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Université de Neuchâtel (Suisse) Institut de zoologie

ORGANIZATION OF A TROPICAL HERPETOFAUNAL ASSEMBLAGE ON AN ELEVATIONAL GRADIENT

par

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diplômé en biologie

Thèse présentée à la Faculté des Sciences de l'Université de
Neuchâtel pour l'obtention du grade de Docteur ès sciences

2000

IMPRIMATUR POUR LA THÈSE

Organisation d'une communauté de reptiles et d'amphibiens tropicaux le long d'un gradient altitudinal

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UNIVERSITÉ DE NEUCHÂTEL

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Mme M. Rahier, MM. C. Mermod (directeur de thèse),
L.-F. Bersier, D.M. Newbery (Berne) et
R.F. Inger (Chicago)

autorise l'impression de la présente thèse.

Neuchâtel, le 28 octobre 1999

Le doyen:

J.-P. Derendinger

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I INTRODUCTION

COMMUNITIES – INTERACTIVE AND NON-INTERACTIVE

A long-standing and ongoing debate in community ecology concerns the question of whether communities are „real“ or are the products of our imagination. Are many community-level properties simply epiphenomena that arise from pooling component populations, or do communities possess truly emergent properties that transcend those of mere collections of populations (Pianka 1992)? Stated as a dichotomy, the community as an integrated and repeatable complex having evolved as a unit contrasts with a haphazard multispecies association resulting from species-specific responses to the environment, where species are encountered in one place and time due to a correspondence of their independent life histories and physiological constraints. Proponents of the first view assign biotic interactions, namely competition, overriding importance in structuring communities. Their opponents claim environmental stochasticity, habitat and resource heterogeneity, and predation to account predominantly for observed patterns. Cornell and Lawton (1992) suggested that real communities lie on a continuum from *interactive* to *non-interactive*. While for many invertebrates such as phytophagous insects, non-interactive communities may be the norm, some vertebrate groups, particularly tropical bird assemblages, were considered prime examples of highly interactive communities by some authors, and the publication of Diamond's (1975) assembly rules provoked a debate that spanned more than two decades in the ecological literature.

HERPETOFAUNAL COMMUNITIES IN TROPICAL FORESTS

Although community ecology still tends to be dominated by studies on plants, invertebrates and birds, research on amphibians and reptiles in tropical rainforests resulted in important contributions to the subject. Studies on diversity and abundance over space and/or time (Scott 1976, Gascon 1991, Inger and Voris 1993, Duellman 1995), and on patterns of resource use (Inger and Colwell 1977, Duellmann 1978, Toft 1980, Vitt and Caldwell 1994, Vitt and Zani 1998) provided insight in the structure and functioning of vertebrate assemblages in some environments of presumably high predictability and therefore conventionally considered prime areas for species interactions. Most analyses of resource utilisation revealed some degree of organisation in these assemblages, and raised the question about the extent to which species interactions accounted for the patterns of niche segregation. Although non-random structures and guild formation that could be the result of competitive interactions were confirmed (Inger and Colwell 1977, Vitt and Caldwell 1994, Vitt and Zani 1998), the relation of observed patterns to underlying processes was rarely straightforward (e.g., Vitt and Zani 1998). Cadle and Greene (1993) recognised a substantial impact of philogeny and historical events on the composition and species richness of Neotropical rainforest snake assemblages, suggesting that many community properties do not necessarily result from contemporary ecological factors. In a review on the composition and resource use of the herpetofaunas from four Neotropical lowland forests, Duellman (1990) questioned the importance of interspecific competition and suggested predation and climatic fluctuations to be the most important regulators of amphibian and reptile populations. On the other hand, the results of a removal experiment by Inger and Greenberg (1966) in Sarawak, involving three syntopic species of stream-dependent frogs, congeners and similar in habits, suggested that some species may in fact reach abundances that bear the potential for interspecific competition. At this stage, rather than searching for a general explanation, it is probably more appropriate to ask what outcomes we expect from a given process in a particular environmental setting.

METHODOLOGY

Reductionist and holistic approach

Nature and degree of interaction within species assemblages are commonly explored by analyses of patterns of co-occurrence and relative abundance, community assembly, species-area relations, stability and complexity properties in food webs, patterns of resource utilisation and guild structure, and within-guild effects of biotic interactions. Evidence is obtained by two fundamentally different lines of investigation: The *reductionist*, or bottom-up approach to communities usually examines the dynamics of biotic interactions of two or three-species systems by detailed experimentation, attempting to reassemble a picture of the community and its operation as a jigsaw of component interacting parts. The *holistic*, or top-down approach attempts to study communities as a statistical entity, based on aggregate variables or „macrodescriptors“ that summarise presumably important system properties, such as species diversity, niche relationships, and trophic structure. Hairston (1989) questioned the contributions of the non-experimental model building approach to community ecology, arguing that models tend to explain what is already known and frequently incorporate unjustified assumptions. On the other hand, Maurer (1999), emphasising the limitations of competition experiments as revealed by Gurevitch et al. (1992) in a meta-analysis, considers much of the experimental approach to communities an meaningless focus on noise, and calls for a macroecological perspective. Be that as it may, the discussions about the appropriate scale and methodology in community ecology are unlikely to cease in the near future. Meanwhile, the difficulty of disentangling ecological complexity still requires many approaches (Hanski 1999), and all of them may continue to yield substantial insights.

Null Models

A major challenge to the holistic approach constitutes the establishment of pattern and inference of mechanism. Without any comparison to some form of a replicate, there are no means to evaluate if indeed the patterns we observe in a given community could result from the biological process invoked to explain them. *Comparative studies*, occasionally termed „natural experiments“, aim at obtaining replicates by involving several communities that mainly differ in the factor of interest, but do not account for stochastic effects and for the patterns that may result in the absence of the mechanism under study. Such deficiencies can be resolved by the use of *null models*. Gotelli and Graves (1996) defined the null model as „a pattern-generating model that is based on randomisation of ecological data or random sampling from a known or imagined distribution. The null model is designed with respect to some ecological or evolutionary process of interest. Certain elements of the data are held constant, and others are allowed to vary stochastically to create new assemblage patterns. The randomisation is designed to produce a pattern that would be expected in the absence of a particular ecological mechanism“. Thereby null models allow the falsification of the predictions of a single alternative hypothesis. The null hypothesis, however, can be an aggregate of several possible mechanisms, and the testing of mutually exclusive alternative outcomes would require multiple null models. Unlike mathematical models, null models are built with reference to real data sets. By incorporating stochastic effects, they reflect the natural variability in community structure and require that the signal of mechanism be stronger than the noise of natural variation. Despite the efforts of the proponents to account for biological realism in their construction, some key properties and the frequent contradiction to conventional

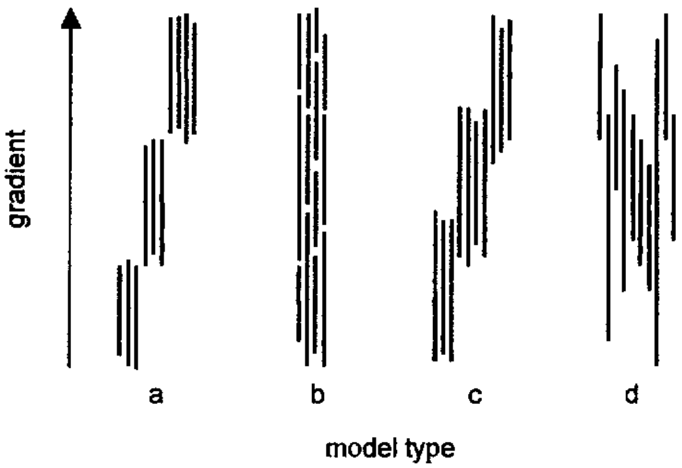

Fig. 1. Four models of the arrangement of species on a gradient (Whittaker 1967), and arrangement in studied assemblage. Each line corresponds to a species range.

wisdom made null models controversial in ecology. For an even-handed discussion and a comprehensive review of the applications in community ecology, readers are referred to the book by Gotelli and Graves (1996).

Null models provide the methodological background for this study, where I used them to assess the relative importance of competitive interactions, environmental discontinuities and major habitat characteristics in the spatial organisation of a herpetofaunal assemblage along a tropical forest elevational gradient. A common feature in community research, the rigorous application of null models to the data at hand and to the hypotheses tested proved an intellectual challenge and is an integrative part of this project. As a result, two chapters include original modifications and extensions of existing testing devices, which I hope will entail a wider application.

COMMUNITIES ON GRADIENTS

The theory and its application in a comparative study

The distribution of species along one-dimensional gradients provides some of the best examples of the organisation of natural communities. The conspicuous zonations of vegetation associations along elevational gradients or of organisms in the rocky intertidal suggest that strong non-random forces determine position and range length of each species within the gradient. Whittaker (1967) described four models of community organisation on gradients, distinguished on the basis of whether or not species occur in discernible groupings and the extent to which distributional boundaries between species are exclusive (Fig.1). The four models are: (a) distinct groups of species with sharp exclusion boundaries; (b) sharp exclusion boundaries between competing species but no natural groupings; (c) groupings of species that are not exclusive; (d) 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.

Terborgh (1971, 1985) made an explicit attempt to test for the relative importance of the first three mechanisms in limiting species' distributions. 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), 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.

The null model approach to communities on gradients

Unfortunately, the difficulty of finding truly comparable gradients even on a regional scale, as well as the logistically demanding and time-intensive sampling left Terborgh's approach an example hard to follow. Moreover, conclusions obtained by natural experiments can be questioned for reasons stated in the Methodology section. In the light of these drawbacks, null models offer a real alternative, provided a systematic procedure comparable to Terborgh's approach can be established. To obtain meaningful results from null model applications to one-dimensional gradients, an appropriate sampling design has to meet three criteria: (1) data on elevational ranges must be obtained from a single location, (2) the sampling must occur on a continuous scale or at regularly spaced intervals, and (3) it must be done with equivalent intensity at each point on the gradient. The main null models for presence/absence data have been developed by Pielou (1977, 1978) and Dale (1984, 1986, 1988), and were originally applied to sessile organisms on a *continuous* scale, i.e., seaweed species on a latitudinal gradient and intertidal algae. Mobile organisms on gradients in terrestrial ecosystems, however, are typically sampled at several points regularly spaced along a gradient, i.e., at a *discrete* scale with comparatively few fixed intervals. The application of some of Pielou's and Dale's models to samples at discrete scales required an appropriate adjustment of the tests; the corresponding modifications are suggested in the first chapter. In combination with chronological clustering (Legendre et al. 1985), the modified set of null models constitutes an analysis protocol aimed at evaluating the relative importance of interspecific *competition* and *ecotones* in the gradient distribution of an assemblage.

Due to their restriction to distributional data, however, the above mentioned models provide only indirect estimates of the effects of the putative mechanisms underlying the observed patterns. A more subtle measure of the potential importance of competitive interactions can be obtained by including in an analysis procedure the range of interactions that may result from overlaps in resource use. In Andean birds, Terborgh and Weske (1975) found diffuse competition (as distinguished from the directly observable exclusion of congeners) to have a significant effect on the gradient distribution pattern of the assemblage. In fact, it was the primary mechanism limiting elevational distributions for most of the species previously assumed to be limited by physiological constraints. I therefore intended to relate the pattern of niche overlap of the herpetofaunal assemblage directly to its spatial organisation along the elevational gradient. Specifically I asked whether the species' distributional ranges are co-adjusted in a way as to reduce the potential for interspecific competition resulting from niche overlap. Tests of a corresponding hypothesis must account for the *non-linearity* in the relationship of the two overlap matrices: In a competitively structured assemblage, we would expect species with high niche overlap to segregate geographically (in our example, along the gradient), i.e., show small geographic overlap, but species with small niche overlap must not exhibit high geographic overlap. Testing devices based on a linear correlation, e.g., the Mantel test, are therefore not applicable. The problem is resolved here by an approach built on two methods designed to test for niche segregation and guild formation in communities, the nearest-neighbour analysis pioneered by Inger and Colwell (1977) and the subsequent development of the pseudocommunity analysis by Winemiller and Pianka (1990).

For an assessment of the importance of *abiotic limits*, i.e. the physical factors varying in parallel with the gradient, relative to *ecotones*, in the spatial organisation of the herpetofaunal assemblage along the gradient, several ordination techniques known as direct gradient analysis are available. I used canonical correspondence analysis (CCA) (ter Braak 1987) to explore the community response to major habitat characteristics assumed to absorb a substantial part of the variation of the species' abundances along the gradient, and to variables describing the elevational gradient. The null model philosophy is maintained here by submitting the results to a Monte Carlo permutation procedure, which tests for the overall significance of the ordinations and the significance level of each canonical axis.

COMPARATIVE DIVERSITY AND ABUNDANCE

The first comparisons of tropical forest herpetofaunal samples across continents involved neotropical and Indo-Malayan lowland rainforests and revealed frog and lizard densities to be an order of magnitude higher in the New World than in Southeast Asia. The difference seemed that striking that the phenomenon and potential explanations for it were eventually discussed by Robert May in a letter to 'Nature' (May 1980). Afrotropical herpetofaunas, however, remained virtually excluded from the subject, as data sets equivalent to those from the other two continents were scarce.

This prompted me to evaluate diversity and abundance properties of Mount Kupe's herpetofauna by a comparison to an assemblage from either a neotropical or Indo-Malayan upland site. Comparisons of sites across continents are often biased by a number of unresolved differences in site characteristics and sampling protocol, and it soon turned out that no published data set resembled my own one to an extent that meaningful results could be expected. I therefore compiled a sample from a neotropical site where I tried to account for most of the potential sources of bias. The analyses largely followed the suggestions from a recent review on the subject by Colwell and Coddington (1994).

STUDY SITES

In this work I use two original data sets, obtained by the same methodology from comparable forest types, elevational ranges and seasons, Mount Kupe in Cameroon and Bosque Protector Palo Seco in western Panama.

The main study site was *Mount Kupe* (4°45'N / 9°42'E) in the southwest province of Cameroon, a steep-sided, cone-shaped mountain 2064 m in height and situated approximately 100 km northeast of Mount Cameroon (Fig.2). It forms part of the Cameroon highlands, an extensive volcanic mountain range running from Bioko Island to Mount Cameroon in the south-west on to the Bamenda and Adamawa highlands in the north-east, with the Obudu and Mambila Plateaus extending into Nigeria. By the time of the sampling the mountain was covered by ~ 2100 ha of undisturbed closed canopy submontane forest, characterised by a fairly uniform structure with a sparse ground layer and a thin understory. Below 900 m the forest has been logged or severely degraded except for a few patches on the southwestern and southern slopes. In the primary forest, we found permanent streams between 900 and 1500 m and at 1900 m. The single standing water body found within the primary forest was a puddle on a log in a treefall. Mount Kupe receives mean annual rainfall of 4891 mm (Suchel 1972). The rainy season lasts for seven months from April to October, with no month receiving less than 70 mm.

The *Bosque Protector Palo Seco*, (8°47'N / 82°12,5'E) in the Bocas del Toro province of Panama, is situated on the Caribbean slope of the Cordillera Central. It is a vast area of primary forest extending from the lowlands up to the continental divide, with ridge tops and peaks at around 1400 to 2300 m, and from the main road crossing the divide further west towards Costa

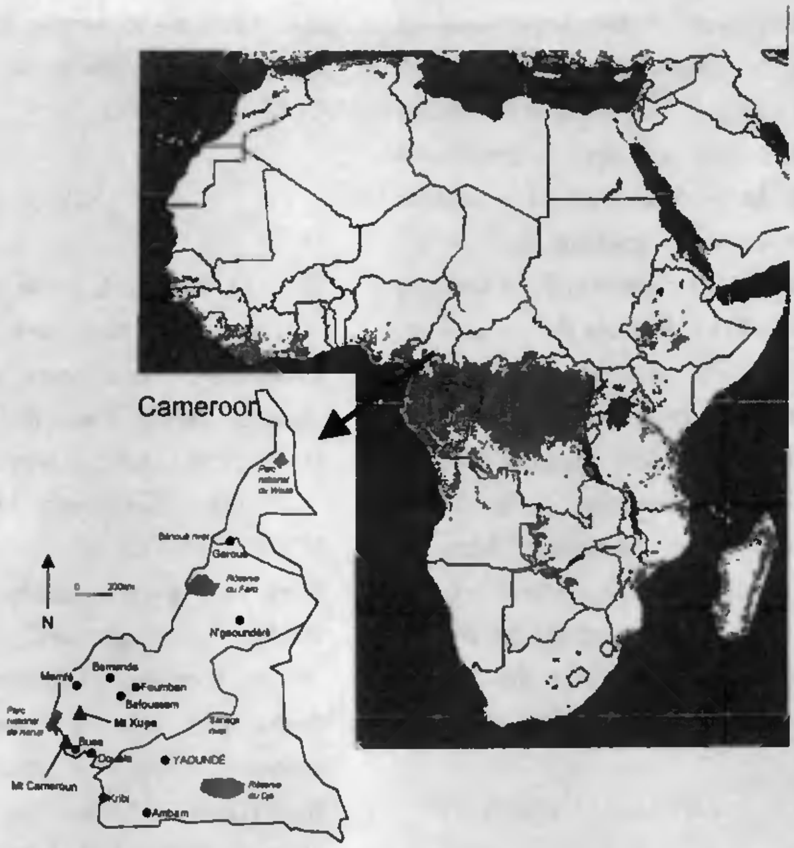

Fig. 2. Study site in Cameroon.

Rica. Despite the status of a protected forest, human impact is increasing, with pastures along the valley bottoms and plantations on the adjacent slopes. Estimated from regional climate maps (CAP 1975), the Bocas del Toro province receives annual rainfall from ~ 3000 mm in the lowlands to 5500 mm at higher elevations. Other than on the Pacific slope, rainfall is abundant throughout the year and, as on Mount Kupe, a pronounced dry season is absent. We found permanent streams at all elevations sampled, whereas puddles along an unpaved road outside the forest were the only standing water located. As on Mount Kupe, most stream bottoms are on bedrock, with moderate to steep gradients, rapids and splash zones.

