

SPATIAL ORGANIZATION OF A HERPETOFAUNA ON AN ELEVATIONAL GRADIENT REVEALED BY NULL MODEL TESTS

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Abstract. Five null model tests were applied to the herpetofaunal assemblage on the western slope of Mount Kupe, Cameroon. Based on the pattern of species range boundaries and abundances along the primary forest elevational gradient, ranging from 900 to 2000 m, the relative importance of interspecific competition and ecotones in structuring the assemblage was assessed. Tests were run for (1) all species, (2) amphibians, (3) reptiles, (4) amphibians dependent on streams for reproduction, and (5) amphibians that do not use streams for reproduction.

For three null models, the observed patterns did not differ from random expectations. The results indicated that there are very few species whose gradient distributions may be limited by interspecific competition between congeners. Significant discontinuities in abundance patterns and range boundary dispersion revealed zonations in all subsets analyzed but neither indicated distinct species groups with sharp exclusion boundaries nor a strong response to vegetational ecotones. Physical factors varying in parallel with the gradient and specific habitat components, particularly water bodies suitable as amphibian breeding sites, are suggested to be the dominant factors limiting gradient distributions of amphibians and reptiles on Mount Kupe. The zonations revealed suggest a pattern of three spatially nonexclusive species groups: physical factors separate distinct lowland and montane species limited by physiological constraints and produce faunal discontinuities in the lower submontane forest around 1300 m; this boundary is encompassed by the range of a group of anuran species, whose distributions on the gradient are centered at intermediate elevation and appear to be limited by specific habitat requirements. The response to predominantly abiotic factors suggests a basic difference from endotherms, where biotic factors seem to be of major importance in limiting elevational distributions.

Keywords: *Amphibia; Cameroon; ecotone; gradient distribution; interspecific competition; null model; Reptilia; species groups; tropical forest.*

INTRODUCTION

The pioneering approaches by Whittaker (Whittaker and Niering 1965, 1975, Whittaker 1967) and Terborgh (1971) provided the basis for a research domain that aimed at elucidating the structure of communities along environmental gradients. The majority of faunal studies focused on diversity and endemism on elevational gradients. Declining species richness with increasing elevation has been demonstrated for many taxa and is now widely accepted as a general pattern (Rahbek 1995), but attempts to establish further uniformity have proven difficult. That species richness does not necessarily decline monotonically with altitude was demonstrated in birds and insects. In an analysis of all South American tropical land birds, Rahbek (1997) examined four species richness/elevation models, two describing a monotonic relationship and two postulating hump-shaped patterns, one of the latter based on a null model expectation formulated by Colwell and Hurtt (1994). By factoring out area, Rahbek showed that species rich-

ness is not highest in the 0–500 m zone, but peaks between 500 and 1000 m. In insects, mid-elevation peaks in species richness were observed by Janzen (1973) and Olson (1994), but not by Lawton et al. (1987) and Wolda (1987). In mammals, hump-shaped patterns have been found in small mammals (Patterson et al. 1989), whereas bats exhibit a monotonic decline (Graham 1990, Patterson et al. 1996). On a coarse scale, amphibians and reptiles essentially show a monotonic decline in species richness (Heatwole 1982), although opposite trends have been observed in particular habitats (Heyer 1967).

Authors usually claim a complex interplay of factors to explain the variability of observed gradient patterns, including nonbiological ones such as differences in sampling regime (Wolda 1987, McCoy 1990), scale differences (Patterson et al. 1996), and species–area effects not adequately accounted for (Rahbek 1995, 1997). Lawton et al. (1987) explain the decline of insect species richness with altitude by a decrease in habitat

area, resource diversity, and primary productivity, emphasizing the changes in host plant diversity and plant architecture. Vegetational habitat structure has also been found to affect elevational distributions of small mammals on Taiwan (Yu 1994) and of Andean birds (Terborgh 1985), although competitive interactions seem to transcend the effect of vegetational ecotones in the latter case (Terborgh and Weske 1975, Terborgh 1977). From a macrogeographic perspective, the impact of phylogeny and speciation modes on diversity patterns on local gradients has been repeatedly emphasized (e.g., Duellman 1979, Cadle and Patton 1988, Patterson et al. 1996). For most regions, however, more historical data are required to elucidate these processes. In all, the various effects accounting for the distribution patterns of assemblages on elevational gradients are well recognized, but attempts to unravel them by explicitly testing for the relative importance of single factors remain sparse.

Whittaker (1967) described four models of community organization on gradients, distinguished on the basis of whether or not species occur in discernible groupings and the extent to which boundaries between species are exclusive. The four models are: (1) distinct groups of species with sharp exclusion boundaries; (2) sharp exclusion boundaries between competing species, but no natural groupings; (3) groupings of species that are not exclusive; (4) no groupings and no exclusion. The models themselves are generated by four mechanisms: (1) biotic interactions, (2) abiotic limits, (3) ecotones, and (4) dispersal constraints. An explicit attempt to test for the relative importance of the first three mechanisms in limiting species' distributions was made by Terborgh (1971, 1985). By comparing the elevational distributions of bird species on one reference and three control gradients in the Andes, Terborgh identified direct and diffuse competitive exclusion as the factor of "overriding importance" in limiting avian distributions (Terborgh 1985). 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 this paper, we make use of null model tests to analyze the gradient distribution pattern of a herpetofaunal assemblage from Mount Kupe, Cameroon. The main models have been developed by Pielou (1977, 1978) and Dale (1984, 1986, 1988), and disregard abundances. Therefore, we also used chronological clustering (Legendre et al. 1985), a constrained permutation method that retains abundances. The application of some of Pielou's and Dale's models to sampling designs based on discrete points at regularly spaced intervals required modifications that are also dealt with in this paper. In combination, these tests help to assess the relative importance of interspecific competition and ecotones in the gradient distribution of an

assemblage, based on its patterns of range boundaries and abundances. Potentially competing species pairs can be singled out and, at the assemblage level, non-random patterns can be identified.

