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Spatial and Temporal Patterns of Abundance and Diversity of an East African Leaf Litter Amphibian Fauna

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ABSTRACT

We present data on sample richness, relative abundance, and community structure of a leaf litter amphibian assemblage from globally important miombo-mopane woodlands characteristic of western Tanzania. We describe patterns of diversity across major habitat types and between different seasons from an annual pitfall-trapping campaign. We recorded 28 species of amphibians, which is significantly higher than existing richness estimates for other miombo woodland sites elsewhere in sub-Saharan Africa. We found that cultivation of native habitat reduces frog diversity, a conclusion that has important implications in light of the rapid conversion of miombo woodland for agriculture and fuel-wood across much of southern and central Africa. Many species showed strongly ansynchronized patterns of seasonality in relative abundance, which has significant implications for the establishment of successful monitoring programs and biodiversity surveys. These conclusions emphasize the importance of stratified long-term sampling in biodiversity studies and demonstrate that superficial levels of sampling effort can lead to erroneous conclusions regarding patterns of diversity in amphibian communities. The relatively poor focus on herpetofaunal research in African miombo-mopane woodland is out of proportion to its ecological and conservation significance.

Key words: amphibians; miombo woodland; patterns of biodiversity; Tanzania; tropical dry forest.

There is now a growing consensus in the scientific community that amphibian populations have been experiencing catastrophic declines across many areas of the world within the last few decades (Houlahan *et al.* 2000, Semlitsch 2003, Lips *et al.* 2005a), declining at a faster rate than either mammals or birds (Stuart *et al.* 2004). Amphibians therefore currently represent some of the most endangered vertebrate taxa (IUCN 2004, Stuart *et al.* 2004). Although we are starting to understand the nature of threats faced by amphibian populations, including habitat change (Sala *et al.* 2000), and the role of more enigmatic stressors such as disease, global climate change, UV-radiation, and aquatic pollutants (Semlitsch 2003), we still know surprisingly little about amphibian ecology including patterns of spatial and temporal variability in richness and abundance (Pechmann *et al.* 1991). In light of their sensitivity to environmental change, it is particularly important that we understand baseline patterns of amphibian diversity and habitat preferences in areas that still retain relatively intact habitat. Such basic data are necessary to monitor population declines, and evaluate impacts of different conservation options.

There is a paucity of data on tropical amphibian populations and communities, owing to a biogeographic bias in studies toward temperate and subtropical regions. Studies that do focus on patterns of habitat use of tropical amphibian populations are further biased toward research in tropical wet forests (*e.g.*, Crump 1971, Scott 1976, Inger & Colwell 1977, Duellman 1978), with the majority of studies having been conducted in the Neotropics (Crump 1971, Scott 1976, Duellman 1978, Aichinger 1987, Gentry 1990, Allmon 1991, Heinen 1992, Duellman 1995, Pearman 1997, Lips *et al.* 2005b), and SE Asia (Lloyd *et al.* 1968, Scott 1976, Inger & Colwell 1977, Inger 1980, Inger & Voris 1993). Few data are available from any African ecosystem, with most existing studies having also focused on wet tropical forests (Hofer & Bersier 2001, Vonesh 2001) or wetland habitat (*e.g.*, Raxworthy & Attuquayefio 2000), with a virtual absence of ecological data on amphibian communities from seasonally arid African savannahs or dry forests (but see Hinde *et al.* 2001, Flemming & Loveridge 2003). Despite this lack of attention to savannas and dry woodlands, these biomes have been identified as globally important wilderness areas, and

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are therefore worthy of conservation attention (Mittermeier *et al.* 2003).

In this study, we provide information on the diversity and ecology of a dry forest amphibian fauna from western Tanzania, within the miombo-mopane wilderness area (Mittermeier *et al.* 2003). Although miombo woodland has been recognized to be of global importance for biodiversity conservation, much of the area is increasingly threatened by habitat degradation following conversion to agriculture or overharvesting (Abbot & Homewood 1999, Caro 1999a, Mittermeier *et al.* 2003). Information on the consequences of habitat conversion for East African amphibians is scarce and mostly restricted to wet forest habitats (*e.g.*, Vonesh 2001), with few studies having focused on miombo woodlands (but see Hinde *et al.* 2001). To our knowledge, ours is the first study to report on the consequences of the conversion of miombo woodland to cultivated land for amphibians in East Africa.

