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ON THE EVALUATION OF RESOURCE USE  
AND COMMUNITY STRUCTURE

By

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## ABSTRACT

### ON THE EVALUATION OF RESOURCE USE AND COMMUNITY STRUCTURE

By

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The resource use patterns of individual species and the partitioning of resources among the species in a community are important considerations in community ecology. Most recent resource partitioning studies have employed niche theory in the quantification of overlaps in resource use among two or more species. A potential problem in the use of these point estimates for niche overlaps is that there is no statistical assurance of their reliability. The measurement of niche overlap is less popular than in the past; assumptions of the models are implicated as well as problems interpreting the calculated overlap values. Our inability to accurately measure overlaps has undoubtedly aggravated interpretation problems and could explain in part the increasing abandonment of niche overlaps. In this thesis, I develop an interval estimate of niche overlap which allows the estimation of sample sizes necessary to accurately measure niche overlap. Samples of up to  $10^5$  per species are necessary to measure niche overlap accurately to the second digit right of the decimal. Confidence intervals are calculated for a case study on limiting similarity. Manipulative experimentation provides an appealing alternative to simple observation and overlap estimation based on both logical and statistical grounds.

Patterns of resource partitioning have seemed so similar in certain communities, that it has prompted many authors to ask if there

is an organized pattern in the way communities are assembled. Of course, the only way to uncover presumed consistencies is to examine communities comparatively. Community comparisons are often made between communities with entirely different species assemblages which exist under similar conditions. If it can be shown that structuring forces exist which are powerful enough to force historically and phylogenetically distinct communities to converge in structure, we may be well on our way to establishing any "assembly rules" for community structure which may exist. A neutral model analysis of convergence in resource use patterns provides an alternative hypothesis for two extant hypotheses on convergence. For a case study on lizard community convergence, the model reveals that one of these convergence hypotheses is logically faulty and the data cannot support the other hypothesis.

Interval estimation and neutral modeling are powerful tools which can be applied to a wide class of problems in ecology. Both approaches can aid in experimental design by providing for rigorous testing of alternative hypotheses.

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My wife Judy provided encouragement, support and much love throughout this study; for this I am forever grateful. This thesis is dedicated to the loving memory of Earl M. Crowder and Billie V. Morris.

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## INTRODUCTION

### Resource use and community structure

How organisms find, obtain and use resources has been a major question since man first examined the natural world around him. Naturalists have provided autecological information on diet, habitat and the use of resources for many species. Early studies often examined the habits of single species and how they are constrained by physical factors. Morphological variates were often related to the types of foods eaten or habitats occupied. Grinnell (1904,1917) was among the first of these naturalists to extend the study of single species to the problems of species interactions and resource partitioning. He is credited with originating the niche concept as well as anticipating the competitive exclusion principle (Whittaker and Levin 1975).

The study of species interactions (e.g., competition) places a high priority on understanding resource use patterns within communities of organisms. Physical factors such as temperature or humidity may constrain a species' dynamics, but they are not resources over which two species can compete. Ecologists have employed the naturalist's approach to morphological variates, habitat use and foraging patterns in order to establish how various species interact in the exploitation of resources. While much of modern ecology is based on competition as the major mechanism in the partitioning of limited resources, other

mechanisms clearly influence resource use. Species interactions such as predation, parasitism and various symbiotic or coevolutionary interactions may have profound effects on resource use patterns.

Another often overlooked effect on resource use patterns in communities is that of resource availability--an animal cannot use a resource which cannot be found or obtained. That a species co-occurs with a resource which seems to be obtainable is not evidence for the species use of that resource. Animals traveling through a particular habitat may not actually use any resources there (Schroder and Rosenzweig 1975). Similarly, prey behavior may prevent a predator from eating co-occurring prey of acceptable types and sizes (Charnov, Orians and Hyatt 1976). In assessing resource use, ecologists commonly examine guts or observe animals regularly occupying certain habitats. The concurrent monitoring of resource availability would allow comparisons of use to availability as well as guaranteeing that when competition is claimed, resources are indeed limiting.

Presumably, increased understanding of the differences in morphology and resource use among closely related species would aid our understanding of species diversity within whole communities. The examination of species interactions and resource partitioning has become a basis for much of community ecology. As Schoener (1974a) has pointed out, since Hutchinson (1959) first asked "Why are there so many kinds of animals?" resource partitioning studies have grown exponentially at a rate four times that of typical scientific works. Most recent resource use studies have been couched in terms of the niche hypervolume concept of Hutchinson (1957). The way in which niche space is subdivided by the species in a community may be referred to as community

structure.

Patterns of resource subdivision have seemed so similar in certain communities, that it has prompted many authors to ask if there is structural consistency to these patterns. Diamond (1975) went so far as to propose that there exist "assembly rules" for community structure--that there is an organized pattern in the way communities are assembled. Presumably, all one needs do is examine many communities, uncover consistencies in resource use patterns, and suggest hypothetical assembly rules which are then subjected to test. Of course, the only way to uncover presumed consistencies in resource use patterns is to examine communities comparatively. This may be done by comparing communities composed of the same species at different points in space or time and see if, under similar conditions, resources are partitioned in similar ways.

Community comparisons are also employed with entirely different species assemblages which exist under similar conditions. The question becomes "whether very similar physical environments, acting on phylogenetically dissimilar organisms in different parts of the world, will produce structurally and functionally similar systems" (Di Castri and Mooney 1973). If it can be shown that structuring forces exist which are powerful enough to force historically and phylogenetically distinct communities to converge in structure, we may be well on our way to uncovering any "assembly rules" which may exist.

#### Convergence of community structure

The question is do community properties converge? In particular, does community structure converge? Ecologists have recently begun to

examine the possibility that community structure may converge under a given set of environmental conditions (Cody 1968,1974,1975, Recher 1969, Pianka 1973,1975, Karr and James 1975, Sage 1973, Fuentes 1976).

In its simplest form, convergence may occur in numbers of species in communities in similar environments. Recher (1969) showed that the number of species in Australian bird communities exactly parallels that in American bird communities in comparable habitats. However, many avian niches appear to be fundamentally different on the two continents (Pianka 1974). Cody (1968,1974) has reviewed similar patterns of species diversity for grassland and forest bird communities, but parallels are not exact.

Similarity in resource partitioning was noted in grassland birds by Cody (1968). Data on vertical and horizontal habitat distribution, morphology and foraging behavior of grassland bird communities from Chile and North America implicated some ecological equivalents, but there was no isomorphic mapping of species analogues. Recently (Cody 1974), the approach was extended to a more complex pair of bird communities in shrubby and woodland areas of California and Chile. Some species matching was possible, but no recent attempts by Cody to apply this analysis has shown greater similarities than in the grassland bird communities. Pianka (1973,1975) has compared desert lizard communities from North America, Africa and Australia and has concluded that differences more than outweigh similarities in community structure.

Fuentes (1976) employed a relative criterion for convergence of community structure. His hypothesis of convergence states that community structure should be more similar with respect to habitat, food and time of activity in lizards in similar habitat sites between

continents than in nearby communities on the same altitudinal transect. The relative similarity approach was justified on the basis of allowing for possible historical or phylogenetic constraints which are likely to prevent close convergence. If the hypothesis can be confirmed, the selective effects of environmental similarity can be taken to be more important than taxonomic or historical constraints.

### The evaluation of hypotheses

Given the complex and multiple hypotheses relating resource use patterns and community structure, there is a distinct need to apply careful scientific method. During the early stages of the development of a theory or paradigm (Kuhn 1970) scientists seem to favor attempts to verify or confirm that natural patterns fit (in one way or the other) the predictions of the theory (Kuhn 1970). Popper (1963), however, argues that a theory can be considered "corroborated" only if it has withstood repeated and severe tests of its predictions. This "falsificationist" approach to science considers that theories can only be accepted after stringent testing. In reality, this tack is seldom taken unless the investigators are already aware of some limitations in the theory (Kuhn 1970). That science best proceeds by the elimination of competing hypotheses has been argued thoroughly elsewhere (Popper 1959, 1963, Platt 1964). Platt (1964) summarized a method he refers to as strong inference. The method requires

- 1) Devising alternative hypotheses,
- 2) Devising one or more "crucial experiments," with  
     alternative possible outcomes, each of which will, as  
     nearly as possible, exclude one or more of the hypotheses,

- 3) Carrying out the experiment so as to get a clean result,
- 4) Iterating the procedure.

