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COMMUNITY ASSEMBLY AND STRUCTURE OF TROPICAL LEAF-LITTER ANURANS

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Abstract. We tested two traditional views of community organization relating to the individualistic continuum versus the interactive concept using anuran leaf-litter assemblages in primary and secondary forest habitats in Taï National Park (TNP), Ivory Coast as a model system. Based on biotic data and species occurrence patterns, the relative importance of each of these concepts was assessed. Null model tests of niche and size overlap revealed that the observed multivariate structure was only weakly influenced by biotic interactions, and therefore is most likely not the sole result of present species interactions. Non-metric multidimensional scaling and quadratic regression analyses showed that particular species responded to certain habitat characteristics, in particular the presence or absence of specific breeding sites and tree size classes, the latter being an index of forest degradation in this case. This corresponded to a discrimination of four major functional response groups within the leaf-litter community. However, the strength of these species-specific responses, and therefore the allocation to one or other of these response groups, varied throughout the year. Thus our results indicate that differing individual life histories, rather than interspecific interactions, were likely explanations of the observed pattern. The leaf-litter anuran assemblages of TNP can be best described as a collection of loosely interacting individuals responding to particular sets of physiological constraints imposed by a particular location, rather than as a tightly integrated and highly interacting set of species. *Accepted 11 September 2006.*

Key words: *Amphibia*, *Anura*, *community composition*, *individualistic concept*, *interactive concept*, *Ivory Coast*, *leaf litter*, *rainforest*, *West Africa*.

INTRODUCTION

Interspecific interactions are usually complex in natural communities, and as the number of species increases so does the potential number of interactions. Interactions can be both positive (facilitation) or negative (typically competition and/or predation). Yet abiotic factors might be just as important in structuring communities and determining the distribution and abundance of species (e.g., Beadle 1966, Clark & McLachlan 2003). However, general rules of community assembly remain elusive. There is an ongoing debate about the way in which communities are organized, and a wide spectrum of opinions exists. Both tradeoff-based theories of interspecific competition (Huisman & Weissing 1999, Chesson 2000, Rees *et al.* 2001) and neutral theories (Bell 2001, Hubbell 2001) have been suggested as potential explanations for the assembly, dynamics, and structure of ecological communities. The main discussion focuses on two opposing views. Communities are either seen as integrated, repeatable, tightly structured species assemblages that have evolved as units (Clements 1916, Pianka 1973, Roughgarden 1976), or they are viewed as the result of species-specific responses to the particular set of physiological constraints imposed by particular features of the environment (Gleason 1926, Rotenberry & Wiens 1980, Wiens & Rotenberry 1981, Homes *et al.* 1986). The dispute is personified by Frederick Clements and Henry Gleason (Clements 1916, Gleason 1926). Clements' holistic view stresses interdependence of the constituent species in a community. In contrast, Gleasonian 'communities' are generally characterized as having species that distribute themselves over ecological gradients of conditions, independently of the distributions of other species. In the first view, biotic effects are considered to be the

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major structuring force, and the observed pattern is often interpreted as the result of positive (Bertness & Callaway 1994, Callaway 1997) or negative (Schoener 1968, Brown & Munger 1985, Dayan & Simberloff 1994, Smith & Remington 1996) interspecific interactions. The second concept implies that particular species assemblages simply reflect the fortuitous correspondence of independent life histories of species at one place and time (Ter Braak & Prentice 1988, Gascon 1991). At one extreme, even the very existence of any general assembly rule has been debated (McIntosh 1995).

Strong stochastic elements in the recruitment of component species and environmental fluctuations result in variations in community composition (Hubbell 1979, Chesson & Warner 1981, Dayton 1984, Huston 1994, Allmon *et al.* 1998). The possible role of competition in structuring communities is reduced through predation (e.g., Azevedo-Ramos *et al.* 1999, Hero *et al.* 2001), as well as through habitat and resource heterogeneity, or simply by chance or unpredictable environmental changes. Where competition is inferred to be the major structuring factor studies have concentrated on niche relations among species (Brown & Lieberman 1973, Pianka 1973, Vitt & Carvalho 1995, Caldwell & Vitt 1999), and any observed structure was assumed to be the result of competition. By contrast, several methods of direct or indirect gradient analysis have been used to examine the covariance structure of matrices of species-distribution vectors as a function of environmental characteristics (Whittaker 1956, Parris & McCarthy 1999). In the integrated community view, vectors for many species are correlated in time or space such that discrete units can be observed. In the individualistic view of species associations, these vectors are uncorrelated and repeatable units are not necessarily being observed. By analyzing single species vectors, species-specific correlates of distribution can be found. Historically, the debate has been especially robust among plant ecologists and animal studies have been comparatively underrepresented, but a general applicability of results across various taxa is always desirable in ecological studies. We therefore chose a leaf-litter amphibian fauna for our analyses. They have been shown to be especially appropriate for investigations concerning factors that influence community structure (Gascon 1996) since they comprise a significant proportion of the amphibian fauna at any given site (ca. 25–30 %; Allmon 1991) and because standardized methods exist for estimating their species richness and abundance (Heyer *et al.* 1994, Rödel & Ernst 2004). Amphibians in general also account for a significant proportion of the vertebrates of tropical forests throughout the world, where they are important both as predators and prey (Inger 1980a b; Duellman 1990).

Most of the studies on tropical amphibian assemblages address either questions of community resource partitioning, focusing on niche breadth and overlap (e.g., Crump 1974, Inger & Colwell 1977, Duellman 1978, Toft 1982, Inger *et al.*1987, Lima & Magnusson 1998), or occurrence patterns and habitat use (e.g., Gascon 1991, Parris & MacCarthy 1999, Neckel-Oliveira *et al.* 2000, Parris 2004). To our knowledge no study has combined the two approaches by testing the respective assumptions based on the same set of data. In this study we analyze the relevance of each of the outlined concepts. We take a niche and size overlap-based null model approach to determine the importance of competition in community organization. To test for individualistic or ubiquitous relationships to environmental parameters, and hence the predictive value of these factors with regard to species occurrence, we use non-metric multidimensional scaling analyses and a successive quadratic regression model. This particular approach focuses on predictor variables related to site-specific environmental factors, which may affect species presence and abundance in different ways. Since species presence may change over time, as a result of simple accumulation or dispersal, successional processes, or environmental variation (Nurnberger 1996, Giaretta *et al.* 1999, Brooks 2000), we analyzed data with respect to season, thus addressing temporal variation as an explanatory variable. Additionally, since virtually all types of ecological interactions have been shown to vary with changes in the abiotic environment (e.g., mutualism: Bronstein 1994, competition: Connell 1983), we performed all null model tests of interspecific interactions with regard to disturbance state of the habitat (i.e., primary versus secondary forest).