Today a lot of ecological work on tropical herpetofaunas is devoted to an extension of the temporal and spatial scale, and to the linkage of observed community properties with phylogenetic history. At the same time, there is a remarkable increase in basic ecological information on amphibians and reptiles of tropical rainforests, with species accounts available for more and more sites and numerous papers published on the natural history of hitherto poorly known taxa. To my knowledge, a relatively small fraction of available community-level data was ever subjected to tests for non-random patterns with respect to particular hypotheses. Null models could be helpful in addressing some of the major questions regarding community organisation, provided the data have been collected in accordance with the requirements of corresponding tests. In that sense, I hope this study is a contribution to community ecology as a subject, and to our knowledge on the life of amphibians and reptiles in tropical rainforests.

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ACKNOWLEDGEMENTS

My field counterparts in Cameroon, Elong J. Ebung, Enongene H. Njume, Ngwese S. Epie and Ikechukwu C. Ojiawum, and in Panamá, Melvin A. Aguirre, Aquilino Gonzáles and Otilio Samudio, endured many days and nights of unpleasant working conditions, and by their committment contributed tremendously to the quality of the raw data.

Throughout my stay in Cameroon, I experienced Etone Kenedy Epie and his relatives as my family. Kenedy made me feel at home in Nyasoso and helped me enjoy African village life even more.

The staff from the Mount Kupe Forest Project, namely Chris and Liz Bowden, Ebong Asabe and Ebong E. Ewang, and two teams of porters provided logistic help throughout the fieldwork in Cameroon. By then, the Mount Kupe Forest Project was part of BirdLife International's Cameroon Montane Forest Programme.

The Ministry of Environment and Forest (Cameroon) and the Instituto de Recursos Naturales y Renovables (Panamá) readily issued the necessary research permits. The Bakossi people and Paramount Chief Ntoko kindly allowed me to work on Mount Kupe.

My colleagues André Witschi, Lukas Indermaur, Hannes Baur, Claudia Kühni, Silvia Zumbach, Peter Schlup, Christoph Vonlanthen, Max Dähler, Stephan Dummermuth and Chris Wild, as well as Brigitte und Isabelle Reutter assisted various parts of the fieldwork and/or merely prevented me from becoming all too much addicted to the rainforest environment.

Professor Jean-Louis Amiet kindly shared his impressive knowledge on the amphibians of Cameroon with me, and thus prevented misinterpretations that might have resulted from the inevitable short-term perspective inherent to this study.

Jean-Louis Amiet, Roberto Ibáñez, Jean-Luc Perret, Andreas Schmitz and Wolfgang Böhme helped out with the identification of many specimens.

The commitment and sophisticated help of my colleagues Louis-Félix Bersier and Daniel Borcard contributed substantially to the quality of the manuscript.

The thorough reviews provided by the jury members helped to improve the comprehensibility of some paragraphs and to eliminate major inconsistencies in the discussion of the results.

Professor Claude Mermod, through his interest in herpetological research, encouraged me to do this study as a doctoral thesis project.

The majority of the fieldwork took place in a sabbatical year granted by the supervisory board of the Swiss Amphibian and Reptile Conservation Programme (KARCH), and was generously endured by the staff at the KARCH.

The Swiss Development Corporation, the Swiss Academy of Natural Sciences, and the Natural History Museum of Berne funded the fieldwork.

Professor Marcel Güntert, director of the Natural History Museum of Berne, provided the necessary institutional background throughout the project.

Verena Andres, librarian of the Natural History Museum of Berne, located even the most exotic titles in the shortest time possible, which proved an invaluable help throughout the preparation of the manuscripts.

My parents assisted the preparatory steps of this project. My father‘s modifications of a simple tarpaulin spared the Cameroonian field crew many nights of getting soaked in their tents. Unfortunately, he could not witness the outcome of this project.

II SPATIAL ORGANIZATION OF A HERPETOFAUNA ON AN ELEVATIONAL GRADIENT REVEALED BY NULL MODEL TESTS[1]

INTRODUCTION

The pioneering approaches by Whittaker (Whittaker 1967, Whittaker and Niering 1965, 1975) 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 prove 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 richness is not highest in the 0-500 m zone, but peaks between 500 and 1000 m. In insects, mid-elevation peaks in species richness where 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).

The authors usually claim a complex interplay of factors to explain the variability of observed gradient patterns, including non-biological ones like 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 was also 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 philogeny 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 discernable groupings and the extent to which boundaries between species are exclusive. The four models are: (1) distinct groups

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[1] Chapter published : Hofer U., Bersier L.F. & Borcard D. 1999. *Ecology* **80**: 976-988.

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 a 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 Alcala 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 north-east, 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 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 differenciation between isolated populations of montane anuran species in Cameroon, he concluded that the last extension of montane ranges to low altitudes is 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 afromontane 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 minimal temperature measured during the entire sampling period was 13.8 °C (1900 m, March 13, at night), the maximum was 23.8 °C (900 m, April 21, 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 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 twelve 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 riparian 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 streamsides 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 Appendix 1, but ignored in the analysis. Animals were either collected or 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 x 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 non-overlapping 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 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 where 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

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

	Accessible transect	Accessible riparian zone	Stream	Number of man hours †				No. sampling sessions in each month (March to November)								
Contour	length (m)	length (m)	identity	dt	nt	dr	nr	M	A	M	J	J	A	S	O	N
900	240 m	150 m	A, B	44	34	9	12	2	0	1	4	3	6	1	3	1
1000	140 m	27 m	B	43	36	10	11	3	0	3	3	4	3	2	2	1
1100	230 m	50 m	C	44	36	9	13	0	4	3	4	3	3	1	2	1
1200	200 m	50 m	C	43	37	7	12	0	3	4	4	2	4	1	2	1
1300	220 m	31 m	C	38	31	7	10	0	4	4	6	0	2	1	4	0
1400	220 m	27 m	C	44	32	6	9	0	3	3	7	0	0	2	6	0
1500	240 m	155 m	D	39	38	5	11	0	4	5	6	0	0	3	4	0
1600	500 m	-	-	42	37	-	-	0	3	4	3	0	0	2	2	0
1700	340 m	-	-	42	36	-	-	0	4	2	3	0	0	3	2	0
1800	220 m	-	-	43	35	-	-	5	2	3	0	0	0	4	0	0
1900	400 m	150 m	E	41	35	10	12	10	6	1	0	0	0	5	0	0
2000	790 m	-	-	41	33	-	-	5	3	1	0	0	0	5	0	0

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

groupings, either exclusive (Whittaker's model 1) or non-exclusive (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 towards 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 where 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., B*EB*BE*EB*E, 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 B*EB* (one contiguity), because the ending and the actual beginnings can be located anywhere between the two sampling points. We have three possible sequences: *EB*B, B*EB*, 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

$$\frac{(t-1)!}{(m-1)!}\cdot\binom{t-1}{m}.$$

The corrected number of contiguities is the ratio of the total number of contiguities 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 described above 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, where only the species with a total abundance of ≥10 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 *Buhoma depressiceps.* Several species known to occur at higher elevations 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 overlap 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, where the observed number of contiguities exceeds the expected one ($P = 0.97$, cumulative probability). Congeners exhibiting an ecological contiguity are *Arthroleptis adolfifriderici* - *A.adelphus* and *Chamaeleo quadricornis* - *Ch.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 adolfifriderici* - *A.variabilis* and *A.adolfifriderici* - *A.* species A, overlapping between 1250 and 1350, 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 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 the stream-independent amphibians, where no clumping is indicated by h_m.

Fig. 1 presents the 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 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 non-significant 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 zonations in all

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

Group	S	m	$E(Ls)$	Ls	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 to analyses with abundant species only ($\geq$ 10 individuals); all stream-independent amphibians had abundances > 10. Column head abbreviations are: S, number of species; m, mean span-length of species in the assemblage; $E(Ls)$, expected overlap based on 999 permutations of range boundaries under Pielou's hypothesis 2 (conditional hypothesis); Ls, 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).

subsets. However, where significant boundary clumps appear, they encompass a broad elevational range from 1000 to 1500 m, thereby suggesting an 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 non-exclusive 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 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 which 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

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

		Contiguities ‡			significant partial overlaps §		clumping of range boundaries ¶						
Group	*S* †	$E(c\|n)$	*c*	P_c	small *y*	large *y*	clumps	$E(W_m)$	W_m	P	$E(h_m)$	h_m	P
all species	49	9.8	11.5	0.972	62 (7%)	481 (57%)	3	0.02	0.066	>0.999	0.010	0.019	>0.999
	30	4.0	4.9	0.891	52 (16%)	104 (29%)	0	0.033	0.081	>0.999	0.016	0.029	>0.999
Amphibians	30	3.5	3.5	0.388	27 (8%)	205 (59%)	0	0.033	0.117	>0.999	0.016	0.025	>0.999
	21	2.2	2.0	0.370	22 (13%)	72 (42%)	0	0.047	0.139	>0.999	0.023	0.036	0.998
Reptiles	19	4.3	3.4	0.716	6 (6%)	53 (56%)	0	0.052	0.087	0.997	0.026	0.033	0.966
	9	0.5	1.0	0.856	6 (19%)	0	0	0.111	0.119	0.720	0.052	0.068	0.922
stream-dependent Amphibians	24	2.1	2.1	0.44	0	147 (69%)	0	0.042	0.121	>0.999	0.020	0.029	0.995
	15	1.7	1.3	0.079	0	38 (49%)	0	0.067	0.173	>0.999	0.032	0.027	0.200
stream-independent Amphibians	6	0.5	0.5	0.248	5 (36%)	3 (21%)	0	0.167	0.351	0.997	0.076	0.076	0.520

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

† No. 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.

¶ 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. The larger W_m, the more variable the interboundary distances, the larger h_m, the more clumped the range boundaries.

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., ultimately be limited by temperature. On the Mount Kupe gradient, both mechanisms may approximately be of 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 zonations 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 zonations.

At the community level, the three "competition parameters" exhibit no significant deviations in support of Whittaker's model 2: the

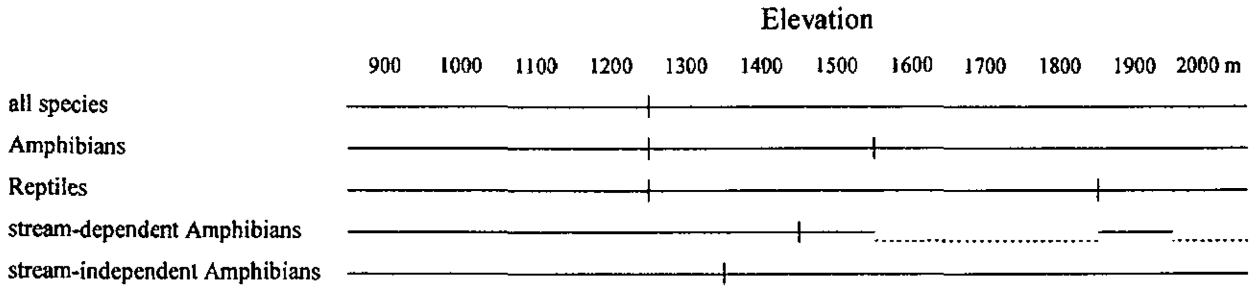

FIG. 1. Discontinuities in species composition and abundance pattern revealed by chronological clustering (Legendre et al. 1985) along the elevational gradient. The raw data are log-transformed. The distance measure used is Steinhaus' coefficient, with the connectance set at 0.5 and *P* set at 0.05. The dotted line indicates the streamless elevations.

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 (*Leptosiaphos*) and arboreal lizards (*Chamaeleo*) and anurans with direct development (*Arthroleptis*). Among the latter, *Arthroleptis adolfifriderici* and *A. variabilis* are the most similar 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 *Leptosiaphos* 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 populations 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 the gradient each account for about one-sixth of the limits (Terborgh and Weske 1975, Terborgh 1977, 1985). Replacements in elevational distributions were also 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, more strongly respond 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 undersampled) 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 where a standard protocol is yet to be established and sampling designs rarely fulfilled 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.

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, 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. For constructive criticism of the manuscript, we thank C. Mermod, D. Meyer, B. D. Patterson, and an anonymous reviewer. This publication is part of a PhD thesis by U.Hofer at the University of Neuchâtel.

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APPENDIX 1: Incidence matrix of amphibians and reptiles recorded on the western slope of Mount Kupe, March-November 1994, as based on an equal sampling effort and subjected to the null model tests. The totals given in the last column include the specimens recorded on the gradient outside sampling sessions and, thus, do not correspond to row totals. Column headers 900-2000 represent sampling zone contours.

Species	Elevation (m) of transect contour												Total
	900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000	
AMPHIBIA													
Bufonidae													
Bufo gracilipes	1	.	.	.	.	.	.	.	.	.	.	.	1
Bufo tuberosus	2	.	.	.	.	.	.	.	.	.	.	.	5
Nectophryne afra	.	.	.	.	.	.	.	.	.	.	.	.	1
Nectophrync batesi	.	.	.	.	.	.	.	.	.	.	.	.	2
Werneria preussi mertensiana	1	1	1	.	.	.	.	.	.	.	.	.	10
Wolterstorffina parvipalmata	.	2	3	6	5	10	42	13	10	4	5	3	124
Ranidae													
Conraua robusta	.	1	1	.	2	1	.	.	.	.	.	.	16
Petropedetes cameronensis	10	9	9	15	.	.	.	.	.	.	.	.	47
Petropedetes perreti	4	4	4	3	11	7	1	.	.	.	.	.	35
Petropedetes newtoni	7	5	3	2	3	3	1	.	.	.	.	.	30
Petropedetes parkeri	2	12	7	5	5	12	.	.	.	.	.	.	45
Phrynobatrachus cricogaster	5	14	2	14	4	1	29	.	.	.	16	1	100
Phrynobatrachus werneri	.	.	.	.	.	.	.	.	.	.	14	.	23
Phrynodon sp.1 †	.	.	.	.	.	.	.	.	.	.	19	.	19
Phrynodon sp.2 †	11	49	28	76	67	17	46	.	.	.	.	.	322
Hyperoliidae													
Afrixalus lacteus	.	.	.	.	1	.	8	.	.	.	8	.	21
Afrixalus laevis	.	.	.	.	.	.	.	.	.	.	.	.	3
Hyperolius acutirostris	.	.	.	.	.	.	.	.	.	.	.	.	12
Leptopelis brevirostris	6	3	.	2	.	.	.	.	.	.	.	.	22
Leptopelis calcaratus	6	1	.	.	.	.	.	.	.	.	.	.	9
Leptopelis modestus	.	.	.	.	.	1	2	.	.	.	9	.	15
Leptopelis rufus	4	.	.	.	.	.	.	.	.	.	.	.	12
Rhacophoridae													
Acanthixalus spinosus	.	.	.	.	.	.	.	.	.	.	.	.	6
Chiromantis rufescens	.	.	.	.	.	.	.	.	.	.	.	.	1
Arthroleptidae													
Arthroleptis adelphus	31	22	7	8	.	.	.	.	.	.	.	.	79
Arthroleptis variabilis	134	76	63	41	8	.	.	.	.	.	.	.	377
Arthroleptis "adolfifriderici" ‡	.	.	.	.	12	36	92	127	268	88	67	47	866
Arthroleptis sp.A §	61	32	35	22	12	3	.	.	.	.	.	.	176
Arthroleptis sp.C §	3	5	9	15	9	2	3	7	24	1	8	8	146
Astylosternus cf.montanus	2	5	1	.	.	.	1	.	.	.	.	.	9
Astylosternus diadematus	3	.	.	.	.	.	.	.	.	.	.	.	4
Astylosternus perreti	5	6	16	14	6	6	.	.	.	.	.	.	66
Cardioglossa elegans	.	.	.	.	.	.	.	.	.	.	.	.	8

Appendix I. Continued

Species	Elevation (m) of transect contour												Total
Cardioglossa gracilis	20	31	3	3	.	.	.	.	.	.	.	.	70
Cardioglossa venusta	8	8	8	.	1	1	.	.	.	.	.	.	27
Leptodactylodon ornatus	6	7	4	1	1	.	.	.	.	.	.	.	20
Leptodactylodon bicolor	.	.	.	.	.	.	.	.	.	.	.	.	1
Trichobatrachus robustus	1	1	.	.	.	.	.	.	.	.	.	.	4
REPTILIA													
Chamaeleonidae													
Chamaeleo montium	21	5	11	12	.	.	.	.	.	.	.	.	55
Chamaeleo pfefferi	.	.	1	2	9	8	4	8	6	.	1	.	49
Chamaeleo quadricornis	.	.	.	.	1	3	18	23	6	10	1	1	85
Rhampholeon spectrum	33	22	26	32	26	19	32	24	7	13	.	.	278
Scincidae													
Leptosiaphos rohdei	1	1	.	.	.	.	.	.	.	.	.	.	9
Leptosiaphos sp.A ¶	.	.	.	.	.	1	1	.	7	2	4	2	19
Leptosiaphos sp.B ¶	.	.	.	.	.	.	1	1	4	1	2	2	17
Leptosiaphos sp.C ¶	.	2	5	2	3	.	.	.	.	.	.	.	13
Panaspis chriswildi	.	.	.	.	.	.	.	.	.	.	.	.	1
Mabuya affinis	1	.	.	.	.	.	.	.	.	.	.	.	1
Lacertidae													
Adolfus africanus	.	.	.	.	.	.	.	.	.	.	.	.	6
Geckonidae													
Cnemaspis koehleri	.	.	.	1	3	3	3	1	.	1	.	.	13
Cnemaspis spinicollis	.	.	.	.	.	.	.	.	.	.	.	.	2
Hemidactylus fasciatus	.	1	.	.	.	.	.	.	.	.	.	.	1
Hemidactylus echinus	.	1	2	1	.	.	.	.	.	.	.	.	9
Boidae													
Calabaria reinhardti	.	.	1	.	.	.	.	.	.	.	.	.	2
Colubridae													
Boiga pulverulenta	.	.	.	.	.	.	.	.	.	.	.	.	1
Bothrolycus ater	.	.	.	.	1	.	.	.	.	.	.	.	3
Buhoma depressiceps	2	.	.	1	.	.	2	1	2	1	2	.	18
Chamaelycus fasciatus	.	.	.	1	.	.	.	.	.	.	.	.	1
Dipsadoboa unicolor	.	.	.	.	.	.	.	.	.	.	.	.	3
Dipsadoboa sp.	.	.	.	.	.	.	1	.	.	.	.	.	4
Mehelya guirali	1	1	.	.	.	.	.	.	.	.	.	.	2
Rhamnophis aethiopissa	.	.	.	.	.	.	.	.	.	.	.	.	1
Viperidae													
Atheris squamiger	.	.	.	.	.	.	.	.	.	.	.	.	2
Bitis gabonica	.	1	.	.	.	.	.	.	.	.	.	.	1

† *Phrynodon* sp.1 and sp.2 told apart by their mating calls (Amiet, *personol communication*).

