

ORGANIZATION IN NATURAL ASSEMBLAGES OF DESERT LIZARDS AND TROPICAL FISHES¹

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Abstract. Techniques are developed for the analysis of community organization and bench tested on a set of simple model systems with known structure (i.e., with and without guild structure, with varying degrees of resource partitioning, with and without “core” resources). Proportional utilization coefficients, p_i , are positively correlated with the abundance of resources, whereas electivities, e_i , correlate negatively with resource abundance. The geometric mean of p_i and e_i , termed g_i , is a superior measure of utilization, more nearly independent of biases associated with resource availability than either of its components, and performs better in bench tests.

Organization in observed patterns of resource utilization by four desert lizard and four tropical freshwater fish assemblages is critically evaluated via comparisons with results from two randomization algorithms. Randomizations follow a Monte Carlo technique whereby the dimensions of the original $m \times n$ resource matrix are preserved during hundreds of independent runs. The first “scrambled zeros” algorithm rearranges observed values for resource utilization by each consumer and retains consumer dietary niche breadths, but destroys guild structure (zero structure) of observed matrices. The second algorithm (“conserved zeros”) also retains observed consumer diet breadths, but only rearranges observed resource utilization coefficients among the particular resources actually used by consumers, thus retaining observed guild structure (i.e., matrix zero structure). By plotting average dietary overlap against ordered niche neighbors, we evaluate (1) relative guild structure using the randomization algorithm that scrambles observed matrix zero structure, and (2) consumer resource segregation within guilds using the algorithm that conserves zero structure.

Statistically significant guild structure is evident to varying degrees in all but one low-diversity fish assemblage. All four tropical fish assemblages reveal significant partitioning of food resources during both the wet and dry seasons, particularly among intermediate to distant neighbors. The most species-rich assemblage exhibits extremely high levels of resource segregation during the period of desiccation of aquatic habitat and increased fish densities. Diverse Australian desert lizard assemblages show significant partitioning of microhabitats among ecologically similar species, even though only 15 microhabitat categories are recognized. Analysis of dietary resource matrices based on only 19 prey resources shows that Australian lizards are piled up on certain prey types, forming functional dietary guilds of lizards that eat termites, ants, other lizards, etc. However, no dietary segregation is evident when only 19 prey resource states are recognized. In contrast, when the analysis is redone on more refined resource matrices based on more than 200 prey types, guild structure essentially disappears but niche segregation becomes evident. In the less diverse Kalahari desert, lizard assemblages are more variable and do not appear to be as tightly organized. Patterns of resource utilization in several of these natural vertebrate assemblages are, however, sufficiently organized to suggest broad effects of internal biotic factors, such as ecological constraints of functional morphology and physiology (leading to guild structure), and possibly interspecific competition.

Key words: assemblages; bootstrap statistics; community organization; core resources; emergent properties; fishes; guild structure; lizards; model systems; Monte Carlo simulations; niche neighbors; niche segregation; pseudo-communities; resource utilization.

INTRODUCTION

Ecological communities are inherently complex. Dynamics of even simple three- and four-species interactions can yield counterintuitive results (MacArthur 1972, Holt 1977, Vandermeer 1980, Bender et al. 1984, Pianka 1987). In addition to complexity, large spatial

scale of interactive units, long time intervals for effective change, as well as spatial and temporal heterogeneity, all hinder development of community theory based on experimentation alone. The scale, complexity, and variation of most ecological communities require that biologists adopt multifaceted, multilevel approaches to problem solving. The full multidimensional complexity of natural systems cannot be conveyed with a handful of descriptive parameters, many of which

¹ Manuscript received 23 September 1988; revised 23 June 1989; accepted 27 June 1989.

are tautologically interconnected (Winemiller 1989b). Consequently, the search continues for a sufficient set of aggregate variables, or macrodescriptors, that will summarize the essential properties of complex interactive networks (Orians 1980).

Patterns of resource utilization constitute a fundamental property of ecological systems, containing vital information on who eats whom, which consumers are potential competitors, etc. Considerable effort has been expended in grappling with the difficult problem of resource availability. Resource availabilities are not easily measured in the field. For example, when insects are sampled with sweep nets, D-vac, Tanglefoot sticky traps, and/or pitfall traps, results differ dramatically. In a study of the herpetofaunas of several sites in the high Andes, Pefaur and Duellman (1980) fenced study plots and conducted exhaustive collections of all herps and insects encountered within the plots with the intention of using the insects as intact whole specimens for comparison standards with the stomach contents of the herps. Yet fewer than 10% of the insect species actually eaten by the herps were collected by diligent humans (W. E. Duellman, *personal communication*). Effective "availability" of any given resource varies in time and space and from consumer to consumer according to behavioral differences, spatial and temporal differences in activity of consumers and prey, and so on. Consequently, to think that a single resource availability vector even exists may be a dangerous and gross oversimplification. Proposed solutions to these problems include resource state weighting factors (Colwell and Futuyma 1971, Pielou 1972), electivity-based measures (Ivlev 1961, Jacobs 1974, Schoener 1974, Toft 1981), maximum likelihood estimators (Petraitis 1979), as well as using community-wide utilization to estimate resource availabilities (Lawlor 1980, Pianka 1986; see also below). No consensus has yet been reached as to how best to proceed and "no standard protocol for community analysis" has yet been established (Inger and Colwell 1977). In this report, we evaluate the performance in null models of various utilization coefficients in bench tests using model systems with simple known structures.

Two commonly used measures of resource utilization are proportional utilization coefficients (p_i) and electivities (e_i). The former correlate positively with resource availabilities (R), whereas the latter are negatively correlated. We employ the geometric mean of p_i and e_i , here termed g_i , as a measure of utilization, which we find superior in part because it is only weakly correlated with R . Performances of all three measures in null models are explored in bench tests and then g_i 's are used to characterize and analyze diverse natural assemblages. We draw upon and unite several concepts and techniques of empirical community analysis developed over the past decade and a half, and apply this methodology to comparisons of natural vertebrate assemblages. This synthesis offers a holistic research pro-

ocol that allows graphical depiction of complex networks and facilitates comparisons between very different systems. It also has promising potential for generating new insights into the structure and function of natural species assemblages.

Empiricists have frequently investigated and described patterns of resource utilization within species assemblages (reviewed in Schoener 1974a, Toft 1985, Ross 1986). A variety of methods are employed in estimating actual use, and fairly large samples are needed to characterize proportional utilizations, or p_{ij} , accurately. Elements in a resource matrix of such utilization coefficients represent the probability that consumer j will use resource state i . In addition, the degree to which consumers actually utilize resources disproportionately to their effective supply can be estimated with electivities, or e_{ij} (Ivlev 1961, Jacobs 1974, Schoener 1974b, Lawlor 1980a, Toft 1981, Pianka 1986).

Even if a matrix describing magnitudes of all pairwise species interactions can be constructed, its multidimensionality poses serious interpretational problems. The simple observation that the number of potential pairwise interactions increases geometrically with number of species creates serious logistical problems for empirical work. Indirect interactions increase at an even faster rate with diversity (Patten 1983, Pianka 1987). Yet we cannot abandon the study of diverse systems simply because they are complex and unmanageable. Simple graphical means of summarizing community structure with operationally tractable parameters are badly needed. Moreover, as Loehle (1987) recently stated, "The mere attempt to define phenomena operationally can dramatically increase theory maturity."

In an attempt to elucidate guild structure while retaining some degree of assemblage connectivity (i.e., the pattern of pairwise interactions in a community matrix), Inger and Colwell (1977) plotted overlap against nearness rank in niche space. Their technique, which permits evaluation of properties of an entire complex network as an operational unit, has since been applied to desert lizard and grasshopper assemblages (Pianka 1980, 1986, Joern and Lawlor 1981). Another promising technique for identifying and interpreting the structure of complex assemblages involves the construction of various randomized null communities (pseudo- or neutral model communities) based on real prototypes. This bootstrap approach to community analysis was pioneered by Sale (1974), and has since been employed in a variety of forms by many other workers (Caswell 1976, Inger and Colwell 1977, Pianka et al. 1979, Joern and Lawlor 1980, 1981, Lawlor 1980b, Ricklefs and Travis 1980, Ricklefs et al. 1981, Schoener 1984, Case 1985, Armbruster 1986, Pianka 1986, Yodzis 1988). Construction of randomized resource matrices from observed data is nontrivial, since inevitably some components of the structure of the pro-

prototype are mirrored in the randomized replicate (i.e., the "Narcissus effect" of Colwell and Winkler 1984). Such randomly constructed model systems differ from real assemblages in some very informative ways. For example, randomized systems differ from their real prototypes in the magnitude and degree of homogeneity of ecological similarities among consumers and in relative guild structure. Moreover, the Monte Carlo approach for statistical inference (Sokal and Rohlf 1969, Ricklefs and Lau 1980, Diaconis and Efron 1983, Pimm 1983, Mueller and Altenberg 1985) offers a means of assessing the significance of patterns generated by randomizations in relation to real prototypes.

Study systems

For the purposes of this study, we evaluate data from eight natural vertebrate assemblages (Appendix I). We selected these particular eight study systems from a larger number of systems we have examined, based on the intensity and completeness of sampling as well as the degree of precision we were able to use in identification of prey resource states. Although horizontal interactions (resource overlap indicating potential for exploitation competition) constitute the primary focus of the present analysis, predator/prey interactions also occur within these vertebrate assemblages, particularly among the fishes. While other taxa interact with many lizards and fishes at the various sites studied, the majority of important horizontal interactions are most likely included within natural groups of vertebrates defined by higher taxonomic categories. Assemblages defined by taxonomic criteria generally exhibit greater morphological similarity, and hence potential ecological similarity. Furthermore, data on resource utilization collected from a taxonomically cohesive assemblage are more likely to be of comparable quality and scope. One could imagine, for example, serious methodological problems with attempting to compare stomach contents of lizards with those of ants. Both diet and microhabitat data were collected from four lizard assemblages in deserts of Western Australia and the Kalahari of southwestern Africa (described briefly below and at greater length in Pianka 1986 and included references). In the current study, only dietary data are analyzed for four fish assemblages studied in freshwater streams and swamps of Costa Rica and Venezuela.

Two lizard study sites are in the Great Victoria desert of remote interior Western Australia. The site referred to as Laverton is an area at the desert's edge some 40 km east of the outback town of Laverton, Western Australia (equals L-area in Pianka 1986). Average annual rainfall is 0.22 m at Laverton. This is a spinifex sandplain area with scattered marble gums and acacias. The Redsands site lies more interior in the desert, \approx 100 km east of Laverton near Yamarna Homestead (average annual precipitation is 0.31 m). This site contains both sandplain spinifex habitats and stabilized sandridges that support a more complex, shrubby vegeta-

tion. Laverton has 32 species of lizards, whereas 42 species are known to occur at Redsands (Pianka 1986). Both these Australian study sites were studied intensely during 1978–1979. Over 3000 lizards were collected on these two sites, and more than 200 different prey resource categories were recognized in construction of dietary resource matrices (201 at Redsands, 217 at Laverton). Two major dietary components, ants and termites, were divided into a number of size and color categories within families to generate some 97 and 58 different resource states. These resource states correspond roughly to castes within separate termite and ant species, many of which have not yet been described. To facilitate comparisons with other sites, all ants and all termites were also lumped to construct a second, substantially simpler, condensed matrix based on a standard 19 prey categories corresponding roughly to insect orders (Pianka 1986).

The other two lizard study areas are located in the Kalahari semidesert of southern Africa. Bloukrans is in the dune area, or sandveld, of the Kalahari in the Republic of South Africa near the Namibian border. Seventeen lizard species were collected at Bloukrans during the 1969–1970 Austral season. The study area south of Tsabong, Botswana has 15 species of lizards (one rare species excluded) and is a sandplain Kalahari site with a mixed open forest–savanna vegetation. Average annual rainfall is 0.15 m at Bloukrans and 0.29 m at Tsabong. Termites, the dominant prey of lizards in the Kalahari desert, were classified by both castes and species, resulting in 46 prey resource states (40 occurring at Tsabong, 41 at Bloukrans). Again, simpler prey resource matrices have also been constructed using the same standard 19 prey resource states to facilitate intercontinental comparisons (Pianka 1986, 1989). In addition to diet, microhabitat resource matrices were assembled for each of the four lizard study systems using the same 15 resource states (see Pianka 1986 and included references for description of methods).

Two fish study sites are located in the western llanos, or flatlands, in the state of Portuguesa, Venezuela. This region receives \approx 2.0 m of rainfall annually, most of which falls during four consecutive months from May through August. Caño Maraca is a seasonal swamp/creek of the Río Apure-Río Orinoco drainage. The broad, sparsely forested floodplain of Caño Maraca typically experiences extensive sheet flooding during the wet season (May–August), followed by gradual desiccation during a transition season (September–December). During the peak dry season (January–April), aquatic habitat is limited to stagnant, vegetation-choked pools within the main creek channel. Eighty-three fish species were collected at Caño Maraca over a 12-mo sampling period in 1984 (site and methods described in Winemiller 1987). In this report, C. Maraca data designated as "dry season" actually correspond to the transition period (September–December). Food resources were partitioned into 117 categories (fish prey

identified to species level) over the course of the study at C. Maraca. The other Venezuelan site, Caño Volcán, is a small stream of the low Andean piedmont on the fringe of the llanos. Caño Volcán also lies within the Apure–Orinoco drainage and was sampled during each month of 1984, yielding 20 fish species. Seasonal rainfall affects C. Volcán differently than C. Maraca in that wet season spates produce flash floods of brief duration, while stream flow is reduced but continuous during the driest months. C. Volcán data were divided into a wet season (May–October) and dry season (November–April). A total of 92 prey resource categories were recognized at C. Volcán over the course of the year.

Two other fish sites are located in Parque Nacional Tortuguero, in the Limón province of Costa Rica's Atlantic lowlands. This region receives from 3.5 to 5.0 m of rainfall annually. Typically, brief dry seasons occur during March–May and September–October each year. Both sites were studied from February through December of 1985, when the dry seasons were delimited as March–May and October. Caño Agua Fría Viejo is a swampy side-channel (“braid”) of the Río Tortuguero flowing through swamp/rain forest dominated in certain stretches by the palm *Raphia taedigera*. Like C. Maraca in Venezuela, the broad, low-lying floodplain of C. Agua Fría Viejo is subject to extensive sheet flooding during the wettest months (June–August). C. Agua Fría Viejo differs from C. Maraca in having much less severe dry season conditions (environmental data available in Winemiller 1987). Fifty-six fish species were collected at C. Agua Fría Viejo during the study period, and 98 prey resource categories were recognized. The other Costa Rican site, Quebrada, is a small creek on the barrier island near the village of Tortuguero. The creek flows into the Laguna Tortuguero and is subject to tidal influence during the dry season. Twenty-three fish species were collected from Quebrada and associated rain forest pools in its upper drainage. A total of 81 food categories were recognized at Quebrada.

METHODS

Resource utilization data

Food resource utilization was estimated by volumetric stomach content analysis. Food categories were assigned following three criteria: (1) estimated discriminatory capabilities of consumers, (2) relative abundance of resource at site, and (3) capability of the investigator to discriminate among resource states in gut contents. In most instances, invertebrate prey are classified at the ordinal level (except for desert ants and termites mentioned above). In the present report, two diet resource matrices are analyzed for Australian sites: expanded matrices containing over 200 resource states, and condensed 19-state matrices based on the same data. Because lizards were infrequently consumed by other lizards, they were assigned to a single resource

state (all vertebrate prey) for this analysis. Fishes are frequently consumed by other fishes. Consequently, fishes are assigned multiple resource states at the species level (sheared fish flesh, scales, mucus-slime, and fin fragments formed separate categories). In an attempt to retain maximum information content from sacrificed specimens, unidentified fishes and terrestrial and aquatic insects were used as separate categories rather than omitted. Microhabitat utilization by lizards is based on observations of spatial positions of undisturbed individual lizards. Microhabitat states are: fosomal, open sun, open shade, grass sun, grass shade, bush sun, bush shade, low sun, low shade, high sun, high shade, on ground under tree in sun, under tree in shade, other sun, and other shade (Pianka 1986).