MATERIALS & METHODS

Study site and data collection. The fieldwork was conducted in Taï National Park (TNP), southwestern Ivory Coast. TNP is the largest remaining protected area of lowland rainforest in West Africa. For a detailed description of the study area, see Riezebos *et al.* (1994). The field data were collected during February–May and September–December 1999, and May–September 2000. Wet season data (months

having precipitation sums above 100 mm) included data from February, April, May, September–November 1999, March–June and September 2000. Dry season data included March, December 1999, and July–August 2000. Study sites were chosen at random within existing macrohabitats (i.e., primary/secondary forest). Although anthropogenic disturbance (selective logging, coffee and cacao plantations) stopped approximately 25 years ago, past human influence was still visible in the area, e.g., absence of a closed canopy. None of our study sites have been logged or cultivated after 1978.

We tested a variety of different methods for their value in representatively assessing the anuran leaf-litter fauna of TNP. Standardized visual and acoustic encounter surveys along established transects proved to be by far the most effective method for our approach (Rödel & Ernst 2004, Veith *et al.* 2004). Therefore we established a total of ten rectangular transects (six in primary forest, four in secondary forest; minimum distance between neighboring transects = 200 m, maximum distance between transects = 6.3 km). The complete transect length of 600 m was subdivided into 25 m subunits [SUs], (24 SUs / transect). SUs were tested for spatial autocorrelation and proved to be independent, thus preventing pseudoreplication in the analyses (see Ernst & Rödel 2005).

We recorded all frogs present in a strip of 100 cm to either side of the transect path. In the case of acoustic sampling we recorded all calling individuals within a distance of 12.5 m on either side of the path, thus creating an approximate 25 x 25 m acoustic sampling plot. To avoid duplicate recordings we marked captured frogs by clipping the most distal part of one toe. Recaptures were excluded from analyses. We characterized all 25-m SUs using variables that were recorded at two defined points (beginning and midpoint of each SU). These variables included vegetation density in four strata, divided into seven categories. We assigned soil to one of seven categories. Substrate moisture was determined in four categories during every transect walk. Leaf-litter coverage was assigned to five categories (accuracy: 20%). The vegetation of all 25-m SUs within a distance of about 100 cm left and right of the transect was recorded by counting the number of plants within each of five classes of stem diameter at breast height (dbh1–dbh5). Dbh-categories can be taken as a measure of forest degradation, assuming that the number of plants with small dbh is greater in degraded, secondary forests, whereas primary forests show increasing numbers of plants of larger dbh (Chatelain *et al.* 1996, Pearman 1997). In order to quantify the availability of potential aquatic breeding sites we registered every aquatic habitat located at a maximum distance of 25 m from either side of the transect (lentic or lotic, surface and depth). The habitat variables that we considered in the analyses were: substrate type, substrate moisture, leaf-litter coverage, four vegetation strata, five dbh-groups, lotic habitats, and lentic habitats (total of 14 variables). For a detailed description of the transect design, the monitoring routine, and habitat parameter definitions see Rödel & Ernst (2004) and Ernst & Rödel (2005).

With respect to niche overlap analyses it has been argued that microhabitat, diet, and activity time are the three most important niche axes, and that most differentiation occurs along the first two of these axes (Schoener 1974). The 70 niche parameters that we used for the niche overlap analyses therefore included all habitat variables (see above) at each site where an individual frog was caught, and species-specific data relating to: reproductive mode (non-aquatic direct development, semiaquatic nidiculous tadpoles, phytotelmata, spawn in lotic sites, spawn in lentic sites), webbing (pronounced, present, absent), toes (enlarged to discs, enlarged but not forming discs, not enlarged), activity (diurnal, nocturnal) and species- and gender-specific mean snout-vent length (SVL, accuracy of dial callipers: ± 0.1 mm).

We registered a total of 11678 individuals of leaf-litter anurans belonging to 24 species during 382.5 hours of transect sampling (765 transect walks, 18360 25-m SUs). Capture probability varied according to size of frogs and climatic conditions, but generally was higher than 90 %. In a comparative analysis, covering amphibian monitoring programs on transects in East Africa, West Africa (including data presented herein), Madagascar, and Borneo, we have recently shown that ≥ 20 independent transect walks seem to be necessary to achieve species saturation (Veith *et al.* 2004). We walked every TNP transect independently at least 41 times. We thus take it as certain that the local species assemblages have been almost completely recorded. For a complete species listing, abbreviation of scientific names of particular species appearing in tables and figures, and a summary of relative abundances of all leaf-litter frogs recorded during transect walks see Appendix 1.

Overlap analysis. According to conventional niche theory, interspecific competition should lead to a reduction in the niche overlap of competing species. Niche overlap analyses are an appropriate tool for the quanti-

fication of actual niche overlap between pairs of species. However it is not enough to show that species differ in their use of resources in a way that reduces niche overlap. Even in the absence of competition, species will differ in their utilization of resources (Connell 1980). Null hypothesis tests by means of null model analyses are therefore an indispensable prerequisite and an important tool in the search for ecologically significant patterns (Gotelli & Graves 1996). We therefore calculated niche overlaps choosing a null model approach.

