Published in Journal of Tropical Ecology 16, issue 4, 517-533, 2000
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Ecotones and gradient as determinants of herpetofaunal community structure in the primary forest of Mount Kupe, Cameroon

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ABSTRACT. The relative effects of the elevational gradient and of environmental discontinuities (ecotones) on the structure of a herpetofaunal assemblage in a tropical upland forest were contrasted by means of canonical correspondence analysis. Qualitative descriptors were used to define the elevational positions of the ecotones of interest, namely transitions in forest type and presence/absence of water bodies. The elevational gradient was coded in a form that accommodated different types of community response. Analyses were run for four subsets of the entire assemblage: (1) reptiles, (2) amphibians, (3) amphibians dependent on streams for reproduction, and (4) amphibians that do not use streams for reproduction. All subsets showed a significant relationship with the gradient, which suggested that most species respond to the physical continuum associated with the change in elevation. A response to ecotones was revealed for the amphibian subset only and associated with the presence or absence of watercourses. However, this response disappeared within subsets 3 and 4. A variation partitioning analysis was used to assess the individual and common contributions of gradient and ecotone descriptors to the elevational variation in the structure of subsets 1 and 2. The gradient descriptors explained more variation in the reptile subset than did ecotones, while the reverse was found in the amphibian subset. The dependence of most amphibians on aquatic breeding sites that were not available at all elevations reduced the relative importance of the gradient on the species distributions in subset 2 and accounted for the difference to the reptiles. In all, these findings add to the results of previous null model tests on the same four subsets, where competitive interactions were assigned a minor importance in limiting elevational distributions. The response patterns revealed by the present approach, with ecotones

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and gradient contrasted in a single analysis, emphasised the role of individual responses to the gradient according to the species' physiological tolerance limits.

KEY WORDS: Amphibia, Cameroon, canonical correspondence analysis, gradient distribution, Reptilia, species groups, tropical forest, variance partitioning

INTRODUCTION

For many vertebrate assemblages in the tropics, the distribution patterns on elevational gradients are well documented. Studies on mammals (Patterson *et al.* 1989, 1996; Yu 1994), birds (Rahbek 1997, Terborgh 1971, 1985), as well as on amphibians and reptiles (Brown & Alcala 1961, Cadle & Patton 1988, Fauth *et al.* 1989, Heyer 1967) provide examples of how species composition, species richness, and abundance change with elevation both at local and regional scales. Declining species richness with increasing elevation emerged as the first general pattern widely accepted for tropical as well as temperate zone communities (Rahbek 1995). The various effects that account for the distribution patterns of assemblages observed on elevational gradients were generally well recognized, but an assessment of the relative importance of single mechanisms proved difficult. Furthermore, with respect to studies on tropical amphibians and reptiles that explicitly addressed elevational patterns (Brown & Alcala 1961, Heyer 1967, Fauth *et al.* 1989, Scott 1976), differences in scale and sampling designs, small sample sizes, or confounded site and year effects contributed to controversial conclusions concerning apparent patterns (Fauth *et al.* 1989).

The systematic approach to communities on gradients essentially started with the work of a plant ecologist: Whittaker (1967) recognized four distribution patterns of species assemblages on gradients (Figure 1), distinguished on the basis of whether species occurred in discernible groupings and by the extent to which boundaries between species were exclusive. Whittaker (1967) suggested four mechanisms that limit species ranges, namely (a) biotic interactions, (b) abiotic limits, (c) ecotones and (d) dispersal constraints. Soon after, Terborgh (1971) began a systematic assessment of the relative importance of competitive interactions and ecotones in limiting elevational distributions in a tropical vertebrate assemblage. By comparing the distributional patterns of Andean birds on four gradients, Terborgh identified direct and diffuse competitive exclusion as the factor of overriding importance in limiting avian distributions (Terborgh 1985), accounting for about two-thirds of the limits, while ecotones and unspecific factors varying in parallel with the gradient each accounted for about one-sixth. Evidence was based on observed displacements of species boundaries in the absence of potentially competing congeners on control transects, and on the response of species to downward or upward shifts of homologous ecotones on the various gradients. In other tropical faunal assemblages, the relative importance of competitive interactions, ecotones and factors varying in parallel with the gradient in limiting elevational distributions

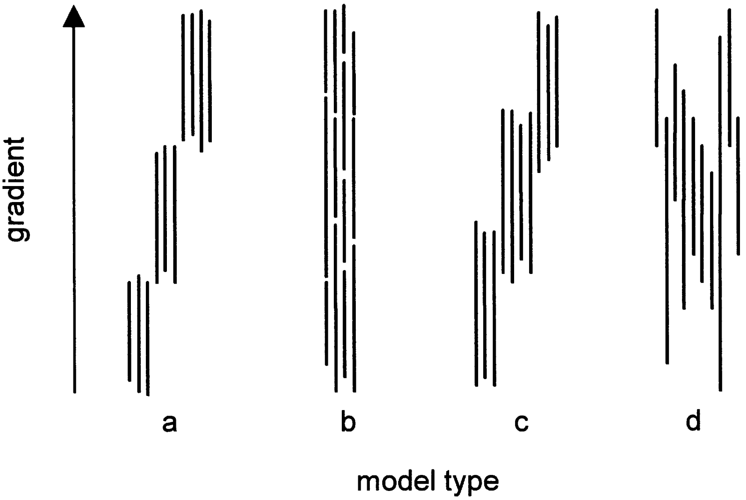

Figure 1. The four models of the arrangement of species on a gradient suggested by Whittaker (1967), adapted from Dale (1986). Each line corresponds to a species range. (a) distinct groups of species with sharp ecotonal exclusion boundaries; (b) sharp exclusion boundaries between competing species but no natural groupings; (c) groupings of species that are not exclusive; and (d) no groupings and no exclusion, species distributions independent of each other.

