



Effects of selective timber harvest on amphibian species diversity in Budongo forest Reserve, Uganda

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ABSTRACT

We studied the effects of forest management on amphibian communities in the Budongo Central Forest Reserve, Uganda. We sampled amphibians from May to August of 2012 in four compartments with different logging and arboricide-treatment histories. We used pitfall traps with drift fences combined with visual encounter surveys to sample amphibians from 36 plots in four 1-km long transects along the Sonso River. From 126 encounters across plots, we recorded 25 frog species belonging to six families and eight genera. Arthroleptidae was the most diverse family represented by 10 species within two genera. *Arthroleptis* had the highest number of species (six), *Ptychadena* the second most (five), followed by *Leptopelis* (four) and *Sclerophrys* (four). Species composition differed across transects. The unlogged study site possessed the highest species richness, diversity, and evenness, and had the greatest frequency of species encounters. The most heavily logged site had the lowest species diversity and fewest amount of species encounters. This site also had the most dissimilar species composition among sites and was significantly different in species richness compared to the unlogged site. The two moderately logged sites had the second and third most species, and had the most similar species composition to each other. Our study provides data on the amphibian species of a protected site in the Albertine Rift, part of the Eastern Afromontane biodiversity hotspot, and results suggest that the forest management regimes in Budongo have exerted an influence over the amphibian communities after more than 50 years of forest recovery.

1. Introduction

At a time when all biodiversity is increasingly threatened by human activities (Kolbert, 2014), some groups of organisms are experiencing more severe losses than others are (Dirzo et al., 2014). Amphibians, in particular, are in one the most salient and rapid declines among vertebrates (Wake & Vredenburg, 2008; Jetz & Pyron, 2018). Many factors have coalesced to erode amphibian diversity, such as globalization and disease (Scheele et al., 2019), but some aspects of amphibian declines remain enigmatic (Catenazzi, 2015). Population studies on how amphibian communities respond to environmental change will help tease apart the causative factors underlying global declines and will also provide evidence-based policies to help conserve wild species (Conde et al., 2019). However, amphibians—like most biodiversity—suffer from a lack of basic research into their population and conservation biology (Howard & Bickford, 2014). Data gaps for biodiversity exhibit extreme biases geographically (Gumbs et al., 2018; Meiri & Chapple, 2016), especially in the tropics (Stroud & Thompson, 2019). In Africa, it

is widely recognized that there is a dire need for baseline research for amphibians (Nori et al., 2018), particularly for herpetofauna in the Afrotropical realm (Tingley et al., 2016; Tolley et al., 2016). Consequently, if we want to understand the conservation outlook for amphibians, we need to collect baseline data in the Afrotropics with the aim to better understand the affect that anthropogenic activities have on species, populations, and communities.

Forest-dwelling amphibians are particularly sensitive to changes because of human-induced transformations (Blaustein et al., 1994). Anthropogenic factors affecting amphibian populations range from the obvious—habitat destruction—to the opaque—natural resource management practices—where some activities have indirect impacts, or the results are context dependent. Timber harvesting is one such management activity for which the results can be mixed, such that both positive and negative impacts have been observed for aspects of amphibian communities (deMaynadier & Hunter, 1995). Consequently, the land-management philosophy adopted by forest managers will influence the survival and persistence of the amphibian communities they oversee

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(deMaynadier & Hunter, 1998; Renken et al., 2004). The montane, tropical rainforests of Uganda harbour high levels of amphibian species diversity (Behangana et al., 2009) and are of global conservation value as a part of the Albertine Rift, the western portion of the Eastern Afrotropical biodiversity hotspot (Plumptre et al., 2007). Regions with such high levels of biodiversity as those in the Albertine Rift demand that their natural resources be managed sustainably and soundly. However, management goals in protected areas are difficult to achieve if they lack site-specific, baseline data on local species and populations, and the responses of these communities to active-management practices (Semlitsch, 2000).

Many Afrotropical rainforest preserves are bereft of ecological data on their amphibian fauna. To inform difficult management decisions, protected forests in the Afrotropical realm would benefit from data on how amphibian communities respond to management practices. We studied amphibians in the Budongo Forest Reserve of western Uganda with the goal to provide site-specific ecological data on how the local communities responded to selective logging treatments. A number of prior studies in Budongo have identified myriad effects of logging on various animal and plant groups (Plumptre, 2001), including primate diets (Tweheyo et al., 2004), climber abundance and diversity (Babweteera et al., 2000), bird communities (Owiunji and Plumptre, 1998), small mammal communities (Musamali, 1996), and primate populations (Plumptre & Reynolds, 1994). We set out to determine the distribution and diversity for various forest-dwelling amphibian species as they relate to forest management regimes along a natural water source. Our results have implications for conservation and management of amphibian communities in protected areas across montane forests of the Afrotropics.

2. Materials and methods

2.1. A note on amphibian taxonomy

The taxonomy of many East African amphibian groups is unstable and unresolved. As a result, we followed the nomenclature and distribution maps of the most recent authoritative sources, such as published books (Schlotz, 1999; Channing, 2001; Channing & Howell, 2006; Channing & Rödel, 2019) and continually updated academic websites that are managed by amphibian experts (AmphibiaWeb, 2019; Frost, 2019). Our species identifications were based on morphological traits, which we note can limit the ability to recognize cryptic species that are delimited by genetic data. Consequently, we made a concerted effort to apply contemporary nomenclature whenever possible by carefully assessing morphological characters, making visual comparison to field guides, determining species distributions from recent phylogeographic studies (Greenbaum et al., 2013; Portillo et al., 2015; Zimkus et al., 2017), taxonomic revisions (Dehling & Sinsch, 2013; Channing et al., 2016; Ohler & Dubois, 2016), and the most comprehensive guide on African frogs published to date (Channing & Rödel, 2019). For example, within the *Ptychadena mascareniensis* complex, *Ptychadena* OTU 6 (as per Zimkus et al., 2017) occurs in Uganda's section of the Albertine Rift, thus we assigned this name to a visually similar species. Also, within the *Leptopelis kivuensis* complex, *L. cf. kivuensis* 1 (as per Portillo et al., 2015) occurs in the mid- to high-elevation forests of western Uganda, thus we assigned this name to a morphological analogous species. Lastly, within the *Arthroleptis poecilnotus* complex, *Arthroleptis* aff. *poecilnotus* (as per Channing and Rödel, 2019) occurs in submontane forests in eastern Democratic Republic of the Congo and thus likely in far western Uganda by extension, thus we assigned this name to a comparable species. Furthermore, Plumptre (2001) identified *A. poecilnotus* from our study region. We took a conservative approach with respect to identifications for which we were unsure by assigning these species as unnamed members of their respective genus.