For niche overlap analyses we used data obtained from visual as well as acoustic transect sampling. The analysis comprised only the seven most abundant species ($n \geq 40$) in comparisons between habitat complexes (primary vs. secondary forest habitats), and the 14 most abundant species ($n \geq 40$) in seasonal comparisons (entire study period vs. dry season vs. wet season). The data that we used in size overlap analyses comprised species- and gender-specific mean SVL-measurements that we took *ad libitum* throughout the entire study period (transect walks + opportunistic visual surveys in other parts of the Taï forest, see Rödel & Ernst 2004). Only mean SVL-measurements of species and/or sexes with a sample size of more than five individuals were used, leaving a total of 18 species included in the analysis. When analyzing data of males, 15 species were considered. Analyses of females considered 14 species (see Appendix 1). Ordinations were performed using data obtained from visual transect sampling exclusively, because these provide the most detailed information on microhabitat parameters potentially correlated with species occurrence. Since it was not possible to distinguish two *Arthroleptis* species morphologically, we treated them as a single species whenever data obtained from visual transect sampling were analyzed. According to the results of the niche overlap analyses, this was a justifiable simplification, as both species were similar with respect to niche partitioning. Separation of the two species was possible using acoustic records. We used relative abundance values referring to number of transect hours (th) for species-related calculations, hence taking into account variations in sampling effort between transects (time-based density measures; Hofer & Bersier 2001). Whenever we pooled categorical data such as different habitat parameters, the respective modes were used for calculation. In niche overlap analyses, resource states are expressed as percent of usage. We transformed "skewed" variables that did not have a normal distribution (Kolmogorov-Smirnov and Shapiro-Wilk tests) by taking their logarithm, or analyzed them by using non-parametric tests. To avoid the problem of zero-log calculations after log-transformation of data, all figures were calculated as $\log x + 1$.

Null model tests of interspecific interactions. In order to elucidate the importance of interspecific interactions, namely competition, in structuring the assemblage, we performed niche and size overlap analyses using the program EcoSim version 7.0 Acquired Intelligence Inc. and Kesey-Bear. We used the index of Pianka (1973) and a randomization algorithm (RA3), which retains the niche breadth of each species but randomizes (1000 iterations) which particular resource states are utilized.

Fixed resource categories such as morphometric parameters that represent unique species-specific features were defined as "hard zeros", representing resource categories that cannot ever be used by a particular species, regardless of whether species interactions are important, and therefore are never reshuffled or randomized. In addition to pairwise comparisons of niche overlap indices, we compared the observed mean niche overlap to the overlap in the simulated communities in order to assess whether it was greater than or less than expected by chance ('pseudocommunity analysis', Winemiller & Pianka 1990). The outcome of this null model test provides information on patterns of competition and resource allocation. Determining dietary preferences or forage ratios of frogs would have required the killing of a great number of individuals. Methods such as stomach flushing to obtain stomach contents would be too invasive and potentially lethal in most of the species, since they also have comparatively small sizes (most frogs < 30 mm SVL). Non-invasive feces analyses do not mirror the real prey spectrum. Hard-bodied prey items, like beetles and ants, will be overestimated in these analyses (cf. e.g. Rödel 1995). We therefore searched for an alternative method to judge the importance of competition for food. The diets of many of the species dealt with here, or close relatives of them, have been investigated by previous workers. All these species have been shown to be opportunistic feeders, feeding on a variety of prey items that are mostly predictable by the frogs' habitats and sizes (Inger & Marx 1961, Barbault 1974). Hence we chose frog body size (SVL) as an indirect index of average prey size (Pacala & Roughgarden 1982, Caldwell 1996, Pough *et al.* 1998, Caldwell & Vitt 1999, but see Lima & Magnusson 1998 for a contradicting example).

Since SVL is a continuous measurement, dietary overlap, expressed as size overlap, was calculated in a separate analysis. We used two different overlap metrics, minimum segment length and variance in segment length. Whereas minimum segment length tests the hypothesis that there is a critical minimum separation necessary for coexistence, the variance in segment length tests the hypothesis that species sizes are evenly spaced, even if there is no particular minimum separation. Variance in segment length is most appropriate for analyses of size overlap in animal communities. The minimum segment length, on the other hand, is most appropriate for analyses of phenological overlap in plant or animal communities (Gotelli & Entsminger 2001). For details on the calculation algorithms and null model assumptions see Gotelli & Entsminger (2001).

Analysis of species response to environmental parameters. We applied non-metric multidimensional scaling (NMDS) using the program PC-ORD for Windows version 4.17 MjM Software Design to describe species response to environmental factors, in order to determine the environmental factors associated with sites used by individual species (McCune & Grace 2002). NMDS appears to provide a better fit to ecological data than may be obtained using other ordination techniques (Kenkel & Orloci 1986). For a general description of the method and iterative algorithm see Kruskal (1964) and Van Deun & Delbeke (2000). In order to minimize the possibility of finding a local minimum rather than global minima, and to determine the appropriate dimensionality and statistical significance, we constructed an initial configuration using a method suggested by Legendre & Legendre (1998). We used the Bray-Curtis distance and the following settings for thorough preliminary runs: maximum number of iterations: 400; instability criterion: 0.00001; starting number of axes: 6; number of real runs: 40; number of randomized runs: 50. We used the resulting configurations as starting coordinates in consecutive ordinations, thereby applying the suggested dimensionality. Since most species showed unimodal rather than linear response to habitat parameters, we chose a quadratic regression model using ordination scores obtained from NMDS performed with habitat parameter matrices as independent, and log-transformed relative species abundance values as dependent variables. The model thus fits a parabola to log-transformed abundances, therefore actually fitting a Gaussian response curve to the original abundance data. For details see Jongman *et al.* (1995). The regression analyses were calculated with SPSS for Windows 10.0, SPSS Inc.

RESULTS

Interspecific interactions. Analysis of the recorded niche parameters revealed high observed mean overlaps, compared with relatively low simulated mean overlaps in both primary and secondary forest habitats. In all cases the observed overlap was significantly greater than the expected overlap index, p (observed ≥ expected) < 0.001; p (observed ≤ expected) = 1.000 (Table 1). This indicates no competition, based upon the underlying assumptions. The observed variances were generally significantly greater than the means of the simulated variances in both primary and second-

TABLE 1. Results of niche overlap randomization test (1000 iterations) of pairwise species comparison; (1) complete: primary and secondary forest habitats were analyzed as pooled sample (14 most abundant species, n ≥ 40); (2) primary, secondary: data from wet and dry seasons were analyzed as pooled sample (seven most abundant species, n ≥ 40). Standardized effect size = (Observed mean – Simulated mean) / (Standard deviation of simulated means). 95% confidence intervals for the standardized effect size: -1.96-1.96.

		Observed mean	Simulated mean	Standardized effect size	Observed variance	Simulated variance
1	Complete	0.616	0.363	37.866	0.011	0.004
	Dry season	0.581	0.351	34.816	0.012	0.004
	Wet season	0.615	0.360	38.452	0.011	0.004
2	Primary	0.682	0.358	23.615	0.016	0.004
	Secondary	0.584	0.374	16.080	0.021	0.004

TABLE 2. Stress in relation to dimensionality (number of axes). Randomized data based on Monte Carlo test (50 randomized runs).

