recording as continuous co-factors). Abbreviations of microhabitat types (Fig. 2): A) Partially flooded rice field, B) dry crop field, C) central ditch/stream, D) irrigation channel with vegetation, E) irrigation channel without vegetation, F) occasionally flooded uncultivated meadow/swamp, G) sedgy reed on abandoned field, H) fish pond, I) mud hole.

cantly between wetlands (2-Factor ANCOVA; $F_{1,287} = 0.91$, $P = 0.3419$), but considerably among the microhabitats (2-Factor ANCOVA; $F_{7,287} = 14.56$, $P < 0.0001$). Fish ponds harboured the highest number of individuals, irrigation channels without shore vegetation the lowest (Fig. 5B).

Kassina senegalensis – Males were found in eight microhabitat types (absent in irrigation channels without shore vegetation), calling from the shore hidden in mud, sometimes in choruses of more than five specimens. Adjusted acoustic abundance was independent from the hour of recording (2-Factor ANCOVA; $F_{1,300} = 2.82$, $P = 0.0943$) and the date within the rainy season (2-Factor ANCOVA; $F_{1,300} = 0.91$, $P = 0.3401$). Abundance was significantly greater in the Butare wetlands than in the Rugeramigozi wetland (2-Factor ANCOVA; $F_{1,300} = 76.69$, $P < 0.0001$), and varied significantly among the microhabitats (2-Factor ANCOVA; $F_{7,300} = 5.64$, $P = 0.0253$). Mud holes, fish ponds and reed swamp harboured the highest number of advertising males, the central ditch the lowest number, but mean numbers of calling males varied only between 1.5 and 2.5 (Fig. 5C).

Amietia nutti – Males used seven microhabitat types for calling from the ground hidden below the vegetation. Adjusted acoustic abundance was independent from the hour of recording (2-Factor ANCOVA; $F_{1,209} = 1.82$, $P = 0.1791$) and the date within the rainy season (2-Factor ANCOVA; $F_{1,209} = 0.13$, $P = 0.7206$). Abundance was significantly greater in the Butare wetlands than in the Rugeramigozi wetland (2-Factor ANCOVA; $F_{1,209} = 6.47$, $P = 0.0117$) and varied significantly among the microhabitats (2-Factor ANCOVA; $F_{6,209} = 2.93$, $P = 0.0092$; maximum abundance in the irrigation channels with shore vegetation).

Phrynobatrachus natalensis – Males used seven microhabitat types for calling from the ground hidden in mud, but hourly acoustic activity was very low (< 0.3 males) in three microhabitats (dry crop fields, sedge reed and mud holes). Adjusted acoustic abundance varied marginally significantly from 7 to 9 pm (2-Factor ANCOVA; $F_{1,243} = 4.76$, $P = 0.0302$), but was independent from the date within the rainy season (2-Factor ANCOVA; $F_{1,243} = 0.01$, $P = 0.9961$). Abundance was significantly greater in the Butare wetlands than in the Rugeramigozi wetland (2-Factor ANCOVA; $F_{1,243} = 21.44$, $P < 0.0001$) and varied significantly among the microhabitats (2-Factor ANCOVA; $F_{6,243} = 8.05$, $P < 0.0001$; maximum abundance in the partially flooded rice fields).

Phrynobatrachus kakamiko – Males used six microhabitat types for calling from the ground. Adjusted acoustic abundance was independent from the hour of recording (2-Factor ANCOVA; $F_{1,215} = 2.02$, $P = 0.1565$) and the date within the rainy season (2-Factor ANCOVA; $F_{1,215} = 0.48$, $P = 0.4914$). Abundance was significantly greater in the Butare wetlands than in the Rugeramigozi wetland (2-Factor ANCOVA; $F_{1,215} = 8.80$, $P = 0.0034$) and varied significantly among the microhabitats (2-Factor ANCOVA; $F_{5,215} = 3.25$, $P = 0.0075$; maximum abundance in the partially flooded meadow).

Afrixalus quadrivittatus – Males used six microhabitat types for calling, usually calling from vegetation 0.2–0.6 m above the ground. Acoustic abundance increased from 7 to 9 pm (2-Factor ANCOVA; $F_{1,215} = 8.05$, $P = 0.0050$) and decreased from October to December (2-Factor ANCOVA; $F_{1,215} = 8.68$, $P = 0.0036$), as in *H. kivuensis*. Abundance did not differ significantly between the two wetlands, but among the microhabitats (2-Factor ANCOVA; $F_{5,215} = 5.05$, $P = 0.0002$; maximum abundance in the irrigation channels with shore vegetation).

Sclerophrys regularis – Males used five microhabitat types for calling from the ground. Adjusted acoustic abundance was independent from the hour of recording (2-Factor ANCOVA; $F_{1,167} = 1.28$, $P = 0.2593$) and the date within the rainy season (2-Factor ANCOVA; $F_{1,167} = 0.11$, $P = 0.7365$). Abundance was marginally significantly greater in the Butare wetlands than in the Rugeramigozi wetland (2-Factor ANCOVA; $F_{1,167} = 3.93$, $P = 0.0492$) and varied significantly among the microhabitats (2-Factor ANCOVA; $F_{4,167} = 5.37$, $P = 0.0004$; maximum abundance in reed swamp).