In this work, I interpret some recent work in resource use patterns and community structure in relation to Platt's method. In addition to creating alternative hypotheses and devising the "crucial" experiment, Platt emphasizes that experiments must be designed and carried out so as to get a clean result. Thus, experimental results must eliminate or support alternative hypotheses in a statistically significant way. Resource use studies have commonly included a measure of overlap in the use of resources by two or more species. In its simplest form, niche overlap is calculated on a single niche dimension such as food size or vertical habitat. Numerous hypotheses relating resource use patterns and community structure have employed point estimates of niche overlap, but none have developed an interval estimate for niche overlap. As I show (in chapter 2) for a particular measure of niche overlap, interval estimation can aid considerably in the design of a "crucial" experiment and the production of a clean result by allowing estimation of proper sample sizes for the resolution of alternative hypotheses. I employ an example from the theory of limiting similarity as a case study to demonstrate the approach.

Of course, the generation of alternative hypotheses is also a non-trivial task. A classic alternative hypothesis is the null hypothesis--for which, in complex situations, a neutral model (Caswell 1976) is an appropriate substitute. Neutral models have provided many insights for biologists from population genetics (Kimura and Ohta 1971) to paleobiology (Raup et al 1973). Caswell (1976,1977) provides a summary of

some extant biological neutral models. In chapter 3, I develop a neutral model for resource use which provides an alternative hypothesis for two extant hypotheses on community convergence.

Finally, I discuss the value of interval estimation and neutral modeling in experimental design. Interval estimates of ecological indices are necessary to determine the validity of a particular hypothesis test and to estimate adequate sample sizes. Neutral models provide alternative hypotheses as well as providing a measure of severity for hypothesis testing. As Caswell (1977) has noted, if a particular pattern is generated by both the theory and a neutral model, then the tests of the theory based on that pattern have absolutely no severity or power. Interval estimation and neutral models are generalized tools; this thesis demonstrates their applicability to some current theory in community ecology and underscores their usefulness to ecologists.

SAMPLE SIZE AND CONFIDENCE INTERVAL  
ESTIMATES FOR NICHE OVERLAP,  $\alpha$ .

Niche overlap: measurement and interpretation

Recently, ecological theory and field work have paid increasing attention to the measurement and interpretation of niche overlaps ( $\alpha$ ) in an effort to understand the processes which have produced them. Estimates of niche overlap have been calculated in several ways and are often referred to as competition coefficients ( $\alpha_{ij}$ ) even though overlap does not necessarily imply competition (Colwell and Futuyma 1971).

Niche overlap measures on single resource axes have been combined in numerous ways to estimate the overlap in resource use for  $n$  dimensions. Cody (1974) has calculated  $n$  dimensional overlaps by taking the product of single axis overlaps (product  $\alpha$ ) and by taking a simple average (summation  $\alpha$ ). But May (1975) has argued that, in general, there is no substitute for directly measuring the species' full multidimensional overlaps.

Niche overlap estimates for all pairwise interactions in a community have been combined into a matrix of coefficients: the community matrix. Stability properties of this matrix have been explored thoroughly (Levins 1968, May 1973a, VanderMeer 1970), as have the relationships between overall competition coefficients and the underlying models of resource use (MacArthur 1969, 1970, 1972). Limiting similarity and community invasibility have also been examined in terms of niche overlap estimates (MacArthur and Levins 1967, MacArthur 1969, 1971, 1972, May and MacArthur 1972, May 1973b, Roughgarden 1974, Abrams 1975). All of these arguments are dependent for their resolution on

reliable estimates for  $\alpha$ .

This chapter examines the overlap estimate of MacArthur (1972), which assumes normal resource use curves. This assumption allows the use of parametric statistics to estimate a confidence interval for  $\alpha$ . Then the range of reliability for overlap estimates over different sample sizes is explored with and without restrictive assumptions about equality of variances. Sample sizes are estimated for hypothesis testing and confidence intervals are calculated for a case study on limiting similarity. Interval estimates of niche overlaps are necessary to provide valid test of hypotheses involving overlaps.

#### Relation of $\alpha$ to the subdivisions of a single resource axis

MacArthur and Levins' (1967) original estimate of niche overlap assumes a community of  $m$  species competing for an array of resources which may be subdivided into  $n$  categories. If the utilization function  $p_{ia}$  ( $i = 1, 2, \dots, m$ ;  $a = 1, 2, \dots, n$ ) is assumed to measure the relative utilization of the  $a^{\text{th}}$  resource by the  $i^{\text{th}}$  species, the two species interaction coefficient is

$$\alpha_{ij} = \frac{\sum_{a=1}^n p_{ia} p_{ja}}{\sum_{a=1}^n p_{ia}^2} \quad (1)$$

Since the utilization functions  $p_{ia}$  are difficult to measure directly, resources are often subdivided into discrete categories and the percentage of time (or diet) spent in each category by the animal describes the utilization function. Weighting terms may be added for resource turnover rates and other effects (MacArthur 1972). Schoener (1974b) has thoroughly discussed the difficulties with estimating  $\alpha$  in

the field. But no matter how difficult it is to estimate  $\alpha$ 's from field data or how difficult estimates may be to interpret, an investigator who chooses to calculate  $\alpha$  must know how reliable his estimates are.

MacArthur (1972) has derived an expression for  $\alpha$  as a function of the distance between two utilization means  $u_1$  and  $u_2$ , which assumes normally distributed utilization functions (Figure 1). For equal variances ( $\sigma_1^2 = \sigma_2^2 = \sigma^2$ ), MacArthur (1972) has shown that

$$\alpha(d) = e^{-d^2/4\sigma^2} \quad (2)$$

When the variances are assumed homogeneous but unknown, both  $d$  and  $\sigma$  must be estimated from the data. In this case,  $\alpha$  is a function of the ratio of  $d$  to  $w$  (the  $\sigma$  estimator).

$$\alpha(d/w) = e^{-1/4(d/w)^2} \quad (3)$$

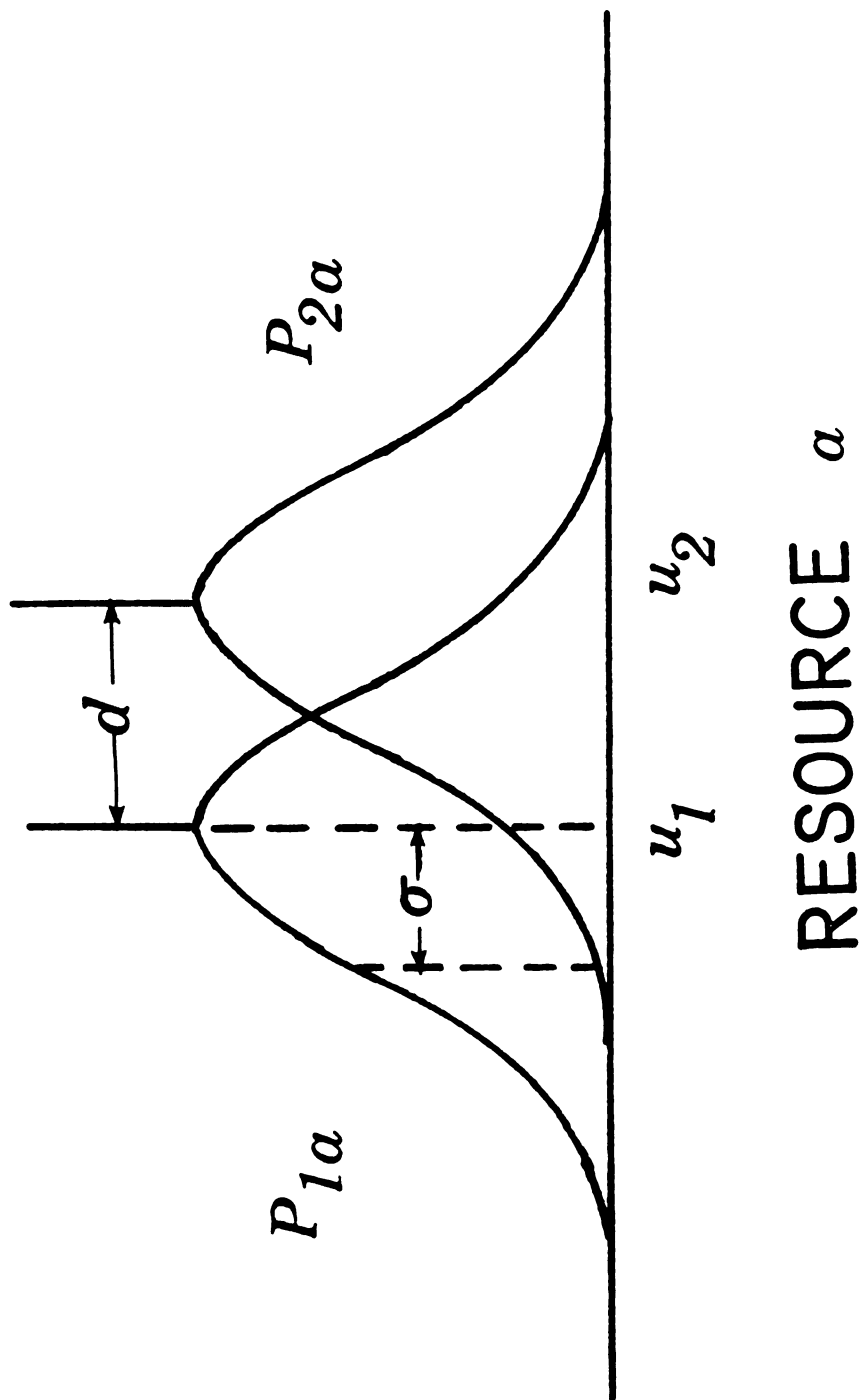
#### Sample size and confidence intervals for $\alpha(d)$