‡ according to Perret (*personal communication*) different from species described as *adolfifriederici* by Nieden from Rwanda.

§ two small *Schoutedenella*-like taxa provisionally included in the genus *Arthroleptis* by Amiet (*personol communication*).

¶ W. Böhme und A. Schmitz, *personol communication*

Abstract of Chapter II

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 do not differ from random expectations. The results indicate 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 or a strong response to vegetational ecotones. Physical factors varying in parallel with the gradient and specific habitat components, particularly waterbodies suitable as amphibian breeding sites, are suggested to be the dominant factors in limiting gradient distributions of amphibians and reptiles on Mount Kupe. The zonations revealed suggest a pattern of three spatially non-exclusive species groups: physical factors separate distinct lowland and montane species limited by physiological constraints and produce the 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 to endotherms, where biotic factors seem to be of major importance in limiting elevational distributions.

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

III RELATING NICHE OVERLAP TO GRADIENT DISTRIBUTION IN A TROPICAL UPLAND FOREST ASSEMBLAGE OF AMPHIBIANS AND REPTILES

INTRODUCTION

A long-standing debate in community ecology concerns the question of how „real“ communities actually are, i.e., whether or not communities possess truly emergent properties that are more than simply epiphenomena that arise from pooling component populations (Pianka 1992). Do observed community-level patterns predominantly result from orderly species interactions (particularly competition, past or present), or do they merely reflect a correspondence of independent life histories and species-specific responses to the environment, due to physiological constraints and selective predator pressures ? Two fundamentally different approaches have been adopted to address this question. The reductionist, or bottom-up approach to communities usually investigates the dynamics of biotic interactions of two or three-species systems by manipulative experiments, using individual-ecological concepts for understanding patterns (Schoener 1986). The holistic, or top-down approach attempts to reveal and interpret patterns and regularities at the community-level, based on aggregate variables or „macro-descriptors“ (Pianka 1992) that summarise presumably important system properties, such as species diversity, relative abundance, niche relationships, and trophic structure.

Community-level research on amphibians and reptiles in tropical rainforest areas resulted in important contributions to the holistic approach. Studies on diversity and abundance over space and/or time (Scott 1976, Fauth, Crother & Slowinski 1989; Gascon 1991; Inger & Voris 1993; Duellman 1995), and on patterns of resource use (Inger & Colwell 1977; Toft 1980; Lieberman 1986; Inger et al. 1987; Duellmann 1978; Vitt & Caldwell 1994; Vitt & Zani 1996, 1998) provided insight into the structure and functioning of vertebrate assemblages in some environments of presumably high predictability and therefore conventionally considered prime areas for species interactions. Most analyses of resource utilisation revealed some degree of organisation in these assemblages, and raised the question about the extent to which species interactions accounted for the patterns of niche segregation. Null model tests confirmed non-random structures and guild formation that could be the result of competitive interactions (Inger & Colwell 1977; Vitt & Caldwell 1994; Vitt & Zani 1996, 1998). However, as a general problem in analyses of community-level phenomena, the relation of observed patterns to underlying processes is rarely straightforward (e.g., Vitt and Zani 1998). Cadle and Greene (1993) recognised a substantial impact of philogeny and historical events on the composition and species richness of Neotropical rainforest snake assemblages, suggesting that many community properties do not necessarily result from contemporary ecological factors. In a review on the composition and resource use of the herpetofaunas from four Neotropical lowland forests, Duellman (1990) questioned the importance of interspecific competition and suggested predation and climatic fluctuations to be the most important regulators of amphibian and reptile populations. On the other hand, the results of a removal experiment by Inger and Greenberg (1966) in Sarawak, involving three syntopic species of stream-dependent frogs, congeners and similar in habits, suggested that some species may in fact reach abundances that bear the potential for competition, both intra- and interspecific. At this stage, rather than searching for a general explanation, we consider it more appropriate to ask what outcomes we expect from a given process in a particular environmental setting. In this respect, null models provide an important tool in the holistic approach to communities, because they allow a statistical comparison of putative patterns to those expected to occur in the absence of a particular mechanism, and hence the exclusion of that mechanism if the null hypothesis is accepted (Gotelli & Graves 1996).

In a previous paper (Hofer, Bersier & Borcard 1999), we used null model tests for one-dimensional gradients to critically evaluate the fit of the observed distribution patterns to the models proposed by Whittaker (1967) to depict community organisation on gradients. The four models are distinguished on the basis of whether species occur in discernible groupings and by the extent to which boundaries between species are exclusive, and are generated by four mechanisms, namely biotic interactions, abiotic limits, ecotones and dispersal constraints. Our results revealed few cases where interspecific competition between congeneric species may have led to spatial exclusion along the gradient or to significantly small range overlaps. However, due to the restriction to distributional data, the fittings to Whittaker's models provide only indirect estimates of the effects of the putative mechanisms underlying the observed patterns. Better insight into the organisation of an assemblage will be gained by a test procedure that provides a link between the overlaps in spatial distribution and the overlaps in resource use, because the full array of potential interactions between heterogeneric species pairs is also accounted for. In Andean birds, Terborgh and Weske (1975) found diffuse competition (as distinguished from the directly observable exclusion of congeners) to have a significant effect on the gradient distribution pattern of the assemblage. It was suggested the primary mechanism limiting elevational distributions for most of the species previously assumed to be limited by physiological constraints.

The observation of Terborgh and Weske (1975) prompted us to relate the pattern of niche overlap of the herpetofaunal assemblage directly to its spatial organisation along the elevational gradient. To do so by means of a null model procedure poses several methodological problems, and, to our knowledge, no single method described as yet can fill the task. Although recent developments such as three-table ordination (Dolédec et al. 1996) and fourth-corner analysis (Legendre, Galzin & Harmelin-Vivien 1997) provide sophisticated methods to link several dimensions important to community organisation, namely environmental conditions and species traits, the problem we are presented with here does not easily fit into one of these procedures. Because our data on spatial and resource overlap between each species pair can be depicted in similarity matrices, the Mantel test (Mantel 1967) may intuitively seem the appropriate method to analyse the relationship between them. However, for reasons explained in the Methods section, we cannot expect a linear or monotonic correlation between spatial and resource overlap matrix; this constitutes a violation of a critical assumption of the Mantel test and therefore invalidates its application in the present context. We eventually built a new approach based on two methods designed to test for niche segregation and guild formation in communities: the nearest-neighbour analysis pioneered by Inger and Colwell (1977) and the subsequent development of the pseudocommunity analysis by Winemiller and Pianka (1990). The microhabitat data we use to demonstrate this new test are original and were acquired in an afrotropical rainforest, an area where quantitative analyses of resource use in herpetofaunal assemblages continue to be rare.

STUDY AREA

Mount Kupe (4°45'N), in the Southwest Province of Cameroon, is a steep-sided, cone-shaped mountain 2064 m im height and situated approximately 100 km north-east of Mount

Cameroon. It forms part of the Cameroon highlands, an extensive volcanic mountain range running from Bioko Island to Mount Cameroon in the south-west on to the Bamenda and Adamawa highlands in the north-east, with the Obudu and Mambila Plateaus extending into Nigeria. By the time of the sampling the mountain was covered by approximately 2100 hectares of undisturbed closed canopy submontane forest, characterised by a fairly uniform structure with a sparse ground layer and a thin understory. Below 900 m the forest has been logged or severely degraded except for a few patches on the south-western and southern slopes. In the primary forest, we found watercourses between 900 and 1500 m and at 1900 m. The perennial streams up to 1400 m are characterised by moderate to steep gradients, rapids, splash zones, and bottoms of bedrock and sand. An intermittent stream is running from 1500 and 1400 m, with a moderate gradient and a bottom of bedrock and silt. The watercourse at 1900 m is perennial and flows through an almost flat area on a bottom of sand and silt. The single standing water body found within the primary forest was a puddle on a log in a treefall. Mount Kupe receives mean annual rainfall of 4891 mm (Suchel 1972). The rainy season lasts for seven months from April to October, and no month receives less than 70 mm.

METHODS

Data acquisition

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 twelve points between 900 and 2000 m, separated by 100 m in elevation, on transects parallel to the contour line. Animals were either collected or marked, and the marked specimens released at the end of each sampling session. We excluded from all analyses recaptured animals and specimens encountered at odd times, i.e., outside the equal sampling effort protocol for all elevations. Sampling procedures are outlined in more detail in Hofer et al. (1999).

In this paper, we depict the organisation of the studied assemblage by the species' microhabitat utilisation. Inger and Colwell (1977) designed a microhabitat code to compute niche overlap between species of herpetofaunal communities in a tropical evergreen forest, a deciduous forest and adjacent agricultural land in Thailand. The code comprised five nominal variables (vegetation / horizontal position / vertical position / substrate / special), and each individual encountered was assigned to one of several alternative states for each variable. We used a similar habitat classification scheme, based on four nominal variables (area / horizontal position / vertical position / substrate), and modified the list of alternative states according to the forest type under study (Appendix 1). Upon first encounter of each individual, microhabitat and activity state were noted. However, as all uses of a microhabitat potentially interact regardless their function in a given species' activity, we did not use the activity states to discriminate between resting, foraging, calling and breeding sites in the analysis. We recorded 101 different resource states, of which 61 in riparian (26 arboreal, 35 terrestrial or at surface level) and 40 in non-riparian situations (21 terrestrial, 19 arboreal).

Computation of resemblance

The similarity in microhabitat use between two species is estimated with the symmetric niche overlap coefficient of Pianka (1973),

$$\Phi_{jk} = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 \cdot \sum p_{ik}^2}} \qquad (1)$$

where p_{ij} and p_{ik} represent the proportions of individuals of species j and k found in microhabitat i. We did not apply any of the procedures suggested to account for resource availability (Colwell & Futuyma 1971, Lawlor 1980, Winemiller & Pianka 1990), because tests of niche overlap based on observed utilisations (p_i)

are conservative with respect to competition hypotheses (Gotelli & Graves 1996: 73). However, as 50 out of 64 species are represented by less than 50 individuals, we had to account for bias in the overlap estimates resulting from low sample sizes. We a priori excluded rare species from the computations, arbitrarily defined as being represented by less than ten individuals, and the single snake species left, which, as a frog predator, is not linked by the same type of interaction to the other species. For the remaining species, we applied the simulations suggested by Ricklefs and Lau (1980) and used the mean of 200 overlaps computed after each bootstrap iteration as the final estimate.

The gradient distribution of a species is characterised by its range length, i.e., the distance between the lowermost and uppermost point of occurrence, and by its abundance curve or amplitude, i.e., the numbers of individuals found at each point on the gradient. As a symmetric measure of the spatial overlap of two species on the gradient, we suggest an index I_{ovl} that gives equal weight to range and abundance overlap:

$$I_{ovl} = \frac{1}{2}\left(\sum_{i}^{m} \frac{\min(p_{ij}, p_{ik})}{\max(p_{ij}, p_{ik})} + \sum_{i}^{m} \frac{\min(q_{ij}, q_{ik})}{\max(q_{ij}, q_{ik})}\right) \qquad (2)$$

where m is the total number of sampled points along the gradient, p_{ij} and p_{ik} are the proportional abundances at point i of species j and k, respectively, and q_{ik} equals 1 if species k is present at site i, and 0 otherwise. This index varies between 0 for no overlap and 1 for complete overlap (when the proportional abundances of two species are equal at all points). To account for species with low abundances, we used the same bootstrap procedure as for the niche overlap index.

The above mentioned restrictions left 29 species of frogs and lizards in the final overlap matrices. The matrix of niche overlap was subjected to a cluster analysis, in order to reveal the general characteristics of habitat use and to obtain distinct subsets for further analysis. For the latter purpose, we chose the complete linkage algorithm, where the fusion of two clusters depends on the most distant pair of objects, a desirable property when clusters with clear discontinuities are sought (Legendre & Legendre 1998).

Linking niche overlap and gradient overlap

In an assemblage where physiological constraints determine the species distributions along environmental gradients, length and position of the ranges primarily reflect individual responses to physical conditions. Provided physiological constraints are of minor importance, species distributions can be constrained by the availability of resources, with two major scenarios possible: 1) If competitive interactions strongly determine the distributional pattern of the assemblage, we expect close neighbours in niche space, i.e., species pairs with high overlap in resource use, to be segregated geographically. The corresponding statement of the alternative hypothesis H_1 (hereafter termed competition hypothesis) is that species with high niche overlap exhibit a significantly smaller geographic overlap than expected by chance, i.e., when species distributions along the gradient were independent from similarity in resource use (H_0). 2) Alternatively, if resource availability rather than interspecific competition is the major determinant of spatial organisation, species pairs with high niche overlap should, by tracking largely the same resources, exhibit a significantly higher geographic overlap than expected by chance. The corresponding statement of the alternative hypothesis H_1 (hereafter termed resource tracking hypothesis, following Cody (1981) and Wiens (1984), who investigated tracking of temporally variable resources by birds) is that species with high niche overlap exhibit a significantly higher geographic overlap than expected by chance. Both alternative hypotheses should result in a non-random adjustment of the species' distributional ranges and their overlap in resource use. To what extent a community response is in accordance with either form of organisation can be revealed by a test procedure in which ecological and geographic organisation of an assemblage are related.

Note that in both scenarios outlined above, H_1 only predicts the relationship between the closest neighbours in niche space. Species pairs with small overlap in resource use may exhibit high (no competition, geographically overlapping resources) or small (geographically non-overlapping resources) geographic overlap. In other words, the geographic overlap between distant members in niche space is unpredictable. As a consequence, H_1 cannot be addressed by testing for a linear or monotonic correlation between the two resemblance matrices, which means a standard Mantel test (Mantel 1967) is not applicable. The solution to the problem we suggest here is based on an extension of the pseudocommunity analysis (Winemiller & Pianka 1990). This analysis critically evaluates niche segregation and guild formation in assemblages by ordering the n - 1 neighbours of each of n species on the basis of their niche overlap. The ordered values are then averaged to give the mean overlap of the first, second, ... n – 1 neighbours in niche space. In the pseudocommunity approach, mean niche overlap at each rank of neighbour is compared to the niche overlap values obtained from permutations of the resource matrix. Here, we compare mean geographic overlap at each rank of neighbour in niche space.

We therefore use the same aggregate statistic as the pseudocommunity analysis, i.e., mean overlap at a given rank of neighbour. As main differences, our test refers to two matrices (niche and geographic overlap) rather than a single one, and the distributions of the statistic are not obtained by randomising a resource matrix, but from permutations of the niche overlap matrix, as outlined below.

1) *Raw data.* Given are a resource matrix (**R**) and a geographic distribution or spatial matrix (**G**), both describing the same assemblage.

2) *Computing resemblance among species.* For R, species are related by a symmetrical niche overlap coefficient. The appropriate coefficient describing geographic similarity or overlap depends on whether **G** contains abundances, or ranges only. Both resemblance matrices (termed S_R and S_G) must be symmetrical and of the similarity type (distance coefficients must be converted to similarities).

3) *Setting diagonals to zero.* In both overlap matrices, the diagonal elements (the species-with-itself comparisons) must be given the value of 0 (TABLE 1).

4) *Constrained rearranging (ordering) of the columns of the geographic overlap matrix.* For each column in the niche overlap matrix, values are arranged in decreasing order. Simultaneously, the corre-sponding cells in the geographic overlap matrix are rearranged accordingly, i.e. in the order imposed by the sorting of the niche overlap matrix (TABLE 1). The zero diagonal elements all fall at the last row of the matrix. A technical problem occurs if observed niche overlaps are zero, in that they could appear in this last row. We accounted for that by replacing all zero niche overlaps, except those in the diagonal, by random values smaller than the smallest non zero overlap in each column. Note that these zero indices do not hamper our test because they fall in the last ranks in niche space, which are not part of the hypothesis.

5) *Computing the test statistic.* Mean geographic overlap at each rank of neighbour in niche space is computed.

6) *Randomisation of the niche overlap matrix.* The permutable units are whole objects, i.e., the entire species vectors, and not single overlap values, since the reference distribution is built upon comparisons of randomised pairs of species. If the columns are permuted, the rows have to be rearranged in the same sequence in order to restore the symmetrical structure of the matrix (TABLE 1), or vice-versa. Steps 4 and 5 are repeated following each permutation, always ordering the columns of the original geographic overlap matrix according to the sorted columns of the permuted niche overlap matrix.

7) *Evaluation of statistical significance, graphic representation of results*. For each rank of neighbour in niche space, the two-sided probability that mean observed geographic overlap differs significantly from random expectation is computed, based on the reference distribution obtained from the permutations. Observed geographic overlap (y-axis) is plotted against rank of neighbour in niche space. To facilitate the interpretation of the results, curves representing the permutational means of the geographic overlap and the rejection limits can be added to the nearest neighbour plot (FIG.2). H1 predicts that observed geographic overlap of at least the first rank of neighbour in niche space lies in the upper or lower rejection zone. Since our procedure tests the n-1 ranks simultaneously, we applied a sequential Bonferroni correction to the P-values (Holm 1979, Rice 1989).

To evaluate the sensitivity of our procedure, we applied a benchmark test, whose description and result are presented in Appendix 2. In the application to real data, we run the test with the entire set of species, and with two series of subsets. The first one corresponds to the subdivision separating species according to class and amphibians according to reproductive mode: (1) amphibians; (2) reptiles, represented here by lizard species only; (3) amphibians depending on streams for reproduction, i.e., tadpole development in lotic water or lentic microhabitats associated with streams; and (4) stream-independent amphibians, i.e., species reproducing by direct development or breeding in ponds, puddles, and tree holes. The second series of subsets followed the subgroups defined by the cluster analyses of the niche overlap matrix (see Results). It is within these subgroups of ecologically similar species that we expect the strongest effect of competition. For a complete list of all 64 species recorded on Mount Kupe, readers are referred to Hofer et al. (1999, Appendix 1).