For the present analysis, lizard data for the entire annual sampling period are combined to form resource matrices. Fish data are separated into wet and dry seasons at each site as defined above. Similarity in resource utilization between two consumers is estimated with the symmetric niche overlap coefficient (Pianka 1973):

$$\phi_{jk} = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}}$$

where p_{ij} and p_{ik} represent the proportional utilization by volume of resource state i by consumer species j and species k . The p_{ij} and p_{ik} are replaced by standardized e_{ij} and e_{ik} for an electivity-based analysis, and by the geometric means g_{ij} and g_{ik} (standardized to sum to unity) for the analyses we present in detail. This overlap index is an analogue of a correlation coefficient and generates values ranging from zero when no resources are shared to 1.0 for complete identity in resource utilization between two species.

Some investigators have argued for the use of electivities rather than proportional utilization coefficients for approximations of interspecific competition (Sale 1974, Schoener 1974b, Lawlor 1980a). We do not claim to estimate interspecific competition directly from niche overlap. Rather, we simply seek to detect segregation and to analyze observed patterns of similarity in resource utilization within diverse natural assemblages. If an appropriate comparative basis is achieved (e.g., periods of resource scarcity vs. resource abundance, or diverse vs. depauperate assemblages), patterns of resource overlap can be used to evaluate the likelihood of interactive effects. Both p_{ij} and e_{ij} were employed during preliminary data analysis. Electivities were estimated following the methodologies of Sale (1974), Jacobs (1974), and Lawlor (1979), in which the availability of a given resource is estimated based on the total amount of that resource utilized by the entire community. In spite of the built-in circularity, such “bioassays” of availabilities are probably superior to attempts to estimate availability in more direct but less unbiased ways. Uneven relative abundances among resource states pose potential problems for direct es-

TABLE 1. Pearson product moment correlation coefficients and significance levels of log-log plots of proportional utilization coefficients (p_i), electivities (e_i) and the geometric mean of the former two (g_i), each with resource availabilities (R_i) estimated for the 18 systems examined.

System	N	$r_{p,R}$	$r_{e,R}$	$r_{g,R}$
Redsands (15 microhabitats)	178	+.346**	-.085 NS	-.000 NS
Redsands (19 prey)	298	+.288**	-.330**	-.000 NS
Redsands (201 prey)	870	+.552**	-.366**	+.110**
Laverton (15 microhabitats)	162	+.494**	-.226**	+.138 NS
Laverton (19 prey)	193	+.566**	-.170*	+.261**
Laverton (217 prey)	684	+.608**	-.224**	+.249**
Bloukrans (40 prey)	232	+.551**	-.413**	+.077 NS
Bloukrans (15 microhabitats)	83	+.592**	+.071 NS	+.366**
Tsabong (41 prey)	289	+.677**	-.235**	+.303**
Tsabong (15 microhabitats)	85	+.339**	-.267*	+.032 NS
Caño Maraca (wet)	1328	+.212**	-.380**	-.130**
C. Maraca (dry)	1515	+.255**	-.423**	-.127**
Caño Volcán (wet)	478	+.547**	-.263**	+.173**
C. Volcán (dry)	515	+.447**	-.323**	+.045 NS
Caño Agua Fria (wet)	721	+.431**	-.354**	+.000 NS
C. Agua Fria (dry)	735	+.431**	-.295**	+.071 NS
Quebrada (wet)	414	+.425**	-.224**	+.055 NS
Quebrada (dry)	368	+.436**	-.316**	+.045 NS

* = $P < .05$, ** = $P < .01$, NS = not significant.

estimates of interspecific competition (Colwell and Futuyama 1971). Given that temporal changes in resource abundance are likely to occur over the duration of sampling (Pulliam 1986), other sources of information are required to estimate interspecific competition based on patterns of resource utilization (e.g., comparisons of temporal shifts in resource availability and niche compression, or other bases of comparison).

Randomization algorithms

One of the major strengths of the pseudo-community (null model) approach is that many different replicates of a randomized real system can be constructed with a computer for comparison with an observed prototype. Confidence limits on the means of the pseudo-communities bracket an expectation against which the observed system can be compared. Standard statistical tests cannot be applied to comparisons involving three or more species because dietary overlaps are not independent, and because pseudo-communities are based on observed ones. A Monte Carlo approach can, however, be employed to generate actual distributions for tests of statistical significance (Pimm 1983). If, say, 95 or 99 of 100 randomized pseudo-communities have mean niche overlaps greater than the observed, results are significant at the $P < .05$ or $P < .01$ level, respectively. Average niche overlap of randomized communities is compared with observed systems at different ranks of neighbors in niche space following Inger and Colwell (1977). Grand means are misleading because pseudo-communities can lie below observed systems at some ranks but above at others. Greater insights into the structure and variation within assemblages can be attained by comparing the proportion of randomized communities above or below the observed prototype at each rank in niche space. For example, the relative height and shape of the curve derived from

plotting the standard deviation in niche overlap against ordered rank in niche space can be used to infer guild structure in an assemblage (Inger and Colwell 1977). Patterns of niche segregation among closest niche neighbors obviously have different implications than segregation between ecologically less similar species (discussed further below). We use Fisher's (1958:99–100) method for calculation of overall probability level from a series of related probabilities by summation of the inverse of the logarithm of component probabilities (i.e., probabilities for n niche neighbor ranks), which yields an overall chi-square value based on null Monte Carlo distributions (Pimm 1980).

Two different randomization algorithms were used to produce 100 pseudo-communities based on each of the 18 observed resource matrices (Pianka 1986). The first algorithm is equivalent to Sale's (1974) randomization and RA3 of Lawlor (1980b). This algorithm, referred to hereafter as the "scrambled-zeros" randomization, retains the original number of consumers, number of resource states, and consumer niche breadths, but randomly reassigns each consumer's observed utilization coefficients among all potentially usable resource states. In other words, the scrambled-zeros randomization retains observed utilization coefficients, but randomly reassigns them among all possible resource states, thus destroying the zero structure of the observed resource matrix (all consumers are "allowed" to use all resource states).

The second algorithm, termed the "conserved-zeros" randomization, is equivalent to RA4 of Lawlor (1980b). This algorithm randomly rearranges utilization coefficients for each species but only among those resources that each consumer actually uses in an observed resource matrix. The conserved-zeros randomization thus retains both observed niche breadths and the zero structure of the original resource matrix (i.e.,

unused resource states remain unused). Zero utilization is an absorbing state or boundary condition, and the zero structure of the resource matrix constrains possible rearrangements.

To aid in the interpretation of results generated by such randomizations of observed resource matrices, we constructed a dozen simple model resource matrices with deliberate, distinctive features (Appendix II). The first three model systems (Trials 1, 2, and 3) were composed of 10 resource states and 10 consumers arranged as two non-overlapping guilds of equal size with overlap between species pairs within guilds being high, intermediate, and low, respectively. Trials 4, 5, and 6 have a similar overlap gradient but each was composed of one large and one small guild. Trials 7, 8, and 9 also have 10 resource states and consumers, but no guild structure, and average overlap between pairs of species is high, intermediate, and low, respectively. Trial 10 also had 10 resource states and 10 consumers overlapping greatly on four core resources. Trial 11 was the same as Trial 10, except that overlap on core resources was lower. Trial 12 was the same as Trial 11, except that a total of 100 resource states was used, 40 of which constituted core resources. These 12 hypothetical "organized" prototype systems are summarized in Appendix II.

The single-linkage algorithm of cluster analysis defines a guild as a cluster of species separated from all other such clusters by a distance greater than the greatest distance between the two most disparate members of the guild concerned (Pianka 1980). This conservative definition allows complex hierarchical patterns of nesting of smaller guilds within larger ones. Fish guilds were defined with both single and average linkage techniques, which usually gave the same results (Winemiller 1987). All such clustering techniques necessarily distort true spacing patterns to some extent because they reduce dimensionality.

RESULTS

Choice of utilization coefficient

Electivities computed with the index suggested by Jacobs (1974) vary from -1 to $+1$, and are positively correlated with their probabilistic counterparts as computed by the methods of Lawlor (1980), which are scaled to that they vary from 0 to unity and sum to 1.0, making them usable in overlap or similarity indices. Electivities give extremely large, counterintuitive weight to seemingly insignificant, trace components in pooled diets, whereas p_{ij} 's overvalue common resource states. Combining the approaches of Hurlbert (1978) and Smith (1982) we employ the geometric mean of p_i and e_i , here termed g_i , as a measure of utilization. Table 1 summarizes the correlations among p_i 's, e_i 's, g_i 's, and R 's for the 18 resource matrices. Correlations between p_i and R are always significantly positive, whereas those between e_i and R 's are usually signifi-

cantly negative. In contrast, correlations between g_i and R 's are weaker and less often significant. In bench tests that follow, the geometric mean, g_i , is more reliable than p_i or e_i , and hence is the most meaningful characterization of patterns of resource use because it reduces the effect of resource availability (R_i) on consumer performance by the square root of R_i . This is illustrated algebraically by $g_i = \sqrt{p_i \cdot e_i}$. Since $e_i = p_i/R_i$, we can substitute, giving the equation $g_i = \sqrt{p_i \cdot p_i/R_i} = p_i/\sqrt{R_i}$. As an estimator of resource utilization, g_i reduces the positive correlation of p_i with R_i and the negative correlation of e_i with R_i , while not eliminating the resource spectrum from the analysis (Table 1). Consequently, g_{ij} performs better than either p_{ij} and e_{ij} for most ecological comparisons requiring estimates of ecological similarity, because neither abundant nor exceedingly rare resources influence niche overlap unduly (see the following analysis).

Bench tests of null models

Graphical results from g -based randomizations using model assemblages (Figs. 1–4) indicate that the scrambled-zero algorithm was most sensitive in revealing patterns of distinctive guild structure and consumer utilization of core resources. The latter was hypothesized a priori to be a common feature of natural communities. For example, various termite species are core food resources for lizards in the Kalahari, whereas mayflies serve as a core resource for many tropical stream fishes. If plots of average overlap (based on 100 scrambled-zeros randomizations) against rank of niche neighbor fall below the observed plot, then consumers are more "piled up" in their utilization of certain resource states than random expectation. The same series of analyses using the conserved-zeros randomization discriminates between random vs. hyperdispersed patterns of resource exploitation. The percentage of randomized mean overlaps that exceed mean observed overlap offers one criterion for judging statistical significance of the community-wide pattern of resource segregation (Joern and Lawlor 1980, Lawlor 1980b). Resource partitioning or niche segregation is occurring when conserved-zero pseudo-communities exhibit higher overlap and "float" above the observed community. Significant assemblage-wide patterns of resource segregation were obtained for Trial 3 (two equal-sized guilds, low overlap) and Trial 9 (no guilds, low overlap), as well as in the low-overlap, core resource models (Trials 11 and 12, Table 1). Increasing the number of resource states without modifying the qualitative pattern of resource utilization (Trial 11 vs. Trial 12) did not increase the likelihood of observing resource segregation, and if anything, it appears actually to decrease somewhat (Fig. 4). Comparisons from these and other model assemblages with their randomized pseudo-communities support an interpretation of the scrambled-zeros algorithm as a test of guild structure (percent pseudo-communities below observed), where-

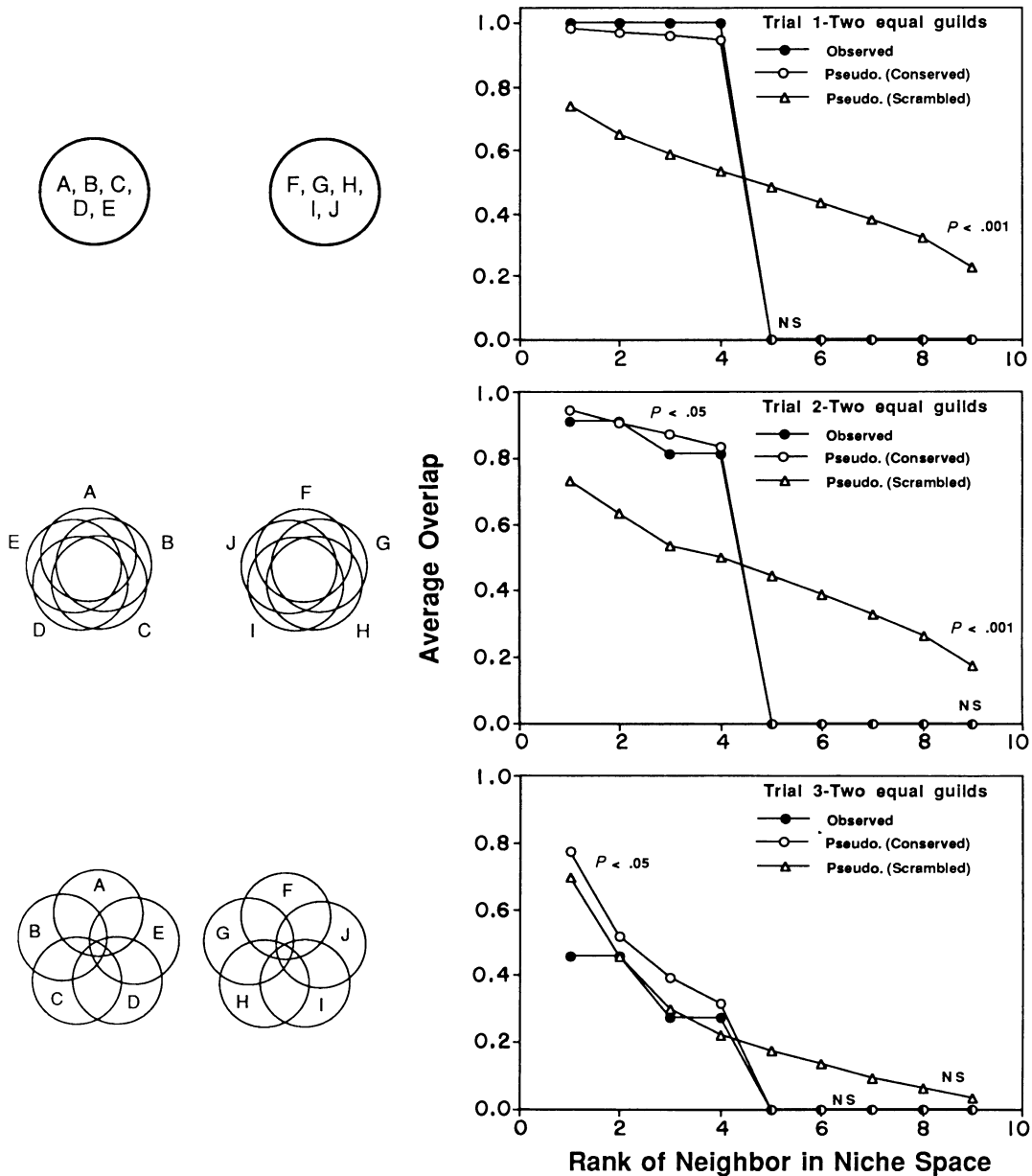


FIG. 1. Plots of average niche overlap against nearness rank of niche neighbor for three model assemblages with guild structure, and the same plots using means from 100 randomizations based on two algorithms (resource matrices for each model are given in Appendix II). Set theory representations of the systems are depicted on the left and Colwellian plots on the right. For all the figures in this paper, neighbors in niche space are ranked from the nearest (most similar) to the most distant (most different from the target species). In all figures except Fig. 5, averages across all species at each nearness rank are plotted. For systems with high overlap, scrambled-zero pseudo-communities fall below observed overlap within guilds but lie above observed systems at more distant between-guild ranks. Trial 1 (two equal-sized guilds, high overlap) plots shows the observed system exceeding both pseudo-community overlaps at 4 out of 9 ranks. Trial 2 (two equal-sized guilds, moderate overlap) plot shows 4 of 9 observed overlaps exceeding pseudo-community overlaps based on the scrambled-zeros randomization algorithm. Trial 2 conserved-zeros pseudo-communities fall above the observed system for 3 of 9 ranks, indicating marginal resource segregation (see Table 4). Note that scrambled-zero pseudo-communities sink at close-in ranks but float significantly at distant ranks in niche space, as a result of destroying guild structure. In Trial 3 (two equal-sized guilds, low overlap), conserved-zero pseudo-communities float significantly at the first four ranks in niche space whereas no other differences are significant. Probability values for Figs. 1-4 are based on Fisher's chi-square summation of probabilities across the first 4 (conserved zero) or all 9 niche neighbor ranks (both algorithms). Conserved zero probabilities based on the fraction of randomized means exceeding observed rank means. Scrambled zero probabilities based on the fraction of randomized means less than observed rank means.