Tanzania hosts one of the most diverse amphibian faunas in sub-Saharan African (Poynton 1998). Understanding of the taxonomy and ecology of Tanzanian amphibians is poor (Howell 2000), as evidenced by the number of new species being described in recent years (Channing & Minter 2004, Crutsinger *et al.* 2004). Those studies that have been conducted are restricted to geographical distribution summaries (Channing *et al.* 2004) or biogeographical comparisons of species lists (Poynton & Boycott 1996, Howell 2000) and information describing community structure and spatiotemporal patterns of species abundance is scarce for Tanzania and largely confined to forest habitats in the Eastern-Arc forests (Howell 1993, 2000; but see also Msuya 2001, Vonesh 2001). Here, we describe patterns of sample richness, relative abundance, and species composition across major habitat types characteristic of the study area (woodland, riverine, flooded grasslands, and cultivated habitat), as well as patterns of richness and relative abundance across three seasons.

METHODS

STUDY AREA.—The study was conducted in and around Katavi National Park (latitude 6°45′ to 7°05′ S, longitude 30°45′ to 31°25′ E, *ca* 800 m a.s.l., in Mpanda District, at the north end of Rukwa Valley, western Tanzania; Fig. 1), between August 2002 and April 2003. The area consists largely of miombo woodland, a dry deciduous forest characterized by *Acacia*, *Brachystegia*, *Combretum*, *Commifora*, *Grewia*, *Kigelia*, *Pterocarpus*, *Sterculia*, and *Terminalia* tree species (Schwartz & Caro 2003). Katavi National Park hosts some of the highest densities of large mammals of any reserve in Tanzania (Caro 1999b). The area generally experiences one wet season between October or November and April. Total rainfall during the study period was 759 mm, which was equal to the total annual rainfall as no further rain fell between May and August.

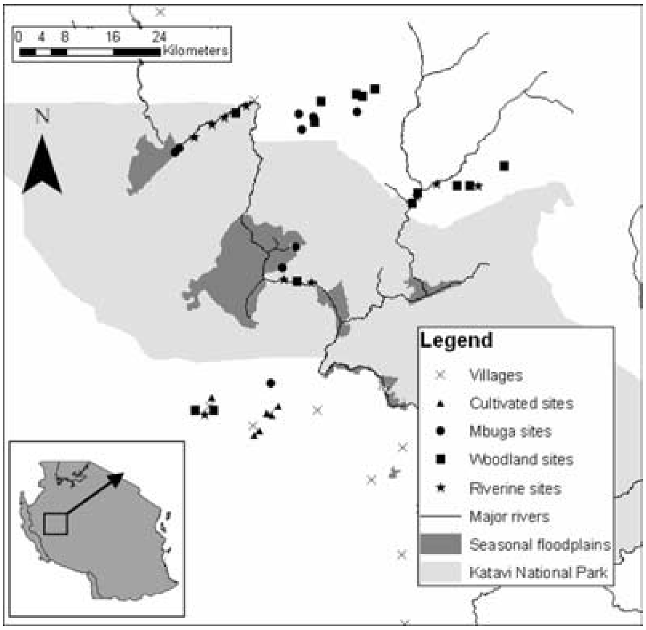

FIGURE 1. Map of study area showing our study sites, Katavi National Park and neighboring areas in Rukwa Region, western Tanzania.

Most of the major rivers that run through the area are seasonal. The main Katuma River connects three large seasonally flooded grasslands: Lake Katavi, the Katisunga mbuga ("mbuga" defines an area of seasonally flooded grassland), and Lake Chada. Both temporary and permanent pools, springs, and wallows can be found throughout the area, although there are relatively few streams. Within this landscape matrix, we stratified our study sites with respect to four major habitat types: woodland, riverine, mbuga, and cultivated habitats (Fig. 1). Woodland habitat refers to areas of miombo woodland with tree canopy cover exceeding 20 percent, and woodland sites were located more than 500 m from a river edge, although often close to seasonal pools and flooded areas. Riverine habitat was defined as the area within a 10 m strip of land adjacent to a major seasonal or permanent river. These areas had varying tree-canopy cover. Mbuga habitats are open grasslands with less than 5 percent tree cover, which are seasonally inundated during the wet season. Cultivated habitat included areas with small-scale, low-intensity farming, mostly for maize, peanuts, bananas, sugarcane and cassava. Prior to cultivation, cultivated areas were covered by miombo woodland, similar to that in the rest of the landscape, with a matrix of open and closed woodland, seasonal rivers and flooded grassland.