If the variances of the resource use curves are assumed equal, the confidence interval for  $\alpha$  is simply functionally related to the confidence interval for  $d$ . Confidence intervals for  $d$  may be estimated using  $t$  statistics (Sokal and Rohlf 1969). A confidence interval for the difference of two means ( $d = u_2 - u_1$ ) from normal populations with common variance ( $w^2$ ) of unknown value may be estimated from a  $t$ -distribution (Sokal and Rohlf 1969). For  $(1-\gamma)$  100% confidence with sample sizes of  $n_1$  and  $n_2$  the estimator is

$$(\bar{Y}_2 - \bar{Y}_1) \pm t_{\gamma/2, n_1 + n_2 - 2} s \sqrt{\frac{1}{n_1} + \frac{1}{n_2}} \quad (4)$$

Figure 1. Resource use curves of two species along a resource axis

a.  $d$  is the distance between means  $u_1$  and  $u_2$ , and  $\sigma$  is the standard deviation common to both curves.



where  $S$  is the pooled standard deviation

$$S = \sqrt{\frac{(n_1 - 1)S_1^2 + (n_2 - 1)S_2^2}{n_1 + n_2 - 2}} \quad (5)$$

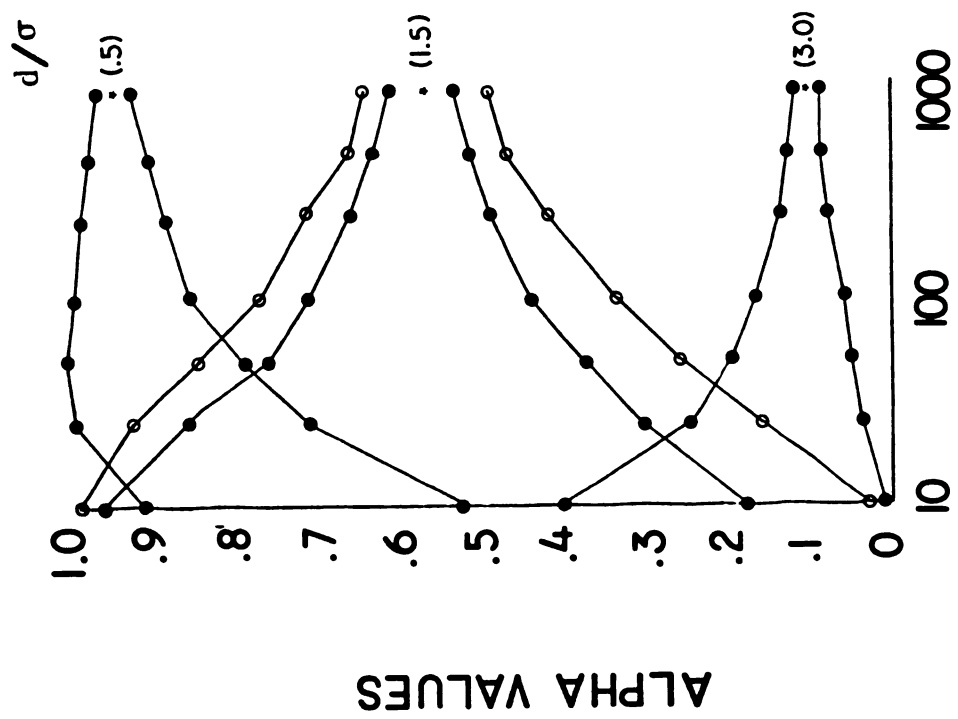
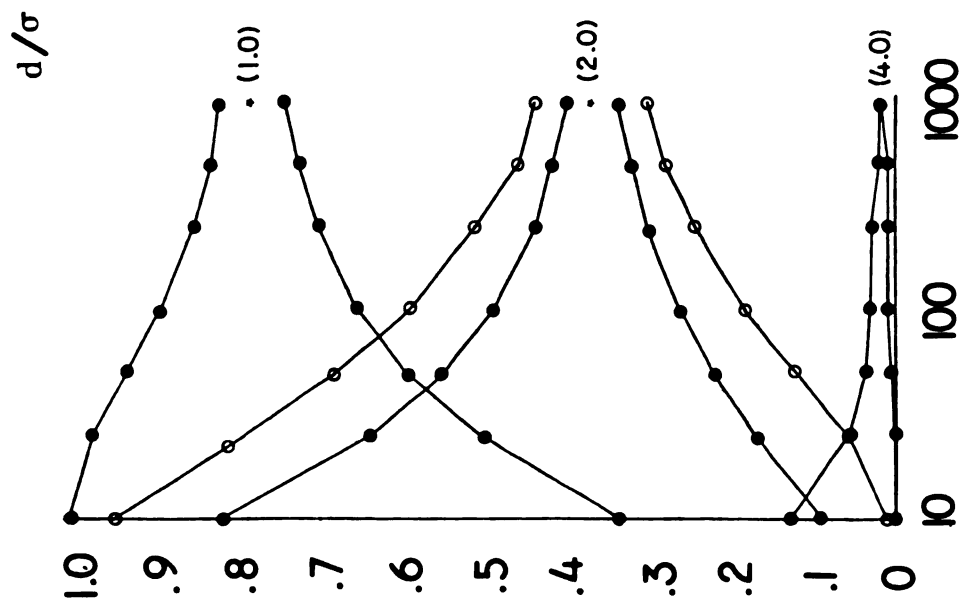
For simplicity, I assume  $\sigma_1 = \sigma_2 = \sigma = 1$  and estimate 95% confidence intervals for  $\alpha(d)$  for various combinations of  $d/\sigma$  (Figure 2). Even at sample sizes of 1000 from each species, the confidence intervals are reasonably large, especially in the midrange of  $\alpha$  values where the slope of the functional relationship between  $d/\sigma$  and  $\alpha$  is the greatest.

Sample sizes for hypothesis tests of differences from a particular overlap value are given in Figures 3 and 4. Samples for each species of up to 100,000 are required to distinguish  $\alpha$ 's to the second digit to the right of the decimal. Of course, necessary sample size is dependent on the proximity of the two species on the resource axis. Intermediate  $\alpha$ 's ( $1 \leq d/w \leq 2$ ) will require the largest sample sizes. Since MacArthur's (1972)  $\alpha$  estimate allows the use of parametric statistics, it also likely provides the minimum sample sizes for other  $\alpha$  measures which may require non-parametric confidence intervals.

#### A confidence interval estimate for $\alpha(d/w)$

If the assumption of normal resource utilization functions is acceptable, it is possible to generate a confidence interval estimate for  $\alpha(d/w)$ . This requires the construction of a confidence region for the joint estimation of  $d$  and  $w$ . Derivations of precise joint confidence regions of this kind are difficult at best (Mood and Graybill 1963, Kendall and Stuart 1963). However, the confidence region may be estimated by using the individual confidence estimates for  $d$  and  $w$ ,

Figure 2. Confidence intervals for various values of  $d/\sigma$  vs. sample size from each species. Solid circles represent 95% confidence intervals for  $\alpha(d)$  and hollow circles represent  $> 95\%$  confidence for  $\alpha(d/w)$ .



SAMPLE SIZE

ALPHA VALUES

Figure 3. Sample sizes required to distinguish particular  $\alpha$  values from values which are larger.



Figure 4. Sample size required to distinguish particular  $\alpha$  values from values which are smaller.



assuming that the probability of both occurrences is the product of their separate probabilities. This will result in a confidence interval overestimate such that one may have confidence of at least  $(1-\gamma)$  100% that the interval contains the true value of  $d/w$ .