		Stress in real data			Stress in randomized data			
	Axes	Minimum	Mean	Maximum	Minimum	Mean	Maximum	p
Complete	3	13.484	20.092	55.718	14.125	19.535	34.795	0.032
Dry season	3	12.309	15.166	21.745	13.980	17.058	29.475	0.032
Wet season	3	8.516	8.691	9.171	9.570	9.995	10.647	0.032

ary forest habitats, p (observed ≥ expected) < 0.001; p (observed ≤ expected) = 1.000 (Table 1). These results were consistent throughout both seasons.

Size overlap analyses revealed that the observed minimum segment length was never significantly larger than that predicted by the null model [males, the entire assemblage: p (observed ≥ expected) = 1.000; females: p (observed ≥ expected) = 0.545], thus not supporting the existence of a critical minimum, and indicating rather convergence in body size, perhaps because of common environmental or foraging constraints. The variance in segment length showed an overall tendency for evenly-spaced body sizes. This resulted in significantly smaller variances than expected by chance [p (observed ≤ expected) < 0.05].

Analysis of species response to environmental parameters. Preliminary NMDS runs, performed in order to minimize stress values and find initial starting coordinates, suggested a three-dimensional (3-d) solution. In all cases, the 3-d solution provided significantly more reduction in stress than expected by chance, accepting a probability of Type I error < 0.05 (Table 2). Three ordination axes explained 95 % of the variance when considering data from both seasons. The efficiency was even greater when looking at dry (96 %) and wet (97 %) season data separately (Table 3).

A first interpretation of the ordination is provided by the calculation of correlation coefficients for each matrix column (species and habitat variables) with each of the ordination axes. These coefficients express the linear (Pearson's r = parametric) and rank (Kendall's τ = nonparametric) relationships between the ordination scores and the individual variables used to construct the ordination. Joint plots provide a graphical representation of the relationship between habitat variables and ordination scores (Fig. 2 a-c). In all cases, correlation with ordination axes was sufficiently strong in only seven of 14 tested habitat variables. These comprised all five vegetation dbh-groups, as well as abundance of potential aquatic breeding habitats (lentic and lotic).

Variables contributed to the three ordination axes (referred to as NMDS 1–3) to varying degrees. Since axis values range from zero to one, negative correlations have to be interpreted as an increased impact of the respective variable moving towards zero, or decreased impact moving towards one. Thus, negative and positive correlations represent a continuum along ordination axes, moving from high impact to low impact and vice versa. In the analysis of the complete set of data, NMDS 1 combines attributes emphasizing small dbh-groups and increasing availability of potential (lentic) aquatic breeding habitats. NMDS 2 was mainly characterized by a combination of the smallest dbh-group, along with decreasing availability of lotic breeding habitats. Lentic breeding habitat availability in combination with an increase in larger

TABLE 3. Coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space (explained variance). Distance measure: Bray-Curtis.

	Axis	Increment	Cumulative
Complete	1	0.019	0.019
	2	0.912	0.931
	3	0.022	0.953
Dry season	1	0.001	0.001
	2	0.020	0.021
	3	0.935	0.956
Wet season	1	0.855	0.855
	2	0.091	0.946
	3	0.023	0.969