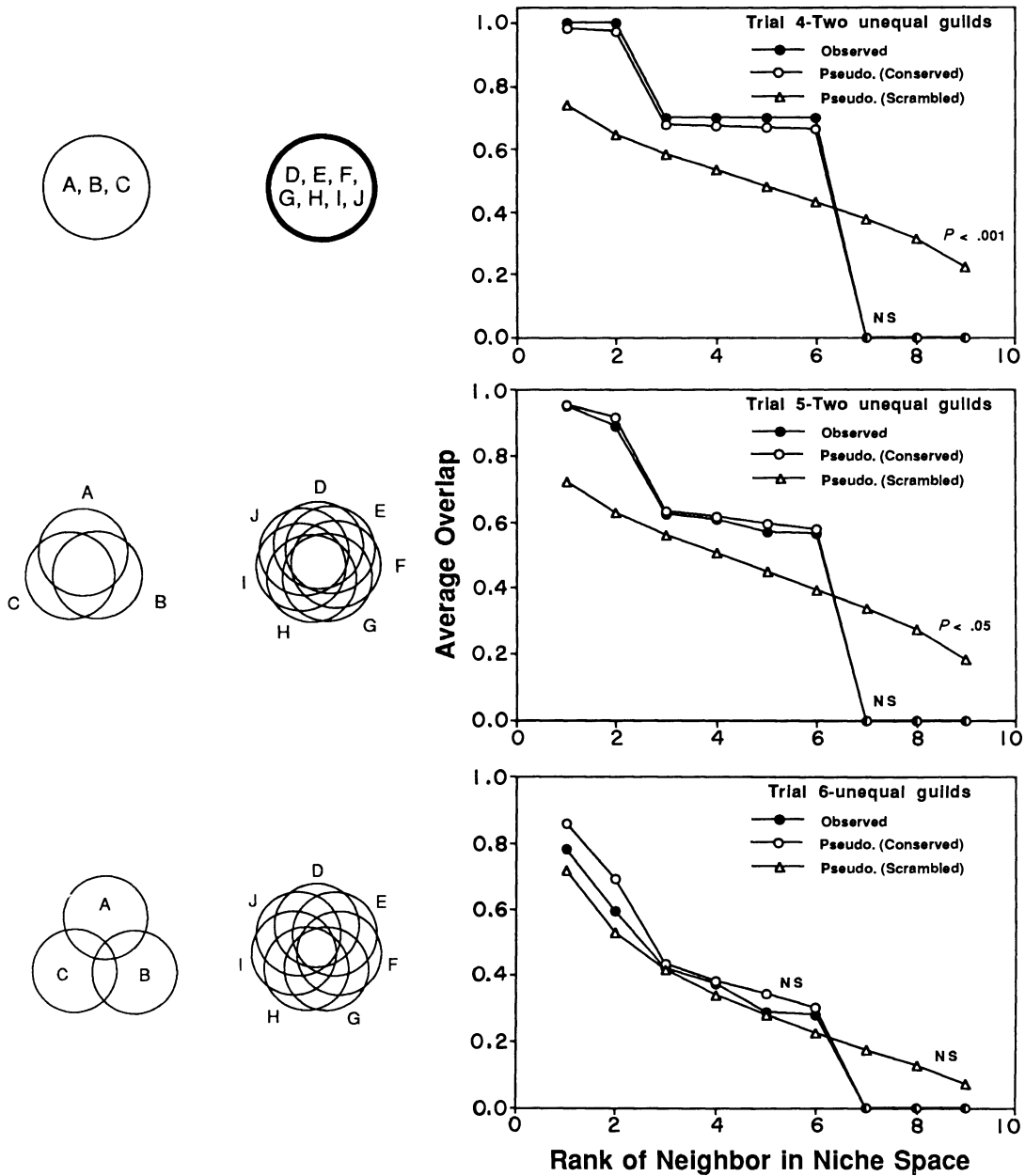


FIG. 2. Plots of average niche overlap against rank of niche neighbor for three model assemblages with guild structure, and the same plots using means from 100 randomizations based on two algorithms (resource matrices for each model are given in Appendix II). Again, for systems with high overlap, scrambled-zero pseudo-communities fall below observed within guilds but lie above observed systems at more distant between-guild ranks. Trial 4 (two distinct guilds of different sizes, intermediate overlap) plot shows the observed system above both types of pseudo-communities at close-in ranks. Scrambled zero pseudo-communities sink close-in but float significantly at distant ranks in niche space, a result of destroying the guild structure. Neither set of pseudo-communities differs from the observed system in Trial 6 (unequal sized guilds with low overlap).

as the conserved-zeros algorithm tests for nonrandom patterns of resource segregation among consumers (percent pseudo-communities above observed). Note that differences in slopes of observed vs. pseudo-community plots can yield radically different patterns at

various ranks in niche space (e.g., Fig. 1, Trials 1 and 2 vs. Trial 3). This within-system variation provides additional information, since the significance level of mean overlap at each niche rank can be examined using the same algorithms (see below).

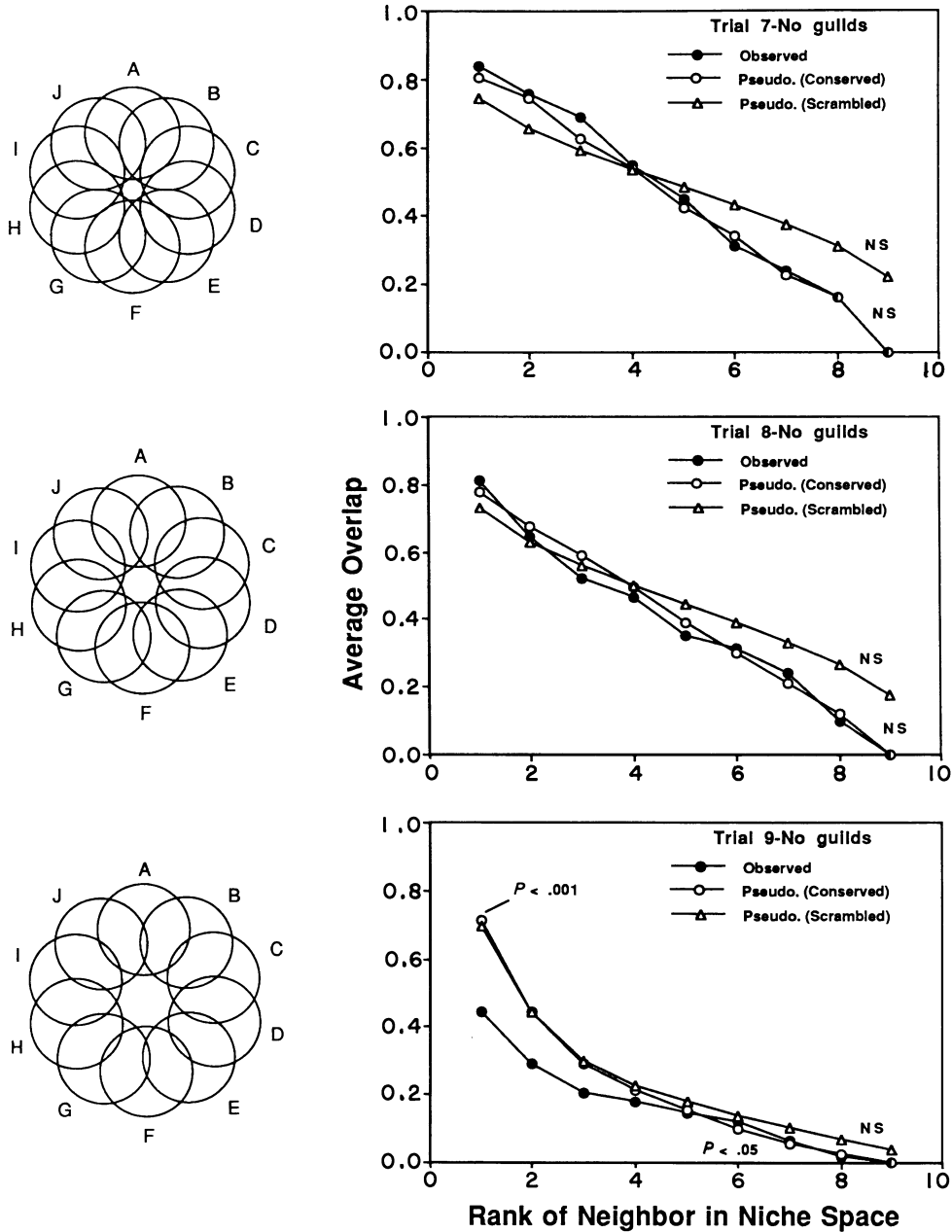


FIG. 3. Plots of average niche overlap against rank of niche neighbor for three model assemblages with no guild structure, and the same plots using means from 100 randomizations based on two algorithms (resource matrices for each model are given in Appendix II). Pseudo-community overlaps at most ranks do not differ significantly from the observed system when overlap is high, but do tend to float at close-in ranks when observed overlap is low (Trial 9).

Performances of each of the three measures of utilization (p_i , e_i , and g_i) in the various model systems are summarized in Tables 2-4.

Guild structure in real assemblages

Number of species in eight vertebrate assemblages investigated varies from 15 (Tsabong and Quebrada) to 59 (Caño Maraca). Fig. 5 illustrates the tremendous complexity and difficulty in attempting to interpret pat-

terns generated by individual species simultaneously, even for relatively low-diversity systems. Large interspecific variation is apparent in both plots of dietary overlap against the rank of neighbors in niche space. Overlap of species exploiting mostly unshared resources (i.e., those at the edge of the multidimensional resource hypervolume) decline quickly, whereas those exploiting core resources (i.e., lying interior in the resource hypervolume) exhibit relatively high overlap

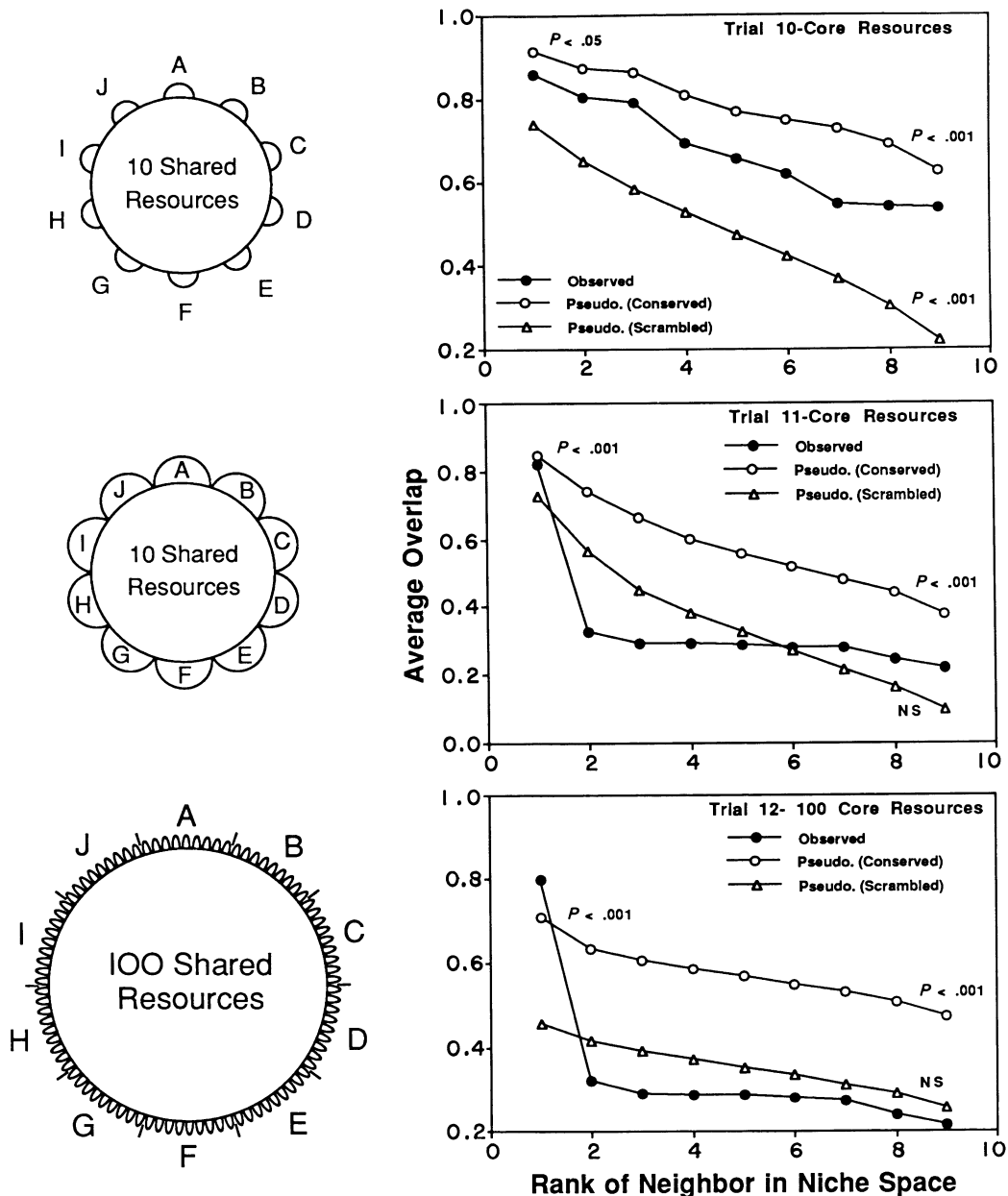


FIG. 4. Plots of average niche overlap against rank of niche neighbor for three model assemblages with no guilds and with consumers segregated on different core resource states, plus the same plots based on means of 100 randomizations using two algorithms (resource matrices for each model are given in Appendix II). In Trial 10 (core resources, high overlap), conserved-zero pseudo-communities float significantly whereas scrambled-zero pseudo-communities sink. In Trial 11 (core resources, intermediate overlap), conserved-zero pseudo-communities float whereas scrambled-zero pseudo-communities do not differ significantly from observed. Trial 12 (core resources, intermediate overlap, 100 resource states) shows a pattern similar to Trial 11, except that conserved-zero overlaps sink in relation to observed values at rank one (nearest neighbor, thus indicating that expanded resource categories are less likely to result in patterns of significant resource segregation).

even with distant niche neighbors. No significant relationship exists between each species' relative abundance (Pianka 1986, Winemiller 1987) and the slope of its curve in Fig. 5 (for Quebrada, linear regression $r^2 = 0.02$) or its y intercept ($r^2 = 0.01$).

To describe empirical patterns of species assemblages, we plot mean overlap against neighbor rank.

Variation around average values in such plots provides an additional description at the assemblage level: relative guild structure (Inger and Colwell 1977). If species in an assemblage are significantly clustered into groups based on similar utilization of resources, a plot of the standard deviation of niche overlap against ranked niche neighbors (from closest to farthest) will produce a curve

TABLE 2. Performance of model 10-species assemblages in p_{ij} -based niche overlap randomizations. The proportion of nearest neighbor ranks with pseudo-community average overlap above (conserved zero) or below (scrambled zero) observed in ≥ 95 cases out of 100 and chi-square significance levels are given.

