

Relating niche and spatial overlap at the community level

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If interspecific competition is a strong structuring force of communities, ecologically similar species should tend to have spatial ranges at local scale that do not overlap. Experimental testing of this hypothesis becomes impracticable with large communities. One possibility to tackle this issue is a correlational approach, by comparing the matrix of niche overlap with that of spatial overlap. The use of the standard Mantel test is however impaired by the non-linearity in the relationship of the two descriptors: in a competitively structured assemblage, species with high niche overlap are expected to be segregated spatially, but species with small niche overlap may or may not exhibit high spatial overlap. To overcome this problem, we devised an original randomization test, which was run for three data-sets comprising frogs, lizards, and birds along altitudinal gradients. The test yielded intriguing results: reptiles and birds revealed an adjustment that would reduce the potential for interspecific competition, while amphibians showed the opposite trend, that is, ecologically similar species co-occurred more than expected by chance. Frogs may be more constrained by resource requirements, possibly breeding sites, than by competition. Our test will help to assess the generality of this pattern with other data-sets.

The effect of competitive interactions on community structure has been confirmed by several well-known reviews of field experiments on interspecific competition (Connell 1983, Schoener 1983, Goldberg and Barton 1992, Gurevitch et al. 1992). Evidence usually came from manipulative experiments that involved two or three potential competitor species (Schoener 1983). One common result of competition was differences in spatial distribution of species, e.g. vertical zonation in barnacles (Connell 1961) or altitudinal zonation in terrestrial salamanders (Hairston 1980a, 1980b). At the same time, prominent observational studies of bird assemblages also revealed differences in spatial distribution, which their authors claimed to result from competition. Diamond (1975) interpreted complementary distribu-

tions of birds among islands of the Bismarck Archipelago to result from interspecific competition. Terborgh (1985) concluded that direct and diffuse competition accounted for two-thirds of the limits of avian elevational ranges along an elevational gradient in the Peruvian Andes. In contrast to those from manipulative experiments, the conclusions of such "natural experiments" (Cody 1974) have been at the heart of heated debates (Connor and Simberloff 1979, Diamond and Gilpin 1982), inviting reanalyses and stimulating the search for adequate analytical procedures, which are usually null model tests (Sanderson et al. 1998, Gotelli 2000, Gotelli and Entsminger 2001).

Within the non-experimental domain of community ecology, null model analyses of whole assemblages have

resulted in some of the most significant contributions to the study of competition. Null models offer a rigorous alternative for investigating community properties that are difficult or impossible to reveal by experiments (Morin 1999). They are pattern-generating models that deliberately exclude a mechanism of interest, e.g. competition, and allow for randomization tests of ecological and biogeographic data (Gotelli and Graves 1996). Controversy persists over the best ways to formulate the appropriate random expectation for a given context and its translation into a computer algorithm. However, the specificity and flexibility in data analysis provided by null models (Gotelli 2001), which is often not possible with conventional statistical tests, has been demonstrated by numerous recent developments. Examples include the analysis of species co-occurrence patterns (Sanderson et al. 1998, Gotelli 2000), elevational distribution patterns (Hofer et al. 1999, Veech 2000), patch distribution patterns (Roxburgh and Matsuki 1999), and the relationship between environmental conditions and species traits (Dolédéc et al. 1996, Legendre et al. 1997).

In the present paper, we test hypotheses that directly link two aspects of community structure: the pattern of overlap in spatial distribution and in resource use. The aim of the test is to detect if there are any statistically significant relationships between spatial overlap and overlap in resource use. For pairs of species with a low resource overlap, competition is expected not to play a role, and these species could segregate spatially or overlap extensively depending on the spatial distribution of their respective resources. It is only for pairs of species with high resource overlap that ecological hypotheses can be formulated. If competition is a strong structuring force, we expect a nonrandom spatial distribution. Two cases are possible: 1) spatial overlap is lower than expected by chance as a result of interspecific competition for similar resources, thus in effect decreasing the intensity of competition; 2) spatial overlap is higher than expected by chance, implying either a) instability whereby competitive exclusion is eventually expected to occur, or b) there are other coexistence mechanisms present, but not detectable in the analysis.