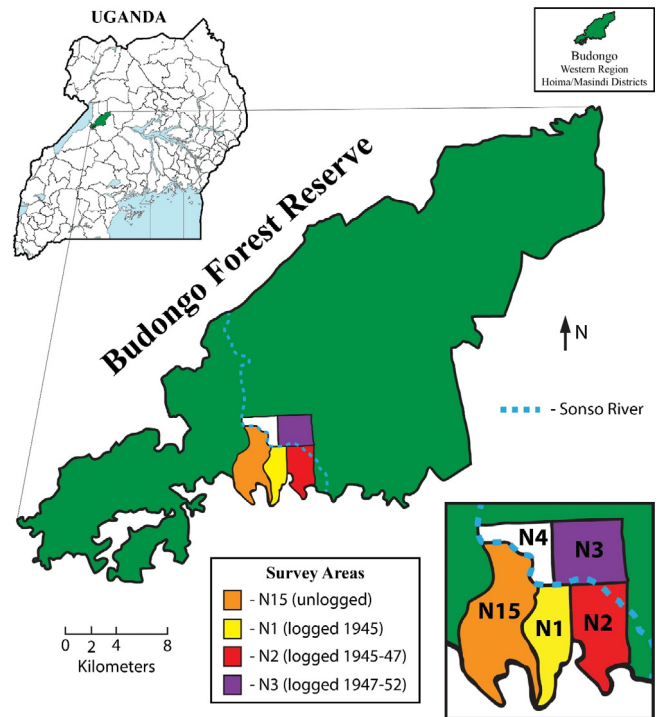


Fig. 1. Location of the four study sites in the Budongo Forest Reserve, Uganda. The map of Budongo was modified from Tweheyo et al. (2004). For the inset map of Uganda, the fine black lines represent country districts and the light-blue shading indicate major lakes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Study area

The study was conducted in Budongo Central Forest Reserve, Western Region, Masindi and Hoima Districts, Uganda (Fig. 1). Budongo was gazetted in 1932 and is one of the longest running forest-research sites in the Afrotropics (Langoya & Long, 1997). The reserve is at a mean altitude of 1100 m above sea level and the largest nearby waterbody is Lake Albert. Budongo is one of the largest of Uganda's 506 central forest reserves, covering a total area of 825 km² and comprising a moist semi-deciduous forest with some grasslands. In Budongo, annual rainfall range is 1200–2200 mm, with the two rainy seasons generally occurring from March to May and again from August to November. The mean monthly temperature range across Budongo is 19–31 °C. Eggeling (1947) identified four types of forest communities in Budongo: 1) *Cynometra* forest that is dominated by an iron wood species (*Cynometra alexandria*); 2) Mixed forest that is dominated by *Chrysophyllum albidum*, *Celtis melbraedii*, *C. zenkeri* and four species of mahoganies; 3) Colonizing forest that is dominated by *Meosopsis emunii*, *Cordia millenii*, and *Diospyros abyssinica*; and 4) Swamp forest that is composed of riparian mixed forest found along streams and where seasonal waterbodies occur. According to Eggeling (1947), the first three main forest types followed an ecological succession from colonizing forest to mixed forest and finally to *Cynometra* dominance. The forest has been under the influence of different management regimes, particularly various degrees of selective logging since the 1920s (Paterson, 1991). Budongo, along its perimeter and in some compartments, has been subjected to human activities, such as illegal logging, charcoal burning, and bush-meat hunting (Mackenzie et al., 2012; Paige et al., 2014).

2.3. History of forest management

Budongo has been divided into compartments for management purposes, each with a unique history of selective timber harvest. From 1910 to 1926, low-level timber harvest was common in Budongo brought about by the arrival of mechanical harvest methods and industrial sawmills (Paterson, 1991). From 1936 to 1957, trees were selectively harvested using an approximate rotation of thirty years to develop an “uneven-aged multi-storied high forest” (Paterson, 1991). After 1957, logging practices changed towards favouring clearcutting and arboricide treatment to alter the forest composition and encourage a more mixed forest type where the mahoganies regenerate most rapidly (Plumptre et al., 1994). The arboricide treatment was intended to kill financially unimportant tree species, such as fig trees and the ironwood species (*Cynometra*). The arboricide had the desired effect in that there was a decrease in *Cynometra* forest and an increase in mixed forest (Plumptre et al., 1994), whereas untreated and unlogged sites moved towards a dominance of ironwoods. By 1960, the Budongo sawmill facilities produced 600 tons of lumber per month, making them the largest in the country (Paterson, 1991). Approximately 80,000 acres of forest had been treated with arboricide by 1966, but this practice was curtailed in the 1970s because more tree species became marketable and it was more difficult to import the tree-killing chemicals (Synnott, 1972). The height of timber harvest and arboricide treatment at Budongo spanned from the 1930s to the 1970s, with an ostensible peak during the 1960s.