SAMPLING METHODS.—We sampled a total of 41 sites in an area of approximately 250,000 ha (Fig. 1), over a period of eight months. Most sites were surveyed across three seasons: late-dry (August–October, total rain = 5 mm), early-wet (November–January, total rain = 474 mm) and late-wet (February–April, total rain = 280 mm). The 2002–2003 wet season was abnormal in that there was almost no rain during February and relatively little in April. Fourteen sites were surveyed three times, 22 were surveyed only during two seasons, and the remaining five sites were surveyed only once.

During a visit, each site was sampled over a 4- or 5-d trapping session. During each trapping session, three drift-fence pit-trap arrays were placed at the site, each separated by at least 100 m. A single array consisted of three 20 liter buckets buried level with the ground, separated by a 0.5-m high, 5-m long, fence of plastic sheeting. Up to five sites were sampled simultaneously during any one trapping session, with an average total sampling effort of 40 trap nights per site in one session. The total sampling effort was 3426 trap nights across all sites during the study.

Each trap array was checked for captures every morning. All individuals captured were identified to species in the field using Channing (2001), and the majority were then released at a similar site more than 500 m away to avoid recaptures, or they were collected and preserved as voucher specimens now held at the California Academy of Sciences, San Francisco, California (catalogue numbers available on request from the authors). Opportunistic surveys were also conducted away from trap lines and among nocturnal breeding choruses of amphibians. However, the focus of sampling effort was on pitfall trapping which provided the data for all analyses in this paper.

ANALYSES.—Owing to differences in abundance and sampling effort, patterns of species richness among habitats and seasons were compared using both rarefaction analyses and a suite of species-richness estimators. To account for spatial heterogeneity in species richness among sites within any one habitat or season, we used sample-based rarefaction curves, with the site as the sample unit (Gotelli & Colwell 2001). Differences in species richness among communities were tested by observing whether the rarefaction curve of the most species poor community lay within the 95% confidence limits of the rarefaction curve of the most species rich community at the point of equal abundance (Magurran 2004). As an alternative technique for controlling differences in sampling effort across habitat types, we employed a suite of true richness estimators. The performance of different richness estimators varies depending on differences in richness, sampling effort, and community evenness (Colwell & Coddington 1994), and the relative biases and inaccuracies remain poorly understood, meaning that the most robust estimates are often only for the lower and upper boundaries (O'Hara 2005). Thus we used a combination of eight parametric and nonparametric indicators (the two coverage estimators ICE and ACE, Chao 1, Chao 2, first- and second-order Jack-knife, the bootstrap, and Michealis Menton [MM] Model; Colwell 2004). Occasional species, which were represented by three or fewer individuals, were excluded from richness analyses. Rarefaction curves and species-richness estimates were produced using EstimateS Version 7 (Colwell 2004).

Patterns of species abundances were evaluated using a relative abundance index calculated as the total number of individuals caught divided by the for a given treatment trapping effort. We recognize that because our data actually represent patterns of frog capturability in pitfall traps, these data are not measures of absolute abundance and therefore only reflect patterns of apparent abundance. Nevertheless, all trapping and sampling techniques contain a systematic bias toward favoring certain more susceptible species and providing the detection biases toward certain species are consistent among habitats and seasons (*i.e.*, their behavior does not overly change), pitfall trapping remains a useful method for the comparison of relative abundances (Heyer *et al.* 1994).

Due to nonnormality in the data, differences in relative abundances between months and habitat types were tested using the Kruskal–Wallis nonparametric equivalent of analysis of variance. Seasonality in relative abundance for individual amphibian species was also tested using a nonparametric serial runs test. Statistical tests were conducted using SPSS v. 11.5 (SPSS, Chicago, IL, U.S.A).