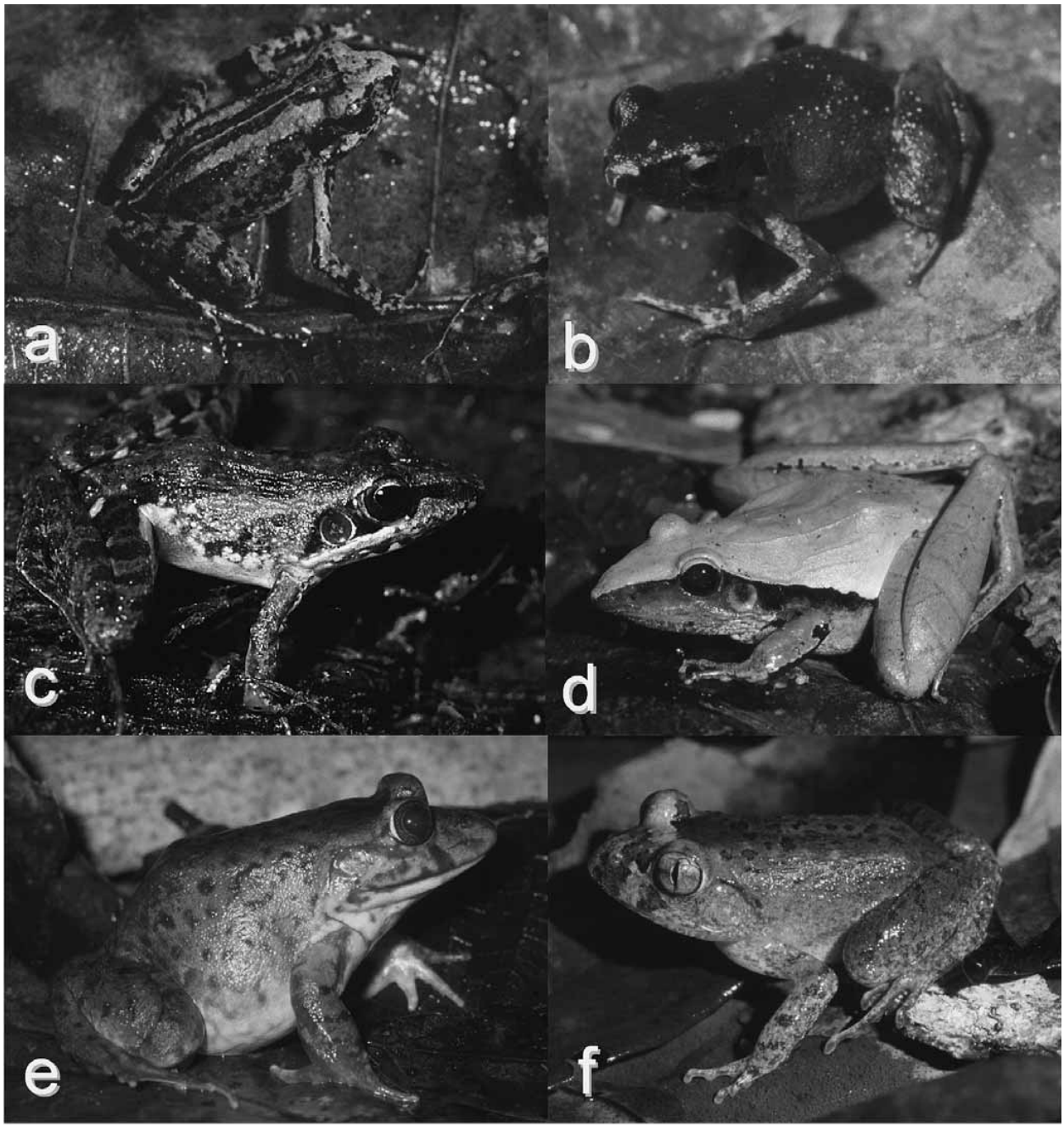

FIG. 1. Typical representatives of the major functional groups within Taï National Park's leaf-litter frogs: a & b represent species with direct development; c-f represent species with aquatic larval stages; a, c & e predominantly occur in primary forest; b, d & f predominantly occur in secondary forest; a & d reproduce in lentic habitats; e & f reproduce in lotic habitats; a: *Arthroleptis* sp. 1; b: *Arthroleptis* sp. 2; c: *Ptychadena aequiplicata*; d: *Ptychadena longirostris*; e: *Aubria subsigillata*; f: *Astylosternus occidentalis*.

dbh-groups had a major impact on NMDS 3. Specific results of correlations with ordination axes are given in Appendix 2.

Some shift concerning the influence of particular variables on ordination axes occurred when taking into account exclusively dry season data. NMDS 1 was more impacted by a decrease in the availability of lotic breeding sites along with a decrease in small dbh-groups. Availability of lentic breeding habitats most influenced NMDS 2. Increases in large dbh-

groups and a decrease in small dbh-groups contributed to the axis to a lesser degree. NMDS 3 was more impacted by lotic, as opposed to lentic, breeding habitats (Appendix 2).

When we took into account exclusively wet season data, the contribution of particular variables to single ordination axes shifted as well. Potential aquatic breeding habitat availability (lotic sites) and small dbh-groups contributed to NMDS 1. NMDS 2 was mainly characterized by decreasing aquatic breeding habitat availability (lentic habitats), as well as the lower dbh-groups. NMDS 3 was almost completely determined by the impact of dbh-groups 2 and 3. Aquatic breeding habitat availability had little influence on NMDS 3 (Appendix 2). Generally, the location of species' centroids in niche space was largely determined by NMDS axes reflecting factors related to dbh groups and aquatic breeding site availability. In other words, the presence or absence of a particular species appears to be determined by these very factors. The analyses of species response to environmental factors by means of quadratic regression revealed that correlations were significant in a number of cases, thus indicating that individual species respond to particular environmental factors (Appendix 3).

NMDS-plots, as well as the results of the regression analyses, therefore form the basis of our definition of four major functional response groups (Fig. 1, Appendix 1). The most prominent discrimination was between species that were restricted to, or most abundant in, secondary or primary forest habitats (Fig. 2 a). This separation was most pronounced during the dry season (Fig. 2 b), but became less distinct during the rainy season (Fig. 2 c). A second, less pronounced, discrimination existed between species that depend on aquatic breeding habitats for reproduction and those that do not depend on these habitats. The first of these two response groups was furthermore subdivided into species that were associated with lotic habitats as opposed to those associated with lentic habitats.

DISCUSSION

Importance of interspecific interactions. A major criticism addressing the interpretation of gradient analyses in the light of the individualistic-continuum concept is the supposed assumption that interactions among species should be similar at all points along environmental axes, and that groups of species should be associated at all points on a gradient if interdependence is to be accepted, yet interactions have been shown to vary over time and on abiotic gradients (Callaway 1997). Variations in the strength of interspecific interactions have been observed e.g., in plants (Connell 1983), neotropical anurans (Toft 1980), and North American lizards (Dunham 1980). Competition has also been shown to be more intense under benign abiotic conditions that permit rapid resource acquisition than under abiotically stressful conditions (Bertness & Hacker 1994). We accounted for this possibility by testing for seasonal and disturbance-gradient-related shifts in competitive patterns. Our results for both the entire assemblage, as well as the assemblage separated by primary and secondary habitats, indicated no, or at least only minor competition between species, regardless of seasonal changes. The observed overlap was high between most species, regardless of season or habitat complex. Hence there was no direct evidence indicating that the intensity or existence of interspecific competition may vary according to changes in environmental conditions. The high observed variances in resource use can be interpreted as an indication of some internal guild structure (Winemiller & Pianka 1990), thereby corroborating the *a priori* designation of a leaf-litter anuran guild, and furthermore implying the existence of "subguilds" or functional groups, most probably based on species-specific responses to environmental parameters. Anurans in the assemblage are most likely feeding on a wide variety of small arthropods (cf. Barbault 1974). Based on the predominant view in herpetological literature that most leaf-litter anurans are opportunistic feeders (e.g., Inger & Marx 1961, Duellman & Trueb 1986), we assume that food partitioning is not one of the major factors structuring the assemblage (Hofer *et al.* 2004).

Although some species seem to respond to particular habitat parameters and thus show different habitat preferences, limitation of these habitats is difficult to quantify and may change throughout the season, with potentially higher impact within secondary forest habitats. However, the relatively high structural heterogeneity of the environment (Ernst & Rödel 2005) is likely to produce a great amount of habitats that can be used by different species and therefore may prevent species from competing. These findings correspond with recently developed stochastic niche theories. These predict that stochastic niche assembly creates communities in which species dominate approximately equally wide "slices" of the habitat's spatial heterogeneity. The niche widths then generate realistic dis-