2.4. Survey sites

The study was conducted at forested sites along the Sonso River in logging compartments of the Nyakafunjo block of Budongo. Based on descriptions provided by Plumptre (1996), we selected four compartments with different logging histories to sample amphibians: N1 is a 412 ha compartment that was logged in 1945 (58.7 m³ ha⁻¹ vol of timber removed) and treated with arboricide during 1962–1963; N2 is a 630 ha compartment that was logged from 1945 to 1947 (46.2 m³ ha⁻¹ vol of timber removed) and treated with arboricide during 1955–1956; N3 is a 620 ha compartment that was logged heavily from 1947 to 1952 (80 m³ ha⁻¹ vol of timber removed) and treated with arboricide from 1959 to 1961; and N15 is a 777 ha unlogged compartment that has been classified as part of the Nature Reserve. The compartment N3 contains a human settlement associated with a field station that is located within a forest gap where Budongo’s main sawmill facilities were historically located. Compartments N1 and N2 were subjected to illegal logging by pit-sawyers between 1990 and 2000 (Babweteera et al., 2000), while N3 and N15 were not (Tweheyo et al., 2004). Even so, we cannot rule out that illegal logging may have occurred in N15 after 2001, but this compartment is protected by the Ugandan government as part of the nature reserve and thus unlikely to have experienced illegal logging (Plumptre and Reynolds, 1994). Along similar lines, we wish to point out a caveat that our reliance on logging histories of each compartment provided by Plumptre (1996) may have overlooked recent changes in forest structure and thus future studies should also include contemporary habitat characteristics alongside measures of amphibian diversity, distribution, and abundance (e.g., Hillers et al., 2008)

2.5. Experimental design and amphibian sampling

In an attempt to standardize amphibian sampling (Rödel & Ernst, 2004; Veith et al., 2004), we established four linear transects, one in each compartment, that spanned 1-km into the forest perpendicularly from the Sonso River. Each transect was established near the approximate centre of their respective compartment at a point where the river crossed through it. Along each transect, nine plots (100 m × 20 m) were demarcated at approximately 120 m intervals, using strings to

mark their boundaries. Drift fences (1 m tall × 100 m long) of plastic sheeting were installed in each of the 36 plots on the diagonal. Six pitfall traps were installed in pairs at both ends and one in the middle of each drift fence. Pitfall traps consisted of 20-liter plastic buckets buried to the rim in the ground. The traps were opened the day before a sampling day, checked for amphibians on the sampling day, and then sealed with a lid during non-sampling days (Enge, 2001). We repeated this standardized sampling regime once per week during May–August of 2012 for a total of 18 trap nights. One surveyor (LW) also sampled amphibians using Visual Encounter Surveys (VES) based on a randomized walking pattern (Crump & Scott, 1994) in each plot by splitting them into four quadrants and searching each systematically starting at dusk (1800 h), which was conducted biweekly at all plots for a total of nine nocturnal VES during the study period. To enhance detection of species that are active during the day, one surveyor (LW) conducted diurnal VES at all plots once per month in the same manner as described above for a total of four diurnal VES. We note that the sampling effort was the same across all plots for both pitfall traps and VES. Individual frogs were captured by hand during VES or retrieved from buckets, identified in the field, and released after some initial voucher specimens were prepared. Specimens were preserved whole in 100% ethanol and taken to the Makerere University Zoology Departmental Museum, Kampala, Uganda, for further examination, verification of species identification, and long-term storage.

2.6. Data analysis

To understand whether amphibian sampling was sufficient to capture most of the species diversity within this sector of the forest reserve, we calculated a sample-based rarefaction curve (Coleman et al., 1982; Gotelli, and Colwell, 2001) and compared it to a species accumulation curve. To compare amphibian assemblages among forest-management regimes, we calculated two community indices for each site: Shannon–Wiener diversity index (H') and Pielou’s evenness index (J') (Pielou, 1966). We estimated evenness at sites using the formula: $J' = H'/H'max$, where H' is the Shannon–Wiener index and $H'max$ is equal to the natural logarithm of specific richness ($\ln S$) (Jost, 2010). The value of J' ranges from 0 to 1, where 0 means species are not equally abundant and 1 means they are all equally abundant. We tested for differences in diversity between sites with different logging histories using non-parametric Mann-Whitney U tests. To test if species composition was similar across sites, we employed an Analysis of Similarity (ANOSIM) with a randomised permutation test in the Community Analysis Package 3.1 (Seaby and Henderson, 2006). The ANOSIM is based on the Bray-Curtis distance as a measure of ecological dissimilarity and evaluates the significance of defined groups by testing for differences within and between assigned groups based on 1000 randomizations (Clarke, 1993). To understand how sites related to each other with respect to shared species composition, we also employed four common similarity measures to generate dendrograms based on similarity: Jaccard Index, Bray-Curtis Similarity Index, Sørensen-Dice Index, and Euclidean Distance (Wolda, 1981).

3. Results

3.1. Heterogeneity test

The Coleman rarefaction curve was found to be slightly above the observed species accumulation curve, indicating some sample heterogeneity (Fig. 2). This result might be expected as the samples were collected from habitats with considerable differences in environmental parameters brought about by forest management regimes. Both curves reached asymptote and saturation around the same plot, thus sampling effort and time was likely sufficient to capture most of the species diversity within this region of the forest reserve. Consequently, the chances of finding more species would be relatively low if sampling was

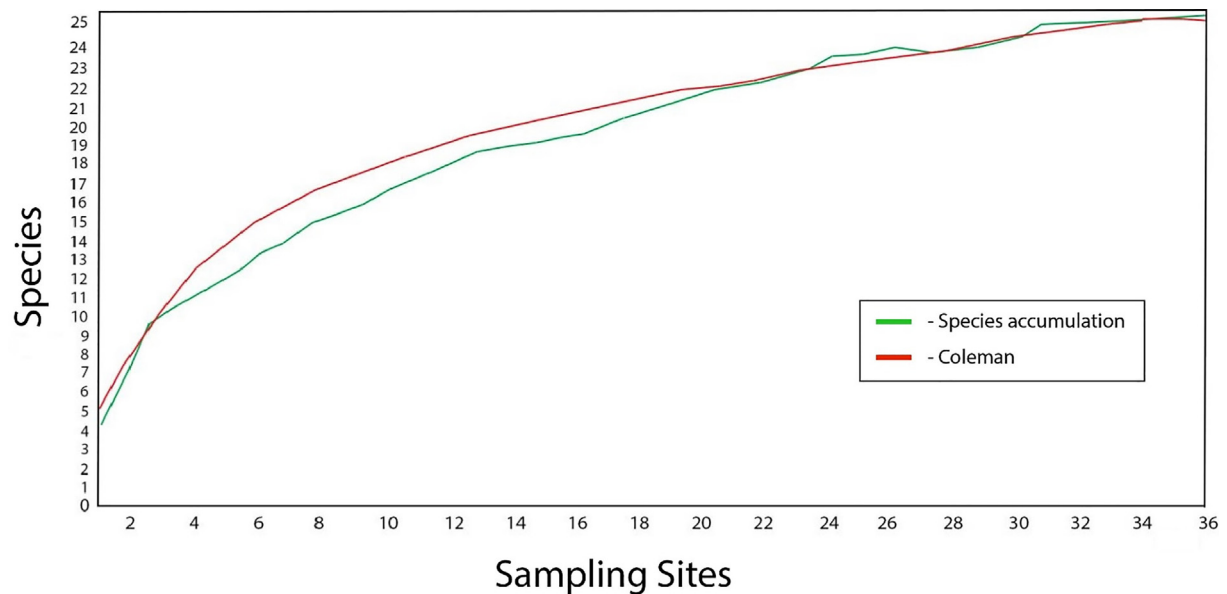


Fig. 2. Species accumulation and Coleman heterogeneity curves for 25 amphibian species across 36 plots from the Budongo Forest Reserve, Uganda.

increased.