Differences in community structure and species composition between habitats were evaluated graphically using nonmetric multidimensional scaling (MDS) ordination. MDS was chosen over other ordination methods because it makes fewer assumptions about the data distribution, and enables the use of a similarity index that excludes joint absences and provides a visually intuitive summary of similarity among sites (Clarke & Warwick 1994). Similar matrices were produced using the site-standardized Bray–Curtis similarity index and square root transformed data, as well as presence–absence data. Site standardization (proportioning each species relative to the site total) reduces the contribution that differences in overall abundance make toward differences in community structure. Differences in the multivariate community structure between habitat types were examined using an analysis of similarity test (ANOSIM; Clarke & Warwick 1994). We tested for the importance of geographic distances among sites in determining patterns of community dissimilarity using the RELATE test (Clarke & Warwick 1994) which is a Mantel-type permutation test of the rank correlation between paired similarity matrices. Multivariate analyses were performed using PRIMER v5 software.

RESULTS

GENERAL DESCRIPTION OF THE AMPHIBIAN FAUNA AND PATTERNS OF RICHNESS.—The pitfall trapping captured 4247 individuals from a combined trapping effort of 3426 trap nights (Table 1). A total of 23 species of amphibian were captured in pitfall traps, and opportunistic searches returned an additional five species, giving a total list of 28 recorded for the Katavi region (Table 1). The overall species accumulation curve approached an asymptote, and the Jack-knife estimate for the total richness for all sites combined was 29 ± 2 (SD).

Three records represent large range extensions for East African amphibians. *Bufo garmani* was not previously known from Tanzania (Poynton 1998), *Pyxicephalus edulis* was previously thought to be restricted to the coastal plain from Kenya to South Africa (Channing 2001), and *Phrynobatrachus stewartae* was only known previously as an endemic from the Rumpi area of Malawi (Channing 2001).

Rarefaction curves demonstrate considerable differences in overall numbers of amphibians captured among habitats and seasons for a given capture effort, with both riverine sites and late-dry season

TABLE 1. *Species and trap success of frogs caught in this study. Values in parentheses are the percentage of total captures of each species found in each habitat, or the percentage of total captures for all species calculated across all sites. An asterisk indicates species that were not sampled through pitfall trapping.*

	Capture success per 100 trap nights (percent of total captures)				
Species	Riverine	Woodland	Mbuga	Cultivated	All sites
Arthroleptis stenodactylus	1.3 (13)	5.2 (67)	1.3 (11)	1.2 (8)	2.6 (2.1)
Breviceps mossambicus		0.09 (100)			0.03 (0.02)
Bufo garmani		0.09 (100)			0.03 (0.02)
Bufo gutturalis	7.1 (40)	1.6 (12)	5.9 (27)	5.6 (21)	4.7 (3.8)
Bufo maculatus	0.44 (80)		0.13 (20)		0.15 (0.1)
Bufo taitanus		0.34 (100)			0.12 (0.09)
*Chiromantis petersi**					
Hemisus marmoratum	16.5 (33)	16.8 (43)	9.2 (15)	6.6 (9)	13.3 (10.7)
Hoplobatrachus occipitalis	0.11 (100)				0.03 (0.02)
*Hyperolius kivuensis**					
Hyperolius viridiflavus			0.27 (100)		0.06 (0.05)
Kassina senegalensis	2.5 (85)	0.17 (7)		0.33(7)	0.79 (0.6)
Leptopelis bocagii		0.34 (100)			0.12 (0.09)
Phrynobatrachus mabiensis	109.5 (61)	17.1 (12)	29.7 (14)	36(13)	47.8 (38.5)
Phrynobatrachus natalensis	74.9 (43)	28.8 (21)	49.8 (23)	33.2(13)	46.4 (37.4)
Phrynobatrachus rungwensis	0.11 (3)3	0.09 (33)	0.13 (33)		0.09 (0.07)
Phrynobatrachus stewertae	0.33 (17)	0.86 (56)	0.27 (11)	0.5 (17)	0.53 (0.42)
Phrynomantis bifasciatus				(0.66) 100	0.12 (0.09)
Ptychadena anchietae	(0.22) 29	0.17 (29)	0.13 (14)	0.33 (29)	0.2 (0.16)
*Ptychadena mascareniensis**					
*Ptychadena oxyrhynchus**				28	
Ptychadena sp. 1	1.86 (52)	0.09 (3)	2.01 (45)		0.96 (0.8)
Ptychadena sp.2			0.13 (100)		0.03 (0.02)
Pyxicephalus edulis	0.22 (67)	0.09 (33)			0.09 (0.07)
Strongylopus sp.	1.21 (92)		0.13 (8)		0.35 (0.28)
Xenopus mulleri	13.49 (74)	2.58 (18)	0.4 (2)	1.82 (7)	4.87 (3.9)
Xenopus petersi	1.75 (73)	0.52 (27)			0.64 (0.5)
All species	231.6 (50)	74.8 (21)	99.6 (18)	86.24 (12)	124
Number of study sites	12	14	9	6	41
Number of trap nights	1101	939	747	639	3426
Number of individuals	871	2112	744	520	4247