Traditionally, analyses of spatial distribution patterns were exclusively based on the arrangement of distributional limits along a gradient, or on the presence/absence pattern with respect to (habitat) islands, with no reference to ecological characteristics of the species (Pielou 1977, 1978, Dale 1984, 1986, 1988, Hofer et al. 1999). A customary practice is to decide prior to the analysis which species are expected to interact, usually congeners (Terborgh 1971) or members of the same, often taxonomically delimited, guild (Diamond 1975). There was however no independent and quantitative assessment of ecological similarity between the species. Thus, the potential effect of these relationships on spatial patterns was accounted for indirectly, and for a

limited number of species pairs. The method presented here allows a direct comparison of the spatial and ecological structure of a species assemblage and, by including all possible pairwise interactions, simultaneously accounts for the effect of diffuse competition (sensu Terborgh and Weske 1975).

The spatial and niche relationships among the members of an assemblage can be described by two overlap matrices. The standard method for the comparison of two similarity or overlap matrices is Mantel's randomisation test (Mantel 1967). This test examines the correlation (or another closely related statistic, Legendre and Legendre 1998) between all pairs of similarity or distance values of both matrices. The significance of the observed correlation between both matrices is evaluated by comparison with the probability distribution obtained by Monte Carlo randomization, where one matrix is held constant and the other permuted. The permutations are constrained in accordance to the fact that the units to be compared are the objects: the procedure is equivalent to permuting the raw data and recomputing a distance matrix. A critical feature of the Mantel test is that it can detect linear or monotonic relationships only. In the context of the hypotheses stated above, we do not expect this because only close neighbours in niche space can be expected to respond in a predictable manner, whereas the spatial relationship between ecologically distant members within the community is unpredictable. We therefore developed a new randomisation test, designed for matrix comparisons where neither a linear nor a monotonic relationship between the similarity matrices can be supposed. Our approach is rooted in 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). After demonstrating that our test is valid and overcomes the stated limitation of the Mantel test, we analyse two original data-sets of frogs and lizards, and a published bird data-set, and reveal intriguing differences.

Methods

Data-sets

The lizard and frog data were obtained between March and November 1994 on Mount Kupe (4°45'N) in the southwest province of Cameroon, a steep-sided, cone-shaped mountain 2064 m in height and covered by approximately 2100 ha of undisturbed sub-montane forest at the time of the study; below 900 m the forest has been logged or severely degraded except for a few patches. The abundance of lizards and frogs was recorded in the primary forest on the western slope of the mountain, at twelve points between 900 and 2000 m,

separated by 100 m in elevation, on transects parallel to the contour line. The sampling procedures are explained in more detail in Hofer et al. (1999), and a detailed description of the study area is given in Hofer et al. (1999, 2000). The microhabitat of each individual frog or lizard was noted upon first encounter. We used microhabitat code similar to the one designed by Inger and Colwell (1977) to compute overlap in microhabitat use between species of herpetofaunal assemblages in Thailand; our code comprised four nominal variables, with several alternative states for each variable (Appendix A). Morphometric data were taken from each individual captured; we measured snout-vent length and, in frogs, mouth-width as well.

The bird data-set was taken from Price (1991). The study area is situated at the Overa Wildlife Sanctuary near Pahalgam, Kashmir, India. The elevational gradient sampled ranged from 2430 to 3725 m and encompassed several forest types, with fir–pine–spruce forest dominating to about 3000 m, whereas birch, willow and rhododendron species dominate at altitudes above 3000 m. The abundance data of nine species of warblers (eight *Phylloscopus* species plus *Regulus regulus*) were obtained between 1985 and 1987 in five 2–20 ha grids (2430 m, 2800 m, 3340 m, 3550 m, and 3725 m) along a continuous primary forest elevational gradient. Methods comprised mist netting and recording singing males in the established grids; morphological data were taken from the trapped birds; feeding behaviour was recorded from direct observation.