Model assemblage	Algorithm	Mean niche overlap	Proportion of pseudo-communities different from observed	
			9 niche neigh.	4 niche neigh.
Trial 1: 2 equal guilds, 10 resources, high overlap	Observed	0.444		
	Scrambled	0.443	.56**	0**
	Conserved	0.395	0 NS	0 NS
Trial 2: 2 equal guilds, 10 resources, moderate overlap	Observed	0.383		
	Scrambled	0.446	.56*	0**
	Conserved	0.395	.22 NS	.50*
Trial 3: 2 equal guilds, 10 resources, low overlap	Observed	0.162		
	Scrambled	0.239	.67 NS	.25 NS
	Conserved	0.217	.33 NS	.75*
Trial 4: 2 unequal guilds, 10 resources, high overlap	Observed	0.533		
	Scrambled	0.447	.33*	0**
	Conserved	0.475	0 NS	0 NS
Trial 5: 2 unequal guilds, 10 resources, moderate overlap	Observed	0.468		
	Scrambled	0.443	.33 NS	0**
	Conserved	0.474	.11 NS	0 NS
Trial 6: 2 unequal guilds, 10 resources, low overlap	Observed	0.303		
	Scrambled	0.308	.33 NS	0 NS
	Conserved	0.329	.11 NS	0 NS
Trial 7: no guilds, 10 resources, high overlap	Observed	0.444		
	Scrambled	0.441	.56*	0**
	Conserved	0.395	0 NS	0 NS
Trial 8: no guilds, 10 resources, moderate overlap	Observed	0.383		
	Scrambled	0.443	.56 NS	0 NS
	Conserved	0.396	.22 NS	.25 NS
Trial 9: no guilds, 10 resources, low overlap	Observed	0.162		
	Scrambled	0.253	.78 NS	1.0 NS
	Conserved	0.220	.44*	1.0*
Trial 10: core resources, 10 categories, high overlap	Observed	0.962		
	Scrambled	0.443	0**	0**
	Conserved	0.733	0 NS	0 NS
Trial 11: core resources, 10 categories, medium overlap	Observed	0.575		
	Scrambled	0.451	0**	0**
	Conserved	0.728	.89**	.75**
Trial 12: core resources, 100 categories, medium overlap	Observed	0.560		
	Scrambled	0.430	0**	0**
	Conserved	0.703	.89**	.75**

* = $P < .05$, ** = $P < .01$, NS = not significant.

with a hump. This is because closest niche neighbors within guilds are piled-up on the same resources; hence overlap is homogeneously high and standard deviations are low at close-in ranks. If two or more guilds are present in the community, standard deviation in overlap increases at more distant ranks, as more mixed between-guild pairings are included in calculations of standard deviation (Inger and Colwell 1977). Standard deviation of niche overlap typically falls off at higher ranks in niche space because distant pairings generally exhibit homogeneously low overlap values. In addition, systems with larger guilds peak at more distant ranks in niche space (Pianka 1980). Presence of guilds of different sizes can result in multiple peaks in standard deviation plots; however, this multiple modality is obscured as the number of consumers increases, and is virtually absent in large assemblages. Large assemblages having many small guilds tend to exhibit shal-

lower curves with a less pronounced negative slope at higher ranks.

Extensive variation among sites is seen in plots of standard deviation in dietary niche overlap by niche neighbors for both wet and dry season tropical fish assemblages, as well as with detailed and condensed resource matrices for the four lizard assemblages (Figs. 6–10). Based on comparisons with the scrambled-zeros computer algorithm (Table 5), guild structure based on diet differed significantly (χ^2 , $P < .05$) from random expectations for Caño Maraca (wet and dry seasons), C. Volcán (wet and dry), C. Agua Fría (wet and dry), Redsands (detailed prey categories), and Laverton (both detailed and condensed categories). Both Caño Maraca and C. Volcán fish assemblages had multiple, indistinct guilds during the wet season. The Maraca assemblage shows more pronounced guild structure during the dry season, whereas Volcán fishes show much weaker pat-

TABLE 3. Performance of model 10-species assemblages in e_{ij} -based niche overlap randomizations. The proportion of nearest neighbor ranks with pseudo-community average overlap above (conserved zero) or below (scrambled zero) observed in ≥ 95 cases out of 100 and chi-square significance levels are given.

Model assemblage	Algorithm	Mean niche overlap	Proportion of pseudo-communities different from observed	
			9 niche neigh.	4 niche neigh.
Trial 1: 2 equal guilds, 10 resources, high overlap	Observed	0.444		
	Scrambled	0.505	.56**	0**
	Conserved	0.444	.22 NS	.50 NS
Trial 2: 2 equal guilds, 10 resources, moderate overlap	Observed	0.383		
	Scrambled	0.440	.56**	0**
	Conserved	0.395	.22 NS	.50*
Trial 3: 2 equal guilds, 10 resources, low overlap	Observed	0.162		
	Scrambled	0.243	.66 NS	.25 NS
	Conserved	0.215	.33 NS	.75*
Trial 4: 2 unequal guilds, 10 resources, high overlap	Observed	0.533		
	Scrambled	0.498	.33**	0 NS
	Conserved	0.533	.22 NS	.50 NS
Trial 5: 2 unequal guilds, 10 resources, moderate overlap	Observed	0.467		
	Scrambled	0.449	.33**	0*
	Conserved	0.479	.22 NS	.25*
Trial 6: 2 unequal guilds, 10 resources, low overlap	Observed	0.312		
	Scrambled	0.336	.33 NS	0 NS
	Conserved	0.347	.33 NS	.50 NS
Trial 7: no guilds, 10 resources, high overlap	Observed	0.444		
	Scrambled	0.501	.56 NS	0 NS
	Conserved	0.444	.22 NS	.50 NS
Trial 8: no guilds, 10 resources, moderate overlap	Observed	0.383		
	Scrambled	0.445	.56 NS	0 NS
	Conserved	0.395	.22 NS	.25 NS
Trial 9: no guilds, 10 resources, low overlap	Observed	0.162		
	Scrambled	0.249	.67 NS	.50 NS
	Conserved	0.219	.33*	.75*
Trial 10: core resources, 10 categories, high overlap	Observed	0.281		
	Scrambled	0.303	.44 NS	.25 NS
	Conserved	0.520	1.0**	1.0**
Trial 11: core resources, 10 categories, low overlap	Observed	0.185		
	Scrambled	0.253	.44 NS	.75 NS
	Conserved	0.422	.89**	.75**
Trial 12: core resources, 100 categories, low overlap	Observed	0.184		
	Scrambled	0.252	.89 NS	.75 NS
	Conserved	0.421	.89**	.75**

* = $P < .05$, ** = $P < .01$, NS = not significant.

tern during the dry season (Fig. 6). These interpretations are corroborated by results from cluster analyses (average linkage using diet overlap as the measure of similarity) based on the combined, annual resource matrices that revealed eight or nine (Maraca) and four (Volcán) feeding guilds arranged hierarchically (Winemiller 1987). The graphical SD analysis suggests few, well-segregated trophic guilds in the Caño Agua Fría Viejo fish assemblage (Fig. 6). Average linkage cluster analysis yielded a very strong carnivore/herbivore split for the combined, annual resource matrix for C. Agua Fría fishes (Winemiller 1987). In contrast, single-linkage clustering produced six trophic guilds for the same matrix (Agua Fría was the only fish assemblage among four tested that yielded different patterns based on the two clustering algorithms). Little trophic guild structure was indicated for Quebrada according to the graphical SD analysis (Fig. 6). At most, few indistinct

guilds were present in the wet season and none in the dry season Quebrada fish assemblage. Average linkage cluster analysis of the annual food resource matrix of the Quebrada assemblage revealed three trophic guilds, two of which were quite similar (piscivore/invertebrate feeders vs. omnivore/invertebrate feeders).

Cluster and graphical SD analyses of Australian lizard assemblages revealed more distinct guild structure for resource matrices based on 19 condensed food resources, as opposed to matrices containing detailed categories (Figs. 7 and 9). This result is perhaps intuitive, since consumers may "pile-up" more effectively in their utilization of lumped resource categories than those more finely divided. For dietary resource matrices, Laverton lizards exhibited the largest, most distinct guilds, followed by the Redsands assemblage with large, yet less distinct guilds. The Bloukrans assemblage appeared to have multiple, less distinct trophic

TABLE 4. Performance of model 10-species assemblages in g_{ij} -based niche overlap randomizations. The proportion of nearest neighbor ranks with pseudo-community average overlap above (conserved zero) or below (scrambled zero) observed in ≥ 95 cases out of 100 and chi-square significance levels are given.

Model assemblage	Algorithm	Mean niche overlap	Proportion of pseudo-communities different from observed	
			9 niche neigh.	4 niche neigh.
Trial 1: 2 equal guilds, 10 resources, high overlap	Observed	0.444		
	Scrambled	0.486	.56**	0**
	Conserved	0.429	0 NS	0 NS
Trial 2: 2 equal guilds, 10 resources, moderate overlap	Observed	0.383		
	Scrambled	0.448	.56**	0**
	Conserved	0.396	.22 NS	.50*
Trial 3: 2 equal guilds, 10 resources, low overlap	Observed	0.162		
	Scrambled	0.242	.67 NS	.25 NS
	Conserved	0.222	.33 NS	.75*
Trial 4: 2 unequal guilds, 10 resources, high overlap	Observed	0.533		
	Scrambled	0.481	.33**	0**
	Conserved	0.516	0 NS	0 NS
Trial 5: 2 unequal guilds, 10 resources, moderate overlap	Observed	0.467		
	Scrambled	0.450	.33*	0**
	Conserved	0.476	.22 NS	.25 NS
Trial 6: 2 unequal guilds, 10 resources, low overlap	Observed	0.306		
	Scrambled	0.322	.33 NS	0 NS
	Conserved	0.336	.33 NS	.50 NS
Trial 7: no guilds, 10 resources, high overlap	Observed	0.444		
	Scrambled	0.482	.44 NS	0 NS
	Conserved	0.429	.11 NS	0 NS
Trial 8: no guilds, 10 resources, moderate overlap	Observed	0.383		
	Scrambled	0.448	.56 NS	.25 NS
	Conserved	0.395	.22 NS	.25 NS
Trial 9: no guilds, 10 resources, low overlap	Observed	0.162		
	Scrambled	0.243	.78 NS	1.0 NS
	Conserved	0.222	.56*	1.0**
Trial 10: core resources, 10 categories, higher overlap	Observed	0.673		
	Scrambled	0.478	0**	0**
	Conserved	0.779	1.0**	1.0*
Trial 11: core resources, 10 categories, medium overlap	Observed	0.336		
	Scrambled	0.353	.33 NS	.75 NS
	Conserved	0.580	.89**	.75**
Trial 12: core resources, 100 categories, medium overlap	Observed	0.332		
	Scrambled	0.353	.89 NS	.75 NS
	Conserved	0.574	.89**	.75**

* = $P < .05$, ** = $P < .01$, NS = not significant.

guilds, whereas Tsubong lizards exhibited little or no significant trophic guild structure according to graphical analysis (Figs. 8 and 10). Trophic guild structure for Laverton and Redsands essentially vanishes when condensed prey categories are replaced with detailed resource states (Figs. 7 and 9). Graphical analysis of lizard microhabitat utilization yielded significant patterns of large, distinct guilds, especially within the speciose Australian assemblages (Figs. 7 and 9).

Community-wide patterns of niche segregation in real assemblages

Statistics and results of both scrambled-zeros and conserved-zeros randomizations are summarized in Table 5 for lizard assemblages based on prey and microhabitat resource utilization, and for fish assemblages based on prey utilization during wet and dry seasons. Scrambled-zero pseudo-communities of all but

one of the eight fish assemblages fell significantly below the observed, indicating piling up on resources (guild structure and/or use of core resources) (Table 5, Figs. 11 and 12). Again, the Quebrada assemblage exhibited no significant guild structure during the dry season (Table 5, Fig. 12). All four fish assemblages demonstrated statistically significant, community-wide dietary segregation during both seasons. Caño Maraca and Quebrada assemblages showed especially striking patterns of resource segregation. At a more microscopic level of analysis, nonrandom diet segregation always occurs at the higher ranks in niche space within tropical fish assemblages (Figs. 11 and 12).

Assemblage-wide patterns for lizard diets appear to be somewhat more variable than those for fishes (Table 5, Figs. 13 and 14). Scrambled-zero pseudo-communities fell below observed for all resource matrices except the two Kalahari microhabitat ones. (Even here,

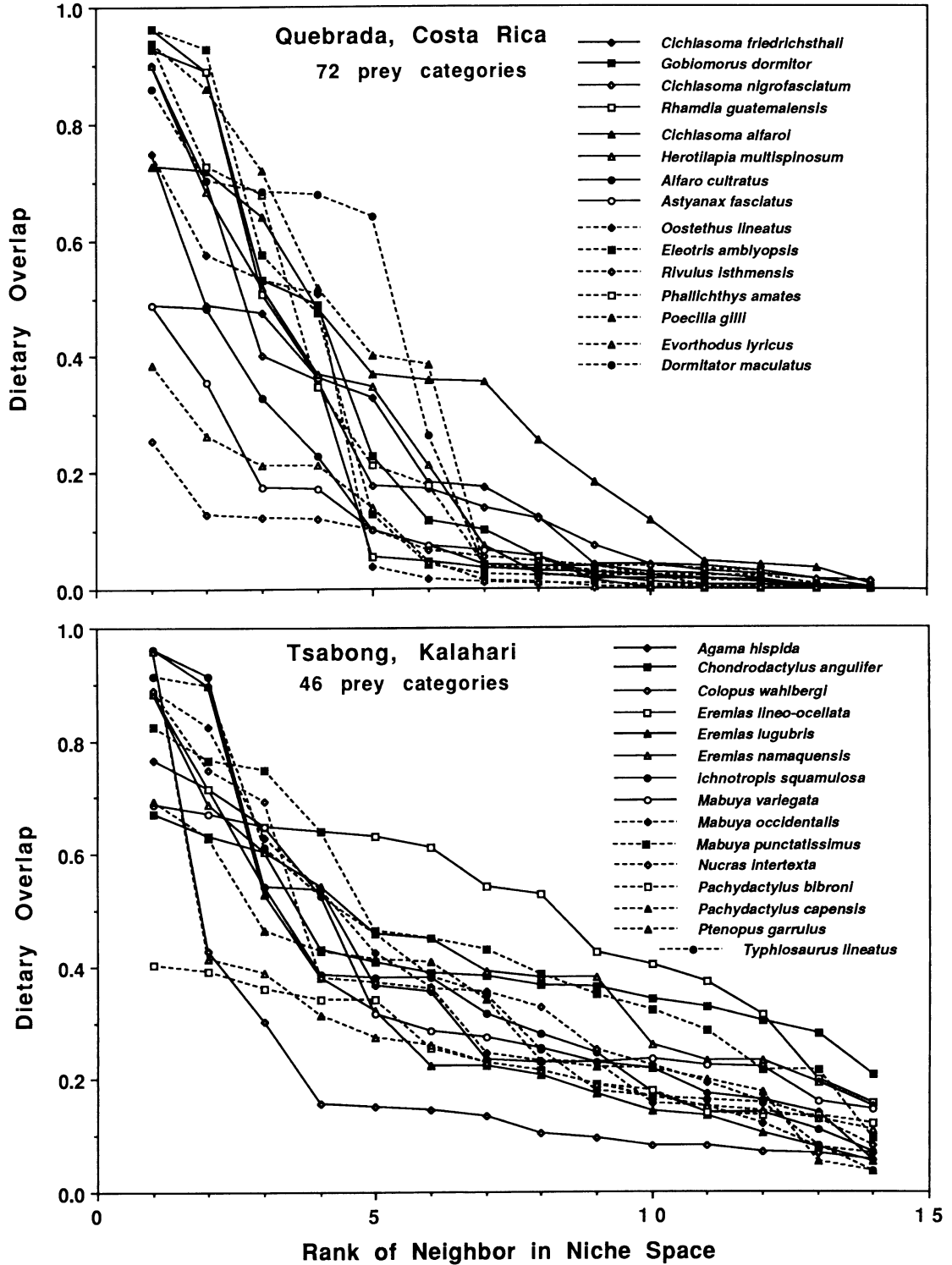


FIG. 5. Plots of dietary overlap with ranked niche neighbors for each fish species at Quebrada, Costa Rica (above) and for each lizard species at Tsabong, Botswana (below). Dietary overlap declines at more distant ranks, but average slopes exhibit large interspecific variation. In the fish system, overlap at distant ranks is homogeneously low, whereas it is higher in the lizard system. Steep negative slopes indicate relatively unique diets and ecological similarity with very few other species, while shallow slopes indicate high or intermediate ecological similarity with many species.