is likely to be different. To substantiate that, however, a systematic procedure comparable to Whittaker's and Terborgh's one is required. Meanwhile, several null model tests have been developed for the analysis of community patterns on one-dimensional gradients (for a review, see Gotelli & Graves 1996), and allow another approach to the topic.

In a previous paper (Hofer *et al.* 1999), we used null model tests for one-dimensional gradients to critically evaluate the fit of the observed distribution patterns to the four models proposed by Whittaker (1967) to characterize community organization on gradients (Figure 1). Our results indicated few cases where interspecific competition may have led to spatial exclusion along the gradient or to significantly small range overlaps. Several null models revealed zonations in the elevational distribution patterns of the species groups tested. With one exception, however, these zonations did not correspond to obvious environmental discontinuities. The overall result of the null models suggested rather that substantial variation within the elevational distribution pattern of this assemblage may be due to the species' individual responses to the physical factors that vary in parallel with the gradient, according to their physiological tolerance limits. This was the implicit null hypothesis in Terborgh's (1971) approach as well as in the null model tests that we applied.

In this paper, we now explicitly assess the impact of the elevational gradient, i.e. the sum of unspecified physical factors varying in parallel with it, on the elevational distribution patterns observed at the level of species groups, relative to ecotones assumed to absorb a substantial part of the variation of the species' abundances along the gradient. In its original definition, the term ‘ecotone’ represents a narrow transition zone between two discrete habitats or ecosystem types (Clements 1905, Jeník 1992) and primarily refers to structural change of vegetation. Here we use it as well to denote the environmental discontinuities along the gradient brought in by the uneven availability of aquatic habitats. It must be noted that we do not search for distinct sets of species associated with a particular ecotone.

By means of canonical correspondence analysis (CCA) (ter Braak 1987) we explore the community response to a set of descriptors that (1) define the elevational position of the ecotones of interest and (2) depict the elevational gradient as a continuum and in a form that accounts for different response types. In contrast to the null model approach used by Hofer *et al.* (1999), CCA allows to detect the patterns of variation in the species abundance data that are best explained by the environmental descriptors. Moreover, the method of partial CCA allows an assessment of the amount of variation explained by either ecotone or gradient descriptors alone.

STUDY SITE

Mount Kupe (4°45′N, 9°42′E) in the Southwest Province of Cameroon, is a steep-sided, cone-shaped mountain 2064 m in height and situated *c.* 100 km northeast of Mount Cameroon. Mount Kupe forms part of the Cameroon highlands, an extensive volcanic mountain range running from Bioko Island to Mount Cameroon in the southwest on to the Bamenda and Adamawa Highlands in the northeast, with the Obudu and Mambila Plateaus extending into Nigeria. The mountain is covered by *c.* 2100 ha of undisturbed closed canopy submontane forest (Thomas 1986). The canopy is closed and to ≤ 30 m, with a few scattered emergent trees. The stature of the forest gradually declines with elevation until near the summit the canopy is at 10–15 m. The summit gives way to small areas of grassland. Typical montane vegetation is lacking on Mount Kupe. Although Thomas (1986) states that the mountain is high enough to support afromontane forest, he does not provide an explanation for the absence of this forest type. Above 1800 m there are a few montane plant species and this part of the forest is best regarded as transitional between submontane and montane. The lower transitional zone on Mount Kupe, between submontane and lowland forest, extends from 700 to 900 m. However, the primary forest below 900 m has been logged or is severely degraded except for a few patches on the southwestern and southern slopes of the mountain. The topography generated three major types of streams (see Methods section), which were found to be mutually exclusive with respect to elevation in the area sampled. In the primary forest, we found streams between 900 and 1500 m and at 1900 m. Permanent ponds are virtually absent from the study area; the single standing water body found during the entire sampling period was a puddle on a log in a treefall at 1560 m.

The mean annual rainfall on Mount Kupe is 4891 mm (Suchel 1972). The rainy season lasts from April to October; of the remaining months, three receive less than 200 mm. Temperature has never been recorded systematically on the mountain. Our measurements taken at the onset and completion of each sampling bout range from 13.8 °C (1900 m, 13 March, night) to 23.8 °C (900 m, 21 April, day). With respect to time and elevation, however, the readings were too irregular to provide a description of the temperature gradient sufficient to be included in the present analysis.