As stated further up, the test is aimed at identifying non-random structures at the community- or guild-level, but does not allow to single out pairs of species. Some information, however, was derived from a plot of gradient against niche overlap, where each species pair is represented by a dot, similar to the graphic representation used by James and Boecklen (1984) to relate density correlations and morphological distances in an avian assemblage. Such a plot not only gives a general impression of the properties we are testing for, but also allows the identification of species pairs showing a particularly strong response in accordance with the hypothesis tested.

RESULTS

General characteristics of habitat use

The vertical stratification for riparian and non-riparian situations is given in TABLE 2 for all lizard and frog species represented by ten or more individuals. The complete linkage clustering of the niche overlap matrix of these 29 species allowed a subdivision of the assemblage into three coarse categories of habitat use (FIG.1): (1) ten species of frogs largely confined to streamsides (median niche overlap 0.542), genera *Afrixalus, Astylosternus, Petropedetes, Phrynobatrachus,* and *Phrynodon*; (2) eleven leaf litter species predominantly found away from streams (median overlap 0.889), where the anuran genera *Arthroleptis* and *Cardioglossa* and the skinks of the genus *Leptosiaphos* form a relatively tight cluster, to which the frog *Leptodactylodon ornatus* is only distantly related; (3) eight species predominantly found away from streams in the herb, shrub and lower tree layer (median overlap 0.166), the lizard genera *Chamaeleo, Rhampholeon* and *Cnemaspis,* and the anuran genera *Leptopelis* and *Wolterstorffina,* where the three *Chamaeleo* are tightly clustered. All three categories include entire genera only, whereas a further subdivision reveals congeners that are rather distantly related (*Leptopelis, Petropedetes*). The more commonly used UPGMA-algorithm

Table 1. Example illustrating the procedure used to relate a niche overlap and a geographic overlap matrix, using a hypothetical assemblage of 5 species (a-e). The numbering of the steps corresponds to the paragraph numbers in the Methods section.

STEP 3: Resemblance matrices are computed and diagonal elements set to 0

matrix S_R (niche overlap)						matrix S_G (geographic overlap)					
	a	b	c	d	e	a	b	c	d	e	
a	0	0.8	0.9	0.1	0.2	0	0.2	0.1	0.9	0.8	a
b	0.8	0	0.3	0.7	0.4	0.2	0	0.7	0.3	0.4	b
c	0.9	0.3	0	0.5	0.6	0.1	0.7	0	0.6	0.5	c
d	0.1	0.7	0.5	0	0.8	0.9	0.3	0.6	0	0.2	d
e	0.2	0.4	0.6	0.8	0	0.8	0.4	0.5	0.2	0	e

STEPS 4 and 5: Sorting of columns in matrix S_R, corresponding cells in matrix S_G are rearranged accordingly. The row means are computed at each rank of neighbour.

rank	a	b	c	d	e	a	b	c	d	e	mean
1st	0.9	0.8	0.9	0.8	0.8	0.1	0.2	0.1	0.2	0.2	0.16
2nd	0.8	0.7	0.6	0.7	0.6	0.2	0.3	0.5	0.3	0.5	0.36
3rd	0.2	0.4	0.5	0.5	0.4	0.8	0.4	0.6	0.6	0.4	0.56
4th	0.1	0.3	0.3	0.1	0.2	0.9	0.7	0.7	0.9	0.8	0.8
	0	0	0	0	0	0	0	0	0	0	

STEP 6: Random permutation of objects (columns) in square, symmetrical matrix S_R

	d	b	a	e	c
d	0	0.7	0.1	0.8	0.5
b	0.7	0	0.8	0.4	0.3
a	0.1	0.8	0	0.2	0.9
e	0.8	0.4	0.2	0	0.6
c	0.5	0.3	0.9	0.6	0

Repeat steps 4 and 5 following each randomization of matrix S_R

yielded the same three categories, but moved *Wolterstorffina* and *Rhampholeon* from the third to the second group; being strongly represented in microhabitats of the herb layer, these two species probably fall in between the third and second group, largely defined on the basis of vertical habitat use, and thus were assigned to the streamside species, where species from all layers except the uppermost are included.

The subdivision is somewhat arbitrary with respect to within-group variation in linkage distance, and because we did not apply any formal guild recognition test (e.g., Jaksic & Medel 1990). Yet, to keep the species groups readily identifiable in the following sections, we prefer to speak of three guilds, namely streamside, leaf litter and arboreal.

TABLE 2: Vertical stratification of 29 frog and lizard species in the primary forest on Mount Kupe, Cameroon. Column ">5m" refers to the lower tree layer, "1-5m" to the shrub layer, "<1m" to the herb layer. Values correspond to number of independent observations in the corresponding strata in a riparian or non-riparian situation.

		non-riparian					riparian				
	n	>5m	1-5m	<1m	on surface	below surface	>5m	1-5m	<1m	on surface	below surface
FROGS											
Afrixalus lacteus	21							8	13		
Arthroleptis adelphus	79			7	71				1		
Arthroleptis adolfifriderici	866		2	157	696	1			4	6	
Arthroleptis sp.A	176			26	144				3	3	
Arthroleptis sp.C	146			22	116					8	
Arthroleptis variabilis	377			9	358				1	9	
Astylosternus perreti	66				2				11	53	
Cardioglossa gracilis	70				56				8	6	
Cardioglossa venusta	27				19				5	3	
Leptodactylodon ornatus	20				11					9	
Leptopelis brevirostris	22		8	3				10	1		
Leptopelis modestus	15		1	2			4	7	1		
Petropedetes cameronensis	47								27	20	
Petropedetes newtoni	30			6	7				9	8	
Petropedetes parkeri	45				7				6	32	
Petropedetes perreti	35								13	22	
Phrynobatrachus cricogaster	100		1	12	13				59	15	
Phrynobatrachus werneri	23			1	5				9	5	3
Phrynodon sp.1	19							1	7	11	
Phrynodon sp.2	322							2	295	25	
Wolterstorffina parvipalmata	124		5	65	7			4	40	3	
LIZARDS											
Chamaeleo montium	55		36	1				17	1		
Chamaeleo pfefferi	49		44	1	1			3			
Chamaeleo quadricornis	85		81	1				3			
Cnemaspis koehleri	13	1	5	3	1			1	2		
Leptosiaphos sp.A	19				18	1					
Leptosiaphos sp.B	17				17						
Leptosiaphos sp.C	13				13						
Rhampholeon spectrum	278		13	194	9			5	57		

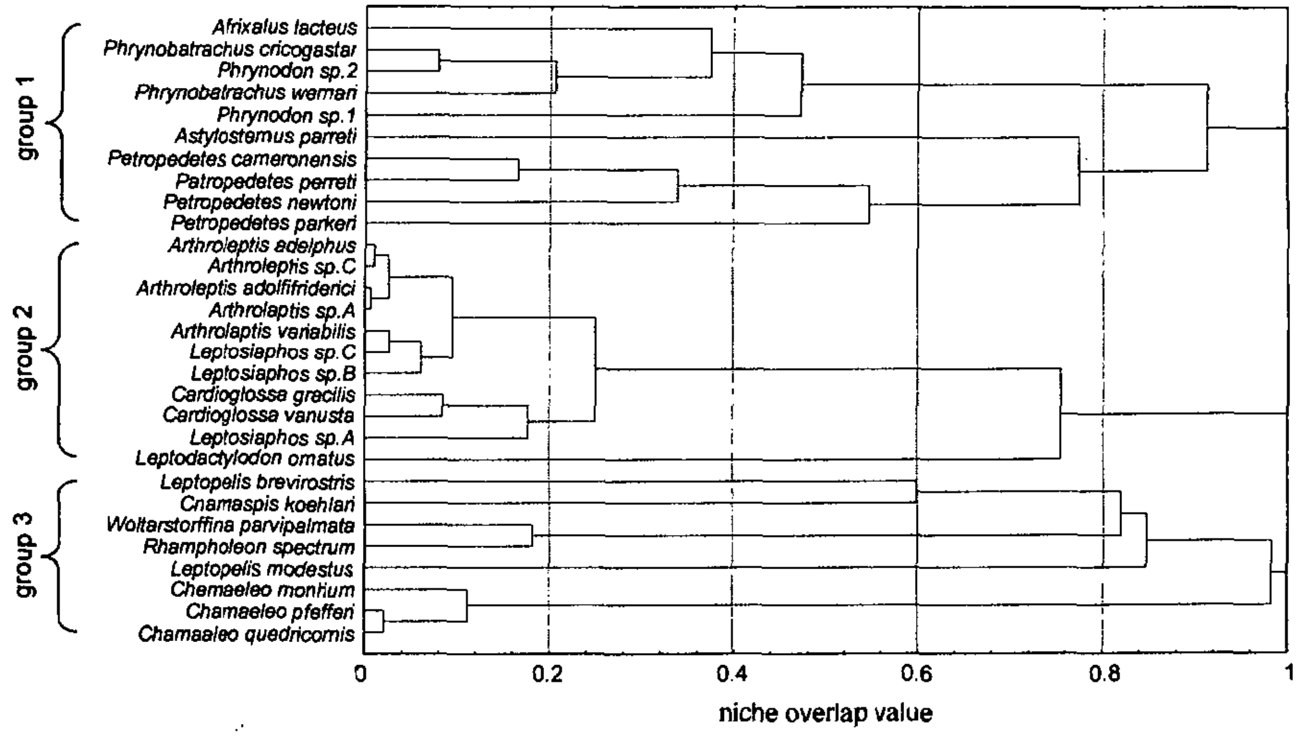

FIG.1: Dendrogram of cluster analysis based on microhabitat use. Group 1: species largely confined to streamsides (termed the streamside guild); group 2: leaf litter species predominantly found away from streams (leaf litter guild);. group 3: species predominantly found away from streams in the herb, shrub and lower tree layer (arboreal guild).

Relationship of niche overlap and spatial overlap

The null model tests revealed no species group where observed gradient overlap within the first three ranks of nearest-neighbour in niche space differs significantly from random expectation (FIG.2). In three subsets, the lizards, stream-independent amphibians and the leaf litter guild, mean gradient overlap at first rank of neighbour in niche space is smaller than expected by the null model, but only marginally so. In the remaining subsets and at the level of the entire assemblage, mean gradient overlap at first rank is higher than random expectation, the streamside guild showing the strongest deviance.

As a control of the above results, we refer to the plot of the indices of all pairwise comparisons (FIG.3). Most species pairs exhibit a small overlap in microhabitat use and are located in the left half of the plot. These are the distant neighbours in niche space whose response is unpredictable. The majority of the dots in the lower right region, where we find species pairs with high niche overlap that avoid each other on the gradient, concerns species of the leaf litter group. However, as demonstrated by the null model tests, the trend in this subset did not result in a non-random adjustment of gradient overlap and niche overlap. This can be explained by the presence of several species pairs of the same guild that are close neighbours in niche space but show a high spatial overlap along the gradient (upper right hand side in FIG.3).

DISCUSSION

The findings of our null model tests reveal no adjustment of niche overlap and gradient distribution that would reduce the potential for interspecific competition. Within the guilds derived from cluster analysis, where we expect the strongest adjustment, only the leaf litter species showed a response in the corresponding direction, but weak and by no means significant. In accordance with a different null model approach to the same assemblage (Hofer et al. 1999), the results suggest that interspecific competition is of

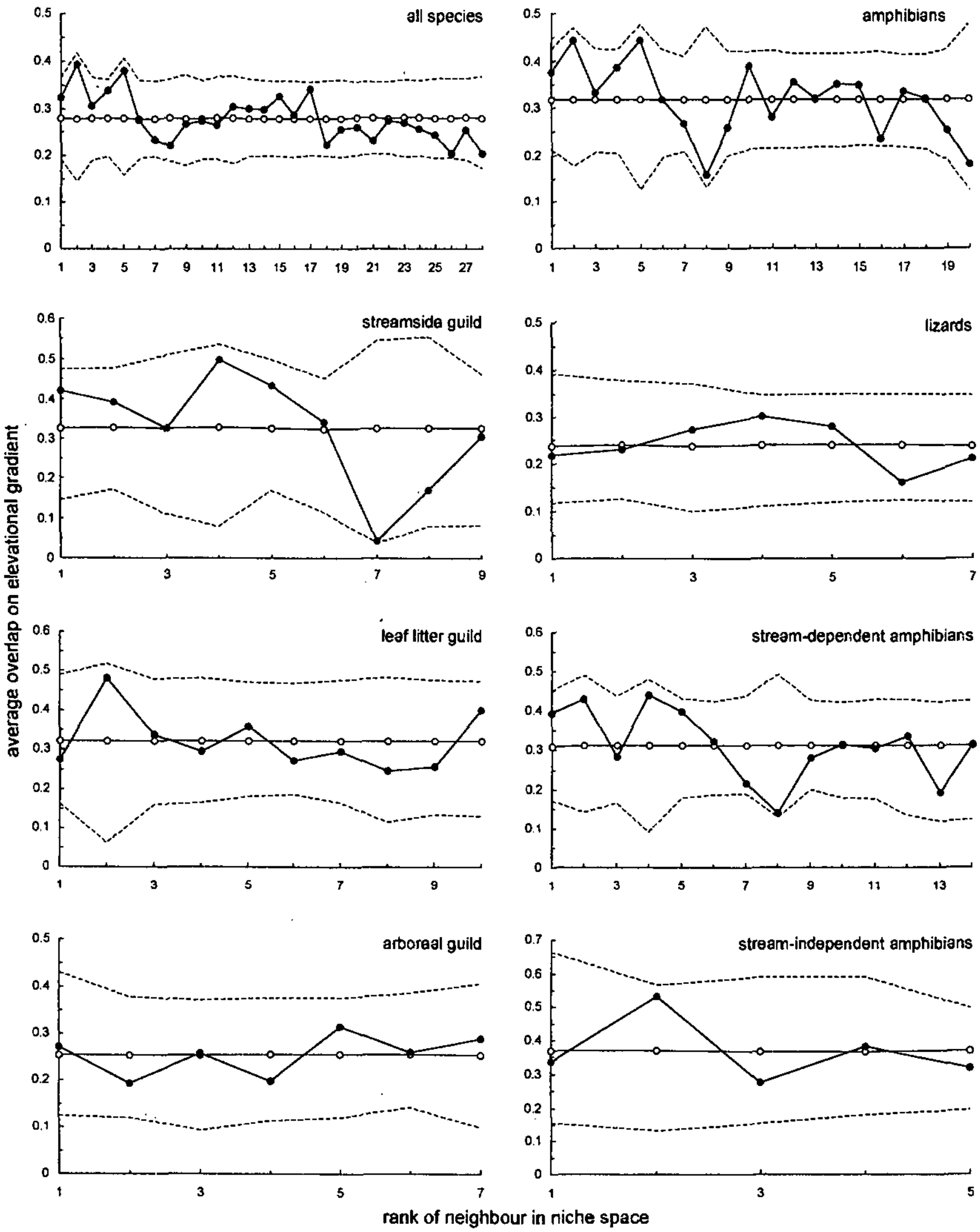

FIG.2: Nearest neighbour plots of average gradient overlap against rank of neighbour in niche space. Dots: mean observed gradient overlap at a each rank of neighbour in niche space; open circles: mean gradient overlap obtained from 10,000 permutations; dashed lines: Holm-corrected 5% rejection regions.

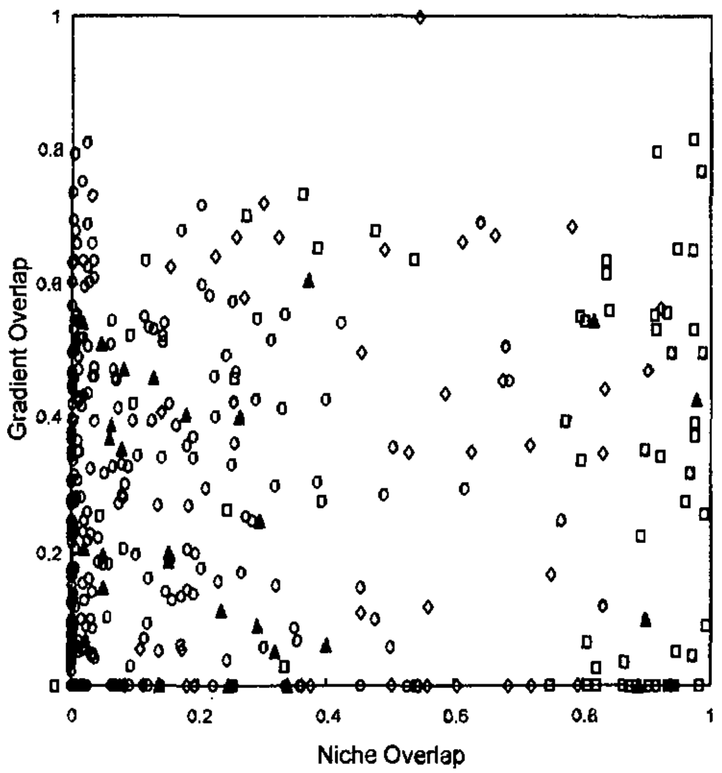

FIG.3: Plot of niche against gradient overlap, representing the 406 possible pairwise interactions in the 29-species assemblage. Open circles: pairs of species from different guilds; diamonds: species pairs of the streamside guild; open squares: leaf litter guild; filled triangles: arboreal guild. If niche overlap had a strong effect on the species' gradient distributions, we would expect a cluster of symbols in the lower right region of the graphic space.

minor importance in structuring the gradient distributions of amphibians and reptiles on Mount Kupe. The conclusions in Hofer et al. (1999) were drawn from a detailed analysis of the distributional patterns along the gradient, but without any consideration of resource use; potential effects of direct competition (sensu Terborgh & Weske 1975) were take into account by considering congeneric species pairs only. The present approach is complementary and provides a deeper insight into the organisation of this assemblage: first, it evaluates the gradient distribution patterns directly on the basis of the similarity in resource use; second, it takes into account the potential effects of diffuse competition, i.e., interactions between heterogeneric species pairs.

Our results clearly contrast with the findings of a study on birds along primary forest elevational gradients in the Peruvian Andes, where direct and diffuse competition was assigned overriding importance, accounting for two-thirds of the limits of avian elevational ranges (Terborgh 1971, 1985, Terborgh & Weske 1975). Despite the fundamental differences between our and Terborgh's approach, the divergent outcomes probably reflect biological realism, a position that may be substantiated by null model tests on the bird data.