3.2. General description of the amphibian community

From 126 encounters, we recorded a total of 25 frog species belonging to eight genera and six families across all sites (Fig. 3; Table 1). The family Arthroleptidae had the highest number of species represented by two genera, *Arthroleptis* (six species) and *Leptopelis* (four species). The families Ranidae and Bufonidae also had relatively high species diversity with five and four species, respectively. The most frequently encountered species was *Leptopelis christyi* (14 plots). *Arthroleptis* aff. *poecilnotus* and *A. stenodactylus* were encountered in 13 and 12 plots, respectively. Four species were found in all four transects and nineteen species were shared by at least two transects. All but four species were found in at least two plots.

3.3. Amphibian diversity across logging regimes

The highest species diversity was found at the unlogged site (N15), with 17 species (Table 2). The moderately logged sites N1 and N2 had 15 and 14 species, respectively. The most heavily logged site (N3) possessed 13 species, representing the lowest diversity across sites. Three species were unique to compartment N15, three were unique to N3, one to N2, yet N1 lacked any unique species. In terms of species encounters at plots, 39 occurred at N15, 34 at both N1 and N2, and 19 at N3. Species diversity index values for the sites generally follow patterns in species richness, with some notable differences (Table 2). Site N15 had the highest diversity and evenness scores, but the lowest for both of these scores was site N2. Sites N1 and N3 were in the middle range for these values, but N3 was closer to the lower-end scores of N2, while N1 was closer to the higher-end scores of N15. Species richness was significantly different only between the unlogged site (N15) and

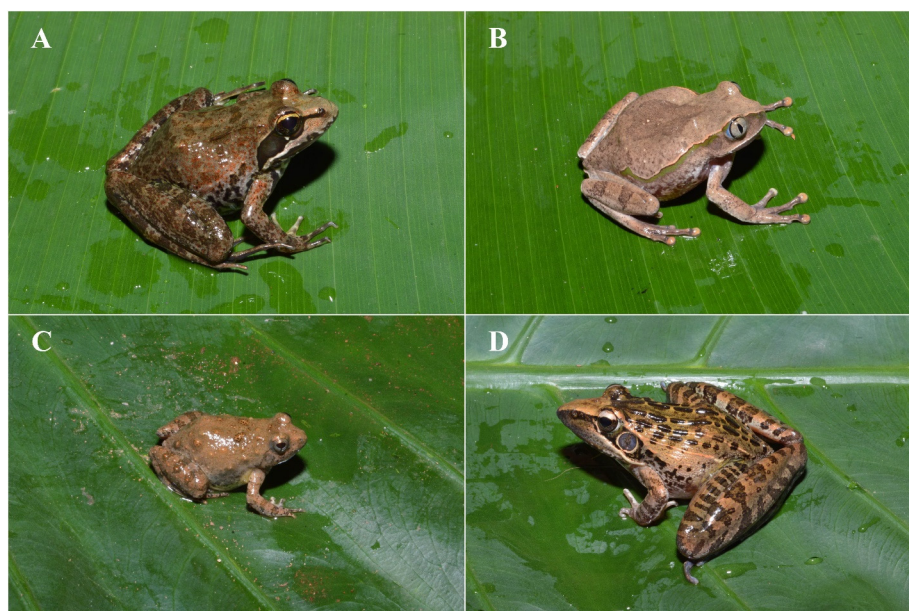


Fig. 3. Representatives of the diversity of amphibian species found in this study within the Budongo Forest Reserve, Uganda: A) river frog, *Amietia nutti*; B) treefrog, *Leptopelis christyi*; C) puddle frog, *Phrynobatrachus natalensis*; D) ridged frog, *Ptychadena oxyrhynchus*. Photos by DFH.

Table 1

Frequency of detection for 25 amphibian species in 36 plots across four transects in one unlogged and three logged compartments in the Budongo Forest Reserve, Uganda. Values represent the total number plots that a species was encountered in at each site. Data were pooled from pitfall traps and visual encounter surveys.

#	Species	N1	N2	N3	N15	TOTAL
1	<i>Ameitia nutti</i>	1	3	2	3	9
2	<i>Afrivalus quadivittatus</i>	–	–	2	–	2
3	<i>Arthroleptis adolfifridgerici</i>	–	–	–	2	2
4	<i>Arthroleptis aff. poecilnotus</i>	3	5	1	4	13
5	<i>Arthroleptis schubotzi</i>	2	–	–	1	3
6	<i>Arthroleptis stenodactylus</i>	4	3	–	5	12
7	<i>Arthroleptis variabilis</i>	3	2	–	1	6
8	<i>Hyperolius viridiflavus</i>	–	–	1	–	1
9	<i>Leptopelis sp.</i>	–	–	–	1	1
10	<i>Leptopelis christyi</i>	4	4	2	4	14
11	<i>Leptopelis cf. kivuensis</i> 1	2	1	–	1	4
12	<i>Leptopelis modestus</i>	–	1	–	1	2
13	<i>Phrynobatrachus auritus</i>	–	–	–	2	2
14	<i>Phrynobatrachus graueri</i>	1	–	1	2	4
15	<i>Phrynobatrachus natalensis</i>	1	–	1	1	3
16	<i>Phrynobatrachus perpalmatus</i>	–	–	1	–	1
17	<i>Ptychadena anchietae</i>	2	5	1	–	8
18	<i>Ptychadena christyi</i>	–	–	–	1	1
19	<i>Ptychadena nilotica</i>	1	1	1	–	3
20	<i>Ptychadena</i> OTU 6	1	–	2	–	3
21	<i>Ptychadena oxyrhynchus</i>	–	1	2	–	3
22	<i>Sclerophrys gutturalis</i>	3	1	2	3	9
23	<i>Sclerophrys kisoaloensis</i>	–	2	–	–	2
24	<i>Sclerophrys maculata</i>	4	3	–	2	9
25	<i>Sclerophrys pusilla</i>	2	2	–	5	9
TOTAL		34	34	19	39	126

Table 2

Amphibian species richness (S), Shannon-Weiner diversity index (H'), Pielou's evenness index (J'), and the history of selective timber harvest and arboricide treatment for four compartments in the Budongo Forest Reserve, Uganda.