METHODS

The data were acquired between March and November 1994 in the primary forest on the western slope of the mountain. Samples of the herpetofauna were taken with equivalent intensity at 12 points between 900 and 2000 m, separated by 100 m in elevation, on transects parallel to the contour line. To adequately sample species potentially confined to watercourses, we examined streams separately; riparian sampling zones could be located at eight of the 12 elevations. The sampling method consisted in 3–5 people moving slowly along the transect, turning logs and stones, ripping apart rotten wood, moving floor debris, digging up soil around the root systems of big trees and under logs and inspecting the herb and shrub layer up to about 10 m; in riparian zones, the stream bed was also examined. Animals were either collected or marked, and the marked specimens released at the end of each sampling session.

Between 14 March and 7 November 1994, 226 samples totalling 1075 man-hours were completed. The first samples taken at the end of the dry season from 26 February resulted in nil to a very few specimens encountered. Most species emerged with the onset of the first rainfalls in early March and then gradually increased in abundance. Beta-diversity values between months indicated moderate changes during the sampling period, but did not result in a pattern that suggests a succession of distinct sets of species. Based on these findings and on dry season sample data provided by A. Schmitz (unpubl. data), we conclude that, with respect to species composition and relative abundance, our data set constitutes a representative subsample of the herpetofaunal community within the study area. We excluded from all analyses recaptured animals and specimens encountered at odd times, i.e. outside the equal sampling effort protocol for all elevations. For a more detailed description of the sampling procedures, see Hofer *et al.* (1999).

We used two qualitative descriptors to define the elevational position of the ecotones introduced by the transitions in forest type and by the presence/absence of a given type of water body. Forest types were assigned according to Thomas (1986) and P. Lane (*pers. comm.*), and include three states: (1a) submontane forest with a closed canopy to *c.* 30 m, with few scattered emergents, on ridges more open and to *c.* 18 m, understorey thin except for ridges, ground layer sparse, typical trees include *Santiria trimera* and Guttiferae spp., gap regrowth characterized by *Cylicomorpha solmsii*, *Macaranga occidentalis*, and the

Table 1. States of the two qualitative descriptors of the ecotones, and values of the first variable coding the gradient at each elevation (the values of X^2 and X^3 variables are simply the values of X raised to the corresponding powers).

Elevation [m]	Ecotone		Gradient X
	Forest type	Type of water body	
900	lower transitional	stream type 1	−5.5
1000	submontane	stream type 1	−4.5
1100	submontane	stream type 1	−3.5
1200	submontane	stream type 1	−2.5
1300	submontane	stream type 1	−1.5
1400	submontane	stream type 1	−0.5
1500	submontane	stream type 2	0.5
1600	submontane	standing water	1.5
1700	submontane	—	2.5
1800	submontane	—	3.5
1900	upper transitional	stream type 3	4.5
2000	upper transitional	—	5.5

tree fern *Cyathea* spp.; (1b) upper transitional zone, with a more open canopy to *c.* 10–15 m, understorey dominated by Rubiaceae spp., ground layer sparse, transitional character denoted by a mixture of species more typical of montane forest, e.g. *Carapa grandifolia*, *Garcinia smeathmannii*, the strangler *Scheffleria mannii*, and the endemic *Pavetta kupensis*, and a few lowland species such as *Xylopia staudtii* and *Macaranga occidentalis*; (1c) lower transitional zone; the transitional character of the forest remnants between 700 and 900 m as emphasized by both Thomas (1986) and P. Lane (*pers. comm.*), but no species list was provided. The type of water body was assigned on the basis of our own fieldwork, with the states: (2a) stream type 1: perennial, with a moderate to steep gradient, with several rapids and splash zones, with bottom bedrock and sand; (2b) stream type 2: intermittent, with moderate gradient, with bottom bedrock and silt; (2c) stream type 3: perennial, with a low gradient, with one rapid, with bottom sand and silt; and (2d) standing water, i.e. a puddle on a fig tree log. The states of the variables at the 12 elevations sampled are shown in Table 1. Both qualitative variables were binary coded prior to analyses (Legendre & Legendre 1998). We added a composite variable called stream, which is the sum of the states stream types 1, 2 and 3, and denotes the presence of watercourses.

The samples were separated by the same elevational distance, therefore the elevational gradient was coded in ordinal form as a series of increasing numbers, X (from 1 to 12). As suggested by Legendre (1990), we added the quadratic and cubic terms, X^2 and X^3, to account for other than just linear gradient patterns in the species data. To eliminate the X–X^2 and X^2–X^3 correlations, we centred the descriptor X prior to the analyses. The values of these three variables appear in Table 1.

The ecotone and gradient descriptors were related to the matrix of species abundances by means of canonical correspondence analysis (CCA; ter Braak

1987, Jongman *et al.* 1995), as included in the software package CANOCO (ter Braak 1988). In contrast to redundancy analysis, which is the canonical version of principal component analysis, CCA assumes unimodal response curves of the species to their environment, which is adequate in the present context (Austin 1999). Species abundances were square root-transformed prior to the analyses, as recommended by Legendre & Legendre (1998) when data were skewed to the right. Results of CCA are affected by rare species (Jongman *et al.* 1995). We accounted for this by downweighting the abundances of a given species in inverse proportion to the number of sites at which it was found, according to an algorithm available in CANOCO. We submitted the descriptors to a forward selection procedure. The overall significance of the ordinations and the significance level of each axis were tested by a Monte Carlo permutation procedure. We used unrestricted permutations in our tests. Constrained permutations for line transects would have been more appropriate in theory, but our 12 sites would allow for only 24 different permutations, reducing the power of the test to an insufficient level. Finally, when we applied multiple tests, P-values were corrected according to Holm (1979).

