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NICHE THEORY

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HISTORICAL ROOTS OF NICHE THEORY

The first use of the word *niche* to refer to an animal's ecological position in the world was in a short paper by Joseph Grinnell in 1924 (14); Grinnell referred to the "ecological or enrivonmental niche" as the ultimate distributional unit of one "species or subspecies." Actually, in a much earlier paper (13), the general notion of the niche as a measurement of an animal's geographical distribution was developed quite completely for several different organisms, although the word *niche* was never actually mentioned. The idea came to fruition in a subsequent paper (15) in which ecological niche was defined as ". . . the concept of the ultimate distributional unit, within which each species is held by its structural and instinctive limitations, these being subject only to exceedingly slow modification down through time." There were two significant aspects of Grinnell's concept of niche: first, its distributional nature—its conceptualization as the distribution of individuals over a geographical area or among habitat types—second, perhaps more importantly, its potential nature—the idealized distribution of individuals in the absence of their interactions with other species. More specifically, Grinnell conceived of the distributional limits of species as being set by various physical or climatic barriers. Only rarely did he refer to the absence of a proper food supply as a limiting factor, and only casual reference was given to adverse interaction with some other species as a limiting factor. This is not to say that Grinnell did not regard such interactions as important in nature, but rather it emphasized his conception of niche as being pre-interactive—the potential area within which a species can live as opposed to the area in which one actually finds it.

At about the time that Grinnell's notion of niche was evolving, Charles Elton was independently developing a conceptual framework of niche in terms of food habits of a species (9). When specifically referring to the ecological niche he was careful to imply a more global meaning to the term—". . . and the 'niche' of an animal means its place in the abiotic environment, its relations to food and enemies," or "the niche of an animal can be defined to a large extent by its size and food habits" (9, p. 64). Yet, when describing various niches, he invariably referred to only the food habits of organisms. For example, his ecological equivalents—such as ophiophagous snakes in

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various parts of the world, tick-eating birds on virtually every continent, or coral-grazing animals in wide-ranging coral formations—always seem to be in reference to food habits. Thus, Elton formally presented his notion of niche as being the species' position in some kind of a larger framework, such as a community or ecosystem; however, his usage connoted the more restricted meaning of the animal's actual food habits. But a more significant aspect of Elton's niche is that it was a post-interactive concept—an organism's actual place in nature as opposed to its potential place in nature.

Thus, the early ideas of niche ranged from the actual physical distribution of organisms to the organism's relationship to other organisms. A subtle interpretation reveals Grinnell's notion of a pre-interactive niche, or potential niche (later to be equated with the modern notion of fundamental niche), as opposed to Elton's notion of a post-interactive niche (later to be equated with the modern notion of realized niche).

It is easy to find references to concepts similar to ecological niche in the writings of Darwin, Wallace, and other early natural historians. I think it is significant that the writings of these early naturalists contain the kernels of many of the currently popular ideas in niche theory.

An exhaustive summary of these historical developments is certainly beyond the scope of a review paper. However, it is becoming more apparent that the insights of the early naturalists are now being quantified and that this quantification is what niche theory is all about. In much the same way that numerical taxonomy is viewed by some as the quantification of processes used by classical taxonomists, we might similarly regard niche theory as the quantification of methods that were intuitively employed by the early natural historians.

During the period 1930–1950, the niche of both Elton and Grinnell became somewhat amalgamated and the vague notion of ecological niche as an organism's profession within an ecological community became accepted in virtually all textbooks of ecology (1, 2, 27). The most significant contribution to niche theory during this period came from Gause. Commonly referred to as *Gause's theorem* or *Gause's axiom,* this generalization states that if the niche characteristics of two species are very similar, the two species cannot occur in the same place; it is somewhat loosely stated as "no two species can occupy the same ecological niche." It is not surprising that naturalists before Gause had noted this principle. Grinnell stated, "no two species in the same general territory can occupy for long identically the same ecological niche" (15); and even earlier he wrote, "two species of approximately the same food habits are not likely to remain long evenly balanced in numbers in the same region" (12). This principle led to a general class of fieldwork which persists to the present day (3, 22, 30, 31) and which demonstrates that for any particular pair of closely related species there exist subtle ecological differences of one sort or another, even though it did not appear initially that the two were ecologically distinct (this supports the notion that no two species can occupy the same ecological niche). The popularity of the concept of ecological niche was probably due in large part to Gause's theorem.