samples having 3–5 times greater capture success than other habitats and seasons respectively (Fig. 2, Table 1). Comparing species richness at a standardized level of abundance suggests a higher richness in woodland sites than elsewhere, although the rarefaction curves at this point are not asymptotic, making comparisons among other habitats is difficult. Nevertheless, comparisons of estimated richness across different estimation techniques support the rarefaction analysis in showing that species richness usually ranks higher in woodland sites, with high variability among mbuga sites. Richness estimates by all methods were similar for woodland (range of values across all sites is 16.6–17.9), riverine (13–14.8), and cultivated (10–11.9). Only mbuga varied widely among methods (12.7–23.5), indicating that estimates for this habitat category are very sensitive to assumptions. Despite capturing many more individuals, late-dry season samples contained many less amphibian species than the same sites sampled in either the early- or late-wet seasons (Fig. 2b).

Of the five species most abundant in our samples, only *Bufo gutturalis* showed a significant difference in capture success among habitat types (Table 1), with lower levels of relative abundance at woodland sites than elsewhere ($H = 8.88$, df $= 3$, $P = 0.03$, all pairwise comparisons significant; Mann–Whitney $U > 16$, $P < 0.05$).

SEASONALITY IN AMPHIBIAN ACTIVITY.—The observed pattern of overall seasonality in amphibian relative abundance was strongly influenced by the response of the two most abundant species in our samples (Fig. 3a–c), the puddle frogs *Phrynobatrachus mababiensis* and *P. natalensis*, both of which had large peaks of relative

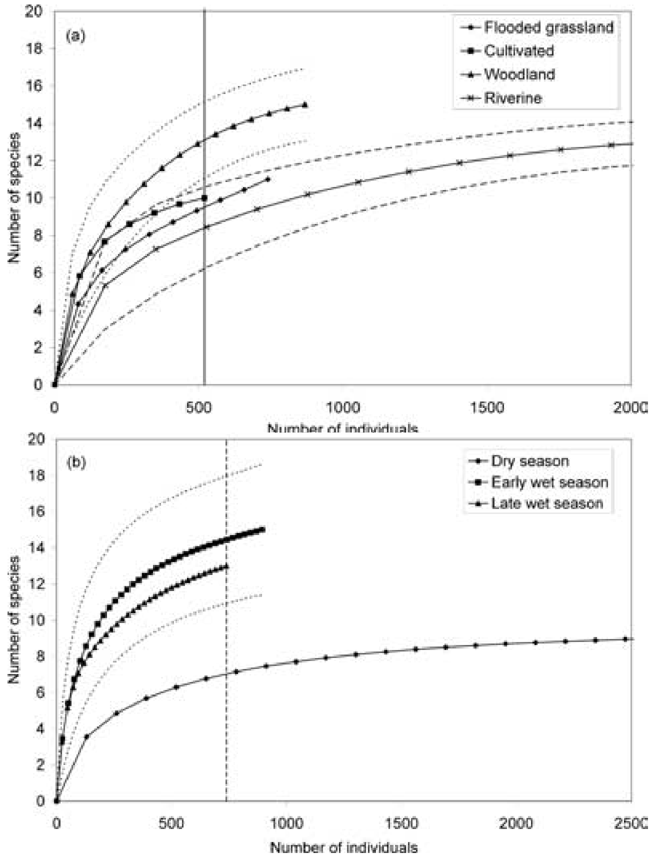

FIGURE 2. Sample-based rarefaction curves. Although the effort is given as the number of individuals, the lines represent expected values for randomization of sample order. (a) Comparison among four habitats. The broken line and dotted lines indicate the 95% confidence interval for the riverine and woodland rarefaction curves respectively. (b) Comparison among three seasons. The dotted line indicates the 95% confidence interval for the early-wet season rarefaction curve. Vertical lines for both plots indicate the point of comparison where sample effort is standardized among treatments.