We further used partial correspondence analysis to distinguish between the relative effects of ecotone and gradient descriptors by applying the variation partitioning method described by Borcard *et al.* (1992). This method consists of three analyses: two CCAs constraining the species ordination by each of the explanatory data sets (ecotones and gradient), and at least one partial CCA, either explaining the species data by the ecotones, controlling for the gradient, or the converse. This allowed us to calculate the percentage of variance due exclusively and in common to the two groups of descriptors. In both explanatory sets, we retained the two descriptors that were best correlated with the species data. It is important that the number of explanatory descriptors be approximately equal in each set, since a set with more descriptors will be comparatively overvalued in partial analyses.

To facilitate a coherent interpretation of the distributional patterns revealed by the previous null model analyses and the present approach, we applied the CCA to the same four subsets of the entire assemblage as used in Hofer *et al.* (1999): (1) the reptiles, i.e., 12 lizard and seven snake species; (2) the 30 amphibian species; (3) the 24 species of amphibians that depend on streams for reproduction, i.e. with tadpole development in lotic water or lentic microhabitats associated with streams; (4) stream-independent amphibians, i.e. five species of *Arthroleptis* reproducing by direct development, and *Wolterstorffina parvipalmata*, using water-filled tree holes for oviposition. In Table 2, we list the species according to the groups subjected to analysis, with relative abundance, elevational range and stratification added. The complete matrix containing the species abundances at each elevation sampled is given in the Appendix in Hofer *et al.* (1999).

Table 2. The three herpetofaunal species groups subjected to canonical correspondence analysis. Note that the amphibian subsets are defined by whether species depend on streams for reproduction, and not by the proportion of individuals found in riparian situations. N: number of individuals recorded. The elevational range denotes the lower- and uppermost transect where a species was observed. Stratification: 1 = aquatic; 2 = terrestrial; 3 = arboreal. The acronyms given refer to those used in the CCA plots (Figures 2 and 3).

Species	Acronym	N	Elevational range (m)	Proportion of individuals in/at streams	Stratification
Stream-dependent amphibians					
Afrixalus lacteus Perret	Afri lact	17	1300–1900	1	3
Astylosternus cf.montanus Amiet	Asty cf.m	9	900–1500	0.33	2
A. diadematus Werner	Asty diad	3	900	0.33	2
A. perreti Amiet	Asty perr	53	900–1400	0.97	2
Bufo gracilipes Boulenger	Bufo grac	1	900	0	2
B. tuberosus Günther	Bufo tube	2	900	1	2
Cardioglossa gracilis Boulenger	Card grac	57	900–1200	0.2	2
C. venusta Amiet	Card venu	26	900–1400	0.3	2
Conraua robusta Nieden	Conr robu	5	1000–1400	1	1
Leptodactylodon ornatus Amiet	Lept orna	19	900–1300	0.45	2
Leptopelis brevirostris (Werner)	Lept brev	11	900–1200	0.5	3
L. calcaratus (Boulenger)	Lept calc	7	900–1000	0.86	3
L. modestus (Werner)	Lept mode	12	1400–1900	0.8	3
L. rufus Reichenow	Lept rufu	4	900	1	3
Petropedetes cameronensis Reichenow	Petr came	43	900–1200	1	2
P. newtoni (Bocage)	Petr newt	24	900–1500	0.57	2
P. parkeri Amiet	Petr park	43	900–1400	0.84	2
P. perreti Amiet	Petr perr	34	900–1500	1	2
Phrynobatrachus cricogaster Perret	Phry cric	86	900–2000	0.74	2
P. werneri Nieden	Phry wern	14	1900	0.74	2
Phrynodon sp.1	Phry sp.1	19	1900	1	2
P. sp.2	Phry sp.2	294	900–1500	1	2
Trichobatrachus robustus Boulenger	Tric robu	2	900–1000	1	2
Werneria preussi mertensiana Amiet	Wern preu	3	900–1100	0.66	2
Stream-independent amphibians					
Arthroleptis adelphus Perret	Arth adel	68	900–1200	0.01	2
A. "adolfifriderici" Nieden	Arth adol	737	1300–2000	0.01	2
A. sp.A	Arth sp.A	165	900–1400	0.03	2
A. sp.C	Arth sp.C	94	900–2000	0.05	2
A. variabilis Matschie	Arth vari	322	900–1300	0.03	2
Wolterstorffina parvipalmata (Werner)	Wolt parv	103	1000–2000	0.38	2
Reptiles					
(lizards)					
Chamaeleo montium Buchholz	Cham mont	49	900–1200	0.33	3
Ch. pfefferi Tornier	Cham pfef	39	1100–1900	0.06	3
Ch. quadricornis Tornier	Cham quad	63	1300–2000	0.04	3
Cnemaspis koehleri Mertens	Cnem koeh	12	1200–1800	0.25	3
Hemidactylus echinus O'Shaughnessy	Hemi echi	4	1000–1200	1	3
H. fasciatus Gray	Hemi fasc	1	1000	0	3
Leptosiaphos rohdei Schmidt	Lept rohd	2	900–1000	0.5	2
L. sp.A	Lept sp.A	17	1400–2000	0	2
L. sp.B	Lept sp.B	11	1500–2000	0	2
L. sp.C	Lept sp.C	12	1000–1300	0	2
Mabuya affinis Gray	Mabu affi	1	900	1	2
Rhampholeon spectrum Buchholz	Rham spec	234	900–1800	0.22	2
(snakes)					
Bitis gabonica Hallowell	Biti gabo	1	1000	1	2
Bothrolycus ater Günther	Both ater	1	1300	1	2
Buhoma depressiceps Werner	Buho depr	11	900–1900	0	2
Calabaria reinhardti Gray	Cala rein	1	1100	1	2
Chamaelycus fasciatus (Günther)	Cham fasc	1	1200	0	2
Dipsadoboa sp.	Dips sp.	1	1500	0	3
Mehelya guirali Mocquard	Mehe guir	2	900–1000	1	2