Hyperolius rwandae – Males used four microhabitat types for calling usually from vegetation 0.2–0.6 m above the ground. Adjusted acoustic abundance was independent from the hour of recording (2-Factor ANCOVA; $F_{1,149} = 0.94$, $P = 0.3335$) and the date within the rainy season (2-Factor ANCOVA; $F_{1,149} = 1.20$, $P = 0.2754$). Abundance did not differ significantly between the two wetlands (2-Factor ANCOVA; $F_{1,149} = 0.75$, $P = 0.3879$), but among the microhabitat types (2-Factor ANCOVA; $F_{3,149} = 6.53$, $P = 0.0004$; maximum abundance in the partially flooded meadow).

Hyperolius cinnamomeiventris*, *Hyperolius lateralis – The two species called exclusively in uncultivated microhabitats with upcoming sedge vegetation which were absent in the Rugeramigozi wetland. In these microhabitats, they often formed choruses. The most important calling habitat was the reed swamp with 1–2 m high sedges or reed. If these habitats were cultivated again, as observed twice in the Butare wetlands, *H. lateralis* emigrated from the area.

Sclerophrys kisoloensis – This toad species was restricted to a single swamp area in the vicinity of the Arboretum du Ruhande (University of Rwanda) at Huye.

Discussion

We provide evidence that the present-day anuran communities in cultivated valley-bottom wetlands in Rwanda are species-rich, harbouring between about a fourth to a third of the total number of species known to occur in Rwanda in areas of a few square kilometres. Local diversity of these agricultural wetlands in Rwanda is by far greater (1,650 m a.s.l.; 13–17 species) than those of the near-natural wetlands Kamiranzovu (1,960 m a.s.l.; 8 species), Rugezi (2,055 m

a.s.l.; 7 species), Uwasenkoko (2,370 m a.s.l.; 7 species) and Lac Ngezi (2,884 m a.s.l.; 5 species) (FISCHER et al. 2011, SINSCH et al. 2011, DEHLING unpubl. data). Considering that the cultivated wetlands and the Kamiranzovu swamp differ only by 300 m in altitude and that species richness along a comparable elevational gradient on Mount Kenya decreased from three to one species (MALONZA & VEITH 2015), we conclude that low elevation does not account alone for the high species richness at the two cultivated study sites. The main difference (besides elevation) between near-natural and cultivated wetlands in Rwanda is that most of the near-natural wetlands are located within forest areas which may act as dispersal barriers for open-land species. The potential richness of anurans known to inhabit the altitudinal range of 1,000–1,700 m is 27 species, of which an amazing 17 were detected sympatrically within only 4 km² in the Huye district (SINSCH et al. 2012, DEHLING & SINSCH 2019, DEHLING unpubl. data). A closer look at the habitat association of the anurans found in cultivated wetlands demonstrates that species richness is based almost exclusively on open-land species and ubiquists (17 = 81.0% of potentially 21 species), whereas forest-associated species are underrepresented (2 = 33.3% of potentially 6 species; IUCN 2019). In agreement with our hypothesis on community structure, the structural complexity of cultivated wetlands including up to nine habitable microhabitat types promoted the local occurrence of most regional, open-land inhabiting species, whereas a millennium of successive forest clearance has reduced the forest-associated anurans to only two disturbance-tolerant species (JOLLY et al. 1997, POULSEN et al. 2005, DEHLING & SINSCH 2019). The actually rather homogeneous species composition in distinct cultivated wetlands is probably the result of at least three processes: environmental filtering by the disappearance of gallery forests (GUERRA & ARÁOZ 2015, RIBEIRO et al. 2017a, b), local competition among species occupying similar niches (CADOTTE & TUCKER 2017), and dispersal/invasion along the interconnected wetland corridors (CAMBREZY 1981; Fig. 1). The available observational data do not allow assessing the relative contributions of environmental filtering and among-species competition (CADOTTE & TUCKER 2017), but the predictions generated from the hypothesis on community structure in cultivated wetlands allow for testable insights on the dispersal process. If homogenisation by dispersal plays a major role in shaping the anuran communities in cultivated wetlands, local species composition, abundance and calling activity should match with corresponding microhabitat types in distinct wetlands.

Prediction 1: Species richness and composition of cultivated-wetland communities is similar and related to the local microhabitat diversity

Our data support clearly the prediction that microhabitat diversity is an important determinant of local species composition, as the two wetlands shared seven (eight includ-

ing the unstudied irrigation channels without vegetation in Butare) out of nine microhabitat types and 13 out of 17 anuran species. The lower environmental heterogeneity (six microhabitat types) in Mugesera wetland (Rwanda, 1,330 m a.s.l.) was associated correspondingly with 15 anuran species, all of them shared with the community of the Butare wetland (FISCHER et al. 2011, MINDJE et al. 2020). Similar analyses on temperate, neotropical and tropical wetlands emphasize the crucial importance of environmental heterogeneity for anuran species richness (e.g., KELLER et al. 2009, COLLINS & FAHRIG 2017, FIGUEIREDO et al. 2019). Microhabitat types becoming more frequent by human action such as fish ponds facilitate the invasion of the aquatic *Xenopus victorinus* that is probably capable of limited overland-dispersal like its congener *X. laevis* (MEASEY & TINSLEY 1998, MEASEY 2016).