The models for analyzing community structure on environmental gradients are well developed, but lack broad application (Gotelli and Graves 1996). To obtain meaningful results, the null model tests must meet three criteria: (1) data on elevational ranges must be obtained from single locations, (2) sampling must occur on a continuous scale or at regularly spaced intervals, and (3) sampling must be done with equivalent intensity. In the case of tropical upland herpetofaunas, elevational ranges of species, when given, were evaluated by pooling data from several localities, e.g., from transects on different mountainsides (Duellman 1979, Cadle and Patton 1988, Inger and Stuebing 1992, Duellman and Wild 1993), or else they encompassed a small elevational range (e.g., Raxworthy and Nussbaum 1994). In studies explicitly addressing regional or local elevational patterns (Brown and Alcalá 1961, Heyer 1967, Scott 1976, Fauth et al. 1989), different sampling designs, small sample sizes, or confounded site and year effects contributed to controversial conclusions (Fauth et al. 1989). Unfortunately, none of the examined papers fulfilled all three criteria to an extent that a reanalysis of published data with null models is likely to yield ecologically relevant results. A broader analysis of gradient patterns and a comparison of performance of the various null model tests using data with different sampling designs and degrees of resolution are still desirable.

STUDY SITE

Mount Kupe, 4°45' N, 9°42' E, in the southwest province of Cameroon, is the first major peak inland from Mount Cameroon, ~100 km northeast, but is smaller and only half as high at 2064 m. It forms part of an extensive volcanic mountain range running from Bioko Island to Mount Cameroon in the southwest, on to the Bamenda Highlands and the Adamawa Highlands in the northeast, with the Obudu and Mambila Plateaus extending into Nigeria. This range, known as the Cameroon Highlands, is the only highland area in tropical West Africa sufficiently high and extended to develop large and distinct floral and faunal assemblages. The highest number of locally endemic amphibians on mainland Africa is found here, with >60 species being restricted to this region (Jenkins and Hamilton 1992) out of roughly 200 anuran species known from Cameroon alone (Amiet 1989).

In the Late Pleistocene, the Cameroon Highlands were exposed to severe climatic fluctuations (Hamilton 1992). Warm and humid conditions, alternating with especially dry and cold phases, caused expansions and contractions of montane biotopes and fragmentations of lowland forest, repeatedly favoring allopatric speciation and subsequent range extensions. During harsh

TABLE 1. Description of the elevational gradient sampled on the western slope of Mount Kupe, Cameroon, March–November 1994, and man-hours of sampling time spent at each elevation.

Contour	Accessible transect length (m)	Accessible riparian zone length (m)	Stream identity	Number of man hours [†]			
				dt	nt	dr	nr
900	240	150	A, B	44	34	9	12
1000	140	27	B	43	36	10	11
1100	230	50	C	44	36	9	13
1200	200	50	C	43	37	7	12
1300	220	31	C	38	31	7	10
1400	220	27	C	44	32	6	9
1500	240	155	D	39	38	5	11
1600	500			42	37		
1700	340			42	36		
1800	220			43	35		
1900	400	150	E	41	35	10	12
2000	790			41	33		

[†] Abbreviations: dt, day transect; nt, night transect; dr, riparian zone during day; nr, riparian zone at night. At the contours 1600, 1700, 1800, and 2000 m, no watercourse was found.

climatic periods, many species survived in several “refuges.” Modern distribution patterns of forest organisms, centers of biodiversity, and gradients of species richness indicate three major centers of forest survival in tropical Africa, Mt. Kupe being part of the “Cameroon/Gabon refuge” (Maley 1987). Present-day patterns in western Cameroon include species with relatively large distributions over widely separated mountains, and other species restricted to a single or small group of mountains. As Amiet (1987) found no differentiation between isolated populations of montane anuran species in Cameroon, he concluded that the last extension of montane ranges to low altitudes was relatively recent and coincided with the last major cold phase, from 25 000 to 15 000 yr BP.

Mount Kupe is a steep-sided, cone-shaped mountain of horst uplifts and syenitic and granitic intrusions formed by block faulting and bounded by structural troughs, within which volcanic activity has created small cones (Tye 1986). Today the mountain is covered by ~2100 ha of undisturbed, closed-canopy submontane forest, characterized by a fairly uniform structure with a sparse ground layer and a thin understory (Thomas 1986). The canopy is closed and is ~30 m in height, with a few scattered emergent trees. On ridges, the forest has a more open canopy ≤18 m tall and a higher density of smaller understory trees. The stature of the forest gradually declines with elevation until the canopy is at 10–15 m near the summit. The summit gives way to small areas of grassland. Although the mountain is high enough to support afro-montane forest, the typical montane vegetation is absent on Kupe. Above 1800 m however, there are a few montane plant species; this part of the forest is best regarded as transitional between submontane and montane. According to Lane (1994), 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. Mount Kupe holds several permanent streams, but, as some run partly underground, no watercourse was found within the study area between 1600 and 1900 m.

Suchel (1972) gives an annual rainfall average of 4891 mm on Mount Kupe, measured over a period of 21 yr. The rainy season lasts for 7 mo. from April to October, with heavy rains almost daily and rainfall peaking in August (878 mm). With no month receiving <70 mm, an appreciable dry season is absent. Reliable temperature data on Kupe are not readily available. The minimum temperature measured during the entire sampling period was 13.8°C (1900 m, 13 March, at night); the maximum was 23.8°C (900 m, 21 April, during the day).

MATERIAL AND METHODS

Data acquisition

Data on gradient distribution were acquired between March and November 1994. Fieldwork was restricted to the primary forest between the village of Nyasoso (800 m) and the summit of the mountain (2064 m). The lower altitudes up to 1200 m were sampled from the village. The work in the higher elevations started from two field camps, set up at 1550 m and 1930 m, respectively. Seven periods of up to 10 d each were spent in the camps, alternating with stays at the village. In July and August, camping was suspended due to continuous rainfall.