RESULTS

All four subsets except the entire amphibian assemblage responded exclusively to gradient descriptors (Table 3), with either X^2 or X^3 entering the model in combination with X. No subset showed a significant response to a transition in forest type. The first descriptor entering the model, which is also the most correlated with the first canonical axis, is always X. In all groups the amount of variation explained by the first canonical axis is larger than 40%. This denotes a strong relationship between the gradient and the elevational distribution of most species.

The stream descriptors were related to the entire amphibian assemblage only (Figure 2), where they primarily reflect the response of the stream-dependent species to the absence of watercourses at several elevations. The majority of these species is lined along the arrow representing stream type 1, on the left-hand side of axis 1. Five stream-dependent amphibian species found predominantly or exclusively at higher elevations (*Phrynodon* sp.1, *Phrynobatrachus cricogaster* and *P. werneri*, *Leptopelis modestus* and *Afrixalus lacteus*) were strongly related to stream type 3, the only watercourse above 1600 m. Negative correlations with the stream descriptors were shown by stream-independent species with extended range lengths, namely *Arthroleptis adolfifriderici*, *Arthroleptis* sp.C., and *Wolterstorffina parvipalmata*, located in the lower right quadrant of the biplot (Figure 2b), close to the streamless sites (Figure 2a). When analysed separately, both stream-dependent and stream-independent amphibians exhibit a significant response to the gradient only, which still explains 71% and 84% of the variation, respectively.

The response of the reptile subset resulted in a much simpler pattern

Table 3. Summary of CCA results. All canonical axes and descriptors are significant at $P \leq 0.05$, after correction by Holm's method. Stream-dependent amphibians were only tested with the eight elevations where watercourses were found.

		Amphibians		
	Reptiles	All species	Stream-independent	Stream-dependent
Number of sites (elevations)	12	12	12	8
Sum of all eigenvalues (total inertia of species matrix)	1.235	1.208	0.788	1.148
Eigenvalues and percentages of variation explained by:				
canonical axis 1	0.516 (42%)	0.634 (52%)	0.638 (81%)	0.583 (51%)
2	0.201 (16%)	0.238 (20%)	0.020 (3%)	0.228 (20%)
3		0.129 (11%)		
4		0.053 (4%)		
Sum of all canonical eigenvalues and percentage of variation explained overall	0.717 (58%)	1.055 (87%)	0.658 (84%)	0.811 (71%)
Significant descriptors	X X^2	X stream stream type 3 stream type 1	X X^3	X X^2