A confidence interval for the standard deviation ( $w$ ) from two normal populations with common but unknown variance may be estimated from a  $\chi^2$  distribution (Sokal and Rohlf 1969). For  $(1-\gamma/2)$  100% confidence with sample sizes of  $n_1$  and  $n_2$ , the confidence interval estimator of  $w$  is

$$\sqrt{\frac{(n_1 + n_2 - 1) S^2}{\chi^2_{\gamma/4, n_1 + n_2 - 2}}} < w < \sqrt{\frac{(n_1 + n_2 - 1) S^2}{\chi^2_{1-\gamma/4, n_1 + n_2 - 2}}} \quad (6)$$

where  $S$  is again the pooled standard deviation (5). The  $(1-\gamma/2)$  100% confidence interval for  $d$  is calculated as in equation 4. The  $(1-\gamma)$  100% confidence interval for  $d/w$  and ultimately for  $\alpha$  may be estimated from the  $(1-\gamma/2)$  100% confidence intervals for  $d$  and  $w$  as follows:

$$\frac{\text{lower limit of } d}{\text{upper limit of } w} < \frac{d}{w} < \frac{\text{upper limit of } d}{\text{lower limit of } w} \quad (7)$$

The confidence interval for  $\alpha$  follows directly

$$L < \frac{d}{w} < U \quad (8)$$

and using equation (3)

$$e^{-1/4L^2} > \alpha > e^{-1/4U^2} \quad (9)$$

Using this technique, confidence intervals for various combinations of  $d/w$  are estimated (Figure 2). Obviously, estimating both  $d$  and  $w$

requires a larger sample size than estimating  $d$  alone. Confidence intervals for  $\alpha(d/w)$  are on average more than twice as large as those for  $\alpha(d)$ . Thus, sample sizes for hypothesis tests involving  $\alpha(d/w)$  must be at least doubled or tripled over those given for  $\alpha(d)$  (Figures 3 and 4).

In the field, both  $d$  and  $w$  must usually be estimated. Antbirds (Formicariidae) of the genus Myrmotherula appear to segregate by foraging height (Figure 5) and have been claimed as a good example for limiting similarity at  $d/w \approx 1$  (MacArthur 1972 from data of Terborgh, but see Abrams 1975). Estimates of  $d/w$  and their  $\geq 95\%$  confidence intervals are shown in Table 1. Clearly, the point estimates are not startlingly close to 1, and the confidence intervals are quite wide with such small sample sizes. The community matrix for Terborgh's antbirds is presented in Table 2. In sub-diagonal pairs--for which limiting similarity has been implied--the average size of the  $\geq 95\%$  confidence intervals is .67 or  $2/3$  of the possible values for  $\alpha$ . Of all estimates in the matrix, the average  $\geq 95\%$  confidence interval is .50 or  $1/2$  of the possible values for  $\alpha$ . Thus Terborgh's data cannot be used as a support for or against MacArthur's hypothesis for limiting similarity.

### Alternatives

The problems with estimating niche overlaps in the field (Schoener 1974b) are only outpaced by the problems of interpreting such measures (Wiens 1977). Given the large samples necessary to measure  $\alpha$  accurately, the frequency of interpretation problems is less surprising. While assumptions of the theory may be problematical, one cannot hope to subject the theory to test if the overlap values cannot even be

Figure 5. Foraging height relationships among the antbirds of genus Myrmotherula. Thickened bars indicate one standard deviation and narrow bars show the entire range of observations. The number of observations for each species is given over the appropriate bar. (After MacArthur 1972, provided by J. Terborgh).

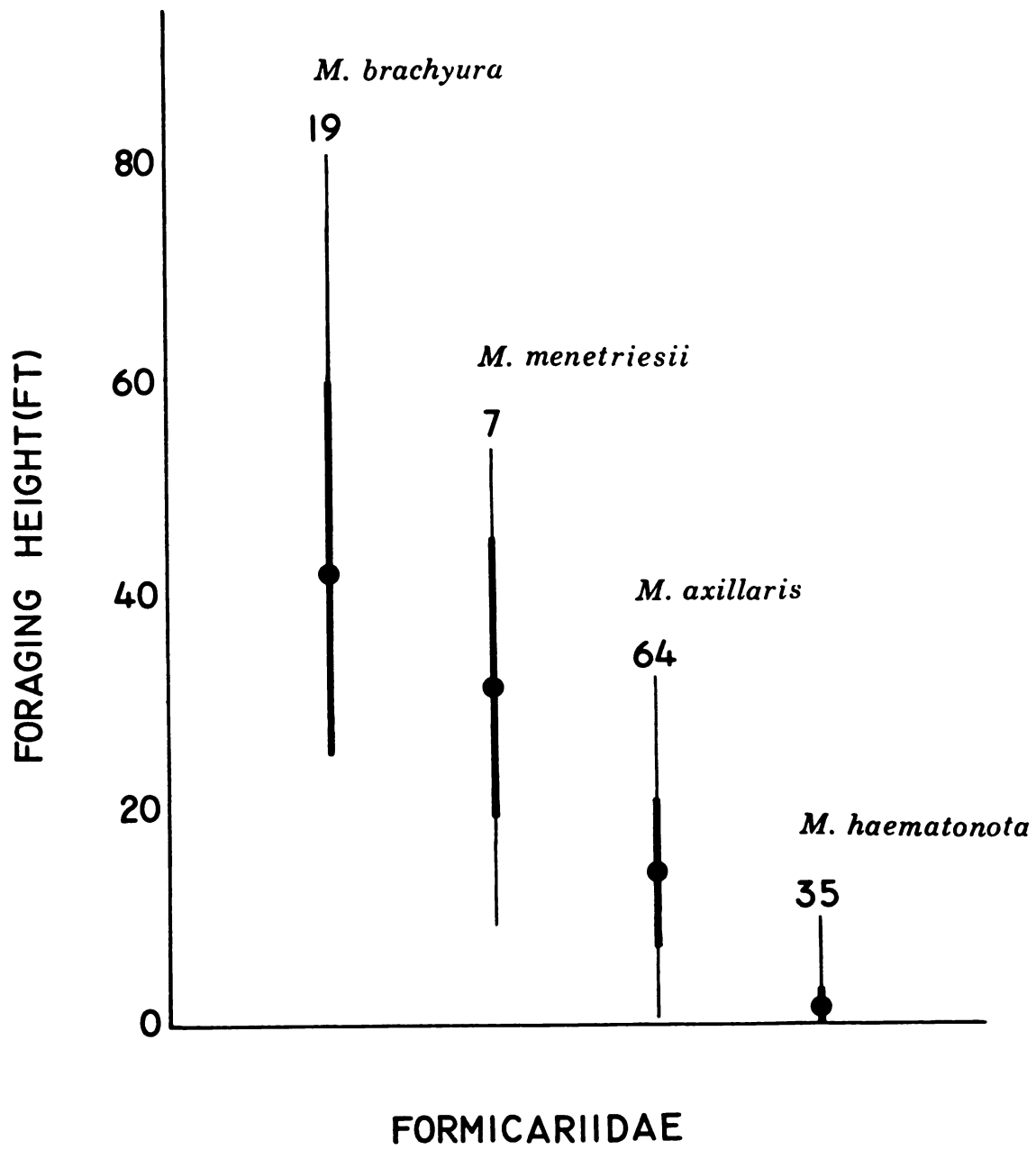


TABLE 1

Antbird species	d/w	$\geq$ 95% confidence interval
<i>Myrmotherula brachyura</i>	.62	.38 < d/w < 2.76
<i>Myrmotherula menetriesii</i>	2.33	1.04 < d/w < 3.99
<i>Myrmotherula axillaris</i>	2.12	1.31 < d/w < 3.07
<i>Myrmotherula haematonota</i>		

Table 1. Point estimate and  $\geq$  95% confidence interval for d/w based on adjacent species pairs from Terborgh's antbird data.

TABLE 2

	<i>M. brachyura</i>	<i>M. mentriesii</i>	<i>M. axillaris</i>	<i>M. haematonota</i>
<i>M. brachyura</i>	1.00			
<i>M. mentriesii</i>	.96>.91>.24	1.00		
<i>M. axillaris</i>	.48>.15>.02	.76>.26>.02	1.00	
<i>M. haematonota</i>	.48>.02>.00	.05>.00>.00	.65>.33>.09	1.00

Table 2. Community matrix for Terborgh's antbirds. Cells contain point estimate for  $\alpha(d/w)$  bounded by the  $\geq$ 95% confidence interval for  $\alpha$ .

estimated accurately.

In view of the large samples necessary to properly distinguish some current ecological hypotheses (e.g., limiting similarity), it may be necessary to consider alternative experimental systems where large sample sizes are possible. For example, if samples of 10,000 are needed, we cannot consider most vertebrates. Yet there are some questions as to whether some current theories even apply to invertebrates (Wilson 1975, Wiens 1977, May 1975).

Given that necessary sample sizes are not available to measure overlaps with sufficient precision, what alternatives are available? Based on problems with theoretical assumptions alone, there are appealing alternatives to measuring overlaps. For example, perturbation experiments (c.f. Schroder and Rosenzweig 1975, Werner and Hall 1976, 1977) are thought to provide much better evidence for competition than simple overlap measures. Even if overlaps are measured, manipulation may lead to large shifts in overlap values (Schroder and Rosenzweig 1975, Werner and Hall 1976, 1977) such that these differences may be detectable at reasonable sample sizes. Without manipulation, we stand little chance of measuring or interpreting niche overlaps accurately.