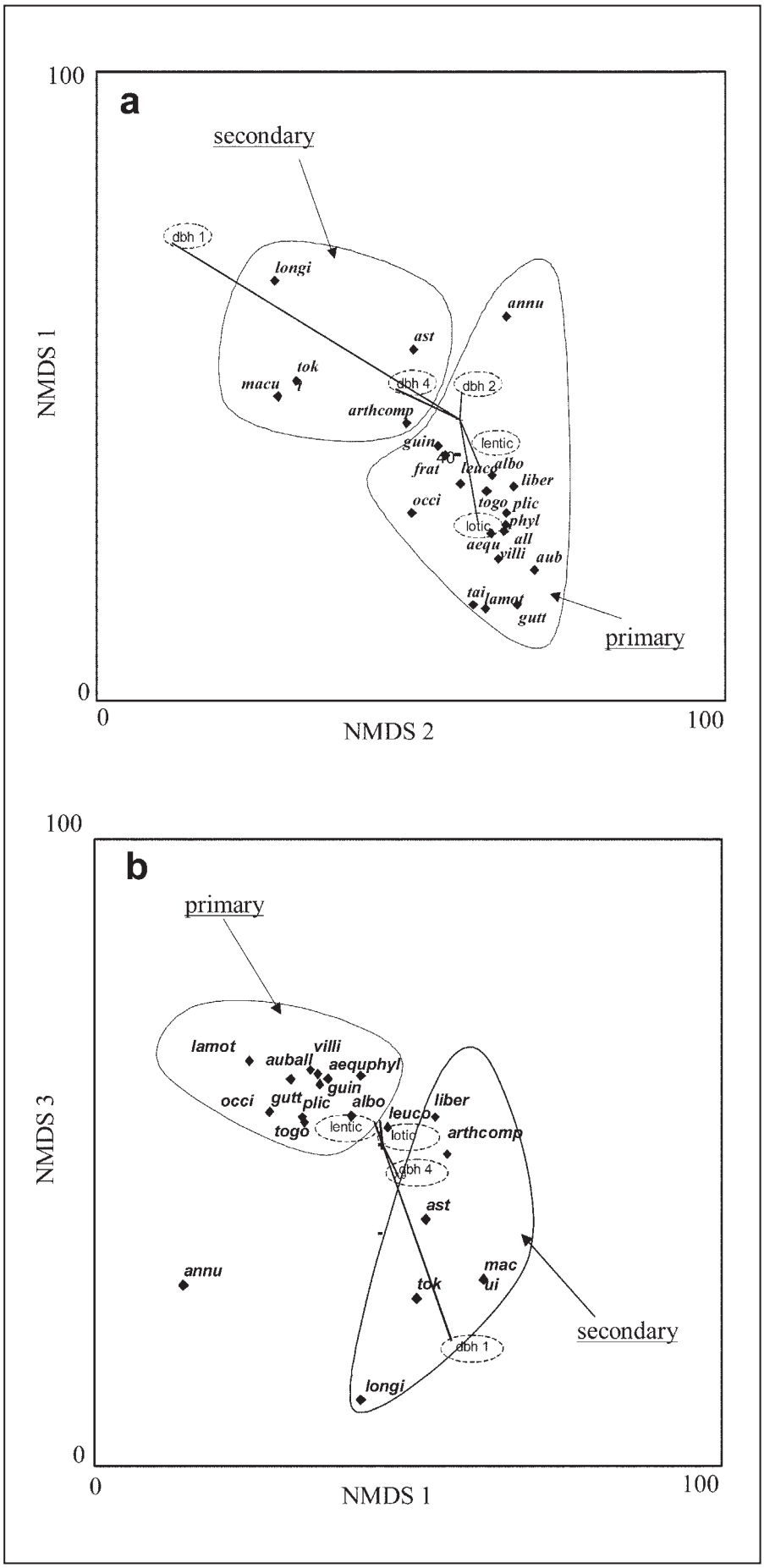

FIG. 2. Typical results of NMDS ordinations on species relative abundance and habitat parameters based on Sørensen distance; (a) entire study period; (b) dry season; (c) wet season. Axes are scaled to the longest axis, thus providing accurate portraits of the similarity relationships among points. Angles and lengths of radiating vectors indicate the direction and strength of relationships of habitat parameters (stippled ellipses) with ordination scores. Ellipsoids indicate species associated with primary and secondary forest sites. For abbreviations and definition of seasons see Material and Methods and Appendix 1.

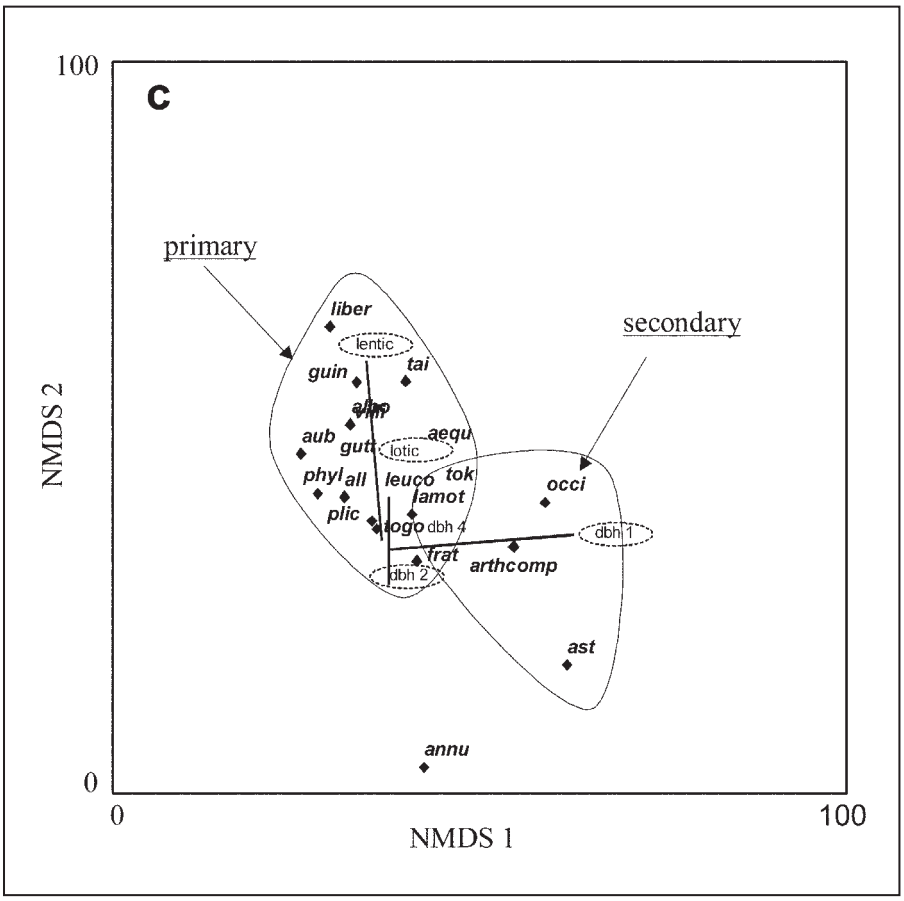

FIG. 2 (continued)

tributions of relative abundance, for which there are strong correlations among species traits, abundance, and environmental conditions (Tilman 2004). In consideration of the integrated community view it can be argued that the anuran species that make up the leaf-litter assemblage of TNP can coexist due to the absence of, or very low pressure from, interspecific competition and that the structure of the assemblage is most probably not, or only weakly influenced by biotic interactions, with the exclusion of predation and parasitism, which have not been investigated in this study. This agrees with results from a study at Mount Kupe, Cameroon, where competitive interactions were assigned minor importance in limiting amphibian distributions (Hofer *et al.* 1999, 2000). These results have recently been confirmed by Sanderson (2004).