At 12 points between 900 and 2000 m (Table 1), separated by 100 m, transects were opened along the contour line and were linked by two vertical main trails. To adequately sample species potentially confined to watercourses, we examined streams separately; riparian sampling zones could be located at eight of the 12 elevations. Because a regular elevational spacing is crucial for the null model analyses presented here, the 100 m was maintained regardless of the suitability of the topography. This caused some transects and ripar-

TABLE 1. Extended.

No. sampling sessions in each month (March–November)								
M	A	M	J	J	A	S	O	N
2	0	1	4	3	6	1	3	1
3	0	3	3	4	3	2	2	1
0	4	3	4	3	3	1	2	1
0	3	4	4	2	4	1	2	1
0	4	4	6	0	2	1	4	0
0	3	3	7	0	0	2	6	0
0	4	5	6	0	0	3	4	0
0	3	4	3	0	0	2	2	0
0	4	2	3	0	0	3	2	0
5	2	3	0	0	0	4	0	0
10	6	1	0	0	0	5	0	0
5	3	1	0	0	0	5	0	0

ian zones to fall at areas where a free extension in length was severely hampered or impossible. Thus, the maximal transect and riparian zone lengths accessible varied from 140 to 790 m and from 27 to 150 m, respectively. The widths were constrained both by the topography and the structure of the understory; where possible, a strip up to 20 m wide was examined along transects and up to 10 m wide on both streambanks at riparian zones. Yet, the topographic heterogeneity among the elevational zones prevented a reasonably accurate delimitation of areas. We therefore based an equal sampling effort (ESE) at all elevations on a time-constrained technique (Campbell and Christman 1982). The basic schedule per elevation was eight day transects (90 min each), five night transects (120 min each), and, for riparian zones, four day (30 min each) and four night visits (45 min each). The sampling method adopted was “cruising collecting” (Inger and Colwell 1977), i.e., 3–5 people moved slowly along the transect, moving floor debris, turning logs and stones, ripping apart rotten wood, digging soil in the root system of big trees and under logs and inspecting the herb and shrub layer up to ~10 m; in riparian zones, the streambed was examined in addition. The amount of time spent at each elevation was counted in man-hours, i.e., the time spans per sample were multiplied by the number of workers involved. Given the indicated method, transect widths, and time spans, the crew covered up to 200 m on a transect and up to 40 m on a riparian zone sample. At the 1000-m elevation with a transect length of only 140 m, we searched a broader strip, which could be extended to 45 m at this site. Heavy rains regularly slowed down or interrupted sampling sessions and required an adjustment. In general, time spans of individual samples were prolonged. In the middle of the rainy season, however, differences increased to such an extent that a sixth night transect had to be added at all elevations from 1500 to 2000 m to maintain approximately equal regimes. Despite our efforts, we could not avoid some variability in the total sampling time spent at each elevation (Table 1).

Between 14 March and 7 November 1994, the crew completed 226 samples totaling 1075 man-hours. Specimens encountered at odd times and during samples broken off due to heavy rains were added to the row totals of the Appendix, but were ignored in the analysis. Animals were either collected or were marked by toe- (skinks, geckos, frogs), gular-crest- (chameleons), or scale-clipping (snakes), and were released at the end of each sampling session. A collection of voucher specimens is deposited at the Natural History Museum of Berne, with additional specimens at the Alexander Koenig Zoological Research Institute and Zoological Museum in Bonn and in the collection of the Mount Kupe Forest Project in Nyasoso.

Analysis

To reveal nonrandom patterns on the gradient, the species \times sample matrix has been subjected to several null model tests developed for the analysis of distributions along one-dimensional environmental gradients. From the null models of Pielou (1977, 1978), originally applied to seaweed species on a latitudinal gradient, and of Dale (1984, 1986, 1988), originally applied to intertidal algae, we selected those applicable to our data and likely to yield meaningful information. For details of the methods, readers are referred to the original papers. The five hypotheses tested are:

1) The species’ ranges, given their observed lengths, are located independently and at random within the total gradient length (Pielou 1977, conditional hypothesis H_2). Each species pair is assigned a λ value according to the pattern of overlap (0, no overlap; 1, partial; 2, complete; 1.5, partial or complete, i.e., the two upper, lower, or all boundaries coincide), the sum of λ giving the observed overlap of the entire assemblage, L_s . This value is compared to the expected overlap for the entire assemblage $E(L_s)$, which is the average of expected amounts of overlap computed for all possible species pairs. Strong deviations of L_s from $E(L_s)$ indicate an unusually nested ($L_s > E(L_s)$) or nonoverlapping assemblage ($L_s < E(L_s)$).

2) The downslope boundary of a species is followed significantly often by the upslope boundary of another, i.e., the number of observed contiguities differs significantly from random expectation (Dale 1984). In the original formulation of the test, boundaries are considered contiguous regardless of the distance between them, provided no other boundary intervenes (“contiguities of sequence”). However, “the contiguity hypothesis refers to ecological contiguities” (Dale 1984: 94), where the upslope boundary of one species coincides exactly with the downslope boundary of another. Significantly more such contiguities than expected are consistent with a competitively structured community, with similar species replacing each other on the gradient.

3) The observed gap (g) or overlap (y) length for any pair of species, given their observed range lengths, differs significantly from random expectation (Dale 1986). Species pairs with significantly small gap sizes or overlaps may competitively interact. If a larger assemblage of potential competitors is analyzed, the numbers of significantly high or low g and y help to reveal the model of community organization. However, the lack of independence in the set of values does not allow significance testing at the community level (Dale 1986).

4) The clumping (or out-spacing) of the species’ range boundaries (either upper or lower) differs significantly from random expectation (Dale 1988). The statistic W_m measures the variability of interboundary distances; the serial autocorrelation statistic h_m measures the degree of clumping of more than two boundaries at a time. Significantly large values of h_m indicate the presence of boundary clumps. Because multiple tests are performed simultaneously (all possible pairs of range boundaries are compared), we applied a Bonferroni correction to this analysis (Rice 1989).

