Guild structure in desert lizards

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How are communities organized? To what extent are species evenly spread out in niche/resource space? Do clusters of functionally similar species exist? If so, are such guilds merely a result of built-in design constraints on consumer species and/or natural gaps in resource space? Or, can guild structure evolve as a means of reducing diffuse competition? (Guilds are presumably arenas of intense interspecific competition with strong interactions within guilds but weak interactions between members of different guilds. A community without guild structure would have greater diffuse competition than one with guild structure.) Do more diverse communities have more guild structure than simpler communities? What are the effects of guild structure on the assembly, structure and diversity of communities? Guild structure may actually foster diversity by means of competitive mutualisms arising from the indirect effects between species that belong to different guilds.

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1. Introduction

Community ecology is in its infancy: "there is no standard protocol for community analysis" (Inger and Colwell 1977). At the community level of organization, choice of appropriate "macro" descriptors or aggregate variables may be vital to progress: community ecology both depends upon and yet is simultaneously constrained by the identification of such conceptual building blocks (Orions 1980). To be useful, these macrodescriptors must oversimplify population-level processes while retaining their essence. Here I explore the utility of such an aggregate variable, the notion of guild structure.

Root (1967) coined the term "guild" to describe groups of functionally similar species in a community, such as foliage-gleaning insectivorous birds. In competitive communities, guilds would represent areas of intense interspecific competition, with strong interactions within guilds but weaker interactions between members of different guilds. Relatively little has been done with the guild concept, although it has begun to attract increasing interest (Feinsinger 1976, Inger and Colwell 1977, Holmes et al. 1979, Pianka et al. 1979, Eckhardt 1979).

To develop thinking about guild structure, the niche concept is useful. The ecological niche has gradually become inextricably linked to the phenomenon of interspecific competition. Moreover, the concept has become increasingly identified with patterns of resource utilization (Pianka 1976). I use the term niche in this narrow sense of resource utilization here, without denying that there are other equally important aspects of an organism's niche such as its reproductive tactics.

Students of resource partitioning seek answers to some fairly fundamental questions about how communities are put together (only after addressing these will we even begin to be able to ask meaningful questions about why communities have particular observed properties). For example, some of these questions are:

1. How many, and which, niche dimensions, separate species?
2. To what extent are species spread out evenly* in niche/resource space? Or, do clusters of functionally similar species ("guilds") exist?
3. How can such guild structure be detected and measured? What are its components?
4. Are such guilds merely a result of built-in design constraints on consumer species, and/or do guilds simply reflect natural gaps in resource space? Or, can guild structure evolve when resources are continuously distributed as a means of reducing diffuse competition? (A community without guild structure would presumably have greater diffuse competition than one with guild structure.)
5. Do more diverse communities have more guild structure than simple communities?
6. What are the effects of guild structure on the assembly, structure and diversity of communities?

I make no pretense of being able to provide definitive answers to any of these questions, but that does not prevent me from exploring them further.

2. Methodological considerations

The basic raw data for most analyses of niche overlap and community structure is the resource matrix, which is simply a rectangular m by n matrix indicating the amount (or rate of utilization) of each of m discrete resource states utilized by each of n different consumer species. Ideally, utilization coefficients in this resource matrix would be expressed in terms of "electivities" (Ilev 1961, Schoener 1974), which reflect the degree to which each consumer's actual pattern of utilization deviates from that of a totally non-selective consumer (i.e., one that uses all resources in direct proportion to their actual supply). In effect, abundant resources and/or those that are used by many different consumer species are given less weight than rare resources and/or those that are used by only a few of the community's consumers. Computation of electivities requires knowledge of resource availabilities, which are typically exceedingly difficult if not impossible to measure. (The row sums of the resource matrix can sometimes be used as a first approximation of resource availabilities.) In the absence of data on resource availabilities, utilization coefficients in the resource matrix are often converted into proportions which sum to unity for each consumer species (this procedure effectively gives each species equal weight).

In any case, once obtained, a resource matrix can then be used to generate an n by n square matrix expressing the ecological distance or overlap between all possible pairs of species. Such an overlap matrix has ones on the diagonal and values less than unity as off-diagonal elements, reflecting the degree of resource sharing between each pair of consumer species. If niche dimensionality is low, an overlap matrix contains mostly zero off-diagonal elements, but, as dimensionality increases, any given target species has more immediate neighbors in niche space (and hence greater prospects for diffuse competition) and the number of positive off-diagonal elements increases.