Computation of overlap

The significance of niche overlap values critically depends on the choice of appropriate descriptors of the ecological characteristics of the species. We described the niche of the species by microhabitat use and morphometry. Reviews by Schoener (1974) on resource partitioning in ecological communities, and by Toft (1985) specifically on amphibians and reptiles, revealed that habitat is the niche axis most frequently partitioned when compared to food and time. MacArthur (1958) classical study on warblers supports this view for birds. We followed the concept of the morphological niche (Ricklefs and Travis 1980, Schoener 1984) in that data on body size are used as a surrogate measure for differences in resource use, in particular for dietary segregation. In fact, within the warbler group mentioned above, Price (1991) found morphological variation to explain 95% of the measured ecological variation. Frogs and lizards in tropical forests are mainly opportunistic feeders, and dietary segregation is often associated with body size (Vitt and Zani 1998a), a segregation we observed for a species subset within the lizard taxocene (Hofer et al. 2003). For lizards, morphometric compar-

isons were based on mean snout-vent-lengths (SVL) and, for frogs, additionally on mean mouth-widths (MW); only the ten largest individuals of each species were retained, as many captured individuals were juveniles. For birds, morphological descriptors were wing length, weight, tarsus length, beak length, beak depth, and beak width, and foraging method served as a proxy for microhabitat use (Appendix 2, Table 3 in Price 1991).

We characterised the gradient distribution of a species 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 sampling point on the gradient. We coded range length at each point along the gradient with a binary variable.

We computed niche and geographic overlap with the use of Gower's coefficient of similarity (Legendre and Legendre 1998), which allows to weight the individual descriptors and to combine binary and quantitative descriptors. For niche overlap, we gave a total weight of 0.5 to all morphological, and of 0.5 to all microhabitat descriptors; for geographic overlap, we gave a total of 0.5 to all binary descriptors describing range length, and of 0.5 to abundances at each point of the gradient. In summary, from the matrices of ecological descriptors (R) and of geographic distribution (G), both describing the same set of species, we obtain two square and symmetrical overlap matrices, termed S_R and S_G , respectively (Appendix B).

Linking niche and spatial overlap

In an assemblage where physiological constraints determine the species distributions along a gradient, length and position of the ranges primarily reflect individual responses to the physical environment. Within these physiologically constrained ranges, species distributions can be limited by the availability of resources, which at its extremes can result in two opposite scenarios: 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 either spatially or temporally. The corresponding statement of the alternative hypothesis H_1 (hereafter termed competition hypothesis) is that species with high niche overlap exhibit a significantly smaller spatial 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 coexistence mechanisms are not detected in the analysis, then species pairs with high niche overlap should exhibit a significantly higher spatial overlap than expected by chance. For example, the presence of resource states may be the major determinant of spatial organisation, and species may coexist

through microhabitat differentiation. 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 spatial overlap than expected by chance. 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 spatial organisation of an assemblage are related.

Note that in both scenarios, 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, spatially overlapping resources) or small (spatially non-overlapping resources) spatial overlap. Thus, spatial 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 that 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 and Pianka 1990). This analysis critically evaluates niche segregation and guild formation in assemblages by ordering the $S-1$ neighbours of each of S species on the basis of their niche overlap. The ordered values are then averaged to give the mean overlap of the first, second, ... $S-1$ 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 spatial overlap at ranks of neighbour in niche space.

The procedure, exemplified in Appendix C, is as follows: 1) setting diagonals to zero. In both similarity matrices S_R and S_G , the diagonal elements (the species-with-itself comparisons) are set to 0 for computational convenience. 2) Constrained rearranging (ordering) of the columns of the spatial overlap matrix. For each column in the niche overlap matrix, values are arranged in decreasing order. Simultaneously, the corresponding cells in the spatial overlap matrix are rearranged accordingly, i.e. in the order imposed by the sorting of the niche overlap matrix. The zero diagonal elements all fall at the last row of the matrix. 3) Computing the test statistic. Mean spatial overlap is computed at the first rank of neighbour in niche space. 4) 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, or vice-versa. Steps 2 and 3 are