5) Pielou’s and Dale’s tests assume sampling on a continuous scale and simplify the community matrix by ignoring abundances and treating the species’ ranges as a “sheave” of line segments. However, many data sets from local gradients (including our own) consist of species abundances measured at discrete points on a gradient. Because the shapes of the species’ amplitudes may add essential information on the mechanisms of distributional limitation (Terborgh 1971), tests that include abundances are desirable. We know of no such test operating at the level of pairwise species comparisons. For an entire assemblage, the chronological clustering of Legendre et al. (1985), applicable on temporal or spatial scales and to abundances as well as to binary data, tests for discontinuities in species composition along a gradient. Although the previous tests operate on the species ranges, here the objects in the raw data matrix are the samples from different points on a gradient, under the single constraint that they appear in their original spatial or temporal succession. A similarity matrix is built, using an appropriate index, and

is submitted to a constrained intermediate-link linkage clustering, where only contiguous samples can be grouped. Each fusion is submitted to a permutation test in which samples are randomly reallocated among groups. The clustering stops at a preset level of probability of fusion between adjacent groups of samples. Despite its entirely different approach, this test is suitable for the detection of species groupings, either exclusive (Whittaker’s model 1) or nonexclusive (model 3). The chronological clustering tests whether or not within-group similarities between samples are significantly higher than among-group similarities.

Correction for ties

Dale’s and Pielou’s tests were designed for ranges measured on a continuous scale. They are, however, suitable for ranges measured on a discrete scale, provided that some small modifications are introduced. In hypotheses 1 and 3, range, gap, and overlap length can be expressed in standard units (e.g., in numbers of point intervals), and no modification is required. However, the tests of hypotheses 2 and 4 are biased toward clumping, because more boundaries will coincide if ranges are measured on a discrete rather than a continuous scale. This requires an appropriate handling of “ties,” i.e., of potentially artificial concentrations of range boundaries on sampled points. Pielou and Routledge (1976) and Underwood (1978) provided tests for the clumping of range boundaries in data sets based on discrete sampling. However, they do not fully replace Dale’s test of hypotheses 2 and 4, as they treat upper and lower boundaries in separate analyses, thereby preventing the identification of competitively structured communities (Gotelli and Graves 1996). Consequently, we retained Dale’s tests (1986, 1988) and corrected for ties in the following ways.

The test of hypothesis 2 deals with contiguous ranges of species, that is, cases in which the ending of a range (event E) is followed by the beginning of the range of another species (event B). Thus, on a sequence of, e.g., *BEBBEEBE*, one will find two contiguities (events *EB*, are in italics). On a discrete scale, one could have, for example, one ending (E) at a sampling point and two beginnings (BB) at the following point. This configuration cannot be simply equated to the sequence *BEB* (one contiguity), because the ending and the actual beginnings can be located anywhere between the two sampling points. We have three possible sequences: *EBB*, *BEB*, and *BBE*, with, for each sequence, 1, 1, and 0 contiguity, respectively. Thus, the expected number of contiguities is $2/3$, that is two contiguities divided by three possible sequences. With t being the number of E’s plus the number of B’s, and m being the number of either E’s or B’s, the number of possible sequences is $\binom{t}{m}$, and it can be shown that the total number of contiguities in these possible sequences is $[(t-1)/(m-1)!] \binom{t-1}{m-1}$. The corrected number of contiguities is the ratio of the total number of conti-

guities by the number of possible sequences, which, after simplification, is $[m(t - m)]/t$. Note that this correction must be applied at each point of a gradient sampled on a discontinuous scale.

The test of hypothesis 4 deals with the clumping of range boundaries and uses the interboundary distances as a parameter. We corrected potentially artificial clumps at sample points by maximizing the interboundary distances; e.g., with a 100-m interval, two boundaries falling at 1300 m are transformed into 1283 m and 1316 m. This is a conservative correction, in that a regular spacing renders more difficult the detection of significant clumps. An unbiased correction, using a broken stick distribution, is very difficult to apply here since the ordering of the interboundary intervals, which is arbitrarily set by the investigator, affects the h_m statistic.

Significance tests

Pielou (1977) provides a formula for the expected L_s value (hypothesis 1), but no significance test for this statistic. We resorted to a permutation test to evaluate the probability that the observed L_s value is smaller or larger than the expected value. In this test, we placed the observed ranges at random positions on the gradient and computed the L_s statistic. We constrained the reshuffling, in that the numbers of range boundaries coinciding with the upper or lower end of the gradient were the same as in the observed distribution of range boundaries. We performed 999 permutations. The position of the observed L_s value in the distribution of randomized L_s is an estimate of the cumulative probability that L_s deviates from $E(L_s)$. Given that Pielou's formula for $E(L_s)$ does not correct for range boundaries coinciding with the endpoints of the gradient, we used the median of the permutation-based distribution as an estimate of the expected value of L_s .

Although Dale (1984) provides a table of critical values for c (the number of contiguities in hypothesis 2), we used the permutation test previously described to assess the probability that the observed c differs from random expectation. Dale's critical values are computed such that beginnings and endings can occur anywhere on the gradient, with the constraint that the first event is a beginning and the last one is an ending. However, when sampling distributions on a gradient, one is very likely to find more than one species range starting with the lowermost sampling point and ending with the uppermost. These beginning and ending events are fixed and cannot be included in a permutation procedure. This constraint is incorporated in the randomization test that we have described, making it suitable for the testing of c . Again, we used the median of the distribution of randomized c values as an estimate of the expected c .

All programs except chronological clustering were written in Visual Basic and were tested with idealized matrices corresponding to the four model distributions.

They are available as Excel Macros by writing to the first author. Chronological clustering was performed with program CHRONO from the R Package Version 3.0 (Legendre and Vaudor 1991).