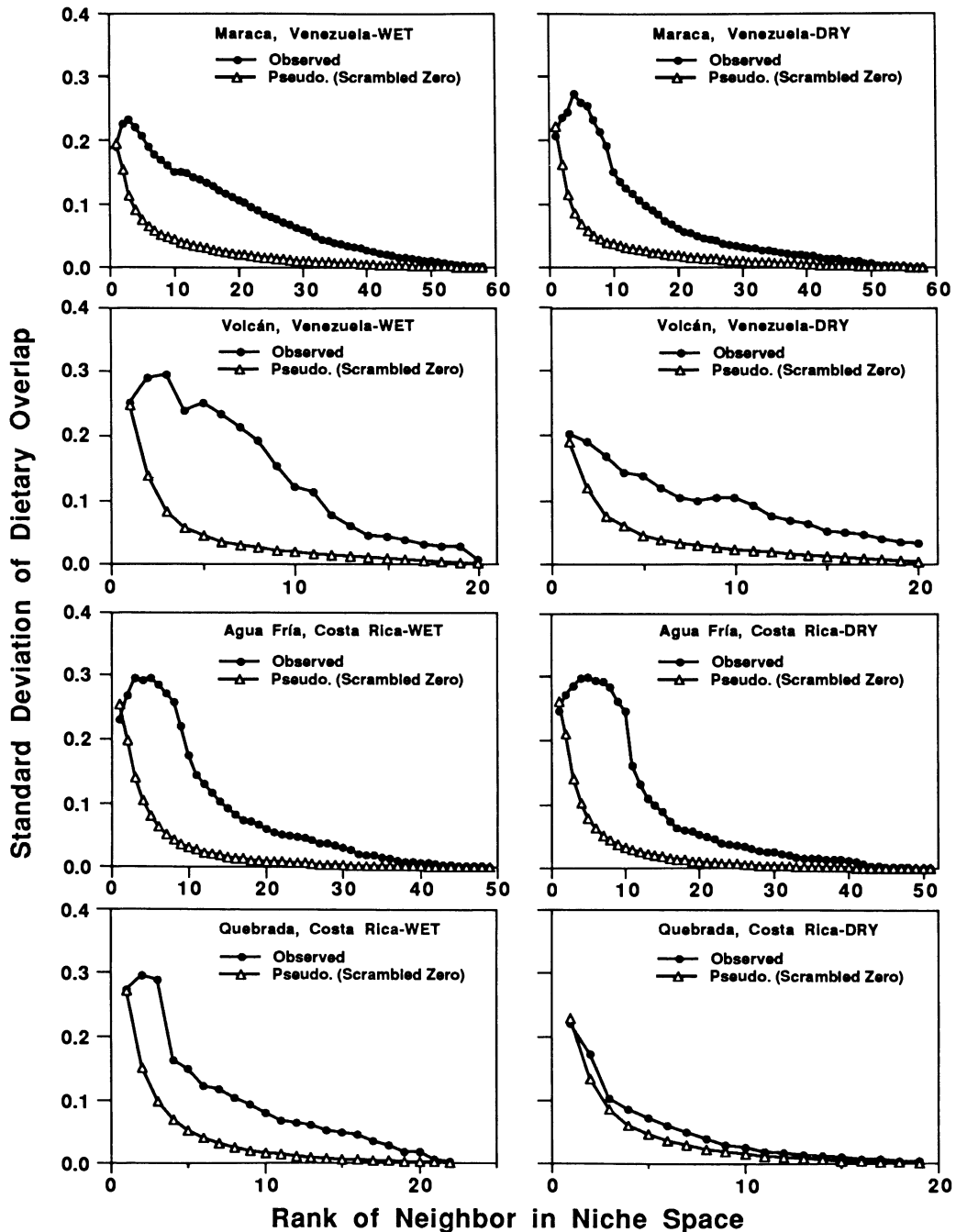


FIG. 6. Plots of the standard deviation of dietary overlap (p -based data) against rank of niche neighbor for two Venezuelan and two Costa Rican fish assemblages during both wet and dry seasons. Guild structure is indicated by the degree that observed curves exhibit a hump and exceed values plotted for the scrambled-zeros pseudo-community.

Bloukrans seems to exhibit a guild structure “hump” in Figs. 8 and 10.) Redsands (201 prey, 15 microhabitats), Laverton (15 microhabitats), and Bloukrans (46 prey) yielded statistically significant patterns of average resource segregation among lizards, and several other tests “lean” in the same direction (Table 5). A scaled-down analysis (overlaps by rank of niche neighbor) shows significant resource segregation among various

niche neighbors in four of the six Australian tests (Fig. 13) and segregation at intermediate ranks among all but one of the four African lizard tests (Fig. 14).

Product moment correlations were performed for number of consumer species, mean sample size, and number of resource states with: (1) percent zeros in resource matrix, and (2) mean observed overlap. Significant correlations ($P < .05$) were obtained for num-

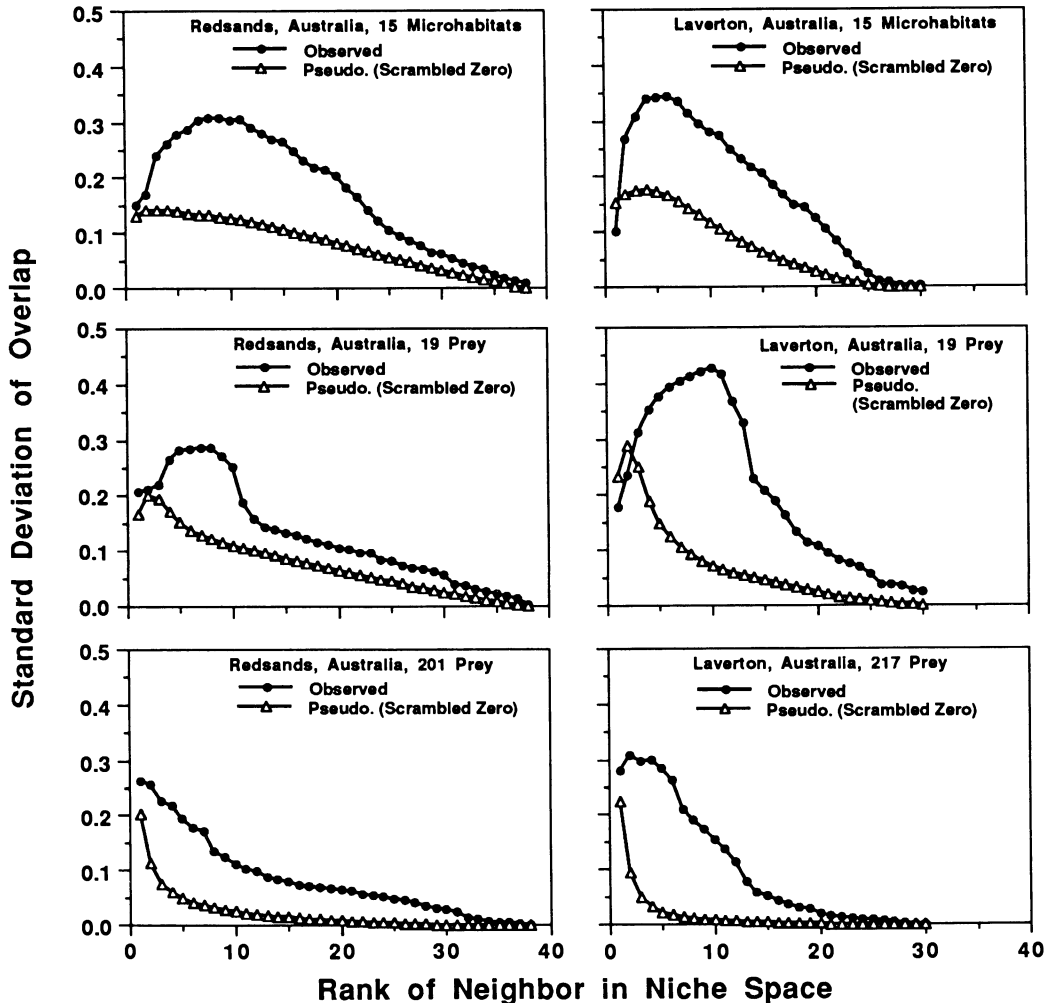


FIG. 7. Plots of the standard deviation (p_i -based data) of microhabitat overlap (top graphs), standard deviation of dietary overlap based on 19 condensed states (middle), and standard deviation of dietary overlap based on detailed prey categories (bottom) against rank of niche neighbor for two Australian desert lizard assemblages. Relative guild structure is interpreted in the same manner as Fig. 6.

ber of consumers with percent zeros in matrix ($r = 0.65$), number of consumers with mean overlap ($r = -0.48$), number of resource states with percent zeros in matrix ($r = 0.75$), and number of resource states with mean overlap ($r = -0.78$). Of the four, only the relationships between number of resource states with average overlap and percent zeros in the resource matrix are appreciably high, and in fact, might be logically expected. (More resource states translate to more opportunities to miss rare items while sampling, either as a consumer, or as an investigator sampling consumers.)

DISCUSSION

The hybrid technique of merging null models with ranked niche neighbors we have developed and adopted here has considerable potential for analyzing patterns of resource utilization in diverse natural assemblages. Obviously this analysis is limited in that only horizontal interactions are addressed (as perceived through vertical interactions in the case of food resource matrices). In this respect, methods proposed here have limited applicability to other aspects of community structure, for example some of the community

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FIG. 9. Plots of the standard deviation (g_i -based data) of microhabitat overlap (top), standard deviation of dietary overlap based on 19 condensed states (middle), and standard deviation of dietary overlap based on detailed prey categories (bottom) against rank of niche neighbor for two Australian desert lizard assemblages. Relative guild structure is interpreted in the same manner as Fig. 6. Compare with Fig. 7.

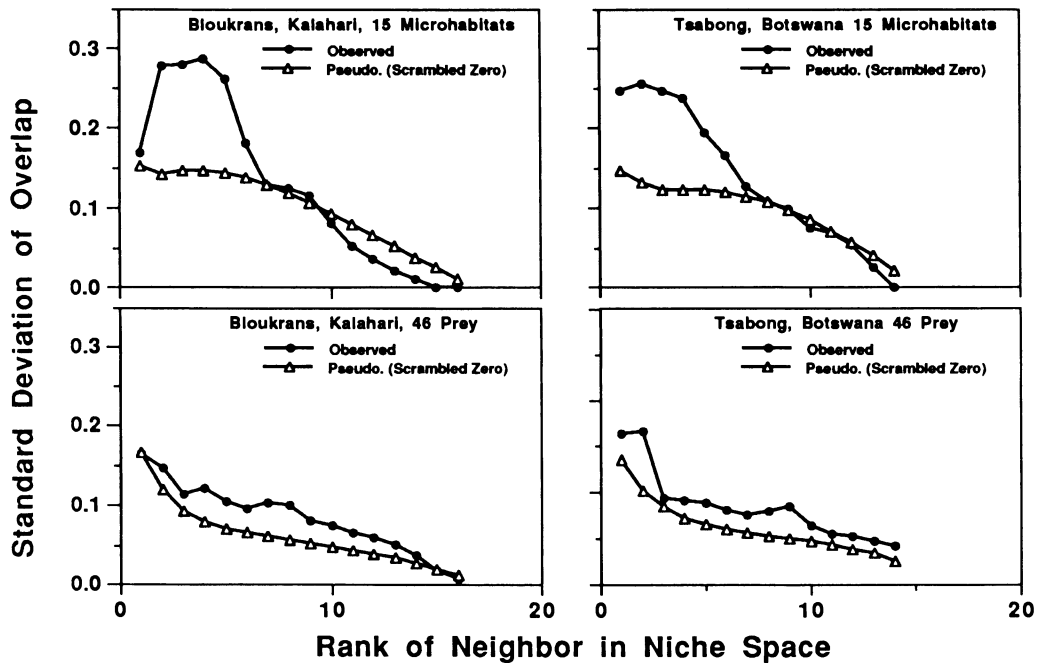
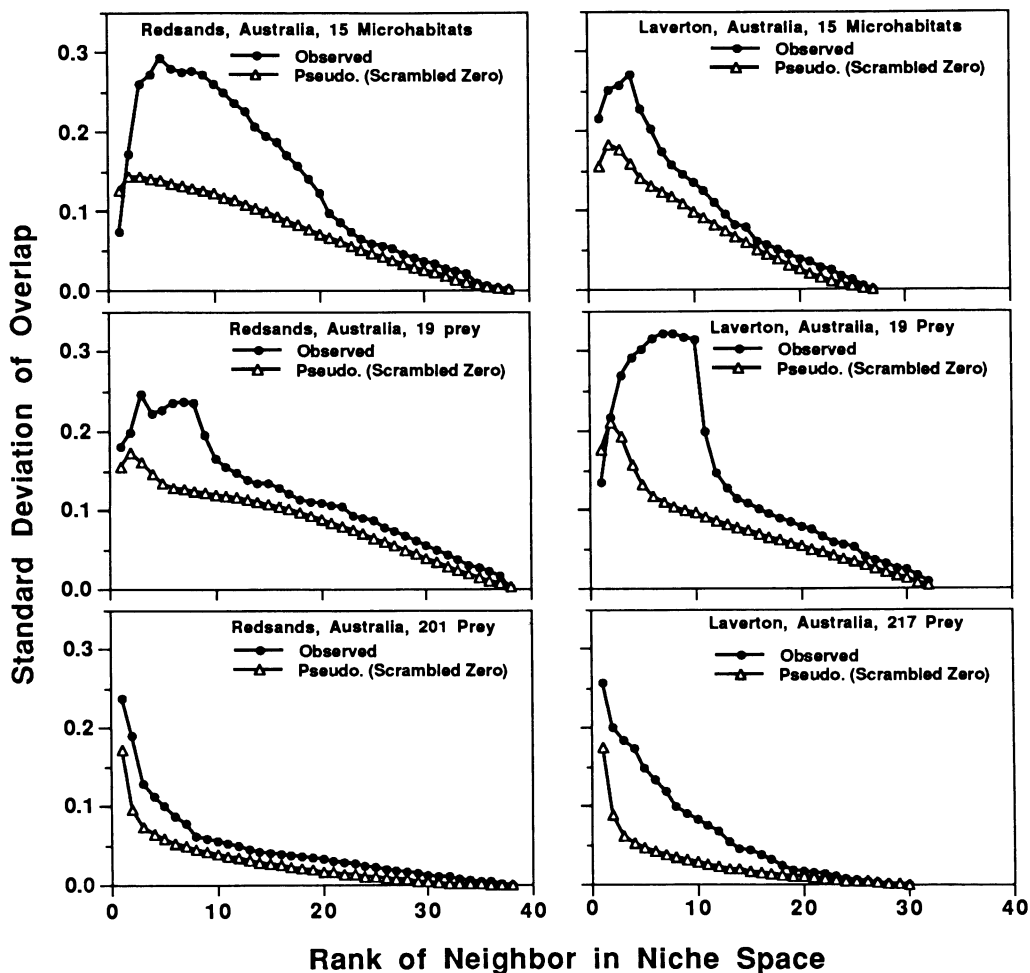


FIG. 8. Plots of the standard deviation (p_i -based data) of microhabitat overlap (top) and standard deviation of dietary overlap (bottom) against rank of niche neighbor for two African desert lizard assemblages.