repeated following each permutation, always ordering the columns of the original spatial overlap matrix according to the sorted columns of the permuted niche overlap matrix. 5) Evaluation of statistical significance. The two-tailed probability that mean observed spatial overlap differs significantly from random expectation is computed, based on the reference distribution obtained from the permutations. If the difference is not significant at the first rank of neighbour, repeat steps 2 to 4, with the following modification of step 3: mean spatial overlap is computed at the first and second rank pooled. Since in this case a second test on the same data is performed, the significance level must be adjusted by a sequential Bonferroni correction (Legendre and Legendre 1998): the p-value obtained by randomization is simply multiplied by the number of simultaneous tests (two in the present case). If significance is still not obtained, repeat the test with more aggregated ranks, each time correcting the significance level. This stepwise procedure accounts for errors in niche overlap estimates that reduce the reliability of the ranking of neighbours. Moreover, focussing on the first rank of neighbour strongly restricts the number of pairwise interactions allowed to contribute to community structure. Note that it is computationally more efficient to perform the tests simultaneously on the first and subsequent aggregated ranks; we suggest not to test beyond $S/2$ aggregated ranks, with S the number of species.

Validation of the test

We evaluated the sensitivity of our procedure by a benchmark test applied to various pairs of matrices with known structure and relationship. First, we evaluated type I errors by the mean of S_R and S_R matrices filled with random numbers. Second, we evaluated type II error with the use of idealized S_R and S_G matrices where all pairs of interspecific overlap are in accordance with either the competition or resource-tracking hypothesis. For the competition hypothesis, this means using a random number x for each cell of S_R , and $1 - x$ in the corresponding cell of S_G . We then increased the level of noise for each overlap value (noise test, Gotelli 2000), and computed the p-value. With a noise level v ($0 \leq v \leq 1$), an initial overlap $y = 1 - x$ in S_G can take any value with lower bound $y-vy$ and upper bound $y + v(1 - y)$. The tests were run for matrices comprising 10, 20, and 30 species, each with 1000 simulations; in all cases we used uniform random numbers.

Results

The bench test with random S_R and S_G matrices revealed that our procedure rejects the null hypothesis 5% of the time at a 5% significance level; it thus performs correctly

with respect to type I error. With patterned S_R and S_G matrices, no type II error (i.e. not rejecting H_0 when it is false) occurred up to a noise level of 0.6; above this threshold, the frequency of incorrect acceptance of the null hypothesis rapidly increased, which is a desirable feature of statistical tests (Gotelli 2000). We further compared the results of our test with those of the Mantel test for idealized combinations of S_R and S_G matrices. In the situation exemplified in Fig. 1a, the Mantel test fails to detect a significant relationship ($p = 0.67$), while our test correctly reveals that pairs of species with high niche overlap exhibit low spatial overlap ($p = 0.01$). This lack of power of the Mantel test is due to a cluster of pairwise

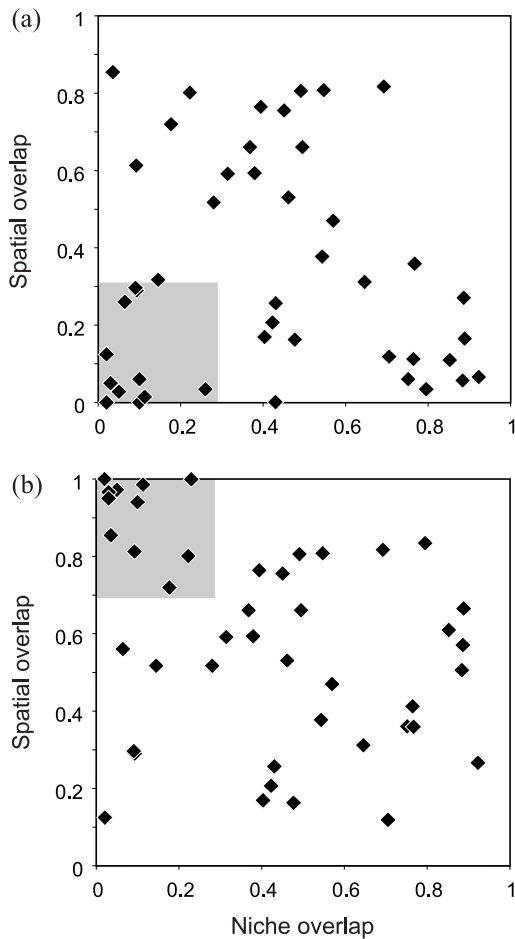


Fig. 1. Relationships between spatial and niche overlap for two idealized communities. Both panels exemplify the problems of using the Mantel test to compare ecological and spatial overlap. (a) Species with high niche overlap exhibit a smaller spatial overlap than expected by chance, which remains undetected by the Mantel test because the relationship is cancelled by the cluster of points in the shaded region. (b) The Mantel test yields a significant negative correlation while there is no relationship between niche and spatial overlap for ecologically similar species; the cluster of points in the shaded region drives the negative relationship.