It is clear that until we know more than we do now, competitive overlaps will have to be examined the hard way--with manipulative experiments (Grant 1972, 1975, DeBenedictis 1974, Schroder and Rosenzweig 1975, Werner and Hall 1976). In this way, the mechanisms underlying the overlaps can be examined rather than the overlaps themselves. Manipulative experiments are preferable because they allow the consideration (and/or elimination) of several alternative hypotheses which may explain the observed overlap equally well.

## ECOLOGICAL CONVERGENCE OF COMMUNITY STRUCTURE:

### A NEUTRAL MODEL ANALYSIS

#### Convergence of community structure

Ecologists have recently begun to examine the possibility that community structures on different continents may converge under similar long term environmental conditions (Cody, 1968,1974,1975, Recher 1969, DiCastrì and Mooney 1973, Sage 1973, Pianka 1973, Karr and James 1975). Since historical and phylogenetic differences between continents may prevent the evolution of identical community structures, Fuentes (1976) proposed a relative measure for convergence of community structures that depends on within-continent comparisons as well as the usual between-continent comparisons (Figure 6). His hypothesis was stated as follows: "Physiognomically similar sites in the two continents should have lizard community structures that are more similar to each other than to the structure of lizard communities in nearby areas on the same [altitudinal-vegetational] transect."

Fuentes examined the convergence of lizard communities from California and Chile by considering the numbers of species, habitat and food use, time of activity, and foraging behavior. Resource use patterns of each species were expressed as a multidimensional vector. The angle between the resource use vectors of two species varies between  $1^\circ$  and  $90^\circ$  as the species vary from identical resource use patterns to completely independent patterns. The major supporting evidence claimed for the species analogue assignments was derived from microhabitat use data (Fuentes 1976). Fuentes also asserted that the general pattern of habitat, food and time use "strongly supports the convergence hypothesis."

Figure 6. Between and within continent comparisons of resource use in California and Chile. Region maps include estimated frequencies of the four microhabitat types.

# CALIFORNIA



**CHAPPARRAL**

**MONTANE**



**BUSHES**



**TREES**



**ROCKS**



**OPEN GROUND**

Fuentes, however, failed to consider an important alternative hypothesis: that convergence patterns in resource use are simply due to similarities in the proportions of available resources on "similar" sites. This "null hypothesis," presented here in the form of a neutral model is as follows: convergence patterns in microhabitat use presented by Fuentes (1976) as support for his hypothesis are not significantly different from what might be expected by chance alone.

#### A neutral model for resource use

A neutral model of an observed phenomenon is one in which the effects of proposed causal mechanisms are completely removed. Moreover, neutral models must be stated relative to a particular hypothesis and are only neutral to mechanisms eliminated explicitly. The model for resource use presented here simply assumes that animals select resources randomly in an environment in which different resources are not equally frequent. The model eliminates all other effects and is therefore neutral to these influences. For further discussion on the neutral model approach see Caswell (1976,1977).

The model does not explain or attempt to account for species differences within a habitat on a continent. It deals solely with comparisons of similar habitats between-continent (e.g., chapparral vs. chapparral) and of different habitats within-continent (e.g., chapparral vs. montane), which Fuentes' hypothesis employs explicitly. Microhabitat use is explored because, according to Fuentes, such data provide strong support for his hypothesis.

In the model, resource availability for each resource category is calculated as a proportion of the total resources available. For example, in chapparral lizards, microhabitat availability for each

microhabitat category (open ground, ground under bushes, rocks, and trees) is based solely on the proportion of these microhabitats in the chapparral environment. Consequently, since the model assumes random resource selection, the proportions of resources actually used are closely correlated with the proportions of resources available.

Since Fuentes did not give estimates of resource availability from his study sites, the model uses data estimated from the literature. Mooney and Parsons (1973) presented data on vegetation types in Monroe Canyon, California, a region that covers 355 ha and includes altitudes in the range of Fuentes' chapparral site. They estimate that 74.6% of the watershed is covered by bushes, 11.9% is sage and barren areas (relatively open) and 13.5% is covered by trees. No data are available for percent cover of rocks. Assuming that Fuentes' microhabitat categories are independent of each other, the model divides the sage and barren area equally into rocks and open ground.

In Australian montane communities trees dominate with an understory of sclerophyllous shrubs (Sprecht 1973). The projective cover for trees is 30-70%. The model assumes that trees account for 50% of the cover in Fuentes' montane system. Since no data are available on the distribution of rocks and open ground microhabitat, the model assumes them to be the same as in the chapparral 6% each. The remaining 38% is assigned to "ground under bushes." Obviously, this analysis would benefit from having frequency data on the microhabitats for Fuentes' study sites (see Figure 6).

The process of random microhabitat selection by the lizards in the model is similar to placing random points on a line segment which has been subdivided into microhabitat categories according to the proportion

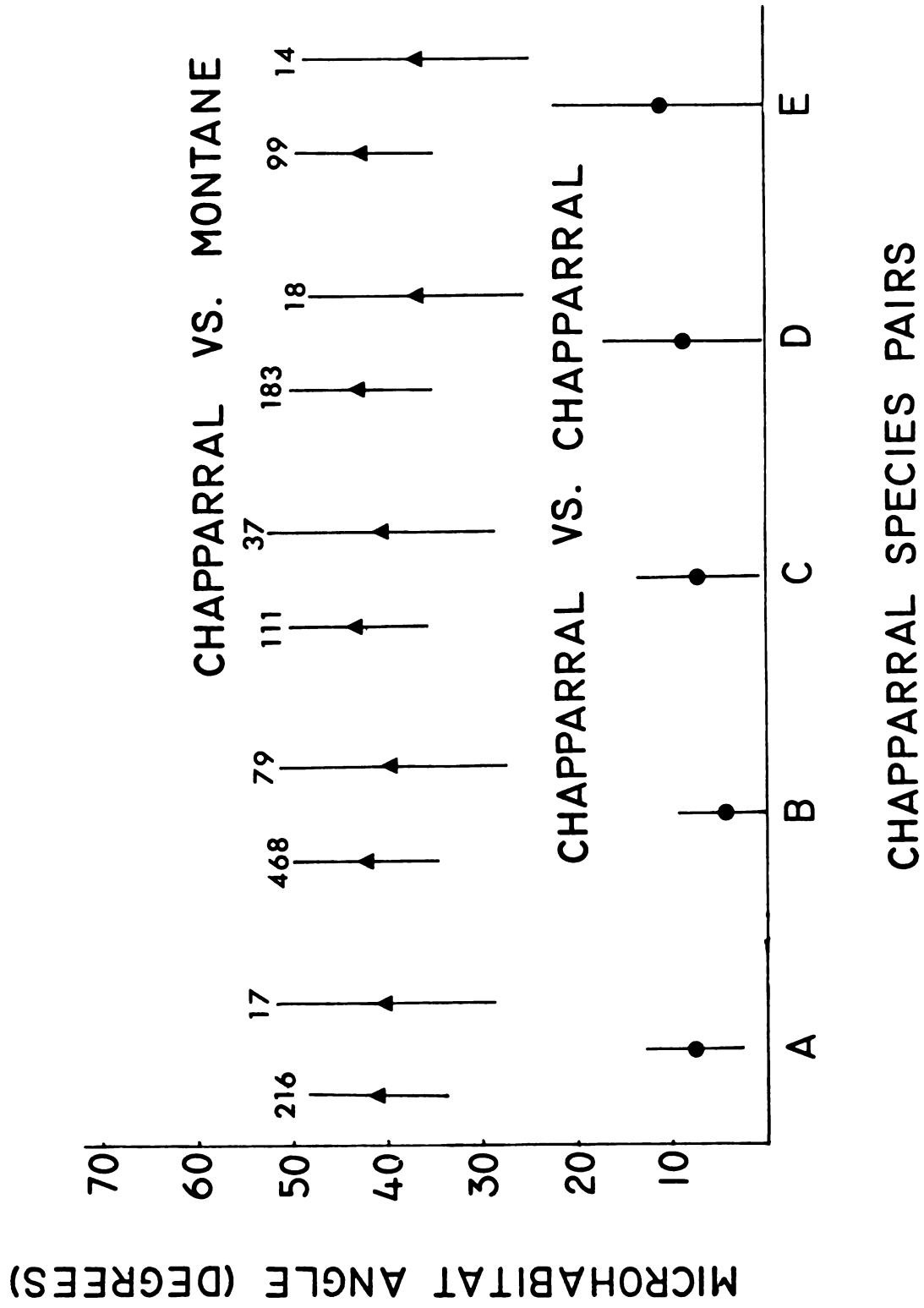
of each category in the environment. For example, in the chapparal environment, a line segment between 0 and 1 would be subdivided into four microhabitat categories: open ground ( $0.00 \leq x < 0.06$ ) ground under bushes ( $0.06 \leq x < 0.81$ ), rocks ( $0.81 \leq x < 0.87$ ), and trees ( $0.87 \leq x < 1.00$ ). Now, if a point were placed randomly on the line, it would necessarily fall into one of the four categories. This is done by a random number call for each lizard and the microhabitats selected by the members of a particular lizard population yield the populations' microhabitat use vector. Angles between microhabitat use vectors of species pairs are calculated as in Fuentes (1976).