Site	Date logged	Volume logged (m ³ h ⁻¹)	Arboricide treatment	Arboricide volume/ha	S	H'	J'
N1	1945	58.7	1962–1963	?	15	2.58	0.80
N2	1945–1947	46.2	1955–1956	11.1	14	2.48	0.77
N3	1947–1952	80.0	1959–1961	22.0	13	2.51	0.78
N15	Never	–	Never	–	17	2.66	0.82

Table 3

Pairwise comparison of amphibian species composition between compartments in the Budongo Forest Reserve, Uganda. ANOSIM R-values top right and corresponding P-values bottom left.

	N1	N2	N3	N15
N1	–	0.45	0.31	0.45
N2	0.001	–	0.23	0.30
N3	0.001	0.005	–	0.39
N15	0.001	0.001	0.001	–

the most heavily logged site (N3) (Mann-Whitney U, $Z = 2.34$, $P = 0.019$). Species composition was found to be dissimilar among the transects (ANOSIM, $R = 0.15$, $P = 0.005$), but with a low R-value suggesting that the effect of logging on species composition across sites was diluted. Pairwise comparisons, however, revealed much higher R-values indicating that sites were statistically dissimilar in species composition when compared directly (Table 3). In terms of shared species, all four similarity measures produced identical branching topologies in the dendrograms, with differences exhibited in the strength of similarity between sites (Fig. 4). The moderately logged sites (N1 and N2) were the most similar to each other, the unlogged site

(N15) was most similar to the N1–N2 cluster, and the most heavily logged site (N3) was the least similar to the others.

4. Discussion

One previous study in Budongo, conducted from June to August in 1996, compared amphibians in two compartments—one logged (B1) and one unlogged (N15) site—and found that two leaf-litter species of the genus *Arthroleptis* dominated captures (greater than 90% at both sites) and that density, but not diversity or evenness, was highest at the unlogged site (Plumptre, 2001). In contrast, we found that the same unlogged site (N15), approximately 16 years later, had the highest diversity and evenness among the four sites we sampled, but we note that we did not measure density, nor did we sample in the same logged site (B1). Plumptre (2001) found 22 amphibian species from 173 captures at N15 and 22 species from 151 captures at B1 with a total of 23 different species combined (i.e., most species were shared across sites). We found a total of 25 species across four compartments: 17 species at N15, 15 species at N1, 14 species at N2, and 13 species at N3 with four species shared across all sites and eight species restricted to single sites. Furthermore, we found that many species were encountered in just one (or two) of the nine plots at each compartment and that no species were encountered in more than five plots at a single site. Among our four study compartments, N3 was the most heavily logged over the longest period and had the highest levels of arboricide treatments; it also, perhaps coincidentally, had the lowest species richness, fewest number of encounters, and was most dissimilar in species composition to other sites. We note that without data on the amphibian communities prior to forest treatments, it is difficult to assess whether the differences we detected among compartments is due to the management regimes or some other factor. The forest management regime at N3 sought to achieve a mixed forest type and thus would have exerted an influence over the canopy cover and consequently moisture retention in the leaf litter. Although we did not measure forest structure, the changes due to logging may be reflected in the frog species found at N3, with a relative dearth of leaf-litter specialists in the genus *Arthroleptis* and generally more species that occupy more open-canopy habitats, such as ridged frogs (*Ptychadena*) and puddle frogs (*Phrynobatrachus*). In contrast, the unlogged site N15, with presumably greater canopy cover and leaf-litter retention, was dominated by more forest-dwelling frogs, such as species of *Arthroleptis* and *Leptopelis*.

Species composition and abundance of amphibian communities in tropical forests are influenced by a variety of biotic and abiotic factors, including vegetation zones (Allmon, 1991), climatic seasonality (Vonesh, 2001), and moisture gradients (Pearman et al., 1995). Anthropogenic factors, such as active forest management practices, can also strongly affect aspects of amphibian communities (deMaynadier and Hunter, 1995), with both positive and negative effects on richness and density (deMaynadier and Hunter, 1998; Ernst et al., 2007). In Kibale National Park, Uganda, Vonesh (2001) found that herpetofauna diversity and evenness was greater in unlogged sites than logged sites, but that a pine-tree plantation unexpectedly had the highest diversity and evenness values. In Edo State, Nigeria, Ogoanah (2011) likewise found a trend of lower amphibian species richness with higher logging intensity in several forest sites. From miombo-mopane woodlands in Tanzania, Gardner et al. (2007) found that conversion of native forest habitats for cultivation reduced amphibian diversity. In the Niger Delta, Nigeria, Akani et al. (2004) found that amphibian species diversity was highest in pristine forest sites, and that oil producing sites had a homogenising effect on the amphibian communities by reducing the community composition to the few most tolerant species. In Tai National Park, Ivory Coast, Ernst et al. (2006) found that amphibian community evenness, but not species richness, was higher in unlogged sites and that functional diversity was higher in primary forests than exploited forests. Across studies, logging not only has shown to affect African amphibian communities with respect to eroding species