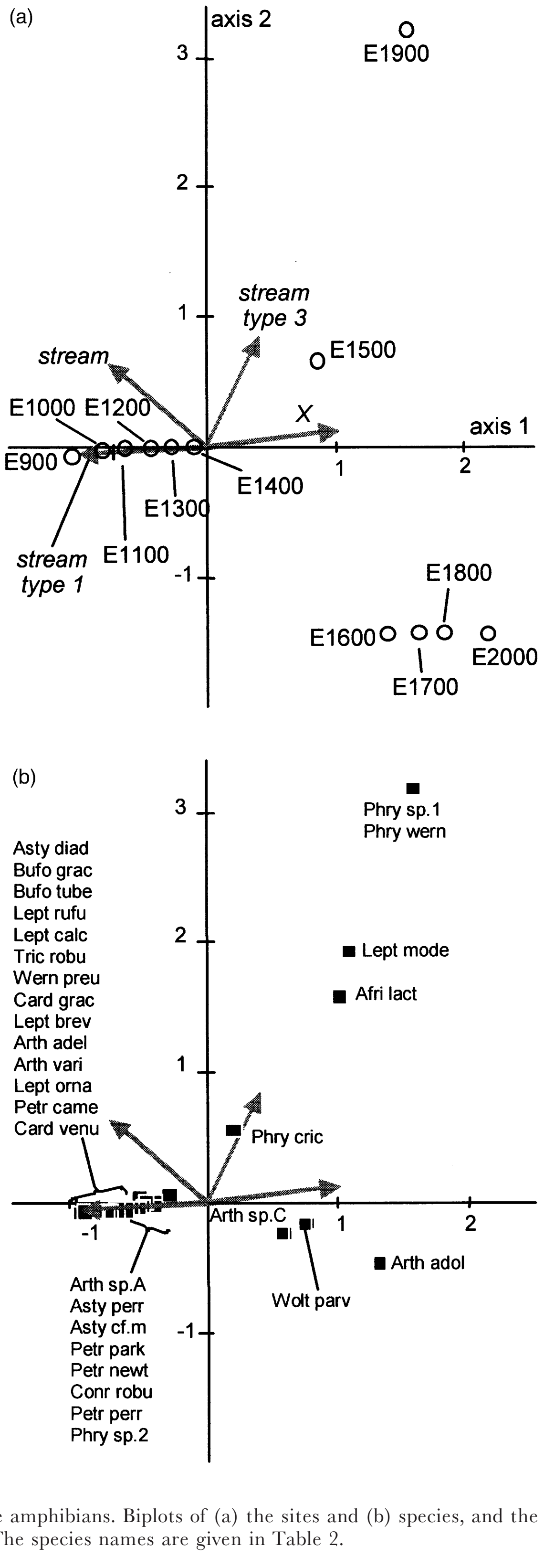

Figure 2. CCA of the amphibians. Biplots of (a) the sites and (b) species, and the significant explanatory descriptors (arrows). The species names are given in Table 2.

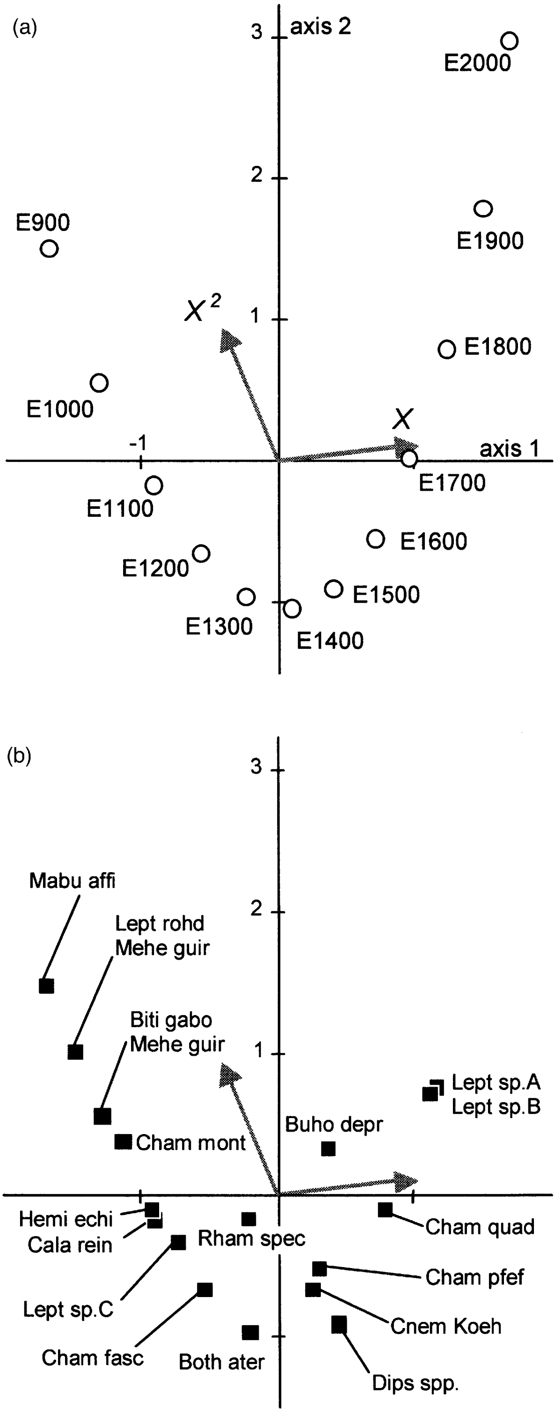

Figure 3. CCA of the reptiles. Biplots of (a) the sites or (b) species, and the significant explanatory descriptors (arrows). The species names are given in Table 2.