In each of ten runs of the model, microhabitats were selected at random up to the number of individuals Fuentes observed for each species. The angle between microhabitat frequency vectors in identical sites would be  $0.0^\circ$ . But if in fact the frequencies of microhabitats in "closely matched" sites are not equal, the angle between microhabitat frequency vectors may be slightly higher. In the simulation, small sample size (few lizards observed) makes convergence of microhabitat use angles to exactly  $0.0^\circ$  unlikely. The angle between the microhabitat frequency vectors of the chapparal and montane sites is 42.6%.

#### Within-continent comparisons

This section describes the results which question the validity of Fuentes' hypothesis. The mean value of microhabitat use angles for ten runs of the neutral model for between-continent comparisons is compared qualitatively with the mean microhabitat use angles for within-continent comparisons. For example, in Figure 7, the mean microhabitat use angles

Figure 7. Within-continent comparisons. Chaparral species pairs. The mean and 2 SD from 10 runs of the neutral model are given for the comparison of each chaparral species with its "analogue" and with the five montane species from the same continent. Species pairs and numbers of observations for each run are given with California species on the left of each pair. Pairs (after Fuentes 1976): A - *Cnemidophorus tigris* (216) & *Callisaurus maculatus* (17); B - *Uta stansburiana* (468) & *Liolaemus lemniscatus* (79); C - *Sceloporus orcutti* (111) & *Liolaemus monticola* (37); D - *Sceloporus occidentalis* (183) & *Liolaemus fuscus* (18); E - *Sceloporus occidentalis* (99) & *Liolaemus tenuis* (14).



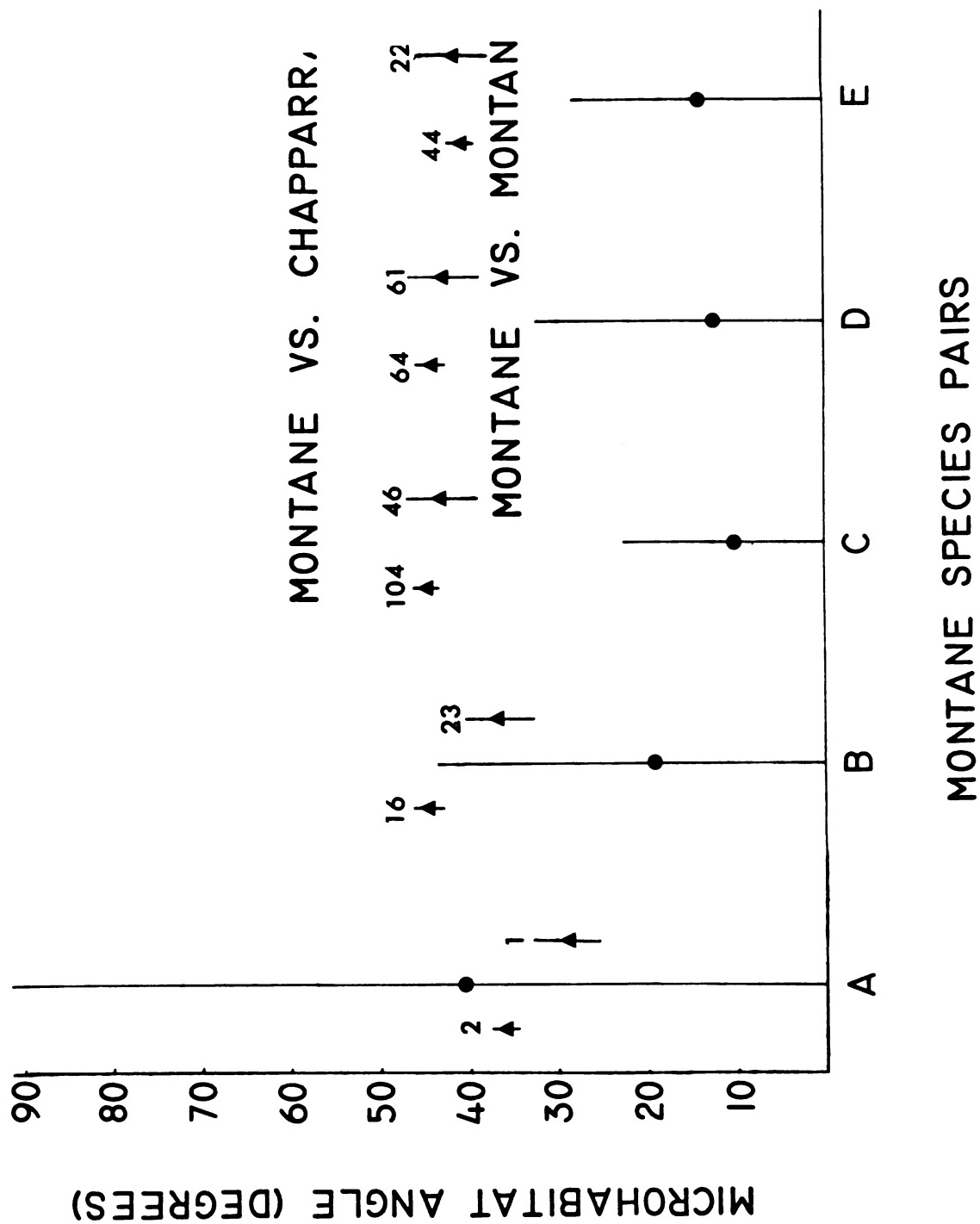
for chapparral species pairs (chapparral vs. chapparral) are compared qualitatively against the mean microhabitat use angles for each chapparral species with each of the montane species from the same continent (chapparral vs. montane). On the whole, within-continent comparisons provide much higher angles than do between-continent comparisons. This qualitative pattern agrees completely with Fuentes' hypothesis, but it is produced by a model which is neutral except with respect to microhabitat frequency differences at the montane and chapparral sites.

Similar data from the neutral model for the montane sites are provided in Figure 8. Each montane species "analogue" is compared with each of the chapparral species from the same continent, and microhabitat use angles are calculated. Again, with one exception (in which sample size is extremely small), within-continent comparisons (montane vs. chapparral) provide angles which are much larger than the angles between species "analogues" (montane vs. montane).

Clearly, if microhabitat frequencies are more different between chapparral and montane habitats than between two chapparral (or montane) habitats, neutral model predictions will always "support" Fuentes' hypotheses. The criteria used to establish the similarities or differences of habitats are precisely those on which the microhabitat utilization comparisons depend.

Since Fuentes' hypothesis can be confirmed even by randomly generated resource use data, it cannot provide a valid approach to the problem of community convergence. But what about the more widely accepted approach to between-continent comparisons of similar sites? Do Fuentes' data confirm the widely accepted hypothesis that communities on

Figure 8. Within Continent Comparisons. Montane Species Pairs. Comparisons similar to Figure 1. Pairs (after Fuentes 1976): A - *Gerrhonotus multicarinatus* (2) & *Urostrophus torquatus* (1); B - *Eumeces skiltonianus* (16) & *Liolaemus schroederi* (23); C - *Uta stansburiana* (104) & *Liolaemus nigroviridis* (46); D - *Sceloporus graciosus* (64) & *Liolaemus nigroviridis* (61); E - *Sceloporus occidentalis* (44) & *Liolaemus tenuis* (22).



different continents tend to converge under similar long term environmental conditions? Are species analogues from Fuentes' between-continent comparisons significantly more alike than would be expected by chance?

#### Between-continent comparisons

In general, Fuentes' chapparral species analogues are no more alike in their microhabitat use than would be expected by chance (Figure 9). Species analogues are those assigned by Fuentes (Note that a similar study of chapparral lizard community structures in Chile and California not cited by Fuentes reported a different species assemblage and assigned different species analogues [Sage 1973]). All microhabitat angles recalculated from Fuentes (1976) (with minor errors in Fuentes' angle calculations corrected) fail to differ significantly from those expected from the neutral model with the exception of one species pair (B), which is significantly ( $p < .001$ ) less similar in microhabitat use than would be expected by chance alone. Significance was assigned by checking the probability that the angle from Fuentes could have come from the distribution given by ten runs of the neutral model. All neutral model distributions did not differ from Normal (Kolmogorov-Smirnov goodness of fit  $p > .2$ ).

Similarly, Fuentes' montane species analogues are not strikingly similar in their use of microhabitats (Figure 10). Two of the five species pairs (C,E) are less alike than would be expected by chance ( $p < .05$ ). All other angles are indistinguishable from those expected from the neutral model.