In studies that demonstrated the spatial, temporal or qualitative partitioning of resources among frogs and/or lizards in tropical forests (Heatwole 1963; Rand & Humphrey 1968; Crump 1971; Heyer & Bellin 1973; Toft 1981; Lieberman 1986; Duellman 1987; Donnelly & Guyer 1994; Vitt & Caldwell 1994; Vitt & Zani 1996), it was usually recognised as a mechanism by which competition among syntopic species was avoided. However, competition was never ascribed overriding importance in the structuring of these assemblages. Duellman (1990) suggested predation and climatic fluctuations (extended dry seasons in particular) rather than interspecific competition to be the dominant regulators of amphibian and reptile populations in Neotropical lowland forests. With respect to an impact of interspecific competition on distributional patterns along a gradient, our null model tests on the herpetofaunal assemblage of an Afrotropical upland forest did not reveal a response at the community-level. Some results strongly suggest that competitive interactions limit the elevational distributions of particular species pairs. On Mount Kupe congeneric species pairs of the genera *Arthroleptis* and *Chamaeleo* exhibit contiguous elevational ranges or significantly small overlaps in gradient distribution (Hofer et al. 1999), and the present study found overlaps in microhabitat use of 0.97 - 0.99 and 0.89 – 0.98, respectively, within the two genera. Confirmatory evidence for interspecific competition to limit gradient distributions in these genera may ultimately be obtained by removal experiments.

Although competitive interactions were the primary interest in our approach, some conclusions regarding the response of the species groups to habitat can be derived from our results. In the stream-dependent amphibians and the streamside guild (itself in fact a subset of the stream-dependent amphibians) observed gradient overlap at the first two ranks of neighbour in niche space is higher than the permutational means, suggesting that species distributions are to some extent affected by resource tracking. In several species pairs the high overlap in gradient distribution may result from a response to the same array of microhabitats. However, the overlaps in gradient distribution are not significantly higher than expected by chance, which means that in both species groups microhabitat availability explains only a small part of the elevational distribution patterns.

In all, the findings of the null model tests leave the possibility that the gradient distribution patterns observed at the level of the entire assemblage and of various subsets essentially reflect individual responses of many species to the gradient, i.e., to the physical factors varying in parallel with it. However, to what extent individual responses shape the spatial organisation of the amphibians and reptiles on Mount Kupe cannot be inferred from the present approach, but needs substantiation by appropriate tests.

In the present study, we based overlap in resource use on a single niche dimension, microhabitat utilisation. Toft (1985) reviewed resource partitioning in amphibians and reptiles with respect to habitat, food and time. With the exception of snakes and amphibian aquatic larvae, habitat was the dimension partitioned first. Inger and Colwell (1977) recognised as well the importance of trophic differences among amphibians and reptiles, but in their analysis of herpetofaunal communities in Thailand considered a parallel study of diets to yield little additional information. Most frogs and lizards are trophic generalists, eating whatever is available in the microhabitats they occupy. Thus, niche metrics computed from food types and microhabitats can be expected to be highly correlated with each other. Furthermore, trophic differences among species with high microhabitat overlap tend to be obvious and are often associated with gross taxonomic differences. A recent study on a taxonomically diverse lizard assemblage (Vitt & Zani 1996) essentially confirmed these assumptions. Some reservations, however, are justified with respect to the leaf litter guild, where several studies demonstrated niche segregation based on food (Toft 1981, Lieberman 1986, Vitt & Caldwell 1994). Our preliminary data on the species' feeding habits suggest that three frogs (the two small *Arthroleptis*, sp.A and sp.C, *Wolterstorffina parvipalmata*) are ant-specialists as defined by Toft (1981), and thus may show dietary segregation from species with which they overlap in microhabitat use. In accordance with the competition hypothesis tested here, any decrease in niche overlap reduces the need for the species to segregate spatially along the gradient, thereby further reducing the probability of rejecting the null hypothesis.

Inger and Colwell (1977) emphasised the problems inherent to statistical analyses of microhabitat data and laid much concern in a reduction of bias in niche overlap estimates. We accounted for their reservations by the procedure outlined in the Methods section. As in Inger and Colwell (1977), only a fraction of the total array of species remained amenable to analysis, 80 % of all lizard and 79 % of all frog species recorded in the study area. Both groups contain equal proportions of the original species pool, and the results from a previous null model approach (Hofer et al. 1999), using both original and reduced matrices, suggest that the 29 species are indeed a representative subset that reflects the major interactions within the assemblage.

Inger and Colwell (1977) further commented on the reasons that justify pooling of all uses of a microhabitat, i.e., resting, foraging, calling and breeding sites, in computations of niche overlap. While their arguments equally apply here, the possible effect of pooling is difficult to assess in our approach. It depends on whether potentially biased niche overlaps concern species pairs that contribute more to the "noise" or to the "signal" part in the relation of the two overlap matrices. Members of the second group, species with high niche but low gradient overlap, increase the probability of rejecting the null hypothesis only if they are disproportionately affected by overestimates of niche overlap. We see no a priori reason for this to be the case. With respect to guilds, the pooling of all microhabitat uses did not result in any counter-intuitive placements (Fig. 1), although the resource vectors of a few species with strongly separated foraging and resting sites can be biased due to low detectability in some microhabitats. Despite the simplification and inaccuracies our decisions may have introduced, we consider the results of our null model tests too far from rejecting the null hypothesis that any change in the niche overlap matrices based on microhabitat use is likely to produce a markedly different outcome.

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APPENDIX 1

Microhabitat classification. Each microhabitat use recorded is a combination of alternative states of the four variables listed below.

Area:	away from stream/pond; permanent stream; intermittent stream.
Horizontal position:	in closed canopy area; in treefall/clearing; in swampy/water logged area; mid stream/pond; above water; on bank; in dried bed.
Vertical position:	lower tree layer 5-10m high; shrub layer 1-5m high; herb layer <1m high; on surface (of soil/water); under surface (of soil/water).
Substrate:	bare soil; on leaf litter; under leaf litter; on swampy/water logged soil/detritus; on rock; under rock; on rocky outcrop; on log/snag; under log; in decaying log; in small puddle on log; in grass; on green leaf; on stem of herbaceous plant; on stem of fine vine; on twig or branch of woody plant; on palm tree/fern frond; epiphyte/moss; on trunk of shrub/tree/stump; under bark of log/stump; in root system of herbaceous plant; between small tree roots; between buttress roots; in tree hole; in landcrab/rodent burrow; in water; in splash zone of running water; in temporary rain pool.

APPENDIX 2

Benchmark test. To evaluate the sensitivity of the test, we applied the procedure to idealised pairs of 10-species overlap matrices, each run with 200 permutations. The niche overlap indices Φ were drawn randomly from a uniform distribution ($U[0,1[$). The values of the geographic overlap indices I_{ovl} were a function of the corresponding Φ:

$$\text{if } \Phi \geq 1-f,\ I_{ovl} = \begin{cases} 1-\Phi-n\cdot(1-\Phi)\cdot U[0,1[& \text{or, with equal probability} \\ 1-\Phi+n\cdot(2\Phi-1)\cdot U[0,1[& \end{cases} \qquad (3)$$

$$\text{if } \Phi < 1-f,\ I_{ovl} = U[0,1[$$

The parameters f and n vary between 0 and 1. f controls the expected proportion of pairwise interactions where high niche overlap corresponds to small geographic overlap, i.e., the proportion of species pairs responding in accordance with the competitive hypothesis. Parameter n allows the addition of noise to I_{ovl}; if $n = 0$, I_{ovl} equals exactly $1-\Phi$; if $n = 1$, I_{ovl} can vary between 0 and Φ. We ran benchmark tests for all combinations of f and n with values changing at 0.1 steps. We additionally applied the benchmark tests to larger matrices, to niche overlap matrices with built-in block structure, and to idealised matrices where high niche overlap corresponded to high geographic overlap (resource tracking hypothesis). As these did not yield different results, they are not presented further. Fig.4A presents the lines of equal percentage of rejection of H_0 ($\alpha = 0.05$, one-tailed) for the first nearest neighbour in niche space. Rejection percentages are computed over 100 simulations with each combination of parameters f and n; the lines were smoothed by a moving average procedure. In the leftmost part of FIG.4A, the niche and geographic overlap matrices are entirely filled with random numbers; in this parameter region, the test correctly produces 5% of rejected H_0. The number of pairwise interactions where high niche overlap is coupled with small geographic overlap (f) increases as one is moving from left to right. The rather abrupt transition from low to high rejection rate at about $f = 0.15$ indicates that at least 15 % of all responses must be of the type high niche overlap coupled with small geographic overlap for the null hypothesis to be rejected. The probability of the test to reject the null hypothesis decreases with the amount of noise added to the interaction (ordinate), but here the transition is gradual over the full range of n values. In all, these results correspond to the desired properties of the test. FIG.4B depicts typical nearest neighbour plots for the combinations of n and f corresponding to the circled letters in FIG.4A. Note that plots C, F, and I of FIG.4B represent biologically unrealistic situations, in that low niche overlap always corresponds to high geographic overlap.

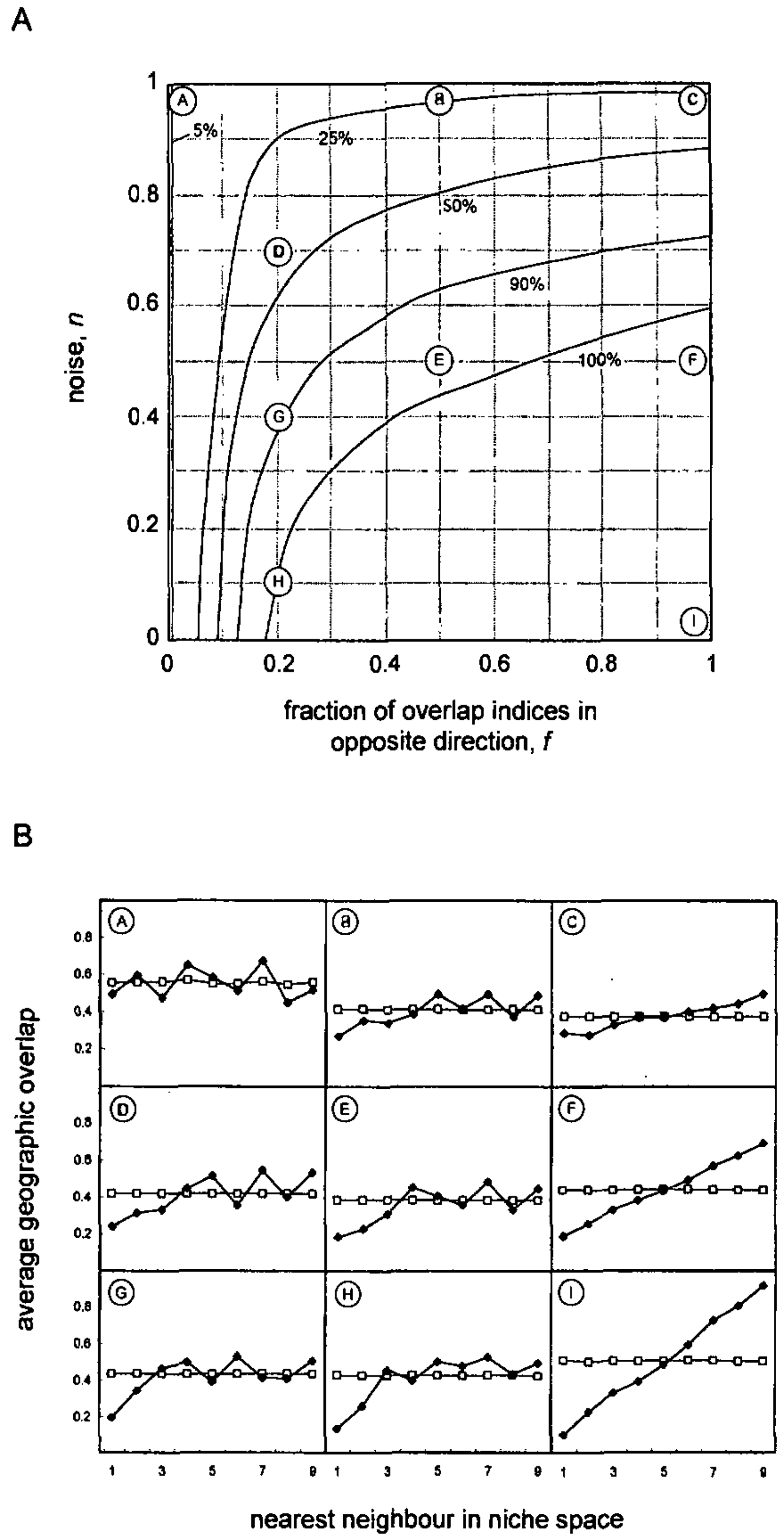

Figure 4. Benchmark test results of the null model test relating niche overlap and geographic overlap within hypothetical ten-species assemblages. A) Plot showing the lines of equal percentage of rejection of H_0 ($\alpha = 0.05$, one-tailed) for the first nearest neighbour in niche space. Benchmark tests were run for all combinations of parameters *f* and *n*, which control the proportion of pairwise overlaps in H_1 direction and noise, respectively. B) Typical nearest neighbour plots of average geographic overlap against rank of neighbour in niche space. Diamonds: observed geographic overlap; squares: mean geographic overlap from 200 permutations. Letters correspond to the combination of parameters values shown in A.

Abstract of Chapter III

The relationship between niche overlap in terms of microhabitat use and overlap in elevational distribution was evaluated in the herpetofaunal assemblage on the western slope of Mount Kupe, Cameroon. Specifically the adjustment of the species' distributional ranges and their overlap in resource use was tested with respect to predictions from an assemblage structured by interspecific competition or by species tracking similar resources.

Tests of corresponding hypotheses must account for the non-linearity in the relationship of the two descriptors: In a competitively structured assemblage, for example, species with high niche overlap are expected to be segregated geographically, i.e., show small spatial overlap along the elevational gradient, but species with small niche overlap must not exhibit high geographic overlap. Testing devices based on a linear correlation, e.g., the Mantel test, are therefore not applicable. This problem is resolved here by an original null model approach based on nearest neighbour analysis.

The null model test was run for the entire assemblage of 29 species and for seven subsets, the amphibians, lizards, amphibians dependent on streams for reproduction, amphibians that do not use streams for reproduction, and three guilds delineated by cluster analysis on the basis of microhabitat use.

For none of the subsets did the null model test reveal an adjustment of the species' gradient distributions that would reduce the potential for interspecific competition resulting from niche overlap. A look at pairwise interactions suggested that only a small proportion may reflect a response to interspecific competition. Some results indicated an impact of habitat, in that species respond to the availability of suitable microhabitats, but the pattern was not sufficiently consistent to consider it the dominant process limiting gradient distributions.

This outcome suggests that the gradient distribution patterns observed at the level of the entire assemblage and of the various subsets essentially reflect individual responses of many species to the gradient, according to their physiological tolerance limits.

Key words: Cameroon; community structure; interspecific competition; nearest neighbour analysis; null model.

IV ECOTONES AND GRADIENT AS DETERMINANTS OF HERPETOFAUNAL COMMUNITY STRUCTURE IN THE PRIMARY FOREST OF MOUNT KUPE, CAMEROON[1]

INTRODUCTION

For many vertebrate assemblages in the tropics, the distribution patterns on elevational gradients are well documented. Studies on mammals (Graham 1990, Yu 1994, Patterson et al. 1996), birds (Terborgh 1971, 1985, Rahbek 1997), as well as on amphibians and reptiles (Brown and Alcala 1961, Heyer 1967, Cadle and Patton 1988, Fauth et al. 1989) 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 and Alcala 1961, Heyer 1967, Scott 1976, Fauth et al. 1989), 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 (Fig.1), distinguished on the basis of whether species occur in discernible groupings and by the extent to which boundaries between species are 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

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[1] Chapter in press: Hofer U., Bersier L.F. & Borcard D. *Journal of Tropicol Ecology*

competitive interactions, ecotones and factors varying in parallel with the gradient in limiting elevational distributions 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 and 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 characterise community organisation on gradients (Fig.1).

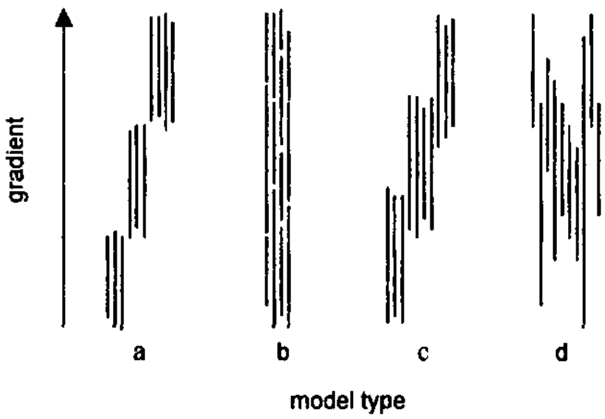

FIG.1: The four models of the arrangement of species on a gradient suggested by Whittaker (1967), adapted from Dale (1986). Each line corresponds to a species range. (a) distinct groups of species with sharp ecotonal exclusion boundaries; (b) sharp exclusion boundaries between competing species but no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

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 rather suggested 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, Jenlk 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 within the study area.

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 to assess the amount of variation explained by either ecotone or gradient descriptors alone.

STUDY AREA

Mount Kupe, 4°45'N / 9°42'E, in the Southwest Province of Cameroon, is a steep-sided, cone-shaped mountain 2064 m im height and situated approximately 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 was covered by approximately 2100 ha of undisturbed closed canopy submontane forest (Thomas 1986). The canopy is closed and to about 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 to 15 m. The summit gives way to small areas of grassland. The 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 south-western 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, March 13, night) to 23.8 °C (900 m, April 21, 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 twelve 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 soil in the root system of big trees and under logs and inspecting the herb and shrub layer up to about 10 m; in riparian zones, the streambed was examined in addition. 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 no 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 Andreas Schmitz (in litt.), 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).