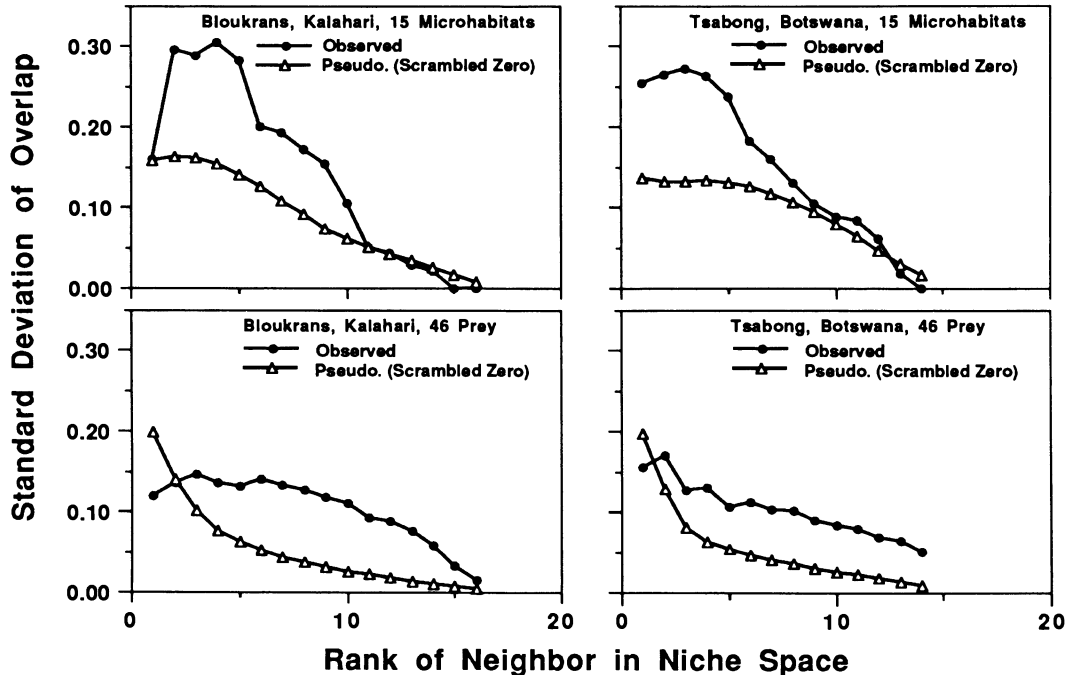


FIG. 10. Plots of the standard deviation (g -based data) of microhabitat overlap (top) and standard deviation of dietary overlap (bottom) against rank of niche neighbor for two African desert lizard assemblages. Compare with Fig. 8.

properties addressed by food web theory (Paine 1980, Pimm 1982). Complex, multidimensional networks of horizontal pairwise interactions can be reduced and graphically summarized in a manner that makes community structure more transparent and easily interpreted (Inger and Colwell 1977). The marriage of the nearest neighbor graphical approach of Inger and Col-

well (1977) with the random models paradigm (Nitecki and Hoffman 1987) provides a powerful research protocol for a young discipline in desperate need of biometric tools for dealing with complex, multidimensional, real-world data.

Several important statements can be made about the eight vertebrate assemblages investigated using the

TABLE 5. Statistics for 18 separate bootstrap tests of observed desert lizard and tropical fish assemblages (g -based). The proportion of nearest neighbor ranks with pseudo-community average overlap above (conserved zero) or below (scrambled zero) the observed value in ≥ 95 cases out of 100 is also given; chi-square significance levels of these comparisons are indicated.

Site (season)	No. species	Mean sample size	No. resource categories	Percent zeros in matrix	Proportion of pseudo-communities different from observed		Mean overlap
					Conserved	Scrambled	
Redsands	39	36.8	201 (prey)	89.1	.92**	1.0**	.071
Redsands	39	36.8	19 (prey)	59.8	0 NS	.92**	.215
Redsands	39	36.8	15 (microhabitat)	69.6	.63**	.94**	.235
Laverton	31	50.5	217 (prey)	89.8	.37 NS	.93**	.088
Laverton	31	50.5	19 (prey)	67.2	0 NS	1.0**	.241
Laverton	31	50.5	15 (microhabitat)	71.4	.81**	.87**	.223
Bloukrans	17	34.4	40 (prey)	65.9	.56*	.87**	.196
Bloukrans	17	34.4	15 (microhabitat)	67.5	.25 NS	.31 NS	.229
Tsabong	15	76.3	41 (prey)	53.0	0 NS	1.0**	.352
Tsabong	15	76.3	15 (microhabitat)	62.2	.29 NS	.14 NS	.255
Caño Maraca (wet)	59	49.5	94 (prey)	76.1	.75**	.98**	.119
C. Maraca (dry)	59	75.6	105 (prey)	75.5	.83**	.68**	.096
Caño Volcán (wet)	19	68.0	68 (prey)	66.5	.35*	.68**	.150
C. Volcán (dry)	19	81.8	78 (prey)	70.0	.52**	.63**	.162
Caño Agua Fría (wet)	50	38.0	82 (prey)	82.4	.61**	.90**	.089
C. Agua Fría (dry)	51	40.5	82 (prey)	82.8	.61**	.90**	.087
Quebrada (wet)	23	46.0	67 (prey)	73.1	.50**	.74**	.088
Quebrada (dry)	20	52.4	68 (prey)	72.9	.84**	0 NS	.075

* = $P < .05$, ** = $P < .01$, NS = not significant.

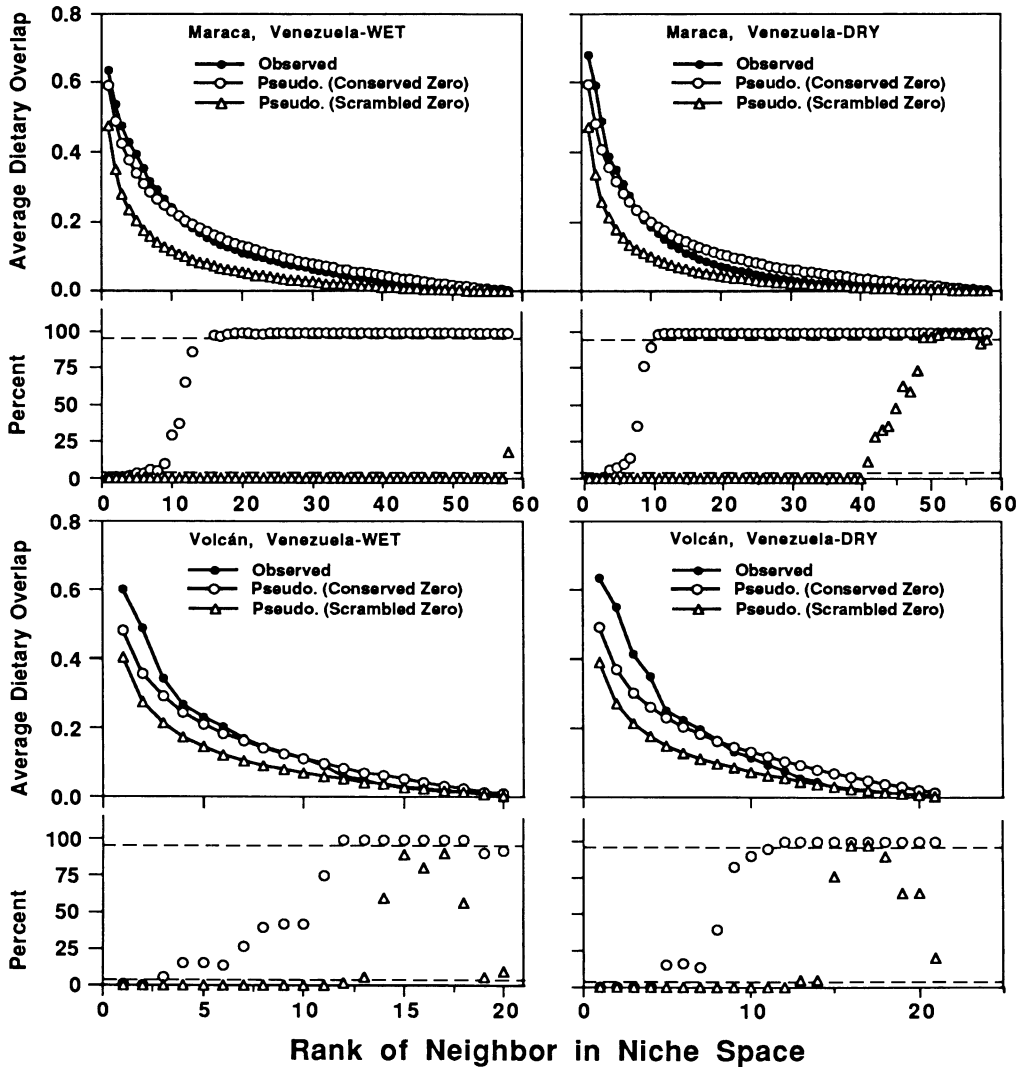


FIG. 11. Plots of average observed dietary overlap against rank of niche neighbors for two Venezuelan fish assemblages during wet and dry seasons (*g*-based data). Pseudo-community data are based on 100 computer randomizations of the observed prototype. Conserved-zeros pseudo-community plots lie above observed plots, indicating a high degree of resource segregation. Scrambled-zeros pseudo-community plots lie below observed plots, indicating guild structure. The lower portion of each plot shows the percent of pseudo-community means greater than the observed mean at each rank in niche space.

community randomization protocol. With the aid of graphical comparisons, the large magnitude of guild structure in desert lizard assemblages is readily apparent (Figs. 7–10). With the possible exception of low-diversity systems during certain seasons, tropical fish assemblages were also well organized into trophic guilds. This result will not surprise fish biologists familiar with various species of algae-, detritus-, invertebrate-, seed-, and fish-eating fishes likely to occur together at a given site in the tropics. Moreover, the graphical technique of analysis developed here permits sensitive comparisons between assemblages; such comparisons would be difficult and largely subjective were each species evaluated independently of the system as a whole. Recent advances in methods for statistical inference in cluster analysis could have considerable promise for

guild analysis as well (Felsenstein 1985, Nemeč and Brinkhurst 1988). Moreover, Monte Carlo randomizations provide an objective basis for statistical inference (Pimm 1979, Diaconis and Efron 1983, Mueller and Altenberg 1985, Wimsatt 1987).

Significant patterns of resource segregation based on the conserved-zeros randomization indicate that some of these communities are highly organized. For example, the proportion of significantly low observed dietary overlaps (i.e., less than predicted by random expectations) at various ranks in niche space was greatest for the 59-species Caño Maraca assemblage during the dry season, when fishes coexist at extremely high densities in shrinking bodies of water in the llanos (Fig. 11). Fish densities during this period are among the highest recorded for freshwaters (Winemiller 1987).

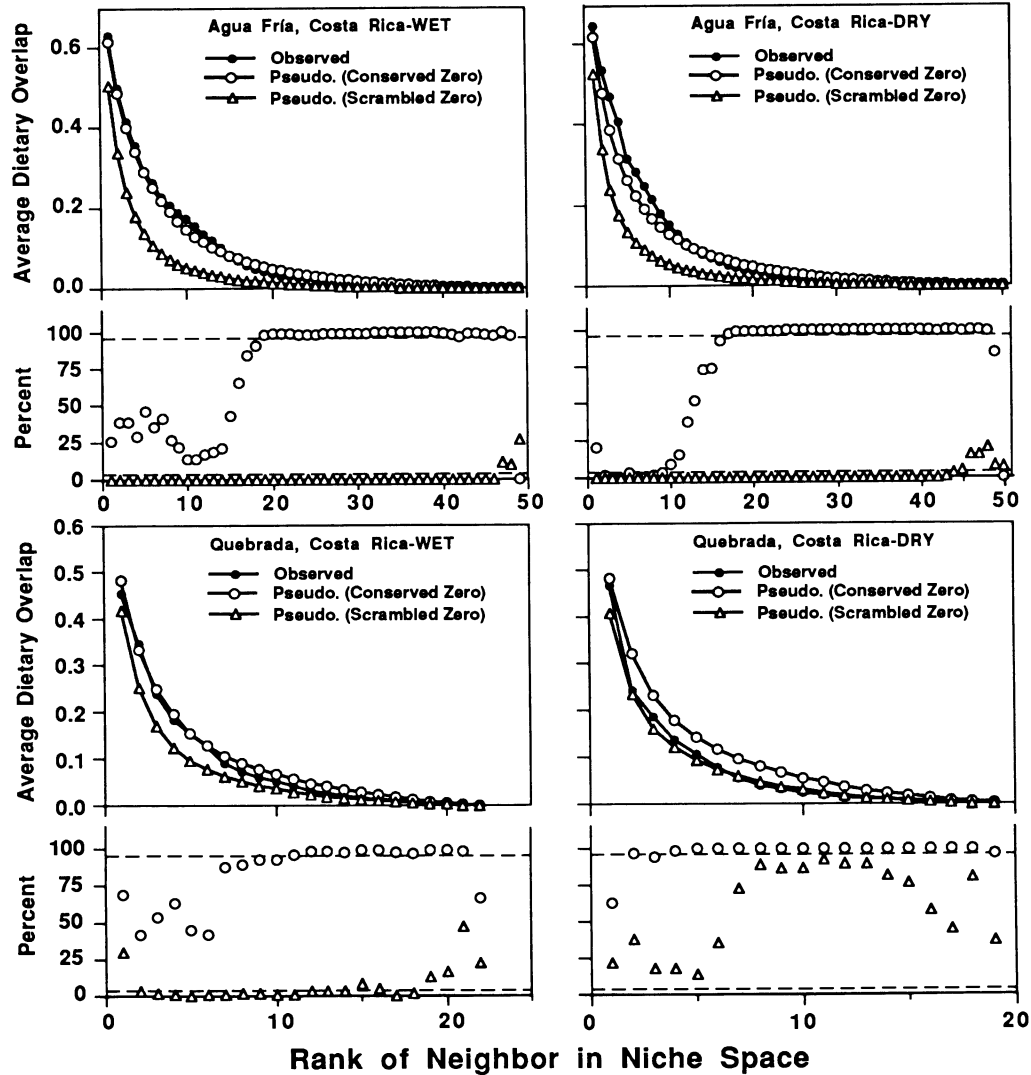
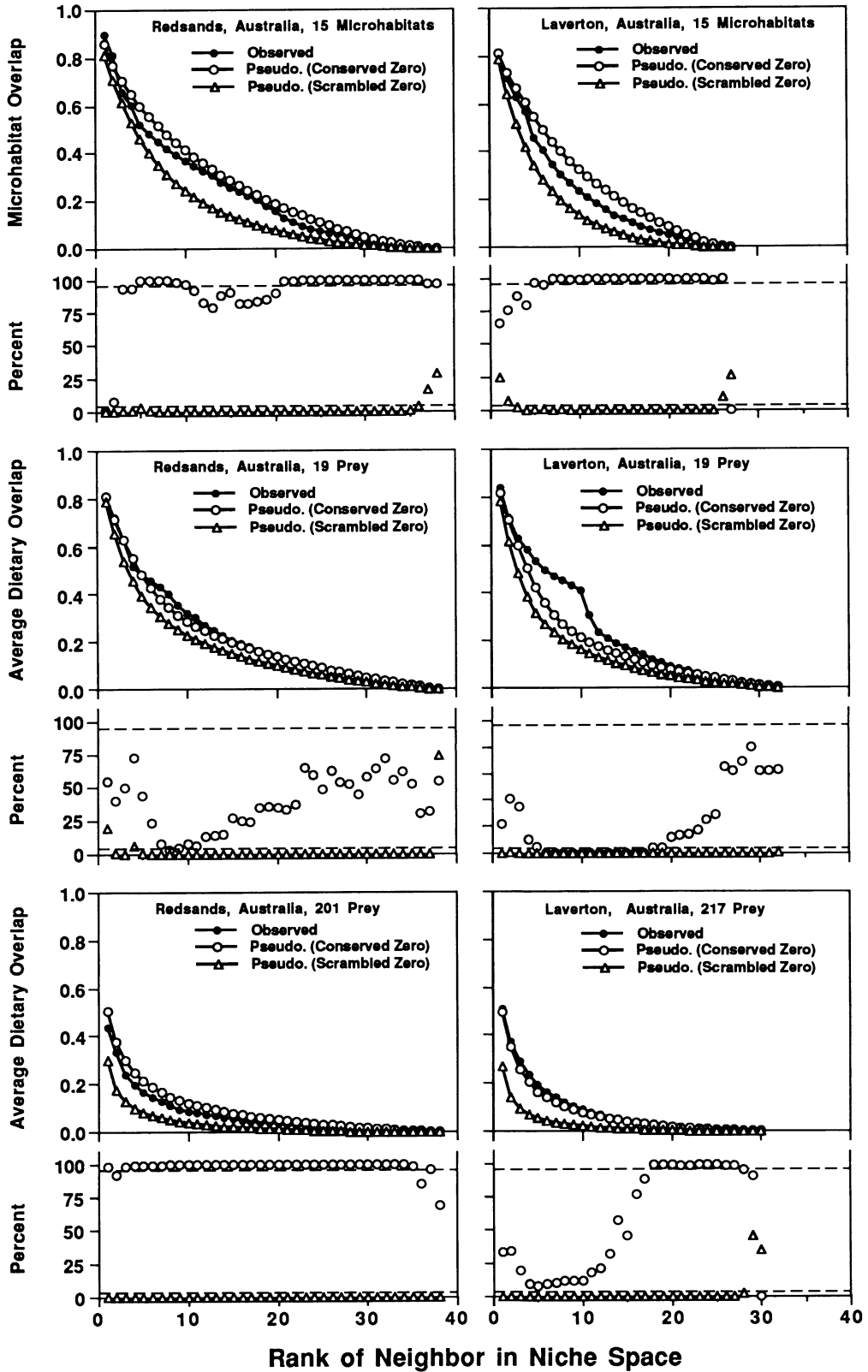


FIG. 12. Average observed dietary overlap plotted against rank of niche neighbors for two Costa Rican fish assemblages during wet and dry seasons (g_i -based data). Again, pseudo-community data are based on 100 computer randomizations of the observed prototype, and the lower portion of each plot shows the percent of pseudo-community means greater than the observed mean at each rank in niche space. Conserved-zeros pseudo-community plots lie above observed, indicating a high degree of resource segregation. For all assemblages except Quebrada-dry, scrambled-zeros pseudo-community plots lie below observed plots, indicating guild structure.