Thus, when Fuentes' data yield microhabitat use angles which

Figure 9. Between-Continent Comparisons. Chapparral Species Pairs.  
Mean and 2 SD are given from the neutral model for similarity  
of species pairs. Triangles are data from Fuentes (1976).  
Species pairs are those given in Figure 7.

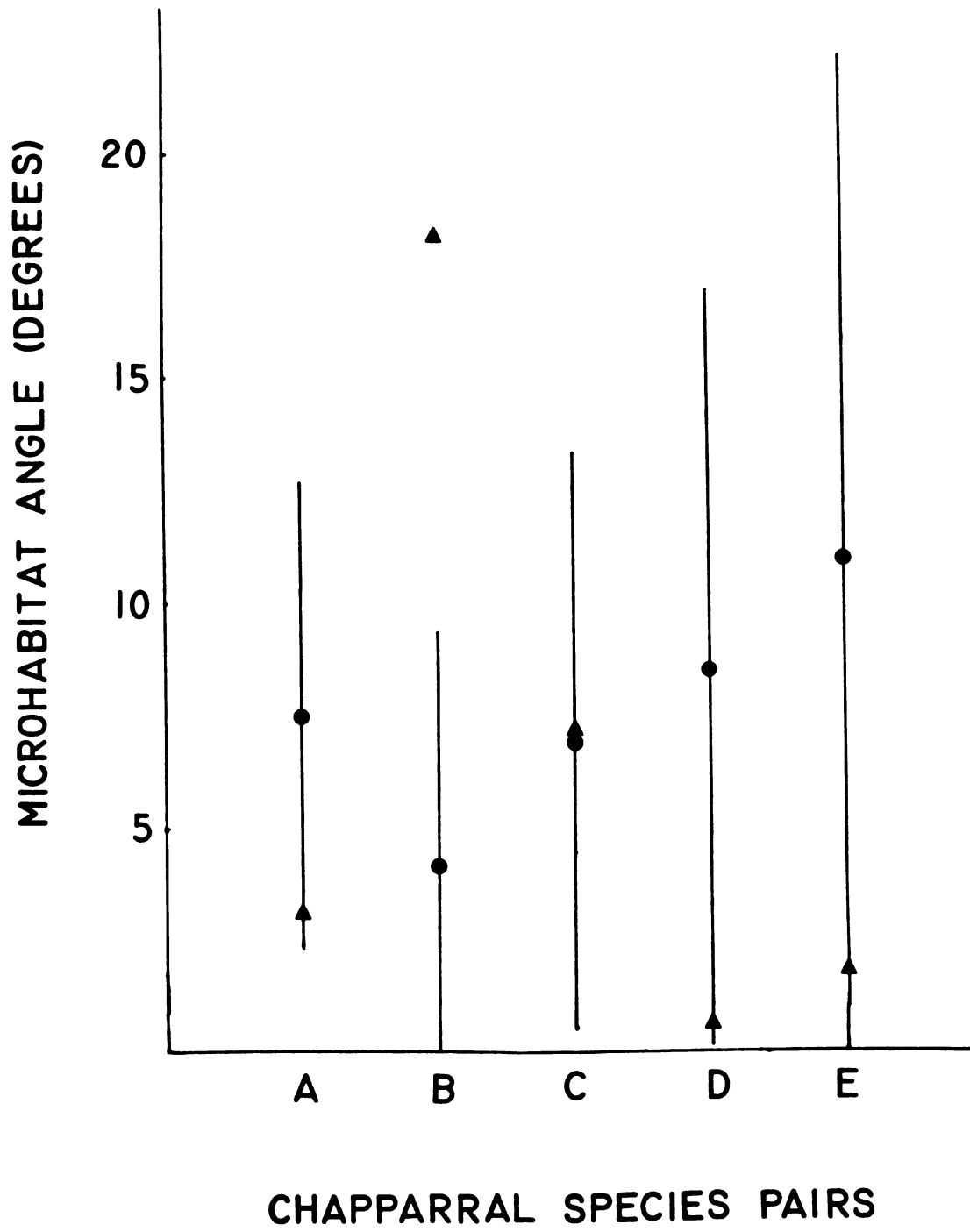
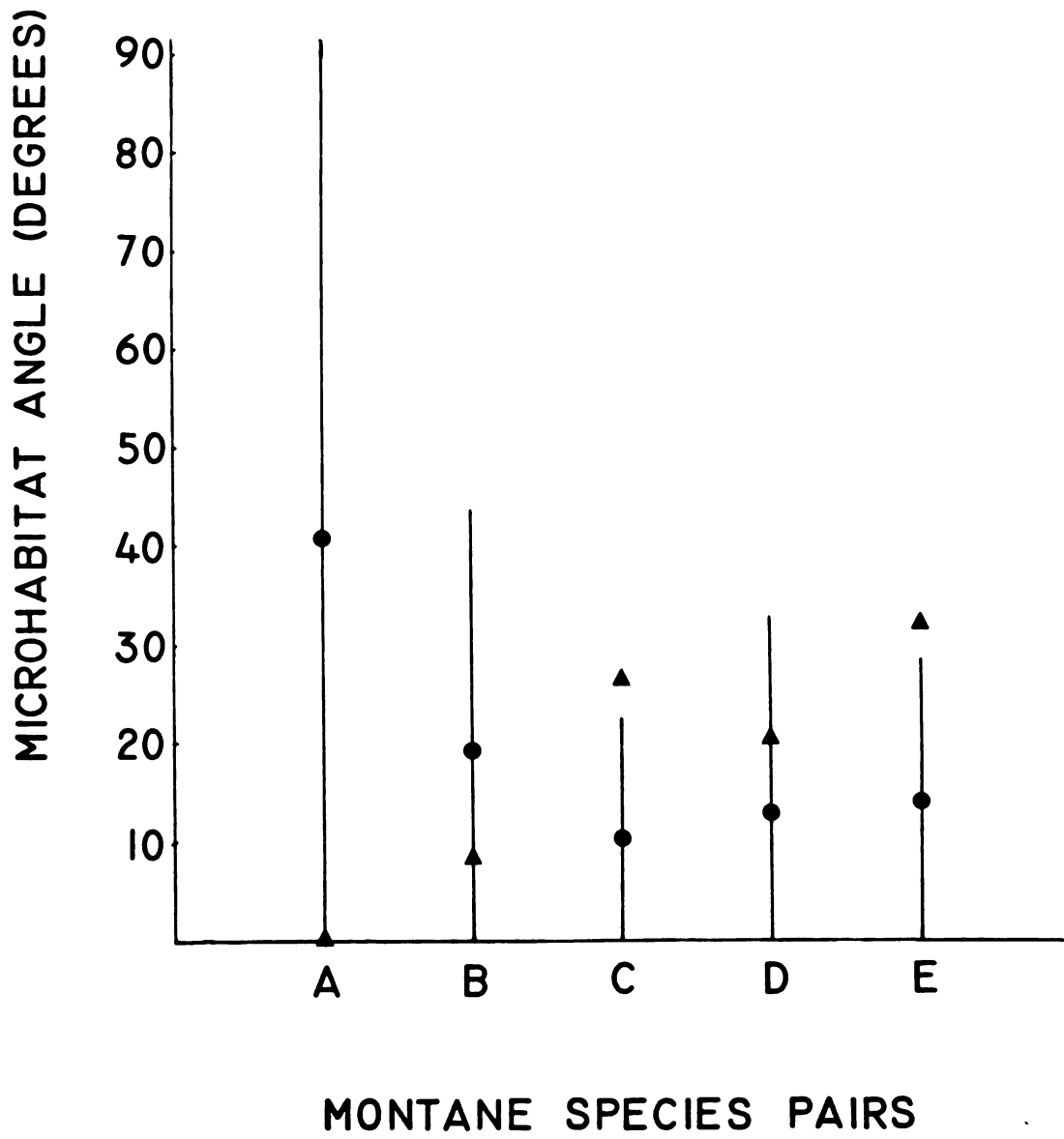


Figure 10. Between-Continent Comparisons. Montane Species Pairs. Mean and 2 SD are given from the neutral model for similarity of species pairs. Triangles are data from Fuentes (1976). Species pairs are those given in Figure 8.



differ significantly from those predicted from the neutral model, they imply greater differences in microhabitat use than would be expected by chance. How might these differences be explained?

- 1) Habitats "closely matched" for vegetational and altitudinal similarity are not precisely alike. The model assumes that two analogous sites have equal microhabitat frequencies. Small differences in microhabitat frequencies would tend to increase the expected values for microhabitat use angles at similar sites. This effect would have to be large to make all "species analogues" (Figures 9,10) significantly more similar than neutral model predictions.
- 2) There may be insufficient data on certain lizard species to predict mean microhabitat use.
- 3) Microhabitat use angles that are higher than neutral model predictions imply that phylogenetic or historical constraints may be more powerful than the effects of environmental similarity on the biological interactions to which the model is neutral.

The results presented here indicate that caution is necessary when comparing "analogous" communities on similar habitat sites between continents.