It can be very difficult to assimilate all the information in such an overlap matrix if it is very large. Indeed, such a matrix may actually describe species as dots in n-1 dimensions if niche dimensionality is great. How can all the information in an overlap matrix be summarized? How can we draw pictures of communities? (Andrew Sheldon pers. comm.) We badly need simpler ways to represent community structure.

* Such overdispersion of species in niche space might be predicted under a competition null hypothesis, with each species minimizing its interactions with all others.
2.1. Histograms of overlap values

Some of the information contained in an overlap matrix can be conveyed pictorially using simple frequency distributions of the magnitudes of overlap values (Pianka 1973, Cody 1974, Pianka et al. 1979). Such histograms of overlaps, however, do not adequately show the extent to which species are clustered or evenly spread out in niche space. Consider, for example, two hypothetical communities with bimodal frequency distributions of overlap values. Such bimodality could arise in either of at least two very different ways: (1) species might be arranged in two or more distinct guilds, with high overlap pairs within guilds, but low overlaps between members of different guilds, or (2) a community might be composed of a central cluster of species surrounded by a diffuse cloud of outlier species (overlaps would be high between members of the central cluster, but low between these and the outliers as well as among outlying species). The first community has more guild structure than the second. Such histograms clearly destroy an important element of the original overlap matrix which might be called its “connectivity.”

2.2. Pictographs of communities

Another way to depict communities is to represent species as dots* in resource space (Pielou 1969). Two species can thus be plotted as points on a line with the distance between them decreasing as overlap increases. Three species can be similarly represented at the corners of a triangle in two dimensions and four species as the vertices of a tetrahedron in three dimensions. But, even a five species community requires a four-dimensional space to depict accurately all the interactions among its component species if several niche dimensions separate species. A community of only a dozen species separated along several niche dimensions clearly defies having its portrait painted! If niche axes are not orthogonal, dimensionality can be reduced by changing coordinate systems with multivariate techniques such as principal components, discriminant functions, and/or factor analysis (Green 1971, James 1971, Dueser et al. 1976, Aspey and Blankenship 1977, Inger and Colwell 1977, Invester and Coull 1977, Holmes et al. 1979).

2.3. Nearness rank in niche space

Still another useful technique that depicts some of the community’s “connectedness” involves ranking each species’ neighbors in niche space from the nearest to the most distant (Inger and Colwell 1977). When overlap is plotted against such nearness ranks in niche space, very similar species (such as those belonging to the same guild) fall out together, whereas species on the periphery of niche space have low overlap with the remainder of the community and tend to fall well below other species. Mean overlap among all members of a community decays monotonically with rank. However, the standard deviation in overlap may increase, decrease, or even rise and then fall as one moves from the nearest niche neighbor to the most distant. Inger and Colwell (1977) argue that humps in such standard deviation curves are indicative of guild structure. The reasoning behind this assertion is that, because close neighbors in niche space tend to belong to the same guilds, standard deviation in overlap is primarily within guilds at low ranks and thus small. But, if a community contains two or more guilds of different size, at a rank one beyond that of the smallest guild, standard deviation should increase because both within-guild overlap pairs and some between-guild pairs occur at the same rank. At still higher ranks, standard deviation in overlap falls because all overlaps are now between members of different guilds (all overlap values are homogeneously small).

2.4. Cluster analysis

A guild may be objectively defined using the “single-linkage” criterion of cluster analysis as a group 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. This conservative definition allows complex hierarchical patterns of nesting of smaller guilds within larger ones. Less conservative “multiple linkage” algorithms have also been developed for cluster analysis. Of course, these techniques necessarily distort spacing patterns since all reduce multiple dimensions to a single dimension.

2.5. Neutral models of community structure

Until fairly recently, students of resource partitioning and community structure have been unable to accomplish much more than merely describe existing patterns of resource partitioning among various coexisting consumer species. Even such descriptive efforts seldom allow very useful comparisons with other studies of communities partially because standardized techniques for community analysis have not been developed or adopted. In some cases with low niche dimensionality, observed estimates of overlap have been compared with values of limiting similarity generated from various theoretical arguments such as those of MacArthur and Levins (1967) or May and MacArthur (1972). (For examples, see Orians and Horn 1969, and/or May 1974.) But such comparisons are not particularly revealing because values of limiting similarity depend strongly on the specific assumptions (often unrealistic) of models concerned (Abrams 1975).