The five null model tests were applied to our original data from Mount Kupe. We ran the tests concerning the assemblage level for (1) all species; and for four subsets: (2) amphibians; (3) reptiles; (4) amphibian guild depending on streams for reproduction, i.e., tadpole development in lotic water or lentic microhabitats associated with streams; and (5) stream-independent amphibian guild, i.e., species reproducing by direct development or breeding in ponds, puddles, and tree holes. To assess to what extent the results are affected by rare species, the tests were rerun for all five sets with a reduced matrix, in which only the species with a total abundance of ≥ 10 individuals are retained. In tests concerning interactions at the species level (hypotheses 2 and 3), we report significant results for congeneric pairs only, thereby disregarding diffuse competition involving heterogeners (sensu Terborgh and Weske 1975).

RESULTS

Composition and quality of the raw data

In all, 2734 amphibians and 596 reptiles were marked or collected, representing 64 species of 35 genera and 12 families (Appendix). The amphibian fauna is dominated by species reproducing by direct development (*Arthroleptis*) or in streams. Species not reproducing in stream-associated water bodies belong to the genera *Wolterstorffina*, *Nectophryne*, *Acanthixalus*, *Chiromantis*, and *Hyperolius*; all but the first are recorded rarely and very locally. About 17 of the 38 species belong to the anurans endemic to the Cameroon Highlands (Gartshore 1986). The remaining are lowland species confined to the western border (*Petropedetes camerunensis*, *Astylosternus diadematus*) or widespread in the Western Equatorial Forest (Amiet 1975). *Chiromantis rufescens* is the only species also reported from the Upper Guinean Forest.

The reptile fauna is dominated by chameleons and scincids. The genera *Chamaeleo* and *Leptosiaphos* exhibit a considerable degree of endemism in the Cameroon Highlands, with the majority of the Kupe *Leptosiaphos* belonging to three new taxa (J.-L. Perret, *personal communication*, W. Böhme, *personal communication*), two with a submontane and one with a premontane distribution. Sightings of the single lacertid recorded, the diurnal, heliophilic *Adolfus africanus*, were restricted to a treefall at 1560 m. The sample includes all lizard genera hitherto known to show montane distributions in Cameroon. With 38 specimens of 11 species, snakes were rarely encountered, the only exception being the small, cryptozoic *Bufo depressiceps*. Several species known to occur at higher ele-

TABLE 2. Results of Pielou's (1977) null model test on the random location of species' ranges.

Group	S	m	$E(L_s)$	L_s	P	Lambda frequencies			
						2	1.5	1	0
All species	49	474	1210.0	1262.5	0.855	173	499	168	336
	30	650	511.5	496.5	0.181	41	195	122	77
Amphibians	30	507	521.5	504.0	0.191	21	270	57	87
	21	614	256.5	243.5	0.113	15	117	38	40
Reptiles	19	421	142.0	144.0	0.571	31	38	25	77
	9	733	41.5	39.0	0.110	4	8	19	5
Stream-dependent amphibians	24	442	306.5	312.0	0.629	9	180	24	63
	15	533	115.5	112.5	0.189	4	61	13	27
Stream-independent amphibians	6	767	17.5	18.5	0.765	0	9	5	1

Notes: In each group, the first row refers to analyses with all species of the respective group; the second row refers to analyses with abundant species only (≥ 10 individuals). All stream-independent amphibians had abundances > 10 individuals. Column heads are: S , number of species; m , mean span length of species in the assemblage; $E(L_s)$, expected overlap based on 999 permutations of range boundaries under Pielou's hypothesis 2 (conditional hypothesis); L_s , observed overlap of tested assemblage; and P , cumulative probability. The lambda frequencies reflect the pattern of overlap (0, no overlap; 1, partial; 2, complete; 1.5, partial or complete overlap).

variations in western Cameroon were only found in the farm bush below 900 m.

To assess the quality of each elevational sample, species accumulation curves were plotted by adding up the species appearing in the chronologically ordered samples. On average, 76% of the species ultimately obtained were recorded in the first half of the samples (minimum 56%; maximum 100%), and 87% after three-quarters of the samples (minimum 67%). We estimated the maximal species richness at each elevation by fitting the Michaelis-Menten equation (Raaijmakers 1987) and by computing Chao's (1984) estimator (reviewed in Colwell and Coddington 1994). Chao's method gave heterogeneous results, with the observed richness varying between 39% and 100% (mean 73%) of the maximum estimated. The Michaelis-Menten procedure yielded more consistent results, with the observed richness ranging from 70% to 90% (mean 78%). To what extent these inadequacies in the raw data affect the direction of the null model results will be addressed in the discussion.

Null model tests

Table 2 lists the results of Pielou's null model test on the random location of species' ranges (hypothesis 1). The permutations revealed no significant differences between observed and expected overall overlap. High proportions of λ values of 1.5 in all groups except the reptiles undoubtedly favored this outcome, the strongest in the stream-dependent species, where observed and expected overlaps are very close. Among the reptiles, the narrow ranges recorded for many species result in the smallest mean span length of all groups and higher proportions of no or nested overlaps ($\lambda = 0$ or 2). As expected, the elimination of rare species increased the mean span lengths of species and reduced the proportion of zero λ values, but the analysis of the reduced matrices again yielded no significant

differences between observed and expected parameters.

Table 3 presents the results of Dale's null models. The test on contiguities (hypothesis 2) reveals a significant difference from random expectation only for the entire assemblage, in which the observed number of contiguities exceeds the expected one ($P = 0.97$, cumulative probability). Congeners exhibiting an ecological contiguity are *Arthroleptis adolfifridericici*–*A. adelphus* and *Chamaeleo quadricornis*–*C. montium* at 1250 m, and *Leptosiaphos* species A–L. species C at 1350 m. The test of hypothesis 3 on gap sizes (g) and partial overlaps (y) revealed no pairs with significantly small or large g , but large numbers of significantly small or large y . However, the test identified only two congeneric pairs with significantly small y : *Arthroleptis adolfifridericici*–*A. variabilis* and *A. adolfifridericici*–*A. species A*, overlapping between 1250 and 1350 m, and between 1250 and 1450 m, respectively. Congeners represent only 3% of all significantly small y and 2.7% of all significantly large y , the majority of the latter concerning the stream-dependent genera *Petropedetes*, *Leptopelis*, and *Astylosternus*. In all groups except the stream-independent amphibians, significantly small y compose $< 7\%$ and significantly large y compose $> 56\%$ of all partial overlaps observed. The test on the spacing of range boundaries (hypothesis 4) reveals a significantly higher variability of interboundary distances W_m than expected by chance in all five groups. Except for the stream-independent amphibians, the serial autocorrelation statistic h_m indicates significant clumping of boundaries in all groups. However, significant clumps are indicated at the level of the entire assemblage only, between 1000 and 1500 m. The apparently contradictory result between the number of significant clumps and the h_m statistic is due to the Bonferroni correction. Results of the analyses with the reduced matrix are largely convergent with those based on the