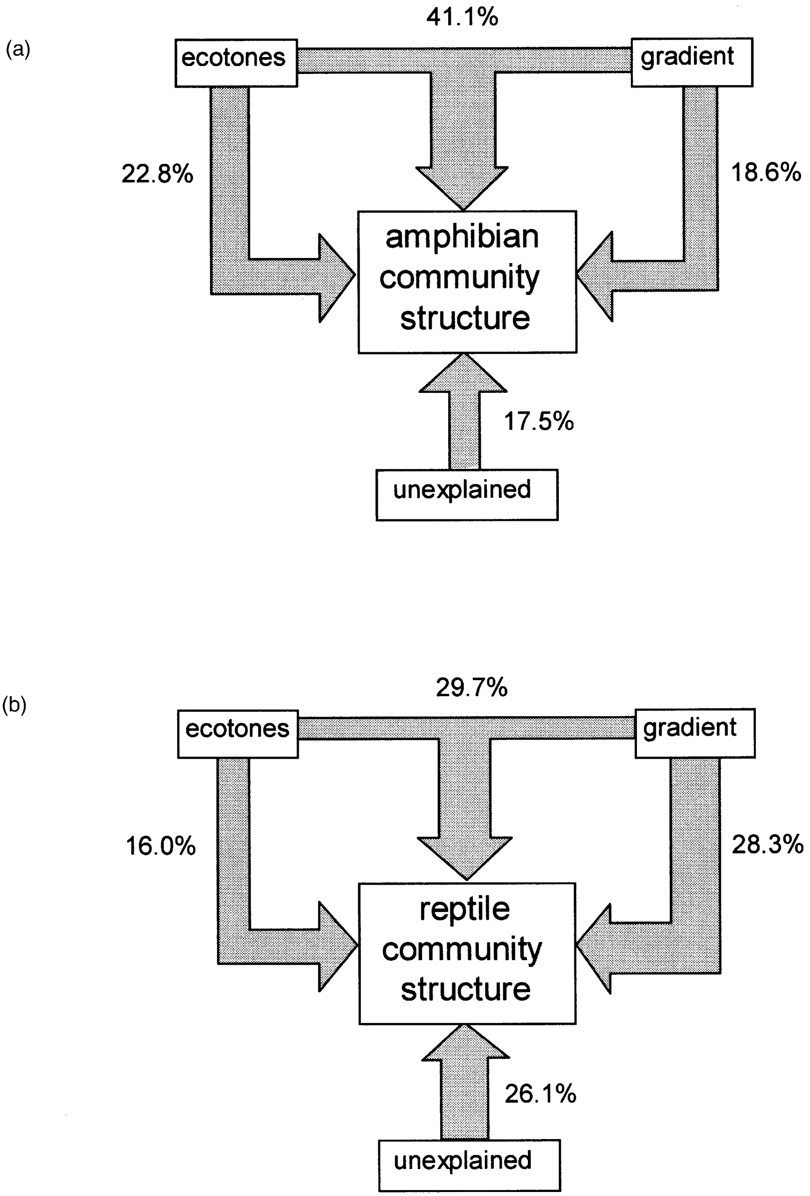

Figure 4. Variation partitioning of the (a) amphibian and (b) reptile communities. Values indicate the percentage of variation explained exclusively or in common by both sets of descriptors.

(Figure 3). The species are ranked on the gradient according to their elevational optima. No effect of the variables describing the ecotones was recognizable.

For the entire amphibian assemblage, the ecotones explain 22.8% of the variation in species' abundances, relative to 18.6% explained by the gradient alone (Figure 4). Both sets of descriptors shared a large amount of common variation (41.1%). For the reptiles the trend is reversed, with the gradient explaining 28.3%, relative to 16% explained by the ecotones alone, and with a much lower common contribution (29.7%). The comparatively low fractions of unexplained variation, 17.5% for the amphibians and 26.1% for the reptiles, result chiefly from the small number of sites included in the analysis.

DISCUSSION

The analyses revealed a significant response to gradient variables of all species groups. The strongest response was shown by the six species of frogs that do not depend on streams for reproduction (subset 4). The dispersion of these species' distributional optima with respect to elevation suggests that species distributions are hardly affected by the environmental discontinuities we simultaneously tested for. In this subset, however, the response pattern is probably enhanced by an effect of interspecific competition (Hofer *et al.* 1999), which resulted in the conspicuous replacement of the two most abundant species along the gradient, *Arthrolpetis variabilis* and *A. 'adolfifriderici'*.

The response of the reptiles (subset 1) to the elevational gradient is less pronounced than in the stream-independent frogs. The reptile subset contains many rare species that were given a small weight in the CCA. Three of the most abundant taxa are arboreal lizards of the genus *Chamaeleo* (Table 2), which, by their relative numbers, are expected to have considerable weight in the response pattern of the reptiles. In a null model that explicitly looked for discontinuities in species data along the gradient, the reptiles showed a zonation that coincided with the change in forest type between 1800 and 1900 m (Hofer *et al.* 1999). Consequently, a sensitivity of the arboreal *Chamaeleo* species to ecotones associated with a change in forest type should decrease the relative effect of the gradient on the distributional pattern at the level of the entire species group. However, when contrasted with the gradient by means of a CCA, ecotone descriptors have no significant effect on the reptile distributional pattern. As revealed by the variation partitioning procedure, 29.7% of variation in species abundance is explained by gradient and ecotones combined. This results from the fact that the ecotones brought in by transitions in forest type are not independent from elevation. As in the stream-independent frogs, interspecific competition probably contributed to the dispersion of elevational optima of the reptiles, with the abundant lizards *Chamaeleo montium* and *Ch. quadriconis* replacing each other along the gradient.