### Discussion

Until the observed patterns are shown to differ significantly from those generated by the neutral model, the arguments for the action of long term environmental similarity leading to the convergence of community structures as presented by Fuentes (1976) must be regarded as premature.

In addition, this case study shows that examining the convergence of community structures in "similar" environments on different continents leads to comparisons which are either not distinguishable from the neutral model or show differences in excess of those expected by chance. Cody (1974) claims that only very similar sites are appropriate for convergence comparisons. If this is so, it may be impossible to show convergence patterns of species pairs which differ significantly from the neutral modeling predictions. Clearly, whenever the criteria for establishing similarities in sites are the same as those for establishing similarities in the use of resources, the "convergent" resource use patterns must be shown to differ from those expected by chance. Like other hypotheses involving resource use, convergence studies must begin to consider resource availability. Finally, community convergence studies may need to abandon pairwise comparisons altogether and in some way compare whole communities in niche space to see how well the "convergent" communities overlay.

Neutral models have provided some powerful insights (Caswell 1976). In general, the neutral model approach provides a valuable tool: for examining a myriad of explanations about naturally observed patterns; for evaluating the validity of hypotheses, and for demonstrating--as in this paper-- that some widely accepted approaches to a problem (e.g., looking at convergence of community structures by comparing "closely matched sites") should be approached with caution.

## DISCUSSION

### Interval estimation of ecological parameters

There are several requirements of the strong inference methodology which must be met to exclude alternative hypotheses. An important point in Platt's (1964) methodology is the crucial experiment. Critical to the conduct of a crucial experiment is the ability to measure outcomes in a way so as to discriminate among competing hypotheses. Clearly, if experimental measurements cannot lead to exclusion of one or more of the alternative hypotheses ecologists cannot progress by continuing that particular approach to the problem.

Interval estimation of ecological parameters (such as niche overlap) may add rigor to the effort to eliminate alternative hypotheses, but only if they are employed in hypothesis testing and/or the estimation of sample size. Despite the fact that Simpson (1949) derived an expression for the standard error of his diversity index, it has rarely been calculated. Similarly, the information measure of diversity ( $H'$ ) has sampling error when calculated for a finite population. Several authors have dealt with the estimation of  $H'$  and its standard error (see Pielou 1969), but again, this has been applied only rarely. Difficulties encountered in the interpretation of diversity measures (Hurlburt 1971) are possibly related to the fact that the available statistical techniques were not employed. This is a generic problem; any indices ecologists use should have estimates of variability. These estimates could indicate where interpretation problems may arise due to the precision of the estimate. I suspect that at least some of the

interpretation problems with overlaps could be traced to estimation problems.

The interval estimates of niche overlap derived here allow the estimation of sample sizes necessary to distinguish  $\alpha$  to whatever degree desired. Thus, for the purposes of hypothesis testing and experimental design, ecological variables with interval estimates can be very helpful. Of course, we may find that to discriminate between competing hypotheses in community structure, we need to be able to detect differences in niche overlaps which are beyond our ability to measure accurately. If this conjecture proves true, the only recourse is to abandon the use of niche overlaps as they are currently employed and try to develop and extend more rigorous paradigms to examine resource use and community structure.

#### Neutral models as null hypotheses

The null hypothesis is rarely overlooked as an alternative hypothesis, but in complex situations, even the null hypothesis may be difficult to formulate. Neutral models can often provide appropriate null hypotheses for complex situations. Caswell (1976,1977) gives some examples of neutral models and discusses the generation and verification of neutral models.

Most often, neutral models are applied to pre-existing data. By considering random variation, one can uncover just where some process is leading to a non-random pattern. Raup et al (1973) set out to show how real phylogenetic clades differ from those generated at random. This would allow the separation of deterministic and chance events in evolution. Surprisingly, real cladograms are not too different from

those generated by the neutral model. The analysis is still proceeding (Raup and Gould 1974, Raup 1977, Gould et al 1977), but they have been able to find few differences between the model and real data.

A proper neutral model is not easy to come by as it must be stated relative to a particular hypothesis and only those mechanisms eliminated explicitly do not influence the outcome. For example, in the neutral model for resource use presented here, all effects except those of resource availability are explicitly eliminated. Surprisingly, the action of random resource use on given resource availability patterns simulates Fuentes' data rather well. For this particular neutral model and for the others discussed earlier, the parsimonious explanation for the observed pattern seems adequate. This is not to say ecological phenomena are random or neutral, rather we need hypotheses and methods which will allow us to rigorously demonstrate the differences from null hypothesis (neutral model) predictions. Thus, the neutral model provides a standard against which the significant patterns can be compared. This is the positive side--we at least have a method for preparing null hypotheses in more complex situations.

It is possible, of course, to generate a neutral model in advance of the experiment. If the primary hypothesis has been well defined along with proposed causal mechanisms, a neutral model which eliminates the proposed causal mechanisms could be developed. The model would yield predictions for systems dynamics due to chance (for example), and differences between the model predictions and observed results could be calculated. As with interval estimation, neutral models can provide valuable design tools.

Recommendations for the evaluation of resource use,  
community structure and convergence

Despite the difficulties, it is becoming increasingly clear that future considerations of resource use must consider resource availability. As a first approximation, it may be acceptable to consider resources to be available in proportion to the frequency of the resource in the environment as I have done in the neutral model. This may be most acceptable for "fixed" resources such as microhabitat space. For resources which may evade capture (e.g., prey escape responses) or depressible resources (Charnov, Orians and Hyatt 1976) density may not be an appropriate measure of availability--although some function of density may suffice. In any case, even crude approximations of resources available may allow us to eliminate some alternative hypotheses.

Where possible, interval estimates of resource use metrics should be established and used. The interval estimates for any ecological index will add rigor and provide guidance as to which hypotheses we can discriminate and which may be impossible to distinguish with reasonable sample sizes. In some situations the interval estimate of niche overlap will suggest an appropriate sample size to test the proposed hypothesis; in other cases it may be impossible even with large samples to show small differences in  $\alpha$ . Unfortunately, even if we can arrive at a technique or sample size which will allow us to rigorously test hypotheses for resource use on a single axis, we are still left with the problem of applying both theory and results to multiple axes (May 1975) or variable environments (Wiens 1977).

The manipulative approach is an attractive alternative to simply measuring overlaps. In this approach, one or more variables affecting

the process are manipulated and the resource is monitored. In this way, the perturbation-response dynamics of the system can help uncover the mechanisms underlying the interaction. Resource levels or size-species composition of food may be altered directly in the lab (Werner and Hall 1974) or in the field (Eisenberg 1966, Hall, Cooper, and Werner 1970, DeBenedictis 1974). Population densities or species compositions may be altered on a fixed habitat or food base (Eisenberg 1966, Connell 1975, Schroder and Rosenzweig, 1975, Werner and Hall 1976), or enclosures may be used to constrain a species' interaction to a particular habitat (Grant 1972, 1975, Werner and Hall 1977, Jaeger 1971). Responses such as competitive release, habitat shift, diet shifts and population density changes may be predicted as alternative system responses to the manipulation. Furthermore, manipulated systems may show large shifts in overlap values (Schroder and Rosenzweig 1975, Werner and Hall 1976) which can be distinguished with reasonable sample sizes.

Convergence in community structure might also be tested rigorously by manipulation. Communities which have been judged "similar" based on functional criteria (resource use patterns) should have similar qualitative responses to a manipulation. For example, if a species (A) and its "analogue" (A') are removed or have their densities severely reduced in the two "convergent" communities, the communities' responses to such a manipulation should be similar (e.g., species B and B' both shift into the former A, A' habitat). This hypothesis has not been tested, but may provide some interesting insights.

Another alternative is to explore ecologically related

morphological variates of the interacting species as well as their resource use efficiencies, physiology and so on. To the degree that these variables reflect the evolutionary outcomes of long term species interactions, this information may be applied to predict community structure. Several investigators have employed this technique and have found it extremely helpful in explaining observed patterns (Werner 1977, Karr and James 1975).

Clearly, both observational and manipulative approaches to resource use patterns have their problems (Schoener 1974a). But both approaches seem to be necessary for our understanding of resource use and community structure. Careful observation of ecological patterns provides needed information which can lead to the formulation of testable hypotheses. However, observation (and/or calculation of summary indices) alone will not provide enough insight into the mechanisms or interactions leading to observed patterns. Manipulative experimentation, perhaps employing the techniques of strong inference should allow the elimination of alternative hypotheses and lead to greater insights.

Resource use patterns, the mechanisms which alter their form and how this is all reflected in community structure is central to community ecology. Competition, predation, environmental variability and other mechanisms are candidates for the factors which structure communities. Only through careful experimental design, perhaps including interval estimates of variables and neutral models as null hypotheses, can we hope to see how these mechanisms influence resource use and ultimately community structure.

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