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, we used two qualitative descriptors. Forest types were assigned according to Thomas (1986) and Philip Lane (pers. comm.), and includes three states: 1a) submontane forest, canopy closed, to about 30 m, with few scattered emergents, on ridges more open and to about 18 m, understorey thin except for ridges, ground layer sparse, typical trees include *Santiria trimera* and Guttiferae species, gap regrowth characterised by *Cylicomorpha solmsii, Macaranga occidentalis*, and the tree fern *Cyathea* spp.; 1b) upper transitional zone, canopy more open, to about 10 to 15 m, understorey dominated by Rubiaceae species, ground layer sparse, transitional character underlined 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 like *Xylopia staudtii* and *Macaranga occidentalis*; 1c) lower transitional zone; the transitional character of the forest remnants between 700 and 900 m is emphasised by both Thomas (1986) and Lane, but no species list provided. The type of water body was assigned on the basis of our own fieldwork, with the states; 2a) stream type 1, perennial, with 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 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 twelve elevations sampled are shown in Table 1. Both qualitative variables were binary coded prior to analyses (Legendre and 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 and Legendre (1998) when data are 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 where it is 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 a meaningless level. Finally, since we applied several tests to the same data, 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 reverse. This allowed us to calculate the percentage of variation 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 hy 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., twelve 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).

RESULTS

All four subsets except the entire amphibian assemblage responded exclusively to gradient descriptors (Table 3), with either X^2 or X^3 entering

Table 1: States of the two qualitative descriptors of the ecotones, and values of the three variables coding the gradient at each elevation.

	Ecotone		Gradient		
Elevation [m]	Forest type	Type of water body	X	X^2	X^3
900	lower transitional	stream type 1	-5.5	30.25	-166.375
1000	submontane	stream type 1	-4.5	20.25	-91.125
1100	submontane	stream type 1	-3.5	12.25	-42.875
1200	submontane	stream type 1	-2.5	6.25	-15.625
1300	submontane	stream type 1	-1.5	2.25	-3.375
1400	submontane	stream type 1	-0.5	0.25	-0.125
1500	submontane	stream type 2	0.5	0.25	0.125
1600	submontane	standing water	1.5	2.25	3.375
1700	submontane	-	2.5	6.25	15.625
1800	submontane	-	3.5	12.25	42.875
1900	upper transitional	stream type 3	4.5	20.25	91.125
2000	upper transitional	-	5.5	30.25	166.375

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 (Fig.2 and 3).

Species	Acronym	n	Elevational range	Proportion of individuals in/at streams	Stratification
Stream-dependent amphibians					
Afrixalus lacteus	Afri lact	17	1300-1900 m	1	3
Astylosternus cf. *montanus*	Asty cf.m	9	900-1500 m	0.33	2
Astylosternus diademotus	Asty diad	3	900 m	0.33	2
Astylosternus perreti	Asty perr	53	900-1400 m	0.97	2
Bufo gracilipes	Bufo grac	1	900 m	0	2
Bufo tuberosus	Bufo tube	2	900 m	1	2
Cardioglossa gracilis	Card grac	57	900-1200 m	0.2	2
Cardioglossa venusta	Card venu	26	900-1400 m	0.3	2
Conraua robusta	Conr robu	5	1000-1400 m	1	1
Leptodactylodon ornatus	Lept orna	19	900-1300 m	0.45	2
Leptopelis brevirostris	Lept brev	11	900-1200 m	0.5	3
Leptopelis calcaratus	Lept calc	7	900-1000 m	0.86	3
Leptopelis modestus	Lept mode	12	1400-1900 m	0.8	3

Table 2 (continued)

Leptopelis rufus	Lept rufu	4	900 m	1	3
Petropedetes cameronensis	Petr came	43	900-1200 m	1	2
Petropedetes newtoni	Petr newt	24	900-1500 m	0.57	2
Petropedetes parkeri	Petr park	43	900-1400 m	0.84	2
Petropedetes perreti	Petr perr	34	900-1500 m	1	2
Phrynobatrachus cricogaster	Phry cric	86	900-2000 m	0.74	2
Phrynobatrachus werneri	Phry wern	14	1900 m	0.74	2
Phrynodon sp.*1*	Phry sp.1	19	1900 m	1	2
Phrynodon sp.2	Phry sp.2	294	900-1500 m	1	2
Trichobatrachus robustus	Tric robu	2	900-1000 m	1	2
Werneria preussi mertensiana	Wern preu	3	900-1100 m	0.66	2
Stream-independent amphibians					
Arthroleptis adelphus	Arth adel	68	900-1200 m	0.01	2
Arthroleptis "adolfifriderici"	Arth adol	737	1300-2000 m	0.01	2
Arthroleptis sp.A	Arth sp.A	165	900-1400 m	0.03	2
Arthroleptis sp.C	Arth sp.C	94	900-2000 m	0.05	2
Arthroleptis variabilis	Arth vari	322	900-1300 m	0.03	2
Wolterstorffina parvipalmata	Wolt parv	103	1000-2000 m	0.38	2
Reptiles					
(lizards)					
Chamaeleo montium	Cham mont	49	900-1200 m	0.33	3
Chamaeleo pfefferi	Cham pfef	39	1100-1900 m	0.06	3
Chamaeleo quadricornis	Cham quad	63	1300-2000 m	0.04	3
Cnemaspis koehleri	Cnem koeh	12	1200-1800 m	0.25	3
Hemidactylus echinus	Hemi echi	4	1000-1200 m	1	3
Hemidactylus fasciatus	Hemi fasc	1	1000 m	0	3
Leptosiaphos rohdei	Lept rohd	2	900-1000 m	0.5	2
Leptosiaphos sp.A	Lept sp.A	17	1400-2000 m	0	2
Leptosiaphos sp.B	Lept sp.B	11	1500-2000 m	0	2
Leptosiaphos sp.C	Lept sp.C	12	1000-1300 m	0	2
Mabuya affinis	Mabu affi	1	900 m	1	2
Rhampholeon spectrum	Rham spec	234	900-1800 m	0.22	2
(snakes)					
Bitis gabonica	Biti gabo	1	1000 m	1	2
Bothralycus ater	Both ater	1	1300 m	1	2
Buhoma depressiceps	Buho depr	11	900-1900 m	0	2
Calabaria reinhardti	Cala rein	1	1100 m	1	2
Chamaelycus fasciatus	Cham fasc	1	1200 m	0	2
Dipsadoboa sp.	Dips sp.	1	1500 m	0	3
Mehelya guiroli	Mehe guir	2	900-1000 m	1	2

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

	Reptiles	Amphibians		
		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%)
canonical axis 2	0.201 (16%)	0.238 (20%)	0.020 (3%)	0.228 (20%)
canonical axis 3		0.129 (11%)		
canonical axis 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 type3 stream type1	X X^3	X X^2

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 relation between the gradient and the elevational distribution of most species. The stream descriptors were related to the entire amphibian assemblage only (Fig. 2b), 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 up 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 parvipalamta*, located in the lower right quadrant of the biplot (Fig. 2b), close to the streamless sites (Fig. 1a). 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 (Fig. 3). The species are ranked on the gradient according to their elevational optima. No effect of the variables describing the ecotones is recognisable.

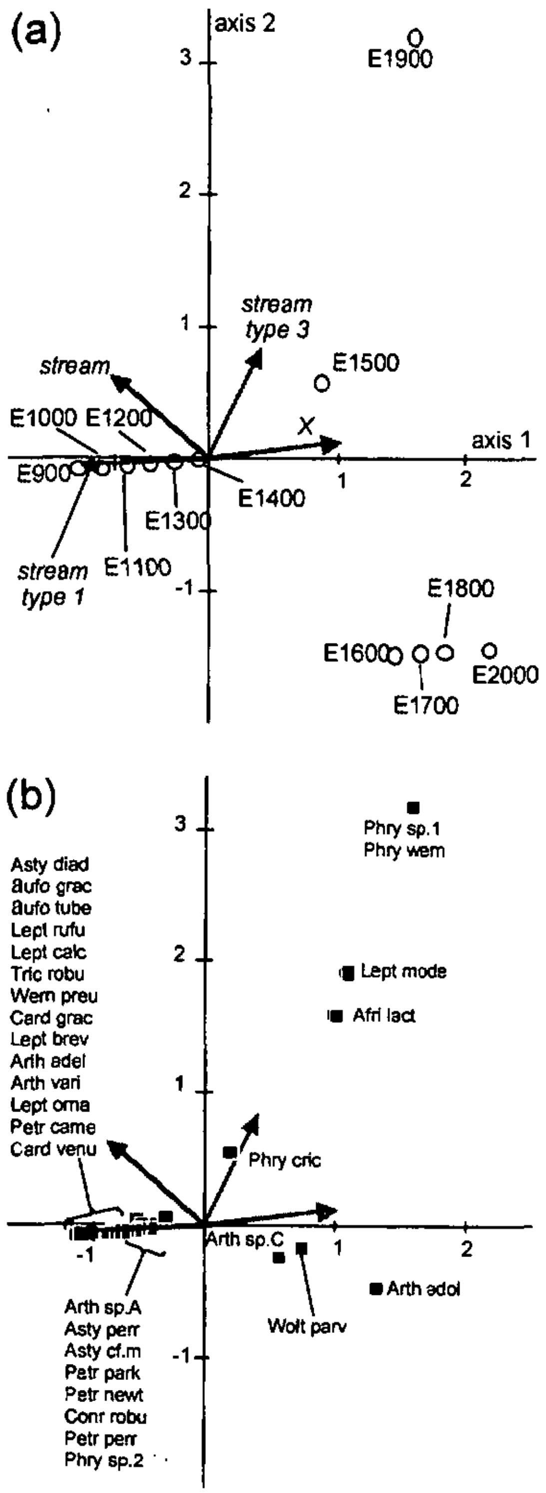

FIG.2: CCA of the amphibians. Biplots of the sites (a) and species (b) and the significant explanatory descriptors. The species names are given in the Table 2.

For the entire amphibian assemblage, the ecotones explain 22.8 % of the variation of species' abundances, relative to 18.6 % explained by the gradient alone (Fig. 4). Both set of descriptors share 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

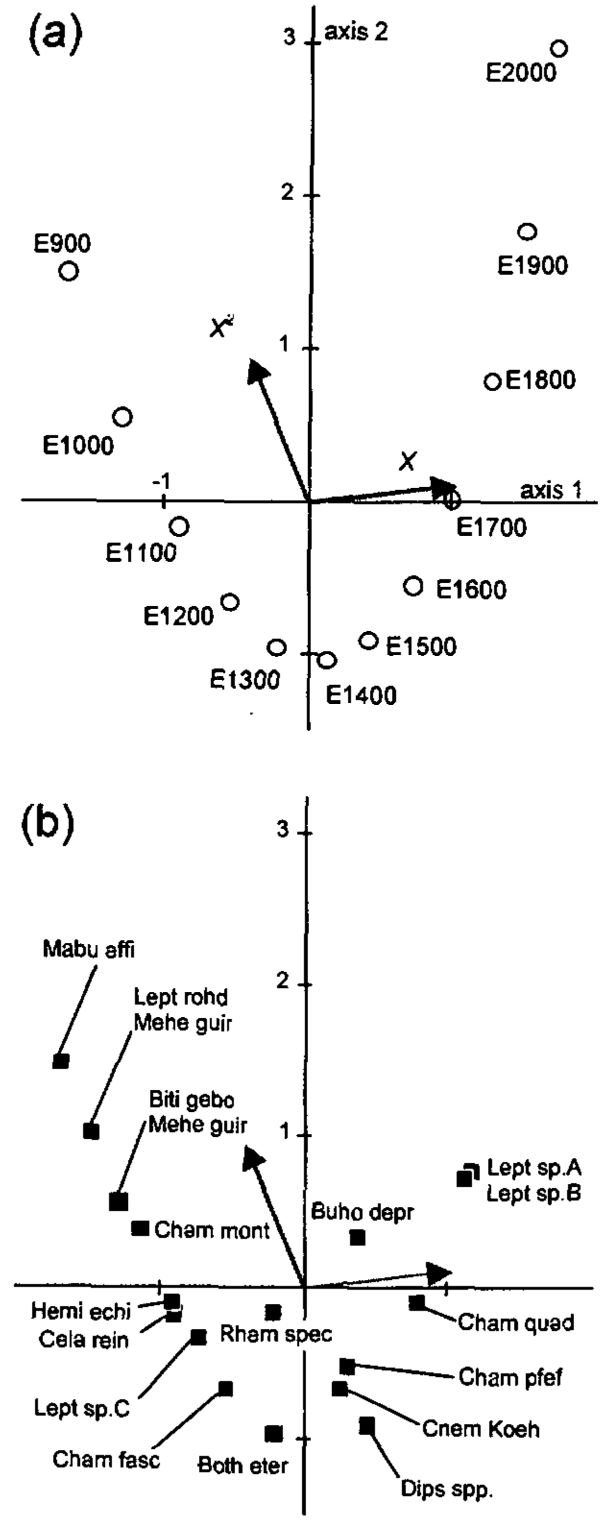

FIG.3: CCA of the reptiles. Biplots of the sites (a) or species (b) and the significant explanatory descriptors. The species names are given in the Table 2.

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 are 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. quadricorrnis* 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

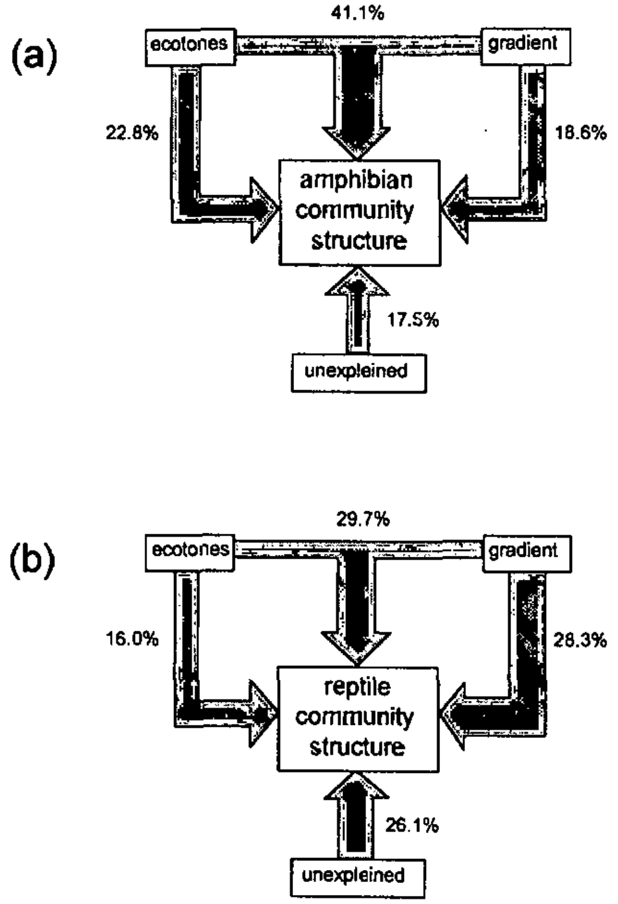

FIG.4: Variation partitioning of the amphibian (a) and reptile (b) communities

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 recognized climatic factors and coarse-grained changes in habitat as limiting the distributions of most species, both at local (e.g., Brown and Alcala 1961, Scott 1976, Inger et al. 1987, Inger and Stuebing 1992) and regional scales (e.g., Heyer 1967, Amiet 1971, Duellman and Wild 1993). With respect to elevational gradients, examples include species that responded to reduced availability of specific microhabitats associated with streams (Inger and Stuebing 1992) or with particular vegetation zones (Brown and 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 to assess 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 and 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 final 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 (Fig.1), where the assemblage would be organised 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, Fig.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 amphibians and reptiles. Within the subsets looked at, 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 (Fig.1). 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.

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Abstract of chapter IV.

The relative effects of the elevational gradient and of environmental discontinuities (ecotones) on the structure of a herpetofaunal assemblage in a tropical upland forest are contrasted by means of canonical correspondence analysis. Qualitative descriptors are 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 is coded in a form that accomodates different types of community response. Analyses are 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 show a significant relationship with the gradient, which suggests that most species respond to the physical continuum associated with the change in elevation. A response to ecotones is revealed for the amphibian subset only and associated with the presence or absence of watercourses. However, this response disappears within subsets 3 and 4. A variation partitioning analysis is 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 explain more variation in the reptile subset than ecotones, while the reverse is found in the amphibian subset. The dependence of most amphibians on aquatic breeding sites that are not available at all elevations reduces the relative importance of the gradient on the species distributions in subset 2 and accounts 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 minor importance in limiting elevational distributions. The response patterns revealed by the present approach, with ecotones and gradient contrasted in a single analysis, appear to reflect individual responses of many species to the gradient according to their physiological tolerance limits.

Key words: Amphibia; Cameroon; canonical correspondence analysis; gradient distribution; Reptilia; species groups; tropical forest; variance partitioning

V HERPETOFAUNAL DIVERSITY AND ABUNDANCE IN TROPICAL UPLAND FORESTS OF CAMEROON AND PANAMA[1]

Comparisons of samples of amphibians and reptiles from neotropical and Southeast Asian lowland rainforests revealed that both diversity and density are higher in the neotropics. Samples usually encompassed the leaf-litter zone or a single type of microhabitat. Heyer and Berven (1973) and Voris (1977) analyzed the tree buttress microhabitat and based their comparisons on average species diversity per individual, thus incorporating both species richness and evenness. Diversity of amphibians and reptiles found on tree buttresses was higher in the neotropical collection and the authors concluded that overall herpetofaunal diversity in a given rainforest largely determines the diversity associated with a particular microhabitat. Scott (1976) and Inger (1980a) compared the densities of non-riparian leaf-litter herpetofaunas. Standardized to the number of individuals per 100 m2, Central American lowland forest densities were about an order of magnitude higher than in Indo-Malayan ones, a result supported by further data from Central American sites (Toft 1980, Lieberman 1986, Fauth et al. 1989). Scott (1976) also included upland sites and found densities of Costa Rican leaf litter herpetofaunas almost six times higher than those reported by Brown and Alcala (1961) for the same elevations on Cuernos de Negros, Philippine Islands. Scott (1976) attributed these differences to greater litter fall and faster decomposition rates in Neotropical forests. Finding no such difference in ecosystem function, Inger (1980a) suggested that population levels in the Indo-Malayan forests are kept below those achieved in neotropical forests primarily by a reduced food supply. The latter would result from the synchronized mast fruiting of the dipterocarp trees dominating these forests, which reduces the number of seed-eating insects and associated arthropod predators on the forest floor. In a brief review of the topic, May (1980) favored Inger's explanation, but emphasized the need for a confirmation of the postulated arthropod density differences.