Toward the end of the 1950s it became apparent to numerous workers that the idea of ecological niche as an animal's "occupation" in a community was excessively vague. At precisely this time G. Evelyn Hutchinson developed the formal notion of the ecological niche as a hypervolume (20), a concept which led to a revolution in niche theory. Hutchinson began by considering two continuous, orderable environmental variables, for example, temperature and humidity. Let temperature equal x, let humidity equal y, and suppose a graph of x against y is plotted. There is some value of x (x') above which a particular species in question cannot survive. There is another value of x (x'') below which the species cannot survive. Similarly, there is a value of y (y') above which the species cannot survive and another value of y (y'') below which the species cannot survive. Between y' and y'' humidity conditions are such that the species can survive. Between x' and x'' temperature conditions are such that the species can survive. Thus, we have defined a rectangular area limited by the quantities x', x'', y', and y'', within which temperature and relative humidity are suitable for the species in question to survive. We could now consider adding a third coordinate, a third environmental variable, to this system. For example, we might add salinity, symbolized by the letter z. Again we conceive of a z' and a z'' above which and below which, respectively, the species cannot survive. We now have defined a three dimensional rectangular solid. Any point within this rectangle represents a state of temperature, humidity, and salinity which is suitable for the survival of the species in question. If environmental variables are continually added until all variables that are important to the species have been added, we extend three dimensional space into a multidimensional space. Every point in this multidimensional space describes states of the environmental variables which are suitable for the survival of the species in question. It is this hypervolume that Hutchinson suggested would adequately conceptualize the fundamental niche.

Perhaps the most important principle derivable from Hutchinson's original formalization is his distinction between *fundamental* and *realized niche*. Later in this paper these terms will be redefined in what I think is a more useful way, but for the present, Hutchinson's fundamental niche is as described above. Hutchinson's notion of the realized niche was essentially that part of a species' fundamental niche which remained occupied by the species after interactions with another species had been completed. It will be seen later that Hutchinson's notion of the realized niche corresponded more closely to what I have called *partial niches*, but the distinction between a preinteractive and a post-interactive niche was quite definitely made by Hutchinson.

The formalization of niche theory by Hutchinson was later modified by several people, most notably Slobodkin (32) and Patten (29). But it was not until Levins (23) and Colwell (5) tried to make niche measurements in nature that the current vigorous activity in the theory of ecological niches came about.

In summary, then, it is possible to trace the development of niche theory

from its origins with Grinnell and Elton to its generation of perhaps the only specific principle or law of nature ever to be proposed in ecology, Gause's axiom. The rigorous formalization of the concept by Hutchinson ultimately led to attempts at applying such theory in nature, simultaneously and independently, by Levins and Colwell.

BASIC DEFINITIONS

In order to set the fundamental theoretical framework, within which all that follows is couched, it is necessary first to describe a basic set of definitions; second, to develop an intuitive notion for several concepts associated with niches; and third, to specify an underlying dynamic framework. We begin with a basic set of operational definitions.

Operational taxonomic unit (OTU) (33).—An operationally identifiable collection of organisms is an OTU. For most ecological considerations this unit more or less corresponds to "species."

Community (C).—A specified set of OTUs is a community. What a "natural" community is, how one recognizes one, etc, is difficult to say. However, I merely wish to use the notion of community to attack the broader aspects of niche theory, and consequently I will not approach the difficult question of what in fact constitutes a natural community. Thus, unless otherwise specified in this development, C refers to an arbitrarily specified set of OTUs.

Operational habitat (resource).—An operationally identifiable unit which is lived in, occupied by, or consumed by one or more of the OTUs in C is an operational habitat. It should be noted that habitats are being recognized as arbitrarily specified cells without questioning whether they are related to one another.

Environment (E).—Environment is a specified set of operational habitats. Note here that it is easy to set up totally nonsensical environments. The difficult question of what constitutes a natural environment, that is, a natural assemblage of habitats, will only be qualitatively approached in this paper. Biologists using "good" biological intuition will probably not set up nonsensical environments, but we would hope that the time will come when an operational procedure will be available for specifying environments that are not nonsensical.

Fundamental niche.—Fundamental niche is the set of elements within E which would be occupied by a particular OTU if no other OTUs in C were present, including the OTU in question. Thus, this use of fundamental niche requires that there be no density dependent feedback effects on an OTU, either inter- or intraspecifically.

Partial niche of OTU i with respect to OTU j.—This is the set of elements within E which will be occupied by OTU i under the presence of density dependent effects felt only from OTU j, where i and j are indices for two particular OTUs in C. Note that the notion of partial niches can be applied to any number of OTUs acting in a density dependent way. For example, we could speak of the first partial of OTU i with respect to OTU j as was done in this definition, or of the second partial of OTU i with respect to OTU j and OTU k, referring to the occupation of the habitats in E by OTU i under the density dependent effects of OTUs j and k only. Similarly, we might speak of the third, fourth, . . . , mth partial niches of OTU i.