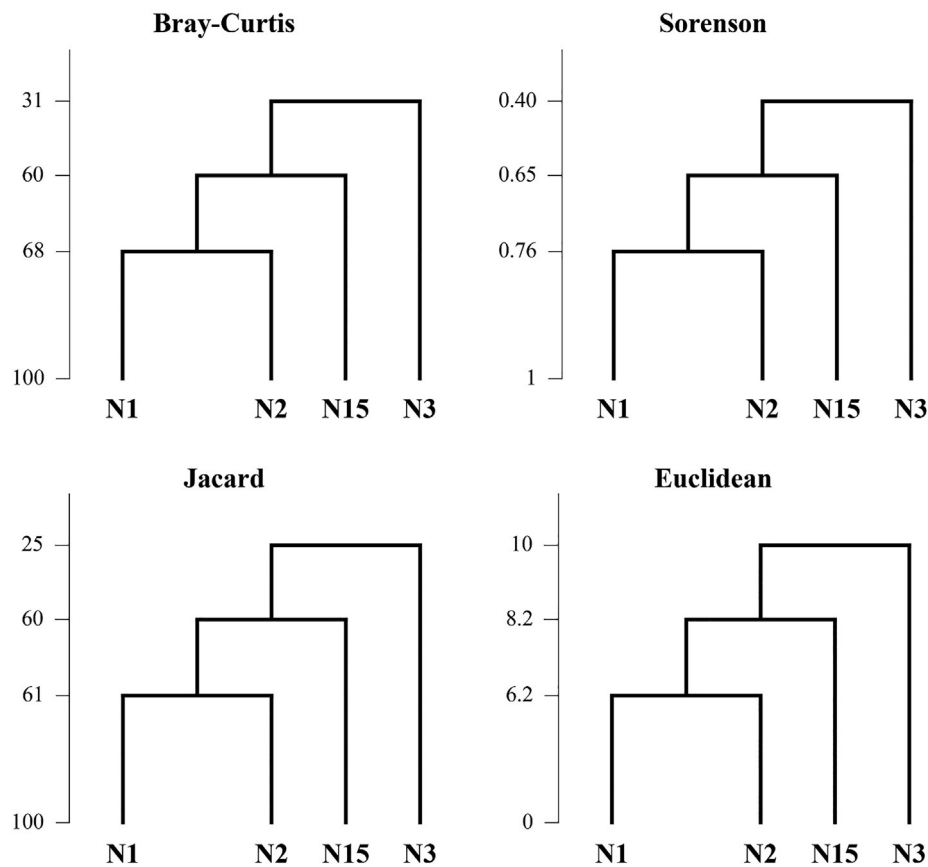


Fig. 4. Similarity dendrograms for amphibian communities at four study sites in the Budongo Forest Reserve, Uganda.

diversity, abundance, and functional diversity (Ernst et al., 2007), but it can also filter out species that cannot cope ecologically or physiologically with altered microclimates (Ernst and Rödel, 2005).

Comparisons between anuran assemblages across the tropical biome can lead to the discovery of general patterns of community structure (Inger, 1980; Scott, 1976) and help us understand how to optimally manage the remaining biodiversity during the Anthropocene (Barlow et al., 2018). The Budongo Central Forest Reserve is within the Albertine Rift, which is a part of the Eastern Afromontane biodiversity hotspot (Plumptre et al., 2007, 2019; Wei et al., 2019). Consequently, understanding the impacts that forest management practices, such as selective logging, have on Albertine Rift amphibians is of global conservation importance (Nori et al., 2018). There is dire need for further surveys into the effects of logging on the amphibians in Budongo, the Albertine Rift, and sub-Saharan Africa in general (Hofer and Bersier, 2001). In fact, this type of study in Africa has lagged far behind those in the Americas, where the impacts of logging on amphibians has been well documented (Allmon, 1991; Bell & Donnelly, 2006; deMaynadier & Hunter, 1995; Renken et al., 2004; Scott, 1976; Vitt and Caldwell, 2001). We found that amphibian communities in Budongo exhibited differences in species richness and composition more than a half-century after selective logging occurred in the forest. Our study highlights the conservation need for long-term studies of amphibian diversity and distribution in Budongo and other protected areas in Uganda (Plumptre et al., 2019) to understand how this globally unique segment of biodiversity responds to management practices at greater spatiotemporal scales in the Afrotropical realm.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to

influence the work reported in this paper.

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Author Contributions

W.L., M.B., and E.N.M. conceived of and designed the experiments; W.L. collected the data with help from M.B.; D.F.H. and W.L. performed the analysis; W.L. wrote the original manuscript with input from M.B. and E.N.M.; D.F.H. wrote the paper with approval from all authors.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117809>.

References

- Akani, G.C., Politano, E., Luiselli, L., 2004. Amphibians recorded in forest swamp areas of the River Niger Delta (southeastern Nigeria), and the effects of habitat alteration from oil industry development on species richness and diversity. *Appl. Herpetol.* 2, 1–22.
- Allmon, W.D., 1991. A plot study of forest floor litter frogs, Central Amazon, Brazil. *J. Trop. Ecol.* 7, 503–522.
- AmphibiaWeb, 2019. <https://amphibiaweb.org>. University of California, Berkeley, CA, USA. Accessed: 1 June 2019.
- Babweteera, F., Plumptre, A.J., Obua, J., 2000. Effect of gap size and age on climber abundance and diversity in Budongo Forest Reserve, Uganda. *Afr. J. Ecol.* 38, 230–237.
- Barlow, J., França, F., Gardner, T.A., Hicks, C.C., Lennox, G.D., Berenguer, E., Castello, L.,