The CCA involving the entire amphibian assemblage (subset 2) revealed a significant response to ecotone variables, namely those that denote the presence/absence of streams along the gradient. A relationship between the availability of watercourses and the elevational distribution of the 24 species of frogs that depend on streams for reproduction (subset 3) was an outcome to be expected. Of particular interest is the response that appears when looking at subset 3 only: Ecotones that result from the uneven availability of watercourses have no longer a significant effect, in contrast to gradient descriptors, which explain 71% of variation (Table 3), an amount that falls in between the one of the stream-independent frogs and the reptiles. A substantial contribution to this result comes from species that drop out at elevations below the upper limits of stream type 1 at 1400 m and stream type 2 at 1500 m (Table 2), e.g. *Petropedetes cameronensis*, *Cardioglossa gracilis* and *Leptodactylodon ornatus*. Among the species of subset 3, the proportions of individuals encountered in riparian situations are on average higher than in the stream-independent frogs and the reptiles, yet they vary from 100% to as low as 20% (Table 2). The variation may to some extent reflect species-specific differences in microhabitat requirements. However, of the 24 species in this subset, only *Petropedetes cameronensis*, *P. parkeri*, *P. perreti*, and the aquatic *Conraua robusta* are largely or exclusively associated with rocky microhabitats confined to streambeds and riparian zones. This suggests that species-specific preferences for microclimatic conditions also account for the different degrees of restriction to streamsides and limit species distributions to the elevations where watercourses are present.

Authors that analysed herpetofaunas in tropical upland areas have recognized climatic factors and coarse-grained changes in habitat as limiting the distributions of most species, both at local (Brown & Alcala 1961, Inger *et al.* 1987, Inger & Stuebing 1992, Scott 1976) and regional scales (Amiet 1971, Duellman & Wild 1993, Heyer 1967). With respect to elevational gradients, examples include species that responded to reduced availability of specific microhabitats associated with streams (Inger & Stuebing 1992) or with particular vegetation zones (Brown & Alcala 1961, Heyer 1967). In a lowland evergreen forest area in South India, Inger *et al.* (1987) found the altitudinal zonation of herpetofaunal distributions to correspond essentially to major shifts in forest type, which they attributed to the climatic zonation rather than to a restriction of suitable microhabitats to some elevations. Scott (1976) emphasized the importance of climatic factors associated with the cloud-forest environment, namely a decrease in temperature and increase in humidity, in limiting or favouring upslope range extensions of neotropical amphibians and reptiles. Yet, in all these studies the environmental data at hand did not allow an assessment of whether climatic factors or habitat changes dominate in their impact on the elevational distribution patterns of the herpetofaunal assemblages. With respect to Bornean frogs, Inger & Stuebing (1992) underlined that no direct evidence exists of a negative effect of lowered temperatures per se on anuran survival.

The present approach does again not allow for an evaluation of the individual contributions of environmental variables to the structuring of herpetofaunal distribution patterns along the elevational gradient. However, the CCA results from Mount Kupe suggest that the physical continuum associated with an elevational gradient absorbs a substantial amount of variation in the elevational distribution of amphibians and reptiles in a tropical upland forest, relative to those environmental discontinuities that reflect the major structural changes of the habitat.

With the null model tests of a previous approach (Hofer *et al.* 1999) and the CCA combined, we can now provide a reassessment of the fit of the distribution patterns exhibited by the amphibians and reptiles on Mount Kupe to the four models of Whittaker (1967). The null model tests of Hofer *et al.* (1999) virtually excluded a response in accordance with model b (Figure 1), where the assemblage would be organized into guilds of competing species that, within guilds, replace one another sequentially along the gradient. The altitudinal zonations that resulted from marked changes in abundance, revealed in all species subsets, were found to correspond best to a model of overlapping species groups (model c, Figure 1). As stated above, the CCA approach used in this paper, where the relative effects of ecotones and gradient were contrasted in a single analysis, assigned environmental discontinuities minor importance in limiting the elevational distribution of reptiles and of both subsets of amphibians. Within these species groups, the dispersion of the elevational optima and range extensions appears to reflect individual responses of many species to the gradient, which result in a pattern in accordance with model d (Figure 1). A combination of model c and d is adequate for the subset comprising all amphibian species, since it responds to both gradient and ecotone descriptors. A more general interpretation of these findings is limited by the relatively small extension (1100 m) of the primary forest gradient that is left on Mount Kupe, with the lower boundary at 900 m at the time of the sampling. The relative importance of the factors that determine elevational distributions need not be the same in the lowland forest range, and in this respect, a wider application of the analysis protocol we used in our approach may provide additional insights.

ACKNOWLEDGEMENTS

Field work was supported by grants from the Swiss Development Corporation, the Swiss Academy of Sciences, and the Natural History Museum of Berne. The Mount Kupe Forest Project provided logistic help and housing in Nyasoso. E. J. Ebung, E. H. Njume and N. S. Epie assisted the whole, C. Wild and I. C. Ojiawum parts of the fieldwork, and C. Wild introduced U. Hofer to the study area. U. Hofer greatly appreciates the support of the Bakossi people in Nyasoso, and in particular, K. E. Epie and E. E. Ewang. J.-L. Amiet, J.-L. Perret, W. Böhme, A. Schmitz and B. Hughes identified many of the collected specimens. J.-L. Amiet made valuable taxonomic and ecological comments, and A. Schmitz provided information on dry season samples from Mount Kupe. For constructive criticism of the manuscript, we thank M. A. Donnelly, D. M. Newbery, and two anonymous reviewers. L.-F. Bersier was supported by the Swiss National Science Foundation grant 31-52566.97 and the Novartis Foundation.

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