While the cited studies revealed consistent differences between Central America and Southeast Asia in diversity and density of lowland forest amphibians and reptiles, Afrotropical herpetofaunas remained virtually excluded from such comparisons, as data sets equivalent to those from the other two continents were scarce. Scott (1982) presented the first inter-site comparison, based on a sample of 15 forest litter plots and 66 man-hours of collecting effort in a Cameroonian lowland forest on white-sand soil. The herpetofaunal species richness in the African leaf litter samples was about half that found in equivalent-sized samples from lowland forests of Borneo and Costa Rica (Scott 1982). Densities of individuals were about 60 % of those found in Central America, but six times the densities on Borneo. Using simple life history data on habitat, activity period, breeding site and size class, Lawson (1992) assessed the similarity in ecological structure of the herpetofaunal assemblages of Korup, Cameroon, and Santa Cecilia, Ecuador. Frogs exhibited little overlap in distribution among life history types, a finding attributed to differences in types of breeding sites available; squamates showed a such dissimilarity,

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[1] Chapter in press: Hofer, U. & Bersier, L.F. *Biotropica*

although they were ecologically more diverse in Korup. The two sites had similar species numbers, but this comparison was not standardized for area or effort. On a broad level, Duellman (1993) and Bauer (1993) provided comprehensive comparisons of the amphibian and reptile faunas of Africa and South America. Standardized to a 106 km2 scale, amphibian species density in montane rainforests of South America was 1.7 times that of Africa, while for lowland forests, density in Africa was 1.2 times that of South America (Duellman 1993). For reptiles, Bauer (1993) compiled continent-wide totals of taxa and country-by-country summaries for the major groups, but did not include standardizations for area and vegetation types.

In this paper we compare local species richness, evenness and density of amphibians and reptiles in an Afrotropical and a Central American upland forest. We use two original data sets obtained by the same sampling method from Mount Kupe in Cameroon, and from Bosque Protector Palo Seco in western Panama. As Voris (1977) pointed out, comparisons of diversity between sites often are biased by unresolved differences in the length of the collecting period, the number of major habitats sampled and the size of the area censused, thus affecting sample sizes and total numbers of species. We accounted for these concerns by adjusting both data sets in a way that total sampling effort, forest type, elevational range and season are comparable.

METHODS

STUDY SITES. — Mount Kupe (4°45'N) in the Southwest Province of Cameroon, is a steep-sided, cone-shaped mountain 2064 m in height and situated approximately 100 km northeast of Mount Cameroon. It forms part of the Cameroon Highlands, an extensive volcanic mountain range in western Cameroon, running from Mount Cameroon in the south-west tip of the country ~ 500 km towards the north-east to the Bamenda and Adamawa Highlands. At the time of the sampling the upper slopes of the mountain, between 900 m and the summit, were 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. Below 900 m the forest has been logged or severely degraded except for a few patches on the southwestern and southern slopes. In the primary forest, we found permanent streams between 900 and 1500 m and at 1900 m. The single standing body of water found within the primary forest was a puddle on a log in a treefall. Mount Kupe receives mean annual rainfall of 4891 mm (Suchel 1972), with monthly precipitation never below 70 mm. The rainy season lasts for seven months from April to October.

The Bosque Protector Palo Seco, (8°47'N) in Bocas del Toro Province of Panama, is situated on the Caribbean slope of the Cordillera Central. It is a vast area of primary forest extending vertically from the lowlands up to the continental divide, with ridge tops and peaks at around 1400 to 2200 m. Horizontally Palo Seco extends from the main road that crosses the divide and links the two provinces of Chiriquí and Bocas del Toro further west to Costa Rica. Despite the status of a protected forest, human impact is increasing, with pastures along the valley bottoms and plantations on the adjacent slopes. Estimated from regional climate maps (Instituto Geografico Nacional Tommy Guardia 1988), Bocas del Toro Province receives annual rainfall from ~ 3000 mm in the lowlands to 5000 mm at higher elevations. Other than on the Pacific slope, rainfall is abundant throughout the year, and with a non-pronounced dry season. We found permanent streams at all elevations sampled, whereas puddles along an unpaved road outside the forest were the only standing water located. As on Mount Kupe, most stream bottoms are bedrock, with moderate to steep gradients, rapids and splash zones. Most herpetological work in western Panama has focused on the Pacific side and the vicinity of Reserva La Fortuna, but the Palo Seco area has received little attention from herpetologists.

DATA ACQUISITION. — At both sites, the sampling method adopted was "cruising collecting" (Inger & Colwell 1977), *i.e.*, three to five people walked slowly along a 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 about 10 m; in riparian zones the stream-bed also was examined. The data on Mount Kupe were acquired between March and November 1994, in the primary forest on the western slope of the mountain between 900 m and the summit; procedures are outlined in more detail in Hofer *et al.* (1999). Data in the Palo Seco area were acquired between April and June 1998. Fieldwork was restricted to the primary forest between 800 and 1600 m elevation at the eastern edge of the forest reserve. The transect samples were taken along 430 m of a trail maintained by workers from the Instituto de Recursos Hidráulicos y Electrificación and by the local citizens, along 1360 m of trails opened by our field crew and along 820 m of stream-sides. Basic information on sampling at both study sites is summarized in Table 1.

On Mount Kupe, animals we did not collect as vouchers were marked and released at the end of each sampling bout, and recaptured animals were excluded from all analyses. The abundance data of two chameleon species we failed to mark reliably were retained in the data set. The mean recapture rate of all species reliably marked was 2.75%.

Due to a drastic decline in amphibian populations in Costa Rica and adjacent Western Panama (see Discussion), our research permits restricted collecting efforts to the minimum number of individuals necessary for accurate species identification, and banned marking of individuals. For the latter reason, the abundance of some species could be overestimated. Assuming a similar mean recapture rate as on Mount Kupe, this sampling error would be five individuals.

Voucher specimens of the two sites are deposited at the Natural History Museum of Berne, the Alexander Koenig Zoological Research Institute and Zoological Museum in Bonn, and in the collections of the Mount Kupe Forest Project, Nyasoso, Cameroon, and of the Círculo Herpetológico de Panamá.

ANALYSIS. — Customarily tropical herpetofaunas have been compared on the basis of species richness, evenness, density and dominance. We restricted our analyses to the first three measures, and, as suggested by Gotelli and Graves (1996), used indices that have a probabilistic basis and tend to be unbiased by sample size. First, we applied an interpolation procedure: species richness of the two samples was compared by rarefaction (Sanders 1968, Hurlbert 1971, Simberloff 1972), whereby samples were standardized for abundance. Second, we extrapolated to total species richness by fitting a Michaelis-Menten equation (Raaijmakers 1987) to the species accumulation curves, and by computing Chao's (1984) non-parametric estimator. As an evenness measure, we computed Hurlbert's (1971) probability of an interspecific encounter. Means and standard errors of this index were estimated by a bootstrap procedure with 1000 iterations (Efron & Tibshirani 1993). Due to the small number of snakes obtained on Mount Kupe, we excluded the snakes from all estimates of species richness.

As a consequence of the field methods chosen, two properties of the data set had to be accounted for. First, because trails were repeatedly searched in the course of sampling both sites, trails cannot be treated as an equivalent to leaf litter plots of previous studies (e.g., Inger & Colwell 1977, Scott 1982, Lieberman 1986). We therefore used samples standardized by time effort to calculate animal densities (number of frogs, lizards or snakes encountered per person-hour of sampling). For each sampling bout we computed the time-based density; from these densities, means and standard errors were estimated for both sites. Second, samples based on cruise collecting encompass a wider array of species than litter plots and usually include taxa associated chiefly with microhabitats above the forest floor. We therefore split three taxonomic groups (frogs, lizards and

TABLE 1: *Sampling characteristics in two tropical upland forests, Bosque Protector Palo Seco, Panama, and Mount Kupe, Cameroon..*

	Palo Seco, Panama	Mount Kupe, Cameroon
elevational range [m]	800-1600	900-1700
total transect length [m]	2610	2820
number of sampling bouts	32	56
person-hours of sampling	9.8 hr / bout	3.8 hr / bout
number of days	35	35
start day	4.V.1998	9.V.1994

TABLE 2. *Results of the runs tests (Zar 1974) performed to evaluate clumping of conspecifics within sampling bouts. For both sites, frogs and lizards were analyzed separately, selecting randomly four bouts from those that contained >7 specimens. For the Palo Seco frogs, only three sampling bouts tested allowed a significant result.*

			number of runs		
		bout	observed	expected	*P*
Frogs	Mount Kupe	1	7	5.99	0.93
		2	18	19.67	0.15
		3	8	8.44	0.33
		4	10	8.66	0.85
	Palo Seco	1	7	7.42	0.37
		2	7	6.93	0.51
		3	5	5.83	0.19
Lizards	Mount Kupe	1	9	9.17	0.42
		2	9	8.35	0.69
		3	7	6.89	0.53
		4	5	5.80	0.21
	Palo Seco	1	8	6.50	0.92
		2	12	11.30	0.68
		3	8	7.79	0.56
		4	6	5.27	0.75

snakes) into an "arboreal" (species known to feed in vegetation) and a "terrestrial" subset and again computed the parameters for these six categories. Because such splitting led to very small sample sizes for some subsets, we do not present the results in tabular form, but refer to them in the Discussion.

We accounted for differences between sites and sampling efforts in two ways. First, we restricted the analysis to data acquired within primary forest (including riparian habitats). Furthermore, we adjusted the elevational range and the lengths of sampling periods by reducing the larger sample (Mount Kupe). This resulted in data sets accumulated over the same number of days starting with the onset of the rainy season. Thus, our density and local species richness estimates are based on data sets obtained by the same methodology from comparable forest types, elevational ranges and seasons. Second, differences in sampling effort (see Table 1) were further taken into account by using rarefaction methods.

For the extrapolations that predicted the total regional species richness, we left the elevational ranges adjusted, but used all data available for the entire collecting periods at both sites. We based the accumulation curves on a similar number of sampling bouts (some chronologically adjacent sampling bouts were pooled). We followed Colwell and Coddington's (1994) procedure to generate species accumulation curves, performing 100 randomizations of the order of sample bouts. The Michaelis-Menten equation was fitted directly by use of a nonlinear regression module in the SPSS package (SPSS 1990). We used the sum of absolute values of the residuals as the loss function, to avoid giving too much weight to outliers. Confidence intervals of Michaelis-Menten parameters were computed by a bootstrap procedure included in SPSS (1990).

RESULTS

The species list from Palo Seco is given in the Appendix, the corresponding data from Mount Kupe are published in Hofer *et al.* (1999). Rarefaction of such data entails several assumptions (Gotelli & Graves 1996). First, the communities compared must be taxonomically similar, come from similar habitats, and be sampled with similar techniques, concerns we accounted for as explained above. Second, sample size must be sufficient to characterize correctly the parent distribution. From inspection of the species accumulation curves (Fig. 1), the frog and lizard sample sizes appear adequate. Finally, the spatial distribution of individuals must be random. In the context of an elevational gradient, this assumption is likely to be violated to some extent, since many species exhibit gaussian-like abundance curves along the gradient. However, the rarefaction model is mostly affected by clumped distributions of conspecifics (Simberloff 1986). We controlled statistically for this property by a runs test (Zar 1974), performed at each site on a random selection of four sampling bouts with > 7 individuals. The tests were run separately for frogs and lizards. The power of the tests was evaluated to ascertain that rejection of H0 was not due to small sample size, which resulted in the elimination of one sampling bout for the frogs at Palo Seco. We found no indication of clumping of conspecifics (Table 2). The fitting of a Michaelis-Menten equation to the species accumulation curves assumes homogeneity of the habitat. The homogeneity can be assessed by comparing the empirical species accumulation curves to those obtained by a random assignment of individuals to sampling bouts (Colwell & Coddington 1994). In a homogeneous habitat, the empirical curves will fit the theoretical ones, in a heterogeneous one they will lie below. We found no strong departure from the assumption of homogeneity, the empirical curves lying at most 1.95 standard deviations below the theoretical ones (Table 3).

Based on equal sample sizes, Palo Seco exhibits a significantly higher richness in frog and lizard species than Mount Kupe (Fig. 2). The two extrapolation methods yield divergent estimates of local species richness, especially for frogs, but variance around these estimates is large (Table 4). Despite their differences, the species accumulation curves (Fig. 1) produce similar estimates to those of the Michaelis-Menten equation, except for the number of lizard species, which is higher on Mount Kupe (Table 4). With the Chao estimator, differences between the two sites are accentuated. However, based on non-overlapping 95% confidence intervals, the higher number of lizard species on Mount Kupe is the only significant difference.

The probability of an interspecific encounter among frogs and lizards is higher in Palo Seco. Although the differences are not significant, the 95% confidence intervals overlap only marginally, particularly in the lizards (Table 4).

Standardized to the number of specimens encountered per person-hour of sampling, there is no difference in lizard density (t-Test, two-tailed; P=0.14). However, frog density is nine times higher on Mount Kupe (t-Test, two-tailed; P<0.0001), and snake density seven times higher in the Palo Seco forest (t-Test, two-tailed; P<0.0001).

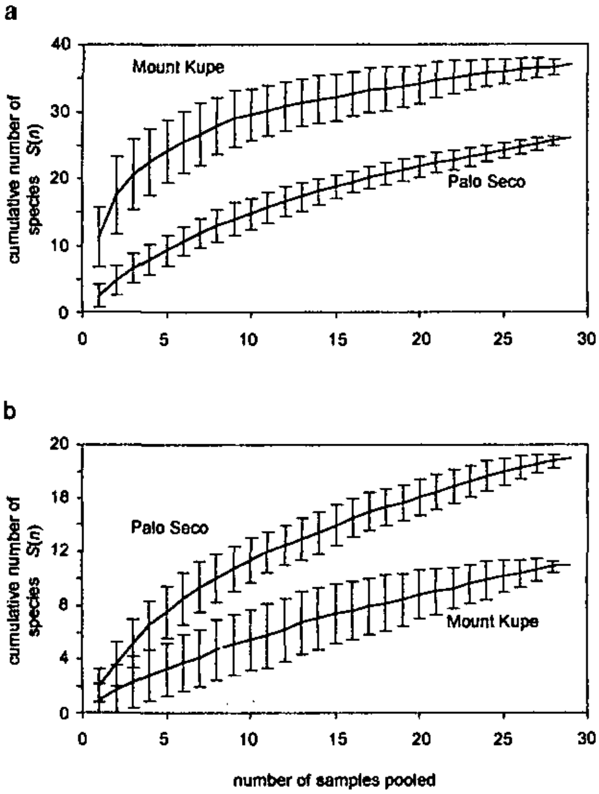

FIGURE 1. *Species accumulation curves for a) frogs, and b) lizards. Due to small sample sizes, no curves were drawn for the snakes. Error bars indicate ± one standard deviation.*

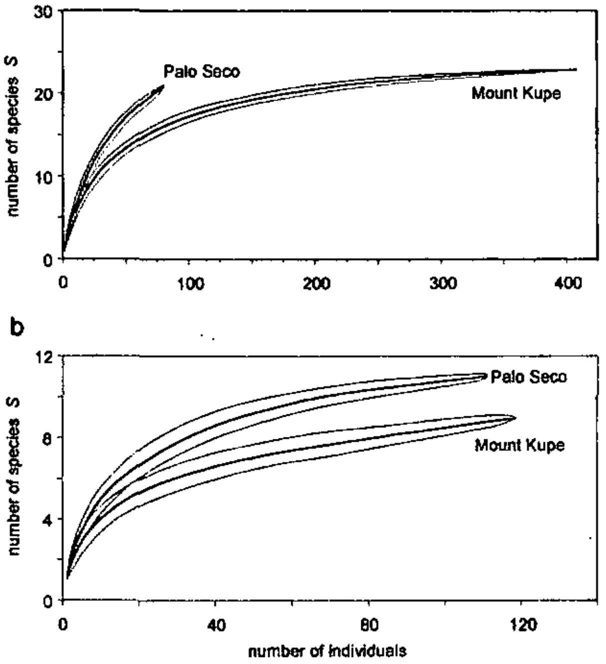

FIGURE 2. *Rarefaction curves for a) frogs, and b) lizards. Due to small sample sizes, no curves were drawn for the snakes. Envelopes indicate the 95% confidence limits.*

DISCUSSION

AMPHIBIAN DECLINE IN CENTRAL AMERICA. — Because no quantitative data are available for the Palo Seco area prior to an amphibian decline reported for Costa Rica and adjacent Panama (Lips 1998, 1999), the effect of this recent disturbance on the abundance and species richness of amphibians and reptiles observed today is unknown. However, the watershed of the Río Chiriquí on the Pacific side of Panama, where Lips (1999) found a sudden and massive decline in anuran abundance and diversity in late 1996, is only separated by a narrow ridge from the nearest watercourse of the Palo Seco area, hardly sufficient to prevent spreading of the suspected fungal pathogen to the adjacent Atlantic side. Furthermore, our frog density estimates are as low as those found by Lips (1999) after the decline. We therefore consider it probable that the phenomenon also affected frog populations in Palo Seco and accounts for the remarkable difference in density observed between this site and Mount Kupe. The difference is largely attributable to higher numbers of individuals of species dwelling on the forest-floor (leaf litter and riparian) of Mount Kupe. Effects on species richness and evenness are less comprehensible, because these properties tend to be biased if some species show a particularly strong response to the pathogen. Lips (1998, 1999) found streamside anurans with an aquatic stage to be more affected than other taxa. The density of these species in Palo Seco is 0.05 individuals per person-hour of sampling, while on Mount Kupe it is 0.7.