- Economu, E.P., Ferreira, J., Guenard, B., Leal, C.G., 2018. The future of hyperdiverse tropical ecosystems. *Nature* 559, 517–526.
- Behangana, M., Kasoma, P.M., Luiselli, L., 2009. Ecological correlates of species richness and population abundance patterns in the amphibian communities from the Albertine Rift, East Africa. *Biodivers. Conserv.* 18, 2855–2873.
- Bell, K.E., Donnelly, M.A., 2006. Influence of forest fragmentation on community structure of frogs and lizards in northeastern Costa Rica. *Conserv. Biol.* 20, 1750–1760.
- Blaustein, A.R., Wake, D.B., Sousa, W.P., 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conserv. Biol.* 8, 60–71.
- Catenazzi, A., 2015. State of the world's amphibians. *Annu. Rev. Environ. Resour.* 40, 1–29.
- Channing, A., 2001. *Amphibians of Central and Southern Africa*. Cornell University Press, Ithaca, New York.
- Channing, A., Howell, K.M., 2006. *Amphibians of East Africa*. Cornell University Press, Ithaca, New York.
- Channing, A., Dehling, J.M., Lötters, S., Ernst, R., 2016. Species boundaries and taxonomy of the African river frogs (Amphibia: Pyxicephalidae: *Amietia*). *Zootaxa* 4155, 1–76.
- Channing, A., Rödel, M.-O., 2019. *Field Guide to the Frogs & Other Amphibians of Africa*. Penguin Random House, South Africa.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18, 117–143.
- Coleman, B.D., Mares, M.A., Willig, M.R., Hsieh, Y.H., 1982. Randomness, area, and species richness. *Ecology* 63, 1121–1133.
- Conde, D.A., Staerk, J., Colchero, F., da Silva, R., Schöley, J., Baden, H.M., Jouvett, L., Fa, J.E., Syed, H., Jongejans, E., Meiri, S., 2019. Data gaps and opportunities for comparative and conservation biology. *Proc. Natl. Acad. Sci. U.S.A.* 116, 9658–9664.
- Crump, M.L., Scott, N.J., 1994. Visual encounter surveys. In: Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.C., Foster, M.S. (Eds.), *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, DC, pp. 84–92.
- Dehling, J.M., Sinsch, U., 2013. Diversity of ridged frogs (Anura: Ptychadenidae: *Ptychadena* spp.) in wetlands of the upper Nile in Rwanda: morphological, bioacoustic, and molecular evidence. *Zoologischer Anzeiger – J. Comp. Zool.* 253, 143–157.
- DeMaynadier, P.G., Hunter Jr., M.L., 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. *Environ. Rev.* 3, 230–261.
- DeMaynadier, P.G., Hunter Jr., M.L., 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conserv. Biol.* 12, 340–352.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the anthropocene. *Science* 345, 401–406.
- Egging, W.J., 1947. Observations on the ecology of the Budongo rain forest, Uganda. *J. Ecol.* 34, 20–87.
- Enge, K.M., 2001. The pitfalls of pitfall traps. *J. Herpetol.* 35, 467–478.
- Ernst, R., Rödel, M.-O., 2005. Anthropogenically induced changes of predictability in tropical anuran assemblages. *Ecology* 86, 3111–3118.
- Ernst, R., Linsenmair, K.E., Rödel, M.-O., 2006. Diversity erosion beyond the species level: dramatic loss of functional diversity after selective logging in two tropical amphibian communities. *Biol. Conserv.* 133, 143–155.
- Ernst, R., Linsenmair, K.E., Thomas, R., Rödel, M.-O., 2007. Amphibian communities in disturbed forests: lessons from the Neo- and Afrotropics. In: Tschirntke, T., Leuschner, C., Zeller, M., Guhardja, E., Bidin, A. (Eds.), *Stability of Tropical Rainforest Margins*. Springer, Berlin.
- Frost, D.R., 2019. *Amphibian species of the world: An online reference*. Version 6.0 (1 June 2019). American Museum of Natural History, New York, USA. <http://research.amnh.org/herpetology/amphibia/index.html>.
- Gardner, T.A., Fitzherbert, E.B., Drewes, R.C., Howell, K.M., Caro, T., 2007. Spatial and temporal patterns of diversity in an East African leaf-litter amphibian fauna. *Biotropica* 39, 105–113.
- Greenbaum, E., Sinsch, U., Lehr, E., Valdez, F., Kusamba, C., 2013. Phylogeography of the reed frog *Hyperolius castaneus* (Anura: Hyperoliidae) from the Albertine Rift of Central Africa: implications for taxonomy, biogeography and conservation. *Zootaxa* 3131, 473–494.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391.
- Gumbs, R., Gray, C.L., Wearn, O.R., Owen, N.R., 2018. Tetrapods on the EDGE: overcoming data limitations to identify phylogenetic conservation priorities. *PLoS ONE* 13, e0194680.
- Hillers, A., Veith, M., Rödel, M.-O., 2008. Effects of forest fragmentation and habitat degradation on West African leaf-litter frogs. *Conserv. Biol.* 22, 762–772.
- Hofer, U., Bersier, L.F., 2001. Herpetofaunal diversity and abundance in tropical upland forests of Cameroon and Panama. *Biotropica* 33, 142–152.
- Howard, S.D., Bickford, D.P., 2014. Amphibians over the edge: silent extinction risk of data deficient species. *Divers. Distrib.* 20, 837–846.
- Inger, R.F., 1980. Densities of floor-dwelling frogs and lizards in lowland forests of Southeast Asia and Central America. *Am. Nat.* 115, 761–770.
- Jetz, W., Pyron, R.A., 2018. The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nat. Ecol. Evol.* 2, 850–858.
- Jost, L., 2010. The relation between evenness and diversity. *Diversity* 2, 207–232.
- Kolbert, E., 2014. *The Sixth Extinction: An Unnatural History*. Henry Holt, New York.
- Langoya, C.D., Long, C., 1997. Local communities and ecotourism development in Budongo forest reserve, Uganda. *Rural Dev. For. Network Pap.* 22e, 1–13.
- Mackenzie, C.A., Chapman, C.A., Sengupta, R., 2012. Spatial patterns of illegal resource extraction in Kibale National Park, Uganda. *Environ. Conserv.* 39, 38–50.
- Meiri, S., Chapple, D.G., 2016. Biases in the current knowledge of threat status in lizards, and bridging the 'assessment gap'. *Biol. Conserv.* 204, 6–15.
- Musamali, P.B., 1996. *The ecology, diversity and relative abundance of small mammals in primary and disturbed forest compartments of Budongo Forest Reserve*. MS Thesis, Makerere University, Kampala, Uganda.