* More realistically, as clouds of dots with a probability density distribution.
Sale (1974) responded to this dire need for null hypotheses by suggesting that communities might be compared to randomized versions of themselves. Overlap in observed communities of grasshoppers did not differ markedly from that in such randomized analogues, leading Sale (1974) to conclude that competition had not been a major force in reducing overlap among or otherwise organizing these communities of insects. In a similar analysis using desert lizard communities, however, Lawlor (1980b) found that average overlap was substantially lower in observed communities than in randomized replicates, suggesting that competition has shaped the organization of these lizard communities. This rather promising "neutral model" approach has now been exploited in a number of studies of community structure (Caswell 1976, Inger and Colwell 1977, Pianka et al. 1979, Taylor 1979, Joern and Lawlor 1980, Connor and Simberloff 1980).

Neutral model algorithms for constructing various randomized analogues of real communities that have been used are by no means exhaustive. Families of such randomized communities with differing degrees of resemblance to observed communities may well help in elucidating the structure of the latter (see Lawlor 1980b, for the beginnings of such an approach). A major virtue of this methodology is that samples of analogue communities can be generated that are adequate for statistical comparisons with observed communities. The approach essentially allows "experimentation" with real communities and is limited only by the imaginative powers of ecologists. A promising but as yet totally unexploited variant on these techniques is the artificial "removal" and/or "addition" of species to existing communities.

One of the more random ways to construct an artificial neutral model community is to assign the utilization coefficients in the resource matrix with a random number generator. This can be done by sampling values from the uniform random distribution over the interval zero to one for each "species," and dividing these values by their sum to give each of the species in a hypothetical community of consumers its utilization coefficient for a given resource state. Overlap matrices computed from such randomized resource matrices have remarkably similar distributions of niche overlap for a wide variety of artificial communities with different numbers of species and resource states (Pianka et al. 1979). Average overlap in such randomly-constructed communities is quite high and variance in overlap is rather low compared to observed communities (Pianka et al. 1979, Lawlor 1980b). Moreover, such neutral model communities have very little guild structure compared to their real prototypes. Insights will presumably come when two different randomization algorithms destroy different aspects of the original community's structure.

3. Preliminary results: desert lizards

With the help of a small army of assistants and colleagues, I have spent much of the past two decades studying the niche relationships of desert lizards. Extensive ecological data were gathered on the saurofaunas of some 30 odd desert study areas, which lie at roughly similar latitudes on three continents: North America, southern Africa and western Australia (Pianka 1967, 1969, 1971, 1973, 1975, 1980). Lizards have evolved in response to desert conditions independently within each of these three continental desert systems. Intercontinental comparisons should thus reflect the extent to which the interaction between the lizard body plan and the desert environment is determinant and predictable. Any convergence observed between such systems could conceivably provide insights into the operation of natural selection and might eventually lead to general principles of community organization.

To gather data on the ecological relationships of these lizard faunas, my assistants and I walked many thousands of kilometers through study sites observing lizards. We spent five full years in the field between 1962 and 1979 and nearly twelve person-years collecting data over essentially the entire annual period of
activity. For most lizards encountered active above ground, microhabitat and time of activity were recorded. As many animals as possible were collected and their stomach contents and reproductive condition analyzed later in the laboratory. Resulting collections of some 20000 lizards, representing 90-odd species in 11 of the 19 extant families of lizards, are lodged in major museums.

Two resource matrices were assembled for the lizards from each study area: one for microhabitats and another for prey taxa (more than a third of a million individual prey items have now been tallied). For simplicity here, I rely primarily on “merged” data sets which treat each continent as a single site; this maximizes sample sizes and hence my confidence in estimating what rare species are actually doing. Area-by-area trends are similar to those found in merged data.

Overlap in microhabitat is plotted against nearness rank in niche space for a nine-species assemblage of North American desert lizards in Fig. 1. Two arboREAL species, Urosaurus graciosus and Sceloporus magister, overlap greatly with each other (0.87) but have very low overlaps with all other members of the community. Terrestrial species fall out together, too, but overlap at a given rank is much higher than it is in the arboREAL species. The presence of this arboREAL guild along with a terrestrial guild generates a hump in the plot of standard deviation in overlap versus nearness rank (Fig. 2). Similar plots for the average and standard deviation in overlap at various ranks are shown for the merged data sets in Fig. 3 (microhabitats) and Fig. 4 (diets). Standard deviation curves tend to have the humps indicative of guild structure, and these humps tend to peak farther out in niche space in more diverse communities, suggesting larger guilds. Area-by-area plots are also characterized by humps. What do such humps mean if guild structure is complex?