interactions in the lower left-hand side of the graph, which cancel the effect of the ecologically similar pairs of species. Fig. 1b shows a scenario where the Mantel test detects a strong negative relationship ($p = 0.02$), while our test indicated that close neighbours in niche space do not segregate spatially ($p = 0.19$). This spurious result of the Mantel test is due to a cluster of pairwise interactions in the upper left portion of the graph, which drives the relationship to be negative. Both examples illustrate how pairwise interactions between ecologically distant species, for which the relationship between niche and spatial overlap is unpredictable, can force the Mantel test to yield inconsistent results. Finally, note that a significant relationship with the Mantel test could be driven solely by one species having a high niche overlap and a low (or high) spatial overlap with most other members of the community. Our test procedure excludes such possibility by giving the same weight to each species; it is thus better suited to a community context.

The application of our test to the frog, lizard, and warbler taxocenes showed divergent results for these three data-sets (Table 1). While pairs of ecologically similar warblers and lizards exhibit a spatial overlap smaller than expected by chance (competition hypothesis), the frogs show a significant adjustment in the opposite direction (resource tracking hypothesis). These divergent results are hardly attributable to methodological differences, because lizards and frogs were sampled and described in the same study area, with the same methods and effort. Note that significance was obtained at the first rank of neighbours in niche space for lizards and frogs; for warblers, significance was achieved for the mean spatial overlap computed over the first three ranks (Table 1), rank one, and aggregated ranks one and two yielded marginally significant results ($p = 0.07$ and $p = 0.08$, respectively).

Discussion

This new development of a null model procedure provides insight into community structure within a context that analysis tools hitherto available could not address adequately. First, previous null models for one-dimensional gradients tested hypotheses on community organization by distributional data only. Our approach is an explicit attempt to assess the extent to which the gradient distribution pattern of an assemblage can be explained by the partitioning of niche space. Moreover, the distributional limits of the species remain unchanged by the permutation procedure. The test is therefore independent from assumptions regarding possible spatial patterns of the community under a null model (e.g. the mid-domain effect in biogeography, Colwell and Lees 2000), which eliminates one of the major controversies regarding null model tests (Gotelli 2001). Second, our

Table 1. Results of the test relating two similarity matrices for three species assemblages along altitudinal gradient. Two-sided probabilities p are given; S : number of species; H_1 : supported alternative hypothesis, “resource tracking” and “competition” refer to situations where pairs of ecologically similar species exhibit a higher or smaller spatial overlap, respectively, than expected by chance. All tests were performed with 2000 permutations.

Group	S	Mean spatial overlap		At ranks	p	H_1
		observed	permuted			
Frogs	21	0.44	0.31	1	0.014	resource tracking
Lizards	8	0.13	0.24	1	0.044	competition
Warblers	9	0.09	0.17	1, 2 and 3	0.045	competition

method overcomes the inherent limitations of the Mantel test (lack of power and spurious correlation when the true relationships among distance matrices are nonlinear) and is more appropriate to a community context, as each species is given the same weight. In the present form our test fails to reveal bimodal patterns, where about equal proportions of pairwise overlap are in accordance with the competitive and the resource-tracking hypothesis. However, the detection of such patterns could be easily implemented by including, in addition to the mean, the variance of similarities at a given rank in niche space as a test statistic. Note that the present test is designed for an analysis at the multispecies level, suited for assemblages of at least four species to satisfy the conventional 5% significance level (24 possible arrangements with four species).