- Nori, J., Villalobos, F., Loyola, R., 2018. Global priority areas for amphibian research. *J. Biogeogr.* 45, 2588–2594.
- Ogoanah, S.O., 2011. Effects of lumbering and farming activities on the amphibians of selected parts of Edo State, Nigeria. *Afr. Sci.* 12, 201–208.
- Ohler, A., Dubois, A., 2016. The identity of the South African toad *Sclerophrys capensis* Tschudi, 1838 (Amphibia, Anura). *PeerJ* 4, 1–13.
- Owionji, I., Plumptre, A.J., 1998. Bird communities in logged and unlogged compartments in Budongo Forest, Uganda. *For. Ecol. Manage.* 108, 115–126.
- Paige, S.B., Frost, S.D., Gibson, M.A., Jones, J.H., Shankar, A., Switzer, W.M., Ting, N., Goldberg, T.L., 2014. Beyond bushmeat: animal contact, injury, and zoonotic disease risk in Western Uganda. *EcoHealth* 11, 534–543.
- Paterson, J.D., 1991. The ecology and history of Uganda's Budongo Forest. *For. Conserv. Hist.* 35, 179–187.
- Pearman, P.B., Velasco, A.M., López, A., 1995. Tropical amphibian monitoring: a comparison of methods for detecting inter-site variation in species' composition. *Herpetologica* 51, 325–337.
- Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.* 13, 131–144.
- Plumptre, A.J., 1996. Changes following 60 years of selective timber harvesting in the Budongo Forest Reserve, Uganda. *For. Ecol. Manage.* 89, 101–113.
- Plumptre, A.J., Reynolds, V., 1994. The effect of selective logging on primate population of Budongo forest, Uganda. *J. Appl. Ecol.* 31, 631–641.
- Plumptre, A.J., 2001. The effects of habitat change due to selective logging on the fauna of forests in Africa. In: William, W., White, L.J.T., Vedder, A., Naughton-Treves, L. (Eds.), *African Rain Forest Ecology and Conservation: An Interdisciplinary Perspective*. Yale University Press, New Haven, Connecticut, pp. 463–479.
- Plumptre, A.J., Davenport, T.R., Behangana, M., Kityo, R., Eilu, G., Segawa, P., Ewango, C., Meirte, D., Kahindo, C., Herremans, M., Peterhans, J.K., 2007. The biodiversity of the albertine rift. *Biol. Conserv.* 134, 178–194.
- Plumptre, A.J., Ayebare, S., Behangana, M., Forrest, T.G., Hatanga, P., Kabuye, C., Kirunda, B., Kityo, R., Mugabe, H., Namaganda, M., Nampindo, S., 2019. Conservation of vertebrates and plants in Uganda: identifying key biodiversity areas and other sites of national importance. *Conserv. Sci. Pract.* 1, e7.
- Portillo, F., Greenbaum, E., Menegon, M., Kusamba, C., Dehling, J.M., 2015. Phylogeography and species boundaries of *Leptopelis* (Anura: Arthroleptidae) from the Albertine Rift. *Mol. Phylogenet. Evol.* 82, 75–86.
- Renken, R.B., Gram, W.K., Fantz, D.K., Richter, S.C., Miller, T.J., Ricke, K.B., Russell, B., Wang, X., 2004. Effects of forest management on amphibians and reptiles in Missouri Ozark forests. *Conserv. Biol.* 18, 174–188.
- Rödel, M.-O., Ernst, R., 2004. Measuring and monitoring amphibian diversity in tropical forests. I. An evaluation of methods with recommendations for standardization. *Ecotropica* 10, 1–14.
- Scheele, B.C., Pasmans, F., Skerratt, L.F., Berger, L., Martel, A., Beukema, W., Acevedo, A.A., Burrows, P.A., Carvalho, T., Catenazzi, A., De la Riva, I., 2019. Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. *Science* 363, 1459–1463.
- Scott Jr., N.J., 1976. The abundance and diversity of the herpetofaunas of tropical forest litter. *Biotropica* 8, 41–58.
- Seaby, R.M., Henderson, P.A., 2006. *Species diversity and richness (SDR) version 4*. Pisces conservation Ltd., Lymington, England. <http://www.pisces-conservation.com/sof-diversity.html>.
- Semlitsch, R.D., 2000. Principles for management of aquatic-breeding amphibians. *J. Wildl. Manag.* 64, 615–631.
- Schiotz, A., 1999. *Treefrogs of Africa*. Frankfurt am Main, Germany: Edition Chimaira.
- Synnott, T.J., 1972. Now an up-to-date report on the Budongo forest chimps. *Africana* 4, 10–11.
- Stroud, J.T., Thompson, M.E., 2019. Looking to the past to understand the future of tropical conservation: the importance of collecting basic data. *Biotropica* 51, 293–299.
- Tingley, R., Meiri, S., Chapple, D.G., 2016. Addressing knowledge gaps in reptile conservation. *Biol. Conserv.* 204, 1–5.
- Tolley, K.A., Alexander, G.J., Branch, W.R., Bowles, P., Maritz, B., 2016. Conservation status and threats for African reptiles. *Biol. Conserv.* 204, 63–71.
- Tweheyo, M., Lye, K.A., Weladji, R.B., 2004. Chimpanzee diet and habitat selection in the Budongo Forest Reserve, Uganda. *For. Ecol. Manage.* 188, 267–278.
- Veith, M., Lötters, S., Andreone, F., Rödel, M.-O., 2004. Measuring and monitoring amphibian diversity in tropical forests. II. Estimating species richness from standardized transect censusing. *Ecotropica* 10, 85–99.
- Vitt, L.J., Caldwell, J.P., 2001. The effects of logging on reptiles and amphibians of tropical forests. In: Fimbel, R.A., Grajal, A., Robinson, J. (Eds.), *The Cutting Edge*. Columbia University Press, New York, pp. 239–260.
- Vonesh, J.R., 2001. Patterns of richness and abundance in a tropical African leaf-litter herpetofauna. *Biotropica* 33, 502–1110.
- Wake, D.B., Vredenburg, V.T., 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proc. Natl. Acad. Sci. U.S.A.* 105, 11466–11473.
- Wei, F., Wang, S., Fu, B., Liu, Y., 2019. Representation of biodiversity and ecosystem services in East Africa's protected area network. *Ambio*. <https://doi.org/10.1007/s13280-019-01155-4>.
- Wolda, H., 1981. Similarity indices, sample size and diversity. *Oecologia* 50, 296–302.
- Zimkus, B.M., Lawson, L.P., Barej, M.F., Barratt, C.D., Channing, A., Dash, K.M., Dehling, J.M., Du Preez, L., Gehring, P.S., Greenbaum, E., Gvoždík, V., 2017. Leapfrogging into new territory: how Mascarene ridged frogs diversified across Africa and Madagascar to maintain their ecological niche. *Mol. Phylogenet. Evol.* 106, 254–269.