Fig. 5 depicts clustering of North American lizard species in microhabitat niche space using the single-linkage criterion of cluster analysis (compare this figure with Fig. 1 which shows most of the same species). The two-species arboREAL guild sets off a large 7-species terrestrial guild, within which are nested two smaller subguilds, one corresponding to three species that frequent the open spaces between plants (Phrynosoma platyrhinos, Callisaurus draconoides, and Uma scaparia) and the other to those species that are usually found closer to cover adjacent to shrubs (Cnemidophorus tigris, Crotaphytus wislizeni, Diplosaurus dorsalis and Uta stansburiana). A tenth species, Coleonyx variegatus, is nocturnal and is not a member of either guild. Lizards in the Kalahari semidesert of southern Africa display similar hierarchical guild structure (see Fig. 7.10, p. 252, in Pianka 1978). Neutral model algorithms tend to break up the guild structure of these saurofaunas.
Fig. 4. Overlap in diet plotted against nearness rank in niche space for the merged data sets for each continental desert-lizard system. Means above and standard deviations below.

Fig. 5. Microhabitat guild structure in North American desert lizards as revealed by single-linkage cluster analysis. The two-species arboreal guild sets off a seven-species terrestrial guild, which includes two subguilds composed of lizards that frequent open spaces versus those species that stay close to shrubs. Only one species is not a member of any guild.

4. Discussion and speculation

Although I can now begin to delimit guilds objectively, an index of guild structure is still needed. Guild structure may well have too many components for a simple single measure to reflect them all (these would include within-guild packing versus between-guild spacing, number of guilds, guild sizes (numbers of species), and hierarchical structure (nesting of smaller guilds within larger ones)).

Once we have been able to describe and quantify guild structure, we can begin to ask questions about the impact of this clustering of species in niche space on community organization and function. Recall some of the questions with which I began this essay: "Does guild structure result from design constraints and/or gaps in resource space?" or "Could guilds evolve without gaps in available resources or modes of life?" or "Could selection favor a few strong competitors over many weaker ones?" "Does guild structure influence coexistence and allow diversity?" "Do more diverse communities have more guild structure than less diverse ones?" The recent notion of competitive mutualism is intriguing in this context.

The traditional approach* to interspecific competitive interactions is strictly pairwise: only the direct effects of each species on any other target species are considered and modelled. Indirect interactions, mediated through other members of the community, must also occur (Levine 1976). Thus, two species with non-overlapping diets preyed upon by a common predator may nevertheless have a net negative effect on each other's population density. Similarly, two predatory consumer species with little or no dietary overlap can benefit each other indirectly if their prey species compete: an

* As, for example, in the "alpha matrix" of competition coefficients for a community (Levins 1968).
crease in either predator population depresses the density of its own resource population hence ameliorating conditions for the other predator's major resource (for greater detail, see Vandermeer 1980). Under certain conditions, pairs of potential competitors can actually act to increase one another's densities if both share other competitors. Such a competitive mutualism may arise when two weak to moderate competitors have a common strong competitor: because both species inhibit this third species markedly, each has a beneficial net effect on the other even though their direct pairwise interaction is detrimental. Lawlor (1980a) has extended this approach to n-species communities, stressing that pairs of such species with the potential for high overlap and strong interspecific competition might in fact interact only weakly in the context of an entire community. Consider two hypothetical guilds and focus on two target species, one a member of each guild (Fig. 6). This pair of species has one weak negative direct interaction: as such, they are competitors in the absence of other species. However, within the left guild, species x has many strong negative interactions (again direct ones), due to its high overlap with other members of its own guild. Thus, species x depresses the populations of other species belonging to its guild considerably. These lowered population densities are translated back as indirect effects, but in this case many weak beneficial interactions, on species y in the other guild. (The process is symmetrical, with species y indirectly helping species x via its strong direct interactions within its own guild.) Such indirect competitive mutualism may affect community assembly: addition of one of a pair of such species could make it easier for the other to invade a community. If members of different guilds are in fact competitive mutualists, guild structure may be instrumental in maintaining community diversity and in holding real communities together. In this light, the question "do more diverse communities have more guild structure than less diverse ones?" assumes new significance. Guild structure could actually foster diversity.

Acknowledgments – I am especially grateful to the John Simon Guggenheim Memorial Foundation and to the National Geographic Society for support during 1976-79. My work has also benefited from intermittent support from the U. S. National Science Foundation. Of the many people who have contributed useful discussion and ideas, I must single out L. R. Lawlor for thanks.

References