Environmental factors determining habitat selection. Our results indicated that different species react differently (positively or negatively) to the same set of environmental predictor parameters represented by particular NMDS-axes. Similar results have been reported for pond invertebrates in Northumberland, U.K. (Jeffries 2003). For the leaf-litter anuran assemblages of TNP this means that different species occur in different habitats. Taking into account the most influential parameters, habitat degradation (indicated via dbh-categories) and breeding site availability, the species could be sorted into four distinct functional groups. The rainy season observation of a comparatively weaker separation between species mainly inhabiting primary versus secondary forest sites can be explained by the increased precipitation, resulting in more favorable conditions in secondary habitats, compared with the conditions during the dry season when humidity drops and availability of aquatic habitats decreases. Indeed an increased occurrence of "primary forest species" in secondary habitats during the rainy season was observed.

A similar explanation may hold true for the observation of the same trend among species that are associated with lotic or with lentic habitats. The enhanced discrimination between these groups during

the dry season may have been an effect of the general reduction in aquatic breeding habitat availability during that period, thus resulting in an aggregation at the remaining sites of species that depend on these habitats. This resulted in an amplified contrast in the NMDS-ordination. Some species seemed to be indifferent to aquatic site availability, instead reproducing whenever and wherever suitable habitats are present. Thus they can be considered opportunistic breeders. In conclusion, individual species responded to the habitat and predominantly occurred in sites having certain environmental attributes. Species-specific responses to habitat characteristics varied throughout the season. These variations were most probably influenced by the availability of open water, especially in secondary forest habitats. Due to their altered vegetation structure, they are microclimatically less stable than primary forest habitats, in which a closed canopy functions as climatic buffer. The strength of these species-specific habitat requirements, although significant in a number of cases, was generally relatively weak and varied considerably between species. This suggests that these factors are not very good predictors of exact sites used by each species. They probably simply describe a set of habitat characteristics within which a species might be encountered. This may, at least, be true for the majority of species that were analyzed, apart from those that display reproductive strategies depending on very special breeding sites (Rödel *et al.* 2004, Rudolf & Rödel 2005).

Integrated communities or individualistic species associations? Linking the observed structure to causal agents remains a problematic task in the analyses of species assemblages. Whether the observed structure is the result of present or past species interactions (Pianka 1973, Diamond 1975, Dayan & Simberloff 1994), or simply the correspondence of independent life histories due to selective pressures from predators, or responses to environmental characteristics (Heyer 1973, Wiens 1973, Homes *et al.* 1986, Gascon 1991, Parris & MacCarthy 1999, Eterovick & Sazima 2000), cannot be easily decided. However, descriptive studies are useful tools in revealing correlative patterns. As can be inferred from the discussion above, interspecific interactions, in general, and competition, in particular, do not seem to influence the structure of the recent leaf-litter anuran assemblage to a considerable extent. This indicates that species are responding individualistically, as does the failure to detect single ubiquitous environmental predictor parameters and the observation of positive and negative correlations with different species and the same sets of these predictors.

Hence, the leaf-litter anuran assemblage of TNP can best be described as a collection of loosely interacting individuals responding to the particular set of physiological constraints imposed by a particular location. Our results thus add more weight to individualistic concepts of community organization and therefore underline the importance of historical and stochastic events in the assembly of particular communities. Deterministic explanations supporting conventional niche theory may thus be challenged if these patterns prove to be consistent.

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APPENDIX 1. Relative abundance matrix of species recorded in primary and secondary forest habitats during the study in TNP, as considered in niche analyses. The size overlap analyses comprised measurements taken inside and outside transects; listed are only specimens that were recorded on the transects. Relative abundance is given as individuals per transect hour. *Arthroleptis* sp. 1 and A. sp. 2 form an artificial taxon, as considered in NMDS and regression analyses; - = no record; § = considered in habitat complex comparisons; * = considered in seasonal comparisons; i/th primary = individuals per transect hour in primary forest transects; i/th secondary = individuals per transect hour in secondary forest transects; i/th total = total number of individuals during whole study period in all habitats; total # of specimens = absolute number of individuals recorded in the study; total # of transect walks = 765 (one transect walk = app. 30 min). Functional groups: a^1: restricted to primary forest sites; a^2: most abundant in primary forest sites; b^1: restricted to secondary forest sites; b^2: most abundant in secondary forest sites; c^1: not dependent on aquatic habitats (direct developers); c^2: breeding in small aquatic habitats (phytotelmata or small depressions); d^1: dependent on larger lotic habitats for reproduction; d^2: dependent on lentic habitats for reproduction.