abundance during the dry season ($H = 38.6$, df = 8, $P < 0.001$, and $H = 49.8$, df = 8, $P < 0.001$, respectively). Other species had contrasting temporal patterns in relative abundance. *Hemisus marmoratum* exhibited two peaks in activity in the early- and mid-wet season (Fig. 3d; $H = 31.2$, df = 8, $P < 0.001$), *Arthroleptis stenodactylus* was captured mainly in the wet season (Fig. 3e, $H = 28.8$, df = 8, $P < 0.001$), and *B. gutturalis*, showed no clear seasonal pattern (Fig. 3f, $H = 9.2$, df = 8, $P = 0.33$). Statistical support for seasonality across months from the serial runs test analyses was found for *P. mababiensis* ($Z = -3.7$, $P < 0.001$), *P. natalensis* ($Z = -4.7$, $P < 0.001$), and *H. marmoratum* ($Z = -3.2$, $P = 0.001$).

Amphibian community structure across major habitat types.—Comparisons of multivariate community structure among habitats revealed significant differences for presence–absence data (ANOSIM: Global $R = 0.12$, $P = 0.019$; Fig. 4), but not for standardized-abundance data (Global $R = 0.071$, $P = 0.06$). MDS scores of an ordination based on presence–absence data indicate that woodland and riverine sites are segregated, but cultivated sites are not distinct from any of the others, indicating that these sites host a subset of species that are also found elsewhere. These observations are supported by the pairwise ANOSIM tests, with all comparisons except cultivated versus riverine and cultivated versus woodland showing significant differences (all cases, $P < 0.045$). There was no significant relationship between differences in amphibian assemblages and the physical distance between sites (Mantel test using site-standardized abundance data: $\rho = -0.045$, $P = 0.83$, or presence–absence data: $\rho = -0.032$, $P = 0.72$).

DISCUSSION

General description of the leaf litter amphibian fauna of the Katavi ecosystem.—The total of 28 species of amphibians recorded for this area is considerably higher than other studies have found in miombo woodland, both within Tanzania (*e.g.*, Hinde *et al.* 2001; 14 species) and elsewhere (*e.g.*, Zimbabwe, Fleming & Loveridge 2003; 13 species). The miombo-mopane woodland biome is known to host at least 138 species of amphibians (Mittermeier *et al.* 2003), and although the Katavi area harbors only 20 percent of the total fauna, it comprises less than 1 percent of the total area. Comparison of the Katavi region with data from the only other area of Tanzania with well-studied miombo woodland habitat (Kilombero Valley, 500 km SE) reveals an assemblage similarity of only 46 percent (Sørenson index; Rees 1964, Hinde *et al.* 2001, Loader *et al.* 2003). This comparison demonstrates that besides altitude and vegetation type, geographical distance is also important in determining high levels of regional beta diversity in Tanzania.

We found that different habitats and seasons had marked differences in richness, sample relative abundances, and species composition, emphasizing the importance of long-term stratified sampling to adequately characterize the amphibian fauna of an area. In particular, sites in cultivated habitat are likely to be less diverse than elsewhere, and harbor only a subset of the wider species pool found in more natural sites. Conversion of miombo woodland for farmland and charcoal production is one of the primary threats facing the conservation of this important biome (Abbot & Homewood 1999, Mittermeier *et al.* 2003).

Consideration of the relative biodiversity value of the Katavi area for amphibians is severely limited by a paucity of data from other areas. It is unfortunate that the deployment of an intensive sampling campaign is both time demanding and financially costly, and accordingly many recent studies of amphibian diversity in both miombo woodland and other African systems have been restricted to a single short season, or a particular habitat type (*e.g.*, Raxworthy & Attuquayefio 2000, Hinde *et al.* 2001, but see Msuya 2001, Vonesh 2001).

Spatial and temporal patterns of amphibian relative abundance and diversity.—Our data suggest that the timing of any one sampling period has a greater influence on the sample richness and relative abundance of amphibians than the spatial location of