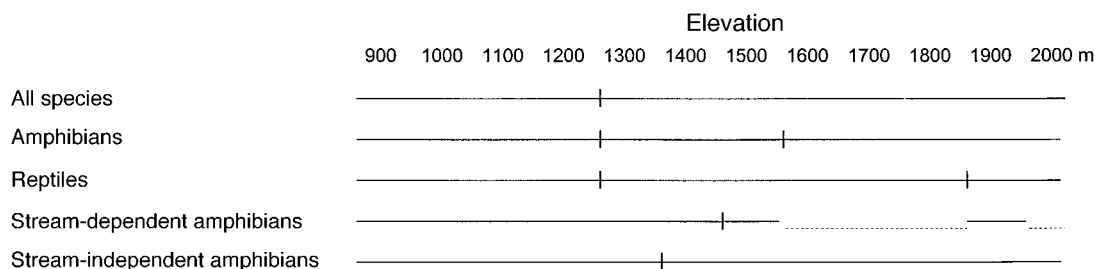


FIG. 1. Discontinuities in species composition and abundance pattern of the herpetofauna of Mount Kupe, Cameroon, revealed by chronological clustering (Legendre et al. 1985) along the elevational gradient. The raw data are log-transformed. The distance measure used is Steinhaus's coefficient, with the connectance set at 0.5 and P set at 0.05. Dotted lines indicate the streamless elevations.

complete set of species. Exceptions concern the reptiles, where significantly large partial overlaps disappear completely and W_m is no more significantly larger than expected, and in the stream-independent amphibians, where no clumping is indicated by h_m .

Fig. 1 presents results of the chronological clustering (hypothesis 5). At $P < 0.05$, the test reveals discontinuities in all five groups. Four discontinuities appear in the lower submontane forest, at 1250 m in the entire assemblage and in both reptiles and amphibians when analyzed separately, and at 1350 m in the stream-independent amphibians. The remaining ruptures farther up coincide with structural changes of the habitat: the stream-dependent amphibians respond to the change of the main watercourse from permanent to intermittent at 1450 m, the reptiles respond to the submontane–montane transitional zone around 1850 m, and all amphibians are pooled to the lower end of the streamless zone at 1550 m. The analysis of the reduced matrices yields the same results in all five groups, i.e., with the connectance set at 0.5 and P set at 0.05, the number and location of discontinuities remain unchanged.

DISCUSSION

The major outcome of the analyses is the dominance of nonsignificant results. The null model tests suggest that the elevational distributions of the majority of the species in the studied assemblage are limited by mechanisms other than direct interspecific competition and vegetational ecotones. The tests on range boundary dispersion and dissimilarities between contiguous elevational samples indicate zonation in all subsets. However, where significant boundary clumps appear, they encompass a broad elevational range from 1000 to 1500 m, thereby suggesting a scattered distribution of boundaries; as revealed by chronological clustering, the local discontinuities at 1250 and 1350 m are expressed by changes in abundances. Taken together, these findings fit Whittaker's model 3 of nonexclusive species groups better than model 1 of groups with sharp exclusion boundaries. Model 3 was tentatively confirmed for the amphibians of Cameroon; Amiet (1975, 1989) recognized a group of anurans provisionally termed "faune

périphérique," whose vertical distribution is centered at intermediate elevations along the western and southern slopes of the Cameroon Highlands and extends into the ranges of both montane and lowland species. On Mount Kupe, this group includes at least *Arthroleptis* sp. A, *Astylosternus perreti*, *Cardioglossa venusta*, *Conraua robusta*, both *Leptodactylodon*, *Leptopelis modestus*, *Petropedetes parkeri*, and *P. perreti*, *Phrynodon* sp. 2, *Werneria preussi mertensiana*, and *Wolterstorffina parvipalmata*. The discontinuities around 1300 m separate the two other groups consisting of distinct lowland and montane species.

The relatively wide transition zone coincides neither with a vegetational ecotone nor with any other obvious habitat discontinuity, but nevertheless seems to mark a change in environmental conditions that is limiting distributions of leaf litter (e.g., *Arthroleptis adelphus*), stream-dependent (e.g., *Cardioglossa gracilis*, *Petropedetes cameronensis*), and probably arboreal (e.g., *Chamaeleo pfefferi*, *Cnemaspis koehleri*, *Hemidactylus echinus*) species alike. Physical factors, such as temperature, precipitation, and evaporation, undoubtedly account for most distributional limits among the lowland and montane species. Moreover, abiotic habitat components such as water bodies suitable for reproduction and specific microhabitats, often spatially and temporally restricted in availability, are known to determine the local abundance of tropical amphibians and reptiles, and may also affect elevational distributions (e.g., Heyer 1967). For example, the anurans *Acanthixalus spinosus*, *Chiromantis rufescens*, and *Hyperolius acutirostris* were chance encounters associated with the single standing water body found during the entire sampling period, a puddle on a log in a treefall at 1560 m. Reduced availability of stream-associated tadpole microhabitats at higher altitudes, suggested by Inger and Stuebing (1992) to limit elevational ranges in Bornean anurans, should also affect stream-breeding anurans of Mount Kupe, in particular the "peripheral" species. Among the reptiles, the heliophilic lizard *Adolfus africanus* may, in higher elevations, depend on large treefalls, grassy patches, and rocky outcrops to meet the preferred microclimatic conditions, i.e., it may ul-

TABLE 3. Results of Dale's (1984, 1986, 1988) null model tests.