The presence or absence of the sedge-related species *Hyperolius cinnamomeiventris* and *H. lateralis* depends probably on the frequency of microhabitat types providing extensive sedge vegetation, a scarce resource in cultivated valley-bottom wetlands. The unexpected detection of *Sclerophrys kisoloensis* in the Gaseke side arm of the Butare wetlands may be due to the neighbouring patch of artificial gallery forest (Arboretum du Ruhande) providing a necessary habitat component of this species not present anywhere else in the studied wetlands. We conclude that geographical distance among the cultivated valley-bottom wetlands in Rwanda does not influence species composition, if they are connected by wetland corridors. Absolute species richness depends mainly on the presence of microhabitat types that are not available everywhere. Saturation of available niches by dispersal along interconnected wetland system may explain the similarity of species composition and the considerably increased species richness (melting pot of generalists) compared to near-natural habitats.

Prediction 2: Species advertising in a given microhabitat type are the same in different wetlands

The overall similarity of communities inhabiting cultivated wetlands raises the question, whether this similarity extends to specific microhabitat types. The low between-wetland variation in species number per shared microhabitat type (Table 2) indicates that available niches for reproductive activities are indeed similar and near saturated. However, rice fields and irrigation channels with vegetation challenge this conclusion because these microhabitats gave room for four additional species in Butare, which were not present in the corresponding microhabitats in Rugeramigozi. We suggest that less intensive and more variable crop production in Butare favoured anuran diversity by smaller homogeneously structured units, similar to the observed effect of field size on local amphibian abundance (COLLINS & FAHRIG 2017).

Testing the prediction that species observed in a given microhabitat type are the same in different wetlands is

hampered by the fact that most of the species advertise in many to all microhabitat types, i.e. opportunistic habitat generalist dominate the communities (low beta-diversity). Yet, mud holes with unique features differing from all other microhabitat types by little to absent vegetation provide the test case comprising a low number of species with tolerance to these conditions (Table 2).

Prediction 3: Average abundance of advertising species is similar in the same microhabitat type in different wetlands

The homogeneity in species composition at wetland and at microhabitat scales did not extend to average abundance of calling individuals in most species indicating that environmental conditions were similar, but not identical. Acoustic abundance was always biased towards the Butare wetlands suggesting generally better conditions for maintaining higher population sizes. Since effects of diel activity variation and of the distinct breeding patterns within the rainy season were accounted for, we speculate that the lower intensity of agricultural use and the more diverse crop production may allow for larger anuran population sizes in the Butare wetlands. This is in agreement with observations in neotropical rice-producing areas that management practices influence species composition and abundance of species (MACHADO & MALTCHIK 2010, GUERRA & ARÁOZ 2015, MALTCHIK et al. 2017). A proximate mechanism may be the increased survival of tadpoles to metamorphosis because of the irrigation regime provides probably longer persistence of water at the oviposition sites. In conclusion, similar species richness and composition does not imply similar population size, which seems sensitive to crop production management.

Prediction 4: Acoustic abundance (= calling activity) varies among microhabitat types

As previously demonstrated for African wetland communities, diel calling activity of anurans varies seasonally and among microhabitats (e.g., SINSCH et al. 2012, MEASEY et al. 2017, MINDJE et al. 2020). Accounting statistically for these factors, distinct strategies underlying generalist microhabitat use for advertisement become evident. *Kassina senegalensis*, one of the “jacks-of-all-microhabitats”, is present with an average density of 1.5 to 2.5 callers in all microhabitats. Omnipresence of this species at high abundances in cultivated wetlands seems to be due to the ability to occupy indiscriminately all microhabitat types without clear preference – a truly generalist habit at all spatial scales. In contrast, the reed frogs *H. kivuensis* and *H. viridiflavus* are also “jacks-of-all-microhabitats”, but show a more profound variation of acoustic abundance among microhabitats. *Hyperolius viridiflavus* was the most abundant species in artificial fish ponds, whereas *H. kivuensis* was most abundant in any kind of habitat providing me-

dium-sized reed. The generalist habit of these species does not extend to the scale of microhabitats; significant preferences for a few among the used microhabitats are discernable. We conclude that the colonisation success of generalists in agricultural wetlands is based on the ability to use all available microhabitat types, either in variable local abundances biased towards few preferred microhabitats or in even abundances at all microhabitats.

In summary, cultivated valley-bottom wetlands become the melting pot of mainly generalist species building up a species richness outnumbering natural habitats about two-fold. Homogeneous species composition is probably the result of the specific landscape configuration of wetland belts connected over hundreds of kilometres allowing for uninterrupted dispersal along these corridors.

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