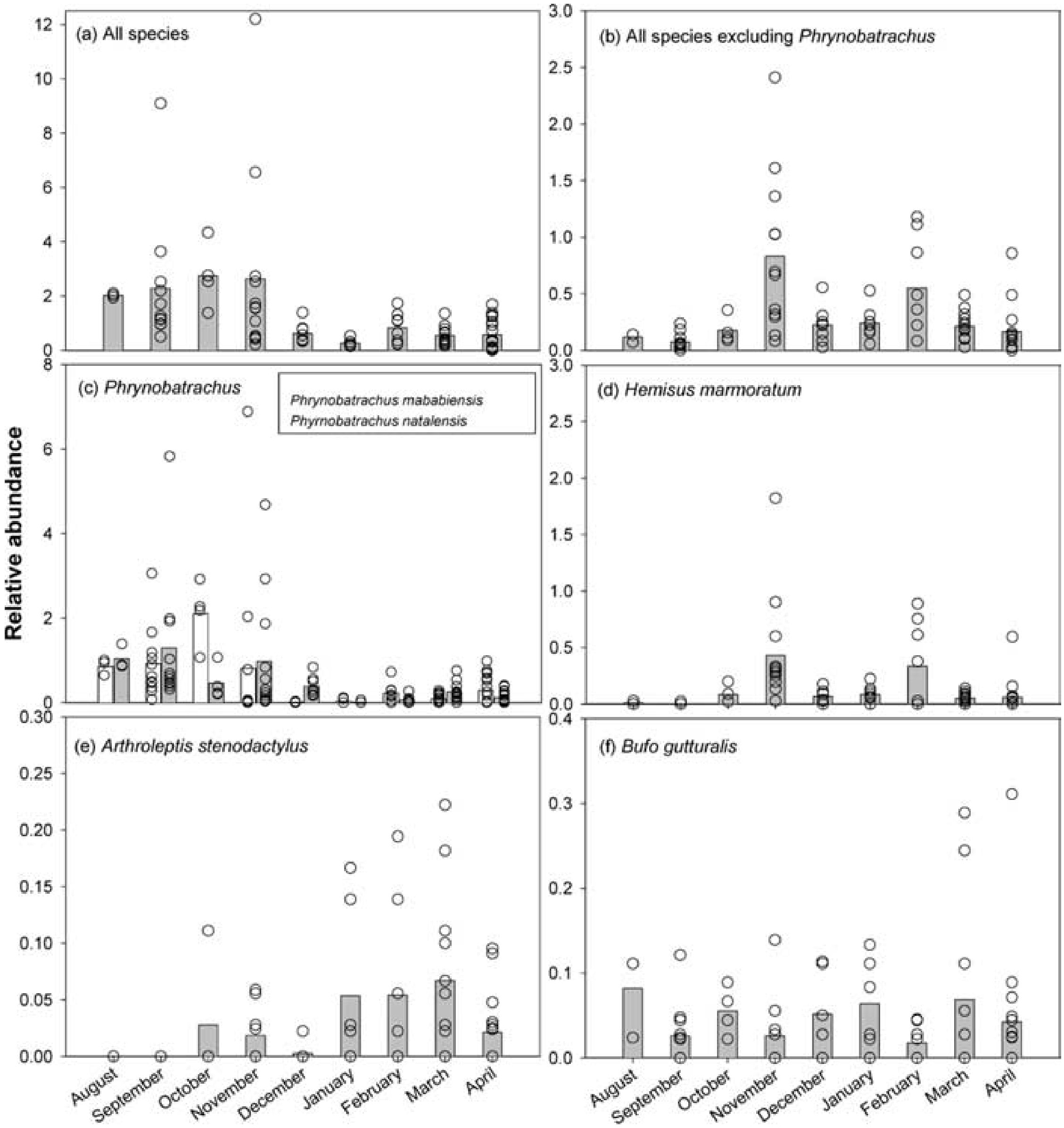

FIGURE 3. Seasonal patterns of relative apparent abundance (trap success) across the three seasons of the study period, late dry, early-wet and late wet. Data are presented for all species combined (a), all species excluding *Phrynobatrachus* (b), and separately for the five most common species (c–f). Relative apparent abundance is expressed as the total number of individuals per trap night. Bars represent the mean trap success for each habitat and circles represent the values for each individual site.

a study site—an observation that has been reported elsewhere both for tropical forests (Lieberman 1986, Aichinger 1987, Watling & Donnelly 2002), and miombo woodland (Fleming & Loveridge 2003). Our data show that different species have very different seasonal patterns of relative abundance. We found that patterns of overall amphibian relative abundance in our samples were strongly influenced by the distribution of the two dominant species (*Phrynobatrachus* spp.), which were relatively more abundant in riverine habitats and dry season samples. Vonesh (2001) also found another member of the same genus (*P. graueri*) to be the most abundant species in leaf litter samples from rain forest in southern Uganda. In contrast, a number of other species in this study also displayed peaks of relative abundance both within (*e.g., H. marmoratum, Leptopelis bocagii*) and throughout (*e.g. A. stenodactylus*) the wet season (see also, Fleming & Loveridge 2003).