Cornell and Lawton (1992) suggested that real communities lie on a continuum from interactive to non-interactive. Following this terminology, our bird and lizard taxocenes are examples of interactive species groups, where niche space is nearly filled and strong interspecific interactions are expected. However, both species groups partition niche space with respect to a physical gradient rather than resources. Price (1991) hypothesised that current competition contributed to the limited elevational distributions of the warblers he studied, and our null model test supports this position. The pattern becomes significant only when considering the first three ranks of neighbour in niche space, i.e. a species may not be limited by a single strong competitor, but by the collective impact of several weak competitors, an effect known as diffuse competition (Morin 1999). The lizard response seems to be stronger, in that closest neighbours in niche space tend to exclude each other on the gradient. A detailed analysis of the three chameleon species of Mount Kupe, while revealing high overlaps in microhabitat use and in prey types selected, confirmed a conspicuous separation in elevational distribution of the two most similar species, and segregation with respect to prey size between the species pairs where gradient distributions overlap (Hofer et al. 2003). The frog assemblage is rather situated on the non-interactive side of the continuum, where population levels are supposed to be reduced due to density-independent

mortality, e.g. fluctuations in the abiotic environment or enemy interactions (Cornell and Lawton 1992). Most frogs on Mount Kupe depend on streams for reproduction. Unusually long dry seasons or strong short-term changes in water and humidity levels can substantially increase mortality at the egg or larval stage, which will in turn depress recruitment rates and adult population sizes. However, such density-independent mortality events can at best only slow competitive exclusion, and are not sufficient to explain coexistence (Chesson and Huntly 1997). Given the (temporal) decrease in intensity of interspecific competition, the species' gradient distributions can expand according to physiological tolerance limits and to individual resource requirements, and coexistence could be achieved by a fine-tuning of the use of specific microhabitats (Hofer et al. 2000).

Numerous studies on frog and lizard assemblages in tropical forests revealed the partitioning of niche space (Heatwole 1963, Crump 1971, Toft 1981, Lieberman 1986, Duellman 1987, Donnelly and Guyer 1994), and null models confirmed distinct structures and guild formation (Inger and Colwell 1977, Vitt and Caldwell 1994, Vitt and Zani 1998b, 1996). However, the relationship between resource partitioning and presence and intensity of competitive interactions remains uncertain (Leibold 1995, Morin 1999), interspecific competition being just one possible explanation for the observed patterns. The results of our null model analysis were obtained in a setting where a hypothesis on the interaction of niche space and spatial distribution could be specified with respect to interspecific competition. An extended application of such null models to a higher number and diversity of taxocenes in comparable settings may help reveal general patterns and thus provide a perspective on communities which is complementary to competition experiments. Of particular interest would be a null model analysis of Terborgh's (1971) bird data.

Acknowledgements – We thank S. Roxburgh for the help and comments. 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, A. Witschi, C. Wild and I. C. Ojiawum parts of the fieldwork. Field work was supported by grants from the Swiss Development Corporation and the Swiss Academy of Sciences, and by the Natural History Museum of

Berne. L.-F. Bersier was supported by the Swiss National Science Foundation grant 31-52566.97 and the Novartis Foundation.

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Appendix A. Microhabitat classification. Each microhabitat use recorded is a combination of alternative states of the four variables listed below. As an example, the most common resource state recorded was “away from stream/pond - in closed canopy area-on surface-on leaf litter”.

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 5–10 m high; shrub layer 1–5 m high; herb layer < 1 m high; on surface (of soil/water); below 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 B. Overlap matrices of the frogs and the reptiles in tropical upland forests of Cameroon, and of the warblers in Kashmir (India). The upper triangular part gives the ecological similarity, the lower triangular the spatial overlap.