SPECIES RICHNESS AND EVENNESS. — Standardized for sample size, frog and lizard species numbers are significantly higher in Panama. Frog species richness in the Palo Seco forest is still 1.3 times greater than on Mount Kupe, but below the value evaluated by Duellman (1993) on a continentwide 10^6 km^2 scale, where amphibian species density in montane rainforests of South America was 1.7 times that of Africa. Inequalities in seasonality and dry season length,

TABLE 3. *Distances between empirical species accumulation curves and those obtained by a random assignment of individuals to sampling bouts. Distances are expressed in units of standard deviation. The higher the value, the stronger the departure from the homogeneity of the habitat for a given species group.*

		distance in SD units	
		mean	maximum
Frogs	Mount Kupe	0.45	0.63
	Palo Seco	0.16	0.33
Lizards	Mount Kupe	0.77	1.46
	Palo Seco	1.33	1.95

TABLE 4. *Diversity and density parameters in two tropical upland forests. Expected species richness for equal sample sizes was estimated by rarefaction; the sizes of the smaller samples are given in parentheses. The number of species at both sites was extrapolated by fitting the Michaelis-Menten equation, and by computing Chao's (1984) estimator. Evenness is expressed as the probability of an interspecific encounter. Densities refer to numbers of individuals per person-hour of sampling. When appropriate, the 95 % confidence intervals (C.I.) are added. Asterisks (*) indicate significant differences between Panama and Cameroon at P £ 0.05. Due to small sample size, snakes were omitted from all species richness estimates.*

	Palo Seco, Panama			Mount Kupe, Cameroon	
Observed number of species					
frogs	21			23	
lizards	11			9	
snakes	13			3	
	estimate	95% C.I.		estimate	95% C.I.
Species richness based on rarefaction					
frogs (*N*=82)	21	-	*	16.1	15.4 - 16.7
lizards (*N*=111)	11	-	*	8.8	8.5 - 9.1
Species richness extrapolated					
a) fitted Michaelis-Menten equation					
frogs	38.1	37.6 - 38.6		37.7	37.0 - 38.4
lizards	13.6	13.4 - 13.8	*	16.6	16.4 - 16.8
b) Chao's (1984) estimator					
frogs	53.3	41.5 - 65.0		44.0	40.2 - 47.8
lizards	13.0	10.8 - 15.2	*	19.5	15.9 - 23.1
Probability of an interspecific encounter					
frogs	0.85	0.80 - 0.91		0.79	0.75 - 0.81
lizards	0.77	0.71 - 0.82		0.65	0.57 - 0.73
Density of individuals [*N*/sampling hour]					
frogs	0.25	0.16 - 0.35	*	2.33	1.65 - 3.00
lizards	0.35	0.23 - 0.47		0.57	0.36 - 0.77
snakes	0.14	0.08 - 0.20	*	0.02	0.00 - 0.04

factors invoked to explain differences in species richness between other sites (Inger 1980b, Scott 1982), are presumably of minor importance in our case. High annual rainfall and a lack of a pronounced dry season at both sites should minimize potential effects of climatic properties.

The higher species richness in the Palo Seco forest, when standardized for sample size, may simply result from a species-area relationship and an island-effect (MacArthur & Wilson 1967). As part of an extended forest range covering the entire Caribbean slope of the Cordillera Central from sea-level to about 2300 m, Palo Seco supports more species than the relatively isolated forest block on Mount Kupe, which is situated in a highland area where about 50 % of the anuran species and at least 40 % of the lizards are endemic. Of the 46 species of amphibians and reptiles endemic to Panama (R. Ibáñez pers. comm.), five amphibian (*Dendrobates speciosus, Eleutherodactylus emceloe, E. museosus, Bolotiglossa minutula, Caecilia volconi*) and two lizard species (*Anolis casildae* and *A. exsul*) were found at Palo Seco, and five presumably new taxa that may be endemic to the area.

Estimates of total species richness do not differ between the two sites for frogs, but lizard species are probably more numerous on Mount Kupe. Mount Kupe is situated in an area known for exceptional herpetofaunal diversity. The Cameroon Highlands may exhibit the highest level of herpetofaunal endemism in all of mainland Africa; more than 60 amphibians species are restricted to this region (Jenkins & Hamilton 1992) and a large number of lizard taxa are undescribed. The adjacent Korup National Park is among the most herpetologically diverse areas in the world (Lawson 1992). However, due to colonization from two directions (South America and the northwest), Panama has probably the most diverse herpetofauna (R. Ibáñez pers. comm.) in Central America. Duellman (1993) explained the higher amphibian species richness in South America in part because of an influx from Central America of taxa inhabiting humid environments, while no equivalent dispersal has occurred into sub-Saharan Africa.

An intriguing result of our study is the discrepancy between rarefaction and extrapolation estimates for the lizards; interpolation indicates higher species richness for Palo Seco, while both extrapolation methods find the opposite. This inconsistency can be explained by inter-site differences in evenness, by differences in the degree of heterogeneity of the habitats, or both. On the one hand, the more uneven the distribution of species abundances, the sooner species are eliminated in a rarefaction procedure. On the other hand, given the same species abundance profiles, the more heterogeneous a habitat the higher is the probability of finding new species during the entire sampling period; consequently the species accumulation curve in a heterogeneous habitat will not attain an asymptote as rapidly as in a homogeneous one; thus higher estimates of species richness will be produced. We found that Palo Seco exhibits a slightly higher degree of heterogeneity than Mount Kupe; thus, differences in habitat heterogeneity cannot explain the conflicting estimates. More likely, they result from a difference in evenness between the two sites, suggested by the higher probability of an interspecific encounter among lizards in Palo Seco (Table 4). This outcome may indeed reflect divergent community structures, in that the Mount Kupe lizard assemblage is dominated by few abundant species. It further demonstrates that the use of different estimators of species richness can reveal subtle differences in community organization otherwise easily overlooked.

DENSITY. --The remarkable inequality in snake abundance results from a much higher density of arboreal species in Palo Seco. The species most commonly encountered in Panama were the arboreal colubrids *Sibon dimidiatus* and *Imantodes cenchoa*, while on Mount Kupe the small leaf litter colubrid *Buhoma depressiceps* was observed most frequently. The conspicuous difference in relative representation of arboreal and terrestrial taxa in the two snake faunas may result from a lack of a lineage of arboreal gastropod-feeders in the African snake fauna, a niche filled by a group of xenodontine colubrids in the Neotropics (in Palo Seco represented by the genus *Sibon*). In a qualitative comparison of the equatorial amphibians and reptiles in Africa and

South America, Laurent (1973) found several examples of empty niches on both continents. An impact of phylogeny and historical events on contemporary patterns of community organization was also suggested by Cadle and Greene (1993) to explain differences in composition and species richness among Neotropical rainforest snake assemblages.

Murphy *et al.* (1994) compared snake densities from several tropical areas based on catch per day. A lack of detailed information on sampling effort and crew sizes for most sites prevented standardizations to catch per man-day, and the numbers of persons involved in sampling undoubtedly accounted in part for observed differences. Despite its inherent inaccuracy, the snakes-per-day measure reveals that Palo Seco and Mount Kupe fall at the opposite ends of the range reported by others. The 2.1 encountered in Palo Seco is close to the 2.25 of Dunn's (1949) large snake collection obtained in Panama and greater than the rates from three South American lowland sites: 0.39 snakes/day in Santa Cecilia, Ecuador (Duellman 1978) and Kartabo, Guiana (Beebe 1946), and 0.47 snakes/day in Manaus, Brazil (Zimmerman & Rodriguez 1990). Our encounter rates at Palo Seco also exceed rates from Southeast Asia (0.97 in lowland sites on Borneo [Murphy *et al.* 1994] and Thailand [Inger & Colwell 1977]). With 0.2 snakes/day, Mount Kupe falls at the lower end of this range. Janzen (1976) suggested that the biomass of African reptiles is depressed by increased predator pressure, a factor that may contribute to the strikingly low snake density on Mount Kupe.

Unlike the snakes, the lizard faunas at the two sites are similar both in density and in relative representation of arboreal and terrestrial taxa. Frog density is higher on Mount Kupe, but provided that the current frog density in the Palo Seco forest resulted from a recent disturbance depressing population levels in western Panama, the difference may ultimately become less pronounced.

Together with Scott's (1982) estimates, our results suggest that frog and lizard densities of African forests may be intermediate to Central American and Asian sites, but closer to the former. However, additional quantitative data from African forests are needed to confirm such a trend. The finding of a consistent pattern may stimulate research related to the mast fruiting hypothesis (Inger 1980a).

Our results suggest that there is no simple relation between species richness and density of individuals. Within the samples at each site, the two parameters show significant positive correlation ($r = 0.60$, $P \leq 0.001$, and $r = 0.85$, $P \leq 0.001$ for all species at Mount Kupe and Palo Seco, respectively), a result also found by Lieberman (1986) for litter plots at La Selva, Costa Rica. When comparing the two sites, however, the higher frog species richness at Palo Seco is not coupled with higher frog density, while the higher number of snake species observed at this site is. Attempts to link herpetofaunal density and species richness between sites led to contradictory conclusions. Scott (1976) suggested density and species richness of leaf-litter herpetofaunas to be inversely correlated. From his Table 1 (p. 43), we found the trend to be strongly affected by a single site (Sarawak, Borneo). Removal of this site results in a correlation in the opposite direction, but neither correlation is significant. Fauth *et al.* (1989) found a significantly positive correlation between several Costa Rican sites. Part of the conflicting results may stem from major differences in site characteristics and in overall geographic range covered by the sites compared. Even so, we doubt that species richness and density are linked in a systematic way (Begon *et al.* 1996); they result from different processes whose relative importance strongly depends on the regions considered, a fact that is difficult to account for in comparisons where both parameters are involved.

ACKNOWLEDGEMENTS

Fieldwork in Cameroon 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, in particular K. E. Epie and E. E. Ewang. J.-L. Amiet, J.-L. Perret, W. Böhme, A. Schmitz and B. Hughes helped with the identification of the collected specimens. Fieldwork in Panama was supported by the Natural History Museum of Berne. L. Indermaur, M. A. Aguirre, A. Gonzáles and O. Samudio assisted the data acquisition. R. Ibáñez D. and the Círculo Herpetológico de Panamá helped with the identification of the collected specimens. For logistic support U. Hofer is indebted to M. A. Aguirre, R. Ibáñez D., N. Gómez, R. Borrell, the Smithsonian Tropical Research Institute, the Instituto de Recursos Naturales y Renovables and the Instituto de Recursos Hidráulicos y Electrificación. For help and constructive criticism of the manuscript, we thank R. F. Inger, N. J. Scott Jr., R. Ibáñez D., B. Benrey, and an anonymous reviewer. L.-F. Bersier was supported by the Swiss National Science Foundation grant 31-52566.97 and the Novartis Foundation.

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APPENDIX. *Amphibians and reptiles recorded in the Bosque Protector Palo Seco, Bocas del Toro Province, Panama, between 800 and 1600 m, April-June 1998. The abundance figures given are those used for further analyses and refer to the numbers of animals taken during the timed sampling bouts. Taxa with no abundances given were encountered outside sampling bouts only, belong to orders not found on Mount Kupe (*Plethodontidae *and* Caeciliidae*), or they were only found in disturbed habitats (*) and therefore not included in the analyses.*

AMPHIBIA		REPTILIA	
Bufonidae		Gekkonidae	
Bufo coniferus *		*Lepidoblepharis xanthostigma*	4
Bufo marinus *		Gymnophthalmidae	
Centronelidae		*Ptychoglossus plicatus*	4
Centrolene prosoblepon	3	Polychrotidae	
Hyalinobatrachium vireovittatum	3	*Anolis aquaticus*	13
Dendrobatidae		*Anolis biporcatus*	5
Colostethus nubicola	1	*Anolis casildae*	3
Dendrobates speciosus	2	*Anolis exsul*	2
Hylidae		*Analis humilis*	44
Agalychnis spurrelli	3	*Anolis limifrons*	9
Hyla debilis	1	*Anolis pachypus*	25
Hyla lancasteri	1	*Anolis* sp. A	1
Hyla picadoi	1	*Anolis* sp. B	1
Smilisca phaeota *		Total lizards	111
Leptodactylidae			
Eleutherodactylus bransfordii	4	Colubridae	
Eleutherodactylus caryophyllaceus	27	*Amastridium veliferum*	1
Eleutherodactylus cf. diastema		*Chironius grandisquamis*	2
Eleutherodactylus crassidigitus	2	*Colubridae* sp. nov.	2
Eleutherodactylus cruentus	11	*Dendrophidion paucicarinatum*	
Eleutherodactylus diastema	4	*Geophis brachycephalus*	1
Eleutherodactylus emcelae	1	*Imantodes cenchoa*	11
Eleutherodactylus fitzingeri	1	*Leptodeira septentrionalis*	2
Eleutherodactylus gollmeri		*Liophis epinephalus*	1
Eleutherodactylus melanostictus	1	*Sibon argus*	3
Eleutherodactylus museosus	1	*Sibon dimidiatus*	17
Eleutherodactylus pardalis	6	*Sibon nebulatus*	2
Eleutherodactylus podiciferus	3	*Urotheca decipiens*	1
Eleutherodactylus ridens	1	*Uratheca euryzona*	
Eleutherodactylus sp. nov.	5	*Xenodon rabdocephalus* *	
Total frogs	82	Elapidae	
		Micrurus alleni *	
Plethodontidae		Viperidae	
Bolitoglossa colonnea		*Bothriechis lateralis*	
Bolitoglossa minutula		*Bothrops asper* *	
Balitoglossa sp nov.		*Lachesis stenophrys*	1
Caeciliidae		Total snakes	44
Caecilia volcani			
Dermophis mexicana			

Abstract of chapter V.

Two tropical upland forests, Mount Kupe in Cameroon and Bosque Protector Palo Seco in Panama, are compared in terms of herpetofaunal species richness and density of individuals. Based on rarefaction, whereby samples are standardized for abundance, Palo Seco has significantly more species of frogs and lizards. Extrapolations to total local species richness, by fitting the Michaelis-Menten equation to the species accumulation curves and by using Chao's estimator, yielded divergent results: more lizard species on Mount Kupe, and an equal number of frogs at both sites. These disparities can be accounted for by differences in evenness, which is higher in Palo Seco. Frog density is significantly higher on Mount Kupe, snake density significantly higher in Palo Seco, and lizards exhibit no density difference. Overall the results reveal a less consistent pattern and more moderate differences than what is known from Southeast Asian–Central American comparisons. This outcome is discussed in the light of available knowledge, but quantitative data from African forests are too sparse to allow general conclusions.

Key words: Amphibia; Cameroon; abundance; evenness; Panama; Reptilia; species richness; tropical wet forest.

VI SUMMARY AND CONCLUSIONS

THESIS OUTLINE

I explore the spatial organisation of an assemblage of amphibians and reptiles in the primary forest on the western slope of Mount Kupe, 4°45'N / 9°42'E, South-West Province, Cameroon. Samples of the herpetofauna were taken in 1994 at the end of the dry season and throughout the entire rainy season, with equivalent intensity at twelve points along an elevational gradient between 900 and 2000 m, separated by 100 m, on transects parallel to the contour line. In all, 2734 amphibians and 596 reptiles were recorded, representing 64 species of 35 genera and 12 families. Variously defined subsets of this sample are tested for the relative importance of a) direct and diffuse *competitive interactions*, b) *ecotones* (environmental discontinuities) introduced by transitions in forest type and by the presence/absence of a given type of water body, and c) the *gradient* itself, i.e., the sum of unspecified factors varying in parallel with elevation, in structuring distributional patterns along the gradient. The two series of subsets tested are 1) amphibians, reptiles, amphibians that depend on streams for reproduction, stream-independent amphibians, and 2) arboreal guild, leaf litter guild, and stream side guild. I make use of null model tests for one-dimensional gradients with some original modifications, of an original null model approach based on an extension of the pseudocommunity analysis, and of canonical correspondence analysis (CCA) in combination with permutation tests.

In another approach I evaluate several community properties of the Mount Kupe sample by comparing it to the herpetofaunal assemblage from a neotropical upland forest, Bosque Protector Palo Seco, 8°47'N / 82°12,5'E, Panamá, sampled in 1998 at the onset of the rainy season. The two sites are compared in terms of species richness, evenness and abundance, based on rarefaction, probability of an interspecific encounter and density of individuals per person-hour of sampling.

BIOLOGICAL CONCLUSIONS

The analyses reveal few cases where competition may have lead to spatial exclusion on the gradient or to significantly small range overlaps between congeners. Species pairs most probably affected are found among terrestrial (*Leptosiaphos*) and arboreal lizards (*Chamaeleo*) and leaf litter anurans with direct development (*Arthroleptis*). Also there is no evidence for an adjustment of the species' gradient distributions that would reduce the potential for competitive interactions resulting from niche overlap. Taken together, these findings suggest a minor importance of direct and diffuse competition in structuring elevational distributions.

Altitudinal zonations are revealed in all subsets of the first series, and in two cases they coincide with an environmental discontinuity: In the reptile subset with the upper transitional zone from submontane to montane forest, in the stream-dependent amphibians with a transition from perennial to intermittent stream.

When ecotones and gradient are contrasted in a single analysis, however, the resulting patterns reflect individual responses of many species to the gradient according to their physiological tolerance limits, rather than to ecotones. At the subset-level a response to ecotones is revealed for the amphibians only, associated with the presence or absence of watercourses. The dependence of most amphibians on aquatic breeding sites that are not available at all elevations appears to reduce the relative importance of the gradient on altitudinal distributions.

A more general interpretation of the null model findings is limited for two reasons: 1) Ongoing deforestation constantly reduces the length of the primary forest gradient, now virtually excluding the lowland forest; the relative importance of mechanisms that determine elevational distributions of tropical herpetofaunas in the lowland forest range need not be the same. 2) The sampling was restricted to a single season. Despite the advantages of null models, a replicate sample from a second season would strengthen any conclusions. In this respect, a wider application of the analysis tools we used (and partly developed) in our approach may yield additional insights.

The comparisons with Palo Seco using rarefaction resulted in Mount Kupe having fewer frog and lizard species than the neotropical site, but the same number of snake species. Extrapolations to total local species richness assigned more lizard species to Mount Kupe, and an equal number of frogs at both sites. These disparities are assigned to differences in evenness, which is higher in Palo Seco. Abundance differences are striking: Mount Kupe has nine times the frog density of Palo Seco, while its snake abundance is seven times less. The first difference could result from a drastic amphibian decline in western Panamá, the difference in snake abundance may have historical reasons. Overall, the patterns are less consistent and differences more moderate than what is known from Southeast Asian–Central American comparisons. We discuss this outcome in the light of available knowledge.

METHODOLOGICAL ACHIEVEMENTS

With the modifications introduced in this study (handling of ties, appropriate permutation procedures), null model tests for one-dimensional gradients are now applicable to communities sampled at discrete scales, i.e. at several points regularly spaced along a gradient, the typical sampling design of most faunal studies on gradients.

The spatial (overlap in gradient distribution) and ecological organisation (overlap in resource use) of a community has been integrated in an single analysis procedure that allows to test for the potential impact of interspecific competition and resource tracking on observed patterns. The test is applicable to different forms of spatial distributions.