Other researchers have also reported increases in the abundance of some amphibians during the dry season (Toft 1980a, Lieberman 1986, Allmon 1991). The abundance of amphibians may be particularly promoted during short dry seasons, when sudden leaffall promotes an increase in arthropod abundance (Toft 1980b, Fauth *et al.* 1989, Watling & Donnelly 2002). However, the dry season in the Katavi area is long (approximately 6 mo) and intense,

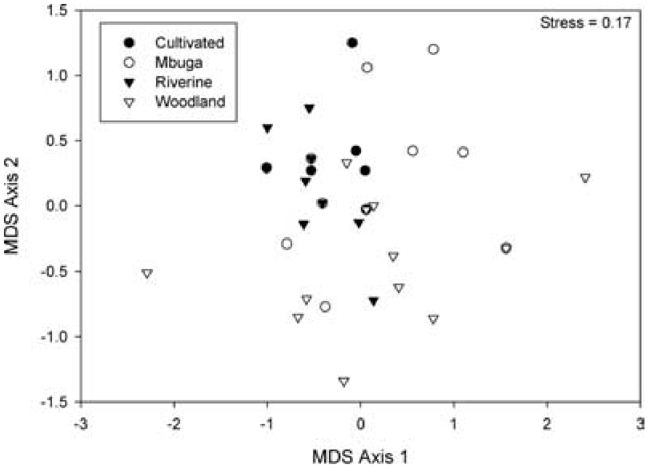

FIGURE 4. Nonmetric multidimensional scaling ordination showing differences in the community structure among four habitats based on presence–absence data and the Bray-Curtis similarity index. Circles represent different study sites. A stress value of 0.17 indicates a fair goodness of fit of the 2D configuration.

suggesting that moisture may be the most important limiting factor for many species—and particularly so for *Phrynobatrachus* which are largely water dependent, and congregate around limited water resources during periods of drought (Stewart 1967). Other observers have also recorded a peak in amphibian abundance during the wet season (Scott 1976, Allmon 1991, Vonesh 2001), and in particular during peaks of heavy rainfall (*e.g.* Duellman 1995), a phenomenon that is related to the phenology of reproductive activity as well as the environmental tolerances of individual species. These observations have important implications for the design of both biodiversity assessment and population monitoring studies.

In contrast to the similarity in amphibian species richness among noncultivated habitats (see also Fleming & Loveridge 2003), we observed significant differences in the composition (presence–absence data) of the frog assemblages. In particular, woodland and riverine habitats exhibited distinct differences in community structure, while sites from cultivated areas were indistinct from other habitats with respect to species composition, indicating they are comprised of a nested subset of the larger species pool found within the wider (unconverted) landscape.

CONCLUSIONS

The data presented here indicate that patterns of diversity in amphibian communities of Tanzanian miombo woodland can vary significantly across ecological and temporal scales. Importantly, we found that cultivation of native habitat reduces frog diversity, a conclusion that has important implications in light of the rapid conversion of miombo woodland for agriculture and fuelwood across much of sub-Saharan Africa (Abbott & Homewood 1999, Mittermeier *et al.* 2003). In addition to the consequences of cultivation for amphibian communities in miombo woodland, the fact that species richness and composition differ among major habitat types means that conservation planners need to give adequate consideration to landscape scale variability in order to ensure maintenance of regional diversity. We have shown that superficial levels of sampling effort, such as a narrow focus on a particular area or in particular a restriction to a single season, can lead to erroneous conclusions regarding patterns of diversity in miombo-mopane woodland.

Simple ecological data such as those presented here are of importance to conservation in the face of growing threats to biodiversity. An understanding of temporal patterns of abundance (both intraannual patterns presented here, but also interannual patterns) among species is vital in effective monitoring of changes in populations (Pechmann *et al.* 1991, Duellman 1995). The findings presented here indicate that the relatively poor focus of herpetofaunal research in miombo woodland is out of proportion to its ecological and conservation significance. The fact that few research projects have the time or resources to deploy sufficient levels of sampling effort remains a major problem for conservation.

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