Mean g -based dietary overlap was 0.12 during the wet season and 0.10 during the dry season. Fish densities were much lower, and aquatic productivity and availability of invertebrate prey were greater during the wet season than during the dry season (Winemiller 1987). While this analysis is purely descriptive, patterns are consistent with a hypothesis of niche compression in response to diffuse competition during temporal reduction in availability of preferred food resources (Pianka 1972, 1974, Rusterholz 1981, Winemiller

1989a). Similar seasonal trends are also evident in the other three fish systems (Figs. 11 and 12). Due to the effect of greater water current velocities from runoff, substrate scouring at Agua Fria, the most energy-rich food resources are probably less available for most fish species during the wet rather than the dry season (Winemiller 1987). Standing stocks of aquatic primary producers are greatest at C. Agua Fria Viejo during the dry season. This illustrates a possible source of variation in assemblage-wide analysis: various trophic

FIG. 13. Plots of average observed overlap (g_i -based data) in microhabitat (top graphs), and diet (middle—19 condensed resource states) and detailed prey categories (bottom) against rank of niche neighbors for two Australian lizard assemblages. Again, pseudo-community data are based on 100 computer randomizations of the observed prototype, and the lower portion



of each plot shows the percent of pseudo-community means greater than the observed mean at each rank in niche space. Except for condensed prey resources, conserved-zeros pseudo-community plots lie above observed at some but not all ranks, indicating significant resource segregation only at certain ranks. In each case, scrambled-zeros pseudo-community plots lie below observed plots, indicating significant guild structure.

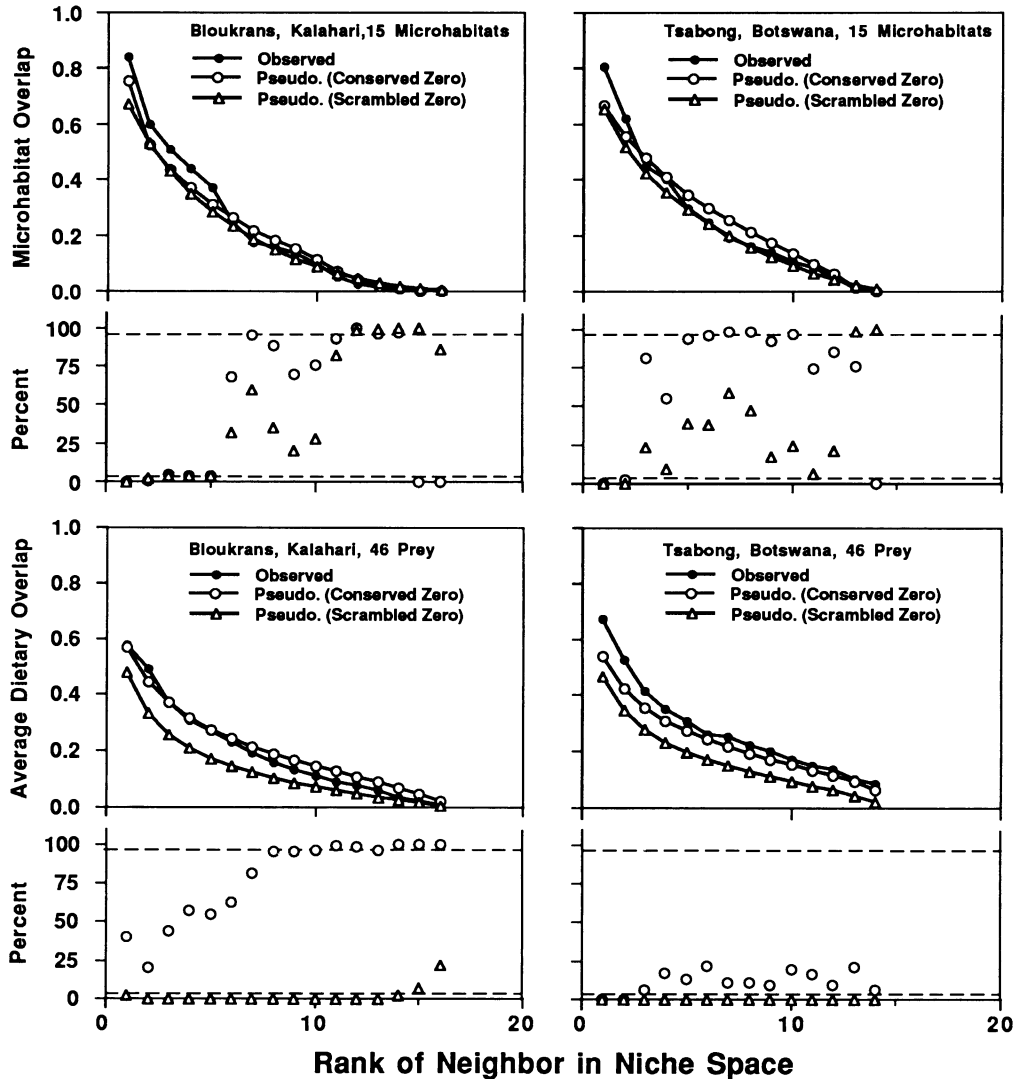


FIG. 14. Average observed microhabitat overlap (g_r -based data) based on detailed resource states (top graphs) and average observed dietary overlap (bottom) plotted against rank of niche neighbors for two Kalahari lizard assemblages. Again, pseudo-community data are based on 100 computer randomizations of the observed prototype, and the lower portion of each plot shows the percent of pseudo-community means greater than the observed mean at each rank in niche space. Conserved-zeros pseudo-community plots lie above observed at some ranks in 3 of the 4 plots, indicating resource segregation. In each case, at some ranks scrambled-zeros pseudo-community plots lie below observed, reflecting guild structure.

guilds probably face resource depression during different seasons. As a consequence, seasonal patterns of diet segregation in response to changing food availability might be more easily interpreted if trophic guilds were analyzed as separate units (Winemiller 1987, 1989a).

Both Australian lizard assemblages clearly exhibited both guild structure and resource partitioning within guilds in diet as well as microhabitat (Figs. 7 and 9). Dietary guilds were larger at Laverton than at Red-sands, whereas the reverse was true for microhabitats (Fig. 7). In the Kalahari, guild structure is more evident for microhabitat than for diets based on SD graphical analysis (Figs. 8, 10). Diets of many Kalahari lizards are dominated by termites, and as a result dietary segregation was weak. In Australia, neighbors in niche

space are segregated for both diets and microhabitats (Fig. 13). As with the *C. Maraca* fish assemblages, these patterns implicate interspecific competition as a potential mechanism. Since tests with model assemblages indicated that a larger number of resource states does not bias the analysis in favor of patterns of segregation (in fact, the tendency is toward a pattern indicating less segregation, Fig. 4), we believe these patterns are robust. Resource segregation was more apparent in Australia than at the Kalahari sites, particularly within guilds. At Bloukrans, both dietary and microhabitat segregation are significant, whereas only microhabitats are significant at the more productive Tsabong site (Fig. 14).

Recently, Schoener (1986) and Slobodkin (1987)

compared and contrasted reductionism and holism in community ecology. Schoener points out that holistic research paradigms deal primarily with description, while reductionistic approaches can ultimately uncover mechanisms that lead to observed patterns. Both authors aptly convey the basic trade-off between dealing with complexity (a major strength of holism) and the ability to infer mechanistic explanations via negation of alternative hypotheses. In Schoener's view, the future of community ecology may ultimately consist of a collection of theories, each having the power of prediction for limited subsets of species under specific environmental conditions. In our view, the demise of the holistic approach in community ecology would limit our ability to generalize and hence be a tragic mistake that could ultimately doom the discipline as a successful field of scientific endeavor. Ecological communities are collections of many species, thus they are exceedingly complex. To some extent, this complexity must be dealt with in a holistic fashion. The biometrics of community ecology will be inherently multidimensional at best, and rather abstract models of reality at worst. Rapid destruction of natural ecosystems by humans makes it urgent and imperative for community ecology not only to survive as a scientific discipline, but also to catch up with other disciplines in biology. Major new discoveries await serious students of community ecology, although good data will always be in short supply. As well as being of fundamental scientific interest, understanding at the community level is essential for wise management of both natural and artificial ecosystems. Ecologists adopting either primarily mechanistic or holistic approaches to communities must seek and maintain dialogue and mutual respect, as well as work towards a greater integration of approaches.

ACKNOWLEDGMENTS

The randomization algorithms exploited here were invented by P. F. Sale and L. R. Lawlor. Massive amounts of computer time were made available by L. Davis and B. Sanders and the University of Texas Computation Center. For constructive criticism of the manuscript, we thank Rob Colwell, Robert F. Inger, Craig Loehle, Peter F. Sale, Thomas W. Schoener, David Tilman, and Peter Yodzis. We greatly appreciate the support of the University of Western Australia, the Western Australian Museum, Conservation and Land Management staff of the Western Australian Wildlife Research Center, the Los Angeles County Museum of Natural History, the Transvaal Museum in South Africa, the Kalahari Gemsbok National Park, the University of the Western Llanos at Guanare in Venezuela, and the National Park Service of Costa Rica at Tortuguero. We are especially indebted to A. R. Main, G. M. Storr, S. D. Bradshaw, A. A. Burbidge, R. B. Huey, W. F. Giles, W. D. Haacke, D. Taphorn, L. Nico, and A. Barbarino. Field research was supported by the National Geographic Society, the National Science Foundation, the John Simon Guggenheim Memorial Foundation, the Los Angeles County Museum of Natural History Foundation, the National Institute of Health, the Tinker Foundation, and the Denton A. Cooley Centennial Professorship in Zoology at the University of Texas at Austin.

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APPENDIX I

TABLE A. Lizard censuses at two study sites in the Great Victoria Desert. Data are number of lizards caught over 1 yr whose stomachs were examined.

Lizard species	Laverton	Redsands
<i>Ctenophorus clayi</i>		16
<i>Ctenophorus fordi</i>		1
<i>Ctenophorus inermis</i>	5	15
<i>Ctenophorus isolepis</i>	530	209
<i>Gemmatophora longirostris</i>		26
<i>Moloch horridus</i>	9	70
<i>Pogona minor</i>	12	10
<i>Varanus eremius</i>	13	7
<i>Varanus giganteus*</i>		1
<i>Varanus gilleni</i>		1
<i>Varanus gouldi</i>	4	5
<i>Varanus tristis</i>	18	38
<i>Ctenotus ariadnae</i>	11	1
<i>Ctenotus brooksi</i>		4
<i>Ctenotus calurus</i>	147	14
<i>Ctenotus colletti</i>		8
<i>Ctenotus dux</i>		112
<i>Ctenotus grandis</i>	39	5
<i>Ctenotus helenae</i>	31	26
<i>Ctenotus pantherinus</i>	21	25
<i>Ctenotus piankai</i>	3	8
<i>Ctenotus quattuordecimlineatus</i>	183	90
<i>Ctenotus schomburgkii</i>	40	
<i>Cryptoblepharus plagiocephalus</i>	53	
<i>Egernia inornata</i>	2	9
<i>Egernia striata</i>	68	13
<i>Eremiascincus richardsoni</i>		2
<i>Lerista bipes</i>	53	5
<i>Lerista desertorum</i>		1
<i>Lerista muelleri</i>	6	
<i>Menetia greyi</i>	4	1
<i>Morethia butleri</i>	1	1
<i>Omolepida branchiale</i>		3
<i>Delma butleri</i>	4	3
<i>Lialis burtonis*</i>	2	2
<i>Pygopus nigriceps</i>	3	3
<i>Diplodactylus ciliaris</i>		43
<i>Diplodactylus conspicillatus</i>	27	10
<i>Diplodactylus damaeus</i>		20
<i>Diplodactylus elderi</i>	4	13
<i>Diplodactylus stenodactylus</i>	2	
<i>Diplodactylus strophurus</i>		12
<i>Gehyra purpurascens</i>	202	378
<i>Heteronotia binoei</i>	1	1
<i>Nephrurus laevis</i>		193
<i>Nephrurus levis</i>	4	
<i>Rhynchoedura ornata</i>	64	31
Total number of individuals	1565	1436
Total number of species	32	42

* Not included in present analyses.

TABLE B. Lizard censuses at two study sites in the Kalahari Desert. Data are number of lizards caught over 1 yr whose stomachs were examined.

Lizard species	Bloukrans	Tsabong
<i>Agama hispida</i>	44	11
<i>Chameleo dilepis*</i>		2
<i>Eremias lineo-ocellata</i>	95	140
<i>Eremias lugubris</i>		125
<i>Eremias namaquensis</i>	19	34
<i>Ichnotropis squamulosa</i>		110
<i>Merole suborbitalis</i>	25	
<i>Nucras intertexta</i>		3
<i>Nucras tessellata</i>	26	
<i>Mabuya occidentalis</i>	29	29
<i>Mabuya spilogaster</i>		222
<i>Mabuya striata</i>	128	
<i>Mabuya variegata</i>	8	3
<i>Typhlosaurus gariepensis</i>	70	
<i>Typhlosaurus lineatus</i>	32	104
<i>Chondrodactylus angulifer</i>	46	71
<i>Colopus wahlbergi</i>	4	74
<i>Lygodactylus capensis</i>	18	
<i>Pachydactylus bibroni</i>	32	1
<i>Pachydactylus capensis</i>	3	34
<i>Pachydactylus rugosus</i>	3	
<i>Ptenopus garrulus</i>	3	182
Total number of individuals	585	1145
Total number of species	17	16

* Not included in present analyses.

TABLE C. Fish censuses at two study sites in Costa Rica. Data are number of fish in subsamples whose stomachs were examined.