1) Frogs

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		
1	0.966																						
2	0.231	0																					
3	0.053	0.651	0																				
4	0.162	0.256	0.496	0																			
5	0.052	0.770	0.045	0.819	0																		
6	0.055	0.472	0.100	0.730	0.319	0																	
7	0	0.800	0	0.559	0.223	0.653	0																
8	0	0.039	0.550	0.064	0.633	0.245	0.614	0															
9	0	0.660	0	0.472	0.182	0.554	0.350	0.603	0														
10	0	0.544	0	0.221	0.140	0	0.054	0	0.033	0													
11	0.036	0.702	0.028	0.652	0.261	0.735	0.514	0.681	0.636	0.495	0												
12	0	0.753	0	0.626	0.278	0.695	0.582	0.681	0.516	0.568	0	0.635	0										
13	0	0.541	0.136	0.718	0.387	0.633	0.640	0.492	0.555	0.395	0.104	0.553	0.508	0									
14	0.055	0.491	0.101	0.690	0.367	0.597	0.720	0.454	0.522	0.337	0.061	0.522	0.496	0.652	0								
15	0.101	0.429	0.131	0.634	0.394	0.532	0.670	0.395	0.462	0.308	0.097	0.458	0.443	0.674	0.686	0							
16	0.360	0.330	0.254	0.428	0.467	0.400	0.422	0.304	0.287	0.284	0.254	0.326	0.345	0.454	0.409	0.435	0						
17	0.350	0	0.086	0	0.067	0	0	0	0	0	0.520	0	0	0	0	0.435	0						
18	0.350	0	0.086	0	0.067	0	0	0	0	0	0.520	0	0	0	0	0	0.117	0.912	1.000	0	0		
19	0.167	0.416	0.177	0.604	0.449	0.505	0.669	0.373	0.414	0.313	0.139	0.425	0.471	0.664	0.624	0.692	0.563	0.733	0	0.800	0	0.786	
20	0.275	0.146	0.547	0.246	0.573	0.194	0.268	0.136	0.156	0.090	0.198	0.154	0.146	0.294	0.273	0.299	0.455	0.058	0.058	0.356	0	0.841	
21																							0.842
																							0.818
																							0.654
																							0.711
																							0.730
																							0.734
																							0.608
																							0.809
																							0.817
																							0.751
																							0.859
																							0.774
																							0.751
																							0.713
																							0.707
																							0.853
																							0.758
																							0.800
																							0.841

Legend: 1, *Afrivalus lacteus*; 2, *Anthroleptis adelphus*; 3, *A. adolfi*; 4, *A. sp.A*; 5, *A. sp.C*; 6, *A. variabilis*; 7, *Astylosternus perreti*; 8, *Cardioglossa gracilis*; 9, *C. venusta*; 10, *Leptopelis brevirostris*; 11, *L. modestus*; 12, *Leptodactylodon ornatus*; 13, *Petropedetes cameronensis*; 14, *P. newtoni*; 15, *P. parkeri*; 16, *P. parkeri*; 17, *Phrynobatrachus cricogaster*; 18, *P. werneri*; 19, *Phrynodon sp.1*; 20, *P. sp.2*; 21, *Wolterstorffina parvipalmata*.

2) Lizards

1	2	3	4	5	6	7	8
1	0.886	0.681	0.664	0.684	0.510	0.481	0.417
2	0.100	0.606	0.709	0.767	0.593	0.564	0.497
3	0	0.425	0.385	0.389	0.215	0.187	0.203
4	0.067	0.458	0.388	0.724	0.692	0.714	0.599
5	0	0.247	0.377	0.161	0.733	0.659	0.478
6	0	0.259	0.397	0.543	0	0.922	0.446
7	0.420	0.218	0.188	0	0	0	0.445
8	0.353	0.369	0.402	0.184	0.184	0.317	

Legend: 1, *Chamaeleo montium*; 2, *C. pfefferi*; 3, *C. quadricornis*; 4, *Cnemaspis koehleri*; 5, *Leptosiaphos sp.A*; 6, *Leptosiaphos sp.B*; 7, *Leptosiaphos sp.C*; 8, *Rhampholeon spectrum*.

3) Warblers

1	2	3	4	5	6	7	8	9
1	0.853	0.775	0.748	0.541	0.403	0.505	0.536	0.767
2	0	0.862	0.772	0.487	0.438	0.520	0.486	0.760
3	0.077	0	0.856	0.589	0.492	0.553	0.542	0.698
4	0.077	0	0.215	0.715	0.462	0.585	0.609	0.651
5	0.580	0	0.036	0	0.306	0.503	0.446	0.550
6	0.750	0	0	0.603	0	0.705	0.646	0.268
7	0	0.684	0.091	0	0	0	0.787	0.287
8	0.383	0	0.098	0.595	0.332	0.018	0	0.337
9	0.167	0.103	0.333	0.314	0.130	0	0.474	

Legend: 1, *Phylloscopus tytleri*; 2, *P. affinis*; 3, *P. pulcher*; 4, *P. inornatus*; 5, *P. proregulus*; 6, *P. magnirostris*; 7, *P. trochiloides*; 8, *P. occipitalis*; 9, *Regulus regulus*.