Group	S^\dagger	Contiguities‡			Significant partial overlaps§	
		$E(c n)$	c	P_c	Small y	Large y
All species	49	9.8	11.5	0.972	62 (7%)	481 (57%)
	30	4.0	4.9	0.891	52 (16%)	104 (29%)
Amphibians	30	3.5	3.5	0.388	27 (8%)	205 (59%)
	21	2.2	2.0	0.370	22 (13%)	72 (42%)
Reptiles	19	4.3	3.4	0.716	6 (6%)	53 (56%)
	9	0.5	1.0	0.856	6 (19%)	0
Stream-dependent amphibians	24	2.1	2.1	0.44	0	147 (69%)
	15	1.7	1.3	0.079	0	38 (49%)
Stream-independent amphibians	6	0.5	0.5	0.248	5 (36%)	3 (21%)

Notes: In each group, the first row refers to analyses with all species of the respective group; the second row refers to analyses with abundant species only (≥ 10 individuals). All stream-independent amphibians had abundances > 10 individuals.

† Number of species.

‡ $E(c|n)$, no. expected contiguities; c , no. observed contiguities; P_c , cumulative probability based on 999 permutations of range boundaries.

§ Small y , no. significantly small partial overlaps; large y , number of significantly large partial overlaps. Percentages of the total number of observed overlaps in tested group are given in parentheses.

\parallel Clumps, no. significant clumps; $E(W_m)$, expected variability of interboundary distances; W_m , observed variability; P , cumulative probability; $E(h_m)$, expected degree of clumping, h_m , observed degree of clumping. Larger values of W_m indicate more variable interboundary distances; larger values of h_m indicate more clumped range boundaries.

timately be limited by temperature. On the Mount Kupe gradient, both mechanisms may be of approximately equal importance: physical factors probably separate the vertical distributions of distinct lowland and montane species at around 1300 m; specific habitat components are suggested as limiting the gradient distribution of the "peripheral" anuran fauna, whose range encompasses the transitional zone. The resulting pattern of overlapping species groups causes sharp zonation to disappear. Within-group variability in range extensions further accounts for the absence of distinct assemblage-level patterns and the weak response to the null model parameters concerning zonation.

At the community level, the three "competition parameters" exhibit no significant deviations in support of Whittaker's model 2: the numbers of contiguities never significantly exceed random expectation, and proportions of significantly small partial overlaps are low in all groups except the stream-independent amphibians. For methodological reasons, the absence of significantly small gap sizes cannot be assigned any ecological relevance. Bench tests showed that, given the degree of resolution within our data set, Dale's test on gap sizes cannot yield significant results at $P = 0.05$. In our data, gap sizes cannot be smaller than 100 m, i.e., 1/12 of the total gradient length, whereas significantly small gaps appear only if the gap size is smaller than 1/40 of total gradient length. In practice, this means that the applicability of this test would require at least 40 sampling points on a discrete scale.

The few gradient distributions probably affected by direct interspecific competition, i.e., between congeners, are found among terrestrial (*Leptosiphos*) and arboreal lizards (*Chamaeleo*) and anurans with direct development (*Arthroleptis*). Among the latter, *Arthroleptis adolfifriderici* and *A. variabilis* are the most sim-

ilar in morphology. The abundances of these two efficiently sampled species show a marked decline toward the contact zone of their amplitudes (Appendix), a phenomenon termed "repulsion interaction" by Terborgh (1971: 27), whereby the abundances of presumably competing species replacing each other along a gradient "fall off sharply in the zone of contact instead of trailing off gradually." In *Chamaeleo*, the pattern is less pronounced, and the low abundances of *Leptosiphos* preclude comparable interpretations.

Congeners of the stream-dependent amphibians exhibit no contiguities or significantly small partial overlaps, and most of the significantly large partial overlaps among congeners were found within this group (genera *Petropedetes*, *Leptopelis*, and *Astylosternus*). The lack of response to the null model parameters related to interspecific competition suggests that this type of interaction does not affect the gradient distributions of stream-dependent anurans. However, Inger and Greenberg (1966) demonstrated with a removal experiment in Sarawak that three syntopic species of stream-dependent frogs, congeners and similar in habits, did in fact compete. For two species, the authors suggested that intraspecific competition fixes maximum population levels, thus allowing their coexistence. Intraspecific competition may also prevent spatial exclusion in stream-dependent anurans on Mount Kupe, along with other factors depressing population levels and possibly niche segregation.

With physical factors and specific, often abiotic, habitat components as dominant mechanisms limiting elevational distributions, the amphibians and reptiles on Mount Kupe differ considerably from tropical endotherms. In Andean birds, competitive interactions account for about two-thirds of the limits, whereas ecotones and unspecific factors varying in parallel with

TABLE 3. Extended.

Clumping of range boundaries						
Clumps	$E(W_m)$	W_m	P	$E(h_m)$	h_m	P
3	0.02	0.066	>0.999	0.010	0.019	>0.999
0	0.033	0.081	>0.999	0.016	0.029	>0.999
0	0.033	0.117	>0.999	0.016	0.025	>0.999
0	0.047	0.139	>0.999	0.023	0.036	0.998
0	0.052	0.087	0.997	0.026	0.033	0.966
0	0.111	0.119	0.720	0.052	0.068	0.922
0	0.042	0.121	>0.999	0.020	0.029	0.995
0	0.067	0.173	>0.999	0.032	0.027	0.200
0	0.167	0.351	0.997	0.076	0.076	0.520