Fish species	Caño Agua Fria Viejo	Quebrada
<i>Atractosteus tropicus</i>	11	
<i>Anchoiella elongata</i>	2	
<i>Anchoa lamprotaenia</i> *	1	
<i>Anguilla rostrata</i>	11	
<i>Astyanax fasciatus</i>	1798	402
<i>Astyanax nasutus</i> *	1	
<i>Bramocharax bransfordi</i> *	1	
<i>Brycon guatemalensis</i>	116	
<i>Carlana eigenmanna</i>	9	
<i>Hyphesobrycon tortuguerae</i>	2	4
<i>Roeboides guatemalensis</i>	123	
<i>Gymnotus cylindricus</i>	3	18
<i>Rhamdia guatemalensis</i>	1	466
<i>Strongylura timucu</i>	7	
<i>Rivulus isthmensis</i>	270	52
<i>Alfaro cultratus</i>	240	917
<i>Belonesox belizanus</i>	221	3
<i>Brachyrhaphis parismina</i>	60	
<i>Phallichthys amates</i>	1343	
<i>Poecilia gilli</i>	1213	518
<i>Melaniris hubbsi</i>	478	
<i>Oostethus lineatus</i>	379	34
<i>Pseudophallus mindii</i> *	1	
<i>Synbranchus marmoratus</i>	7	3
<i>Centropomus ensiferus</i> *	1	
<i>Centropomus parraleleus</i>	5	
<i>Centropomus pectinatus</i>	18	
<i>Centropomus undecimalis</i>	4	
<i>Agonostomus monticola</i>	3	
<i>Mugil curema</i> *	1	
<i>Lutjanus griseus</i> *	1	
<i>Lutjanus jocu</i>	48	
<i>Diapterus plumieri</i>	3	
<i>Diapterus rhombeus</i>	4	
<i>Eucinostomus pseudogula</i>	3	
<i>Pomadasys crocro</i>	122	
<i>Cichlasoma alfaroi</i>	34	24
<i>Cichlasoma centrarchus</i>	345	
<i>Cichlasoma citrinellum</i>	84	
<i>Cichlasoma dovii</i>	159	
<i>Cichlasoma cf. friedrichsthalii</i>	944	162
<i>Cichlasoma maculicauda</i>	451	7
<i>Cichlasoma managuense</i> *	1	
<i>Cichlasoma nigrofasciatum</i>	133	179
<i>Cichlasoma rostratum</i>	11	
<i>Cichlasoma septemfasciatum</i>	7	
<i>Herotilapia multispinosum</i>	4	20
<i>Dormitator maculatus</i>	251	83
<i>Eleotris amblyopsis</i>	1692	934
<i>Eleotris pisonis</i>	278	10
<i>Gobiomorus dormitor</i>	168	55
<i>Evorthodus lyricus</i>	84	48
<i>Gobionellus fasciatus</i>	142	
<i>Gobionellus pseudofasciatus</i>	2	
<i>Gobiosoma spes</i>	10	2
<i>Citharichthys spilopterus</i>	22	
<i>Achirus lineatus</i>	100	
<i>Trinectes paulistanus</i>	117	
<i>Sphoeroides testudineus</i> *	1	2
Total number of individuals	11 537	7719
Total number of species	59	23

* Not included in present analysis.

TABLE D. Fish censuses at two study sites in Venezuela. Data are number of fish in subsamples whose stomachs were examined.

Fish species	Caño Maraca	Caño Volcán
<i>Hoplias malabaricus</i>	521	152
<i>Hoplerethrinus unitaeniatus</i>	14	
<i>Characidium</i> sp. 1	237	
<i>Characidium</i> sp. 2	32	
<i>Lebiasina erythrinoides</i>		473
<i>Pyrrhulina cf. lugubris</i>	363	
<i>Leporinus friderici</i>	72	
<i>Schizodon isognathus</i>	92	
<i>Curimata argentea</i>	2496	
<i>Curimata cerasina</i>	22	
<i>Prochilodus mariae</i>	623	12
<i>Acestrorhynchus microlepis</i> *	2	
<i>Aphyocharax alburnus</i>	757	
<i>Astyanax bimaculatus</i>	1299	191
<i>Astyanax integer</i>		30
<i>Astyanax metae</i>		271
<i>Astyanax superbus</i>		10
<i>Brycon whitei</i>		18
<i>Bryconamericus beta</i>	51	2667
<i>Bryconamericus deuterodonoides</i>		8
<i>Charax gibbosus</i>	331	
<i>Cheirodontops geayi</i>	112	
<i>Colossoma macropomum</i> *	1	
<i>Corynopoma riisei</i>		344
<i>Creagrutus</i> sp.		993
<i>Ctenobrycon spilurus</i>	2390	
<i>Gephyrocharax valenciae</i>	1249	
<i>Gymnocorymbus thayeri</i>	3	
<i>Hemigrammus</i> sp.	231	
<i>Hemigrammus marginatus</i> *	1	
<i>Markiana geayi</i>	1068	
<i>Mylossoma duriventris</i>	8	
<i>Odontostilbe pulcher</i>	3182	
<i>Poptella orbicularis</i>	22	
<i>Piaractus brachypoma</i>	1	
<i>Pygocentrus notatus</i>	238	
<i>Roeboides dayi</i>	1154	280
<i>Serrasalmus irritans</i>	76	
<i>Serrasalmus medini</i>	68	
<i>Serrasalmus rhombeus</i>	50	
<i>Tetragonopterus argentea</i>	200	
<i>Triporthes</i> sp.	744	
<i>Triporthes angulatus</i>	56	
<i>Xenogoniates bondi</i>	16	
<i>Thoracocharax stellatus</i>	412	
<i>Gymnotus carapo</i>	372	
<i>Eigenmannia virescens</i>	276	
<i>Sternopygus macrurus</i>	5	
<i>Hypopomus</i> sp. 1	67	
<i>Hypopomus</i> sp. 2	3	
<i>Apteronotus alburnus</i> *	2	
<i>Adontosternarchus devananzi</i>	59	
<i>Rhamphichthys marmoratus</i>	23	
<i>Ageneiosus vittata</i>	19	
<i>Microglanis iheringi</i>	324	
<i>Pimelodus blochii</i>	8	
<i>Pimelodella</i> sp. 1	9	
<i>Pimelodella</i> sp. 2	332	
<i>Pimelodella</i> sp. 3	217	
<i>Pseudoplatystoma fasciatus</i>	5	
<i>Rhamdia</i> sp. 1	124	
<i>Rhamdia</i> sp. 2		34
<i>Entomocorcorus gameroi</i>	56	
<i>Parauchenipterus galeatus</i>	223	
<i>Ochmacanthus alternus</i>	545	
<i>Bunocephalus</i> sp.	902	
<i>Callichthys callichthys</i> *	1	
<i>Corydoras aeneus</i>	412	

TABLE D. Continued.

Fish species	Caño Maraca	Caño Volcán
<i>Corydoras habrosus</i>	647	
<i>Corydoras septentrionalis</i>	248	
<i>Hoplosternum littorale</i>	232	
<i>Ancistrus</i> sp.	62	243
<i>Cochliodon plecostomoides</i>	6	
<i>Farlowella</i> sp.*	1	
<i>Hypostomus argus</i>	379	337
<i>Hypoptopoma</i> sp.	52	
<i>Loricarichthys typus</i>	501	
<i>Otocinclus</i> sp.	686	
<i>Pterygoplichthys multiradiatus</i>	479	
<i>Rineloricaria caracasensis</i>	628	
<i>Sturisoma</i> sp.*	1	
<i>Pterolebias hoignei</i>	2	
<i>Rachovia maculipinnis</i>	131	
<i>Poecilia reticulata</i>	313	2400
<i>Synbranchus marmoratus</i>	95	6
<i>Apistogramma hoignei</i>	219	
<i>Astronotus ocellatus</i>	176	
<i>Aequidens pulcher</i>	755	651
<i>Caquetia kraussii</i>	795	
<i>Cichlasoma orinocense</i>	365	
<i>Crenicichla geayi</i>	1	174
<i>Crenicichla saxatilis</i>	23	
Total number of individuals	29 324	9294
Total number of species	83	20

* Not included in present analyses.

APPENDIX II

Model resource matrices.

Consumer	Resource									
	1	2	3	4	5	6	7	8	9	10
Trial 1 (Two equal guilds, very high overlap)										
A	.305	.200	.150	.095	.250	0	0	0	0	0
B	.300	.205	.150	.100	.245	0	0	0	0	0
C	.295	.200	.155	.100	.250	0	0	0	0	0
D	.300	.195	.150	.105	.250	0	0	0	0	0
E	.300	.200	.145	.100	.255	0	0	0	0	0
F	0	0	0	0	0	.305	.200	.150	.095	.250
G	0	0	0	0	0	.300	.205	.150	.100	.245
H	0	0	0	0	0	.295	.200	.155	.100	.250
I	0	0	0	0	0	.300	.195	.150	.105	.250
J	0	0	0	0	0	.300	.200	.145	.100	.255
Trial 2 (Two equal guilds, moderate overlap)										
A	.30	.20	.15	.10	.25	0	0	0	0	0
B	.20	.15	.10	.25	.30	0	0	0	0	0
C	.15	.10	.25	.30	.20	0	0	0	0	0
D	.10	.25	.30	.20	.15	0	0	0	0	0
E	.25	.30	.20	.15	.10	0	0	0	0	0
F	0	0	0	0	0	.30	.20	.15	.10	.25
G	0	0	0	0	0	.20	.15	.10	.25	.30
H	0	0	0	0	0	.15	.10	.25	.30	.20
I	0	0	0	0	0	.10	.25	.30	.20	.15
J	0	0	0	0	0	.25	.30	.20	.15	.10

APPENDIX II. Continued.

Consumer	Resource									
	1	2	3	4	5	6	7	8	9	10
Trial 3 (Two equal guilds, low overlap)										
A	.600	.150	.075	.050	.125	0	0	0	0	0
B	.125	.600	.150	.075	.050	0	0	0	0	0
C	.050	.125	.600	.150	.075	0	0	0	0	0
D	.075	.050	.125	.600	.150	0	0	0	0	0
E	.150	.075	.050	.125	.600	0	0	0	0	0
F	0	0	0	0	0	.600	.150	.075	.050	.125
G	0	0	0	0	0	.125	.600	.150	.075	.050
H	0	0	0	0	0	.050	.125	.600	.150	.075
I	0	0	0	0	0	.075	.050	.125	.600	.150
J	0	0	0	0	0	.150	.075	.050	.125	.600
Trial 4 (Two unequal guilds, high overlap)										
A	.300	.200	.150	.099	.251	0	0	0	0	0
B	.300	.200	.150	.100	.250	0	0	0	0	0
C	.300	.200	.151	.100	.250	0	0	0	0	0
D	0	0	0	0	0	.300	.200	.150	.099	.250
E	0	0	0	0	0	.300	.200	.150	.100	.250
F	0	0	0	0	0	.300	.200	.151	.100	.250
G	0	0	0	0	0	.300	.199	.150	.100	.250
H	0	0	0	0	0	.300	.200	.149	.100	.251
I	0	0	0	0	0	.300	.200	.150	.099	.250
J	0	0	0	0	0	.300	.200	.150	.100	.250
Trial 5 (Two unequal guilds, moderate overlap)										
A	.30	.20	.15	.10	.25	0	0	0	0	0
B	.20	.15	.10	.25	.30	0	0	0	0	0
C	.25	.30	.20	.15	.10	0	0	0	0	0
D	0	0	0	0	0	.15	.10	.25	.30	.20
E	0	0	0	0	0	.10	.25	.30	.20	.15
F	0	0	0	0	0	.30	.20	.15	.10	.25
G	0	0	0	0	0	.20	.15	.10	.25	.30
H	0	0	0	0	0	.15	.10	.25	.30	.20
I	0	0	0	0	0	.10	.25	.30	.20	.15
J	0	0	0	0	0	.25	.30	.20	.15	.10
Trial 6 (Two unequal guilds, low overlap)										
A	.500	.150	.100	.050	.200	0	0	0	0	0
B	.150	.100	.050	.200	.500	0	0	0	0	0
C	.200	.500	.150	.100	.050	0	0	0	0	0
D	0	0	0	0	0	.100	.050	.200	.500	.150
E	0	0	0	0	0	.050	.200	.500	.150	.100
F	0	0	0	0	0	.500	.150	.100	.050	.200
G	0	0	0	0	0	.150	.100	.050	.200	.500
H	0	0	0	0	0	.100	.050	.200	.500	.150
I	0	0	0	0	0	.050	.200	.500	.150	.100
J	0	0	0	0	0	.200	.500	.150	.100	.050
Trial 7 (No guilds, high overlap)										
A	.30	.20	.15	.10	.25	0	0	0	0	0
B	0	.20	.15	.10	.25	.30	0	0	0	0
C	0	0	.15	.10	.25	.30	.20	0	0	0
D	0	0	0	.10	.25	.30	.20	.15	0	0
E	0	0	0	0	.25	.30	.20	.15	.10	0
F	0	0	0	0	0	.30	.20	.15	.10	.25
G	.30	0	0	0	0	0	.20	.15	.10	.25
H	.30	.20	0	0	0	0	0	.15	.10	.25
I	.30	.20	.15	0	0	0	0	0	.10	.25
J	.30	.20	.15	.10	0	0	0	0	0	.25

APPENDIX II. Continued.

Consumer	Resource									
	1	2	3	4	5	6	7	8	9	10
Trial 8 (No guilds, moderate overlap)										
A	.30	.20	.15	.10	.25	0	0	0	0	0
B	0	.15	.10	.25	.30	.20	0	0	0	0
C	0	0	.25	.30	.20	.15	.10	0	0	0
D	0	0	0	.20	.15	.10	.25	.30	0	0
E	0	0	0	0	.10	.25	.30	.20	.15	0
F	0	0	0	0	0	.30	.20	.15	.10	.25
G	.20	0	0	0	0	0	.15	.10	.25	.30
H	.15	.10	0	0	0	0	0	.25	.30	.20
I	.10	.25	.30	0	0	0	0	0	.20	.15
J	.25	.30	.20	.15	0	0	0	0	0	.10
Trial 9 (No guilds, low overlap)										
A	.600	.150	.075	.050	.125	0	0	0	0	0
B	0	.075	.050	.125	.600	.150	0	0	0	0
C	0	0	.125	.600	.150	.075	.050	0	0	0
D	0	0	0	.150	.075	.050	.125	.600	0	0
E	0	0	0	0	.050	.125	.600	.150	.075	0
F	0	0	0	0	0	.600	.150	.075	.050	.125
G	.150	0	0	0	0	0	.075	.050	.125	.600
H	.075	.050	0	0	0	0	0	.125	.600	.150
I	.050	.125	.600	0	0	0	0	0	.150	.075
J	.125	.600	.150	.075	0	0	0	0	0	.050
Trial 10 (Core resources, high overlap)										
A	.30	.20	.15	.25	.10	0	0	0	0	0
B	.30	.20	.15	.25	0	.10	0	0	0	0
C	.30	.20	.15	.25	0	0	.10	0	0	0
D	.30	.20	.15	.25	0	0	0	.10	0	0
E	.30	.20	.15	.25	0	0	0	0	.10	0
F	.30	.20	.15	.25	0	0	0	0	0	.10
G	.30	.20	.15	.25	.10	0	0	0	0	0
H	.30	.20	.15	.25	0	.10	0	0	0	0
I	.30	.20	.15	.25	0	0	.10	0	0	0
J	.30	.20	.15	.25	0	0	0	.10	0	0
Trial 11 (Core resources, moderate overlap)										
A	.20	.15	.10	.25	.30	0	0	0	0	0
B	.15	.10	.25	.20	0	.30	0	0	0	0
C	.10	.25	.20	.15	0	0	.30	0	0	0
D	.25	.20	.15	.10	0	0	0	.30	0	0
E	.20	.15	.10	.25	0	0	0	0	.30	0
F	.15	.10	.25	.20	0	0	0	0	0	.30
G	.10	.25	.20	.15	.30	0	0	0	0	0
H	.25	.20	.15	.10	0	.30	0	0	0	0
I	.20	.15	.10	.25	0	0	.30	0	0	0
J	.15	.10	.25	.20	0	0	0	.30	0	0
Trial 12 (Core resources, moderate overlap, 100 states)										
Consumer	Resource									
	1-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100
A	(each) .020	.015	.010	.025	.030	0	0	0	0	0
B	(each) .015	.010	.025	.020	0	.030	0	0	0	0
C	(each) .010	.025	.020	.015	0	0	.030	0	0	0
D	(each) .025	.020	.015	.010	0	0	0	.030	0	0
E	(each) .020	.015	.010	.025	0	0	0	0	.030	0
F	(each) .015	.010	.025	.020	0	0	0	0	0	.030
G	(each) .010	.025	.020	.015	.030	0	0	0	0	0
H	(each) .025	.020	.015	.010	0	.030	0	0	0	0
I	(each) .020	.015	.010	.025	0	0	.030	0	0	0
J	(each) .015	.010	.025	.020	0	0	0	.030	0	0