Taxa	i/th primary	i/th secondary	i/th total	total # of specimens	Functional group
Bufonidae					
Bufo maculatus (macu)	–	0.011	0.003	1	b^1
B. taiensis (tai)	0.004	–	0.003	1	a^1; d^1
B. togoensis (togo)*	0.197	0.097	0.173	66	a^2; d^1
Ranidae					
Aubria subsigillata (aub)	0.017	–	0.013	5	a^1; d^1
Amnirana albolabris (albo)*	0.200	0.086	0.173	66	a^2; d^2
A. occidentalis (occi)	0.007	0.011	0.008	3	a^1; d^2
Ptychadena aequiplicata (aequi)*	0.383	0.011	0.293	112	a^1; d^2
P. longirostris (longi)	–	0.011	0.003	1	b^1; d^2
Petropedetidae					
Phrynobatrachus accraensis (acc)	–	0.011	0.003	1	b^1
P. alleni (all)§*	5.596	0.538	4.366	1670	a^2
P. annulatus (annu)	0.007	–	0.005	2	a^1
P. fraterculus (frat)	0.010	0.011	0.011	4	a^2
P. guineensis (guin)*	0.162	0.075	0.141	54	a^2; c^2
P. gutturosus (gutt)*	0.225	–	0.170	65	a^1
P. liberiensis (lib)§*	2.567	4.344	2.999	1147	b^2
P. plicatus (plic)*	1.157	0.118	0.905	346	a^2; d^2
P. phyllophilus (phyl)*	1.247	0.161	0.983	376	a^2; c^2
P. tokba (tok)§*	0.649	19.796	5.305	2029	b^2; c^1
P. villiersi (villi)*	1.810	0.376	1.461	559	a^2; c^2
Astylosternidae					
Astylosternus occidentalis (ast)	0.004	0.022	0.008	3	b2; d^1
Arthroleptidae					
Arthroleptis sp. 1 (arthcomb)§*	7.081	10.753	7.974	3050	a2; c^1
A. sp. 2 (arthcomb)§*	3.610	2.570	3.357	1284	b2; c^1
Cardioglossa leucomystax (leuco)§*	2.501	0.344	1.977	756	a2; d^1
Hyperoliidae					
Kassina lamottei (lamot)*	0.266	–	0.201	77	a^1; d2
Total	27.700	39.344	30.531	11 678	

APPENDIX 2. Pearson (r) and Kendall (τ) correlations with ordination axes; dbh = diameter at breast height; lentic and lotic breeding sites.

		Axis 1		Axis 2		Axis 3	
		r	τ	r	τ	r	τ
Entire study period	dbh 1	–0.015	–0.057	0.959	0.956	0.138	0.198
	dbh 2	0.537	0.460	–0.008	–0.001	–0.523	–0.439
	dbh 3	–0.062	–0.015	0.118	0.099	0.067	0.057
	dbh 4	–0.170	–0.130	0.133	0.133	0.031	0.012
	dbh 5	–0.140	–0.157	0.025	0.015	0.258	0.003
	lentic	0.313	0.199	–0.153	–0.162	0.566	0.386
	lotic	0.188	0.174	–0.219	–0.211	0.066	0.054
Dry season data	dbh 1	0.007	0.007	–0.007	0.070	–0.959	–0.960
	dbh 2	–0.696	–0.589	–0.384	–0.323	0.020	0.017
	dbh 3	0.085	0.036	0.130	0.095	–0.097	–0.069
	dbh 4	0.076	0.039	0.005	–0.006	–0.123	–0.126
	dbh 5	0.089	0.081	0.290	0.024	–0.046	–0.034
	lentic	–0.150	–0.087	0.673	0.445	0.163	0.161
	lotic	–0.182	–0.170	0.125	0.121	0.217	0.209
Wet season data	dbh 1	–0.853	–0.829	0.431	0.360	–0.074	–0.058
	dbh 2	0.159	0.140	0.337	0.236	0.704	0.569
	dbh 3	–0.070	–0.042	0.015	0.030	–0.256	–0.202
	dbh 4	–0.131	–0.125	0.097	0.100	–0.087	–0.029
	dbh 5	–0.111	–0.066	–0.066	0.059	–0.198	–0.176
	lentic	0.142	0.137	–0.662	–0.420	0.055	0.003
	lotic	0.223	0.209	–0.265	–0.231	0.078	0.062

APPENDIX 3. Quadratic regression of log-transformed (*log*+1) relative species abundance with ordination axes; only significant correlations are reproduced. For species abbreviations see Appendix 1.

	Species	Axis	r^2	*d.f.*	*F*	*p*
Entire study period	togo	2	0.029	224	3.39	0.035
	albo	1	0.062	224	7.45	< 0.001
		2	0.032	224	3.71	0.026
	aub	2	0.035	224	4.09	0.018
	aequ	2	0.057	224	6.73	0.001
	all	2	0.044	224	5.16	0.006
	tok	1	0.054	224	6.42	0.002
		2	0.120	224	15.30	< 0.001
		3	0.027	224	3.10	0.047
	gutt	2	0.048	224	5.70	0.004
	liber	1	0.072	224	8.72	< 0.001
		3	0.171	224	23.13	< 0.001
	phyl	1	0.031	224	3.54	0.031
		2	0.094	224	11.61	< 0.001
	plic	2	0.196	224	27.25	< 0.001
	villi	2	0.176	224	23.84	< 0.001
	ast	3	0.070	224	8.41	< 0.001
	arthcomp	1	0.035	224	4.04	0.019
Dry season data	albo	1	0.032	209	3.47	0.033
		3	0.036	209	3.88	0.022
	aequ	3	0.028	209	3.05	0.049
	all	3	0.192	209	24.90	< 0.001
	tok	1	0.031	209	3.34	0.037
		3	0.164	209	20.52	< 0.001
	liber	1	0.038	209	4.17	0.017
		2	0.174	209	21.95	< 0.001
	phyl	1	0.047	209	5.20	0.006
		3	0.046	209	5.03	0.007
	plic	3	0.073	209	8.29	< 0.001
	villi	3	0.109	209	12.84	< 0.001
	ast	2	0.095	209	11.00	< 0.001
Wet season data	tai	2	0.038	215	4.30	0.015
	albo	2	0.03	215	3.34	0.037
	aub	2	0.028	215	3.09	0.048
	all	1	0.202	215	27.27	< 0.001
		2	0.076	215	8.84	< 0.001
		3	0.056	215	6.42	0.002
	tok	1	0.071	215	8.17	< 0.001
		3	0.028	215	3.06	0.049
	guin	3	0.065	215	7.48	0.001
	gutt	2	0.092	215	10.95	< 0.001
	liber	2	0.216	215	29.67	< 0.001
	phyl	1	0.096	215	11.41	< 0.001
		2	0.128	215	15.73	< 0.001
		3	0.027	215	3.03	0.050
	plic	1	0.101	215	12.06	< 0.001
		2	0.048	215	5.42	0.005
	villi	1	0.09	215	10.65	< 0.001
	ast	1	0.029	215	3.19	0.043
	leuco	3	0.029	215	3.23	0.041
	arthcomp	1	0.033	215	3.63	0.028
		2	0.132	215	16.41	< 0.001
		2	0.032	215	3.59	0.029
		3	0.030	215	3.35	0.037