the gradient each account for about one-sixth of the limits (Terborgh and Weske 1975, Terborgh 1977, 1985). Replacements in elevational distributions also have been found in small mammals on Taiwan (Yu 1994) and on Andean slopes (Cadle and Patton 1988), without addressing the relative importance of interspecific competition. Graham (1990) has suggested that energetic requirements, coupled with trophic resource constraints, determine many gradient distributions of Peruvian bats and the rapid decrease in bat diversity with elevation. Olson (1994) has also recognized resource constraints and species interactions as potential factors limiting elevational distributions of Panamanian leaf litter insects, but emphasizes ecotones produced by sharp physical clines or edaphic gradients to explain pronounced drops in local insect diversity between 1250 and 1500 m. Concerning physical factors, tropical insects and herpetofaunal assemblages may, in fact, share some properties in their response to elevational gradients. Tropical amphibians are known to be markedly sensitive to moisture (Toft 1980, Heatwole 1982). Among lizards in the lowland forests of Southeast Asia, Inger (1980) has found different responses. Arboreal diurnal species tend to be moisture sensitive, whereas terrestrial species, nocturnal and diurnal, respond more strongly to temperature. In the primary forest on the western slope of Mount Kupe, temperature is likely to exhibit a stronger elevational variation than does moisture. Thus, species tolerant to temperature and independent from specific habitat components may ultimately be limited by interspecific competition in their elevational distributions. In our assemblage, *Arthroleptis* and *Chamaeleo* are presumably the only genera meeting these criteria.

As indicated in the *Results*, the differences between observed and estimated maximal species richness revealed inadequacies in the raw data. The Michaelis-Menten estimates indicate that ~22% of the species present at a site were overlooked. Despite the inaccuracies inherent in such extrapolations (Colwell and Coddington 1994), our conclusions may be affected by sampling bias. We tried to assess the effect of the rare species on our results by removing them from the data and repeating the analyses. No additional community-

level patterns emerged, and the general results did not change (Tables 2 and 3). This suggests that the “signal” emerges from the more abundant species and is largely unaffected by the rarer (and possibly under-sampled) ones. Thus, we consider it unlikely that a more thorough sampling would result in conclusions different from ours. To further stay with the quality of the raw data, we restricted our statements concerning interspecific competition and types of elevational responses to abundant (assumed adequately sampled) species representing different adaptive zones and reproductive modes.

In all, we consider null models to be a valuable tool in gradient studies, a field in which a standard protocol is yet to be established and sampling designs rarely fulfill the requirements for proper statistical analysis (Rahbek 1995; see also comments in Yu 1994). With the modifications suggested in this paper, most of the null models based on presence-absence data become equally applicable to assemblages sampled on a continuous scale or at regularly spaced intervals. However, despite the many topographic and logistic difficulties usually encountered when sampling elevational gradients, the three criteria stated in the *Introduction* should be accounted for. An appropriate adjustment of sampling designs in future gradient studies would substantially increase the potential for pattern identification at the community level.

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APPENDIX. Continued.

Species	Elevation (m) of transect contour											Total	
	900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900		2000
Arthroleptidae													
<i>Arthroleptis adelphus</i>	31	22	7	8									79
<i>Arthroleptis variabilis</i>	134	76	63	41	8								377
<i>Arthroleptis "adolffriederici"†‡</i>					12	36	92	127	268	88	67	47	866
<i>Arthroleptis</i> sp. A§	61	32	35	22	12	3							176
<i>Arthroleptis</i> sp. C§	3	5	9	15	9	2	3	7	24	1	8	8	146
<i>Astylosternus</i> cf. <i>montanus</i>	2	5	1				1						9
<i>Astylosternus diadematus</i>	3												4
<i>Astylosternus perreti</i>	5	6	16	14	6	6							66
<i>Cardioglossa elegans</i>													8
<i>Cardioglossa gracilis</i>	20	31	3	3									70
<i>Cardioglossa venusta</i>	8	8	8		1	1							27
<i>Leptodactylodon ornatus</i>	6	7	4	1	1								20
<i>Leptodactylodon bicolor</i>													1
<i>Trichobatrachus robustus</i>	1	1											4
Reptilia													
Chamaeleonidae													
<i>Chamaeleo montium</i>	21	5	11	12									55
<i>Chamaeleo pfefferi</i>			1	2	9	8	4	8	6		1		49
<i>Chamaeleo quadricornis</i>					1	3	18	23	6	10	1	1	85
<i>Rhampholeon spectrum</i>	33	22	26	32	26	19	32	24	7	13			278
Scincidae													
<i>Leptosiaphos rohdei</i>	1	1											9
<i>Leptosiaphos</i> sp. A						1	1		7	2	4	2	19
<i>Leptosiaphos</i> sp. B							1	1	4	1	2	2	17
<i>Leptosiaphos</i> sp. C		2	5	2	3								13
<i>Panaspis chriswildi</i>													1
<i>Mabuya affinis</i>	1												1
Lacertidae													
<i>Adolfus africanus</i>													6
Geckonidae													
<i>Cnemaspis koehleri</i>				1	3	3	3	1		1			13
<i>Cnemaspis spinicollis</i>													2
<i>Hemidactylus fasciatus</i>		1											1
<i>Hemidactylus echinus</i>		1	2	1									9
Boidae													
<i>Calabaria reinhardti</i>			1										2
Colubridae													
<i>Boiga pulverulenta</i>													1
<i>Bothrolycus ater</i>					1								3
<i>Buroma depressiceps</i>	2			1			2	1	2	1	2		18
<i>Chamaelycus fasciatus</i>				1									1
<i>Dipsadoboa unicolor</i>													3
<i>Dipsadoboa</i> sp.							1						4
<i>Mehelya guirali</i>	1	1											2
<i>Rhamnophis aethiopyssa</i>													1
Viperidae													
<i>Atheris squamiger</i>													2
<i>Bitis gabonica</i>		1											1

† *Phrynodon* sp. 1 and sp. 2 are distinguished by their mating calls (J.-L. Amiet, *personal communication*).

‡ According to J.-L. Perret (*personal communication*), different from species described as *adolffriederici* by Nieden from Rwanda.

§ Two small *Schoutedenenella*-like taxa provisionally included in the genus *Arthroleptis* by J.-L. Amiet (*personal communication*).

|| W. Böhme and A. Schmitz, *personal communication*.