Realized niche.—Realized niche is the set of elements within E which will be occupied by OTU i at equilibrium if all other OTUs in C are present in E. Note that this is precisely the same as the mth partial niche of OTU i with respect to OTU $j, k, . . . , m$.

Environmental grain.—Grain is the way in which OTU i moves from habitat j to habitat k. Assuming that there are H habitats in E, for a fixed Δt, which is much smaller than the generation time of the OTU in question, environmental grain is a description of the way in which individuals of OTU i are transferred from habitat j at time t to habitat k at time $t + \Delta t$. Two extremes of graininess are usually identified: Individuals may tend to remain in one specific habitat for long periods of time (coarse grain), or individuals may sort out randomly with respect to the habitats at each Δt interval (fine grain).

The above definitions are only a small fraction of the number that could be made. However, many potential concepts are currently in formative stages of development, and to impose operational definitions on them might indeed hinder their development. I thus choose to make only the above definitions. Undoubtedly, not all of the above definitions will satisfy everybody as to what the defined elements should be. However, definitions are totally arbitrary, and I shall strictly adhere to them in this paper. I hope they prove generally useful.

In the definition of operational habitat I have emphasized the arbitrariness of choice of habitat. It should be further emphasized that the notion is to be applied in both a discrete and continuous case. My development will tend to depend upon division of the environment into discrete habitats rather than upon environmental continua. However, it should be emphasized that everything presented herein applies equally to environments thought of either as continua or as sets of discrete habitats. Naturally, discreteness and continuousness merge, and one might say that as individual operational habitats become smaller and smaller the entire environment approaches the state of a continuum.

Also from the above definitions it should be clear that there is a continuum of types of niches from fundamental niche, to first partial niche, to second partial niche, all the way to mth partial niche (also known as realized

niche), where there are m OTUs in C. That is, we go from a condition in which, at least in principle, an OTU occupies an environment in the absence of any sort of density dependent effects whatsoever, to a situation in which an OTU occupies that environment under density dependent effects from all possible members of the community.

Not to be included under the above definitions, but of central importance in the present paper, is the notion of niche breadth. Niche breadth is likely to remain fuzzy for some time since the idea is currently in a stage of rather rapid development. The concept more or less corresponds to the naturalist's old notions of specialized versus generalized, a specialized OTU being a narrow-niched organism and a generalized OTU a broad-niched organism. Niche breadth was apparently simultaneously invented by Levins (23) and Colwell (5) and refers more or less to the evenness of distribution of individuals throughout a set of habitats. As in the notions of species diversity, in which the species are analogized with habitats in the present context, we have at one extreme an equal number of individuals in every habitat in E, and at the other extreme all of the individuals are congregated in one habitat of the entire set of habitats. When the distribution is extremely even, we say that the niche is extremely broad. When the distribution is concentrated in one (or perhaps just a few) habitats, we say that the niche is extremely narrow. Thus, niche breadth is a measurement on the set of habitats which we have defined as the niche itself. It is important to distinguish between the niche and a measurement associated with that niche, niche being a set of habitats, and niche breadth being a measurement over that set of habitats. As we have defined a variety of different types of niches, we likewise have associated with each of those types a niche breadth.

It is useful to have a standardized notational scheme to associate a measurement with a specific type of niche. Consider a variable with one subscript and a "functional" set of parentheses. The subscript refers to the OTU under consideration, while the parentheses serve to delimit the dependent OTU. For example, B_i (i, k, l) refers to the niche breadth of the ith OTU in C, in the presence of the density dependent effects of species i (intra), k, and l. B_3 $(3, 4, 5)$ is the niche breadth of the 3rd OTU in C, under the influence of the density dependent effects of species 3, 4, and 5. B_2 (2) is the niche breadth of OTU 2 under the density dependent effects of itself alone. Typically, it is useful to apply particular appelations to two specific types of niche breadths since they will be repeatedly referred to: namely. B_i (0) the fundamental niche breadth of OTU i (the 0 refers to the absence of density dependence from any OTU in C), and B_i (m) the realized niche breadth of species i (the m refers to the fact that density dependence is being felt from all other species in C).

Another concept frequently appearing in the recent literature on niche theory is that of niche overlap (6, 7, 19, 23, 28, 35). Unfortunately, niche overlap frequently is equated with interspecific competition, but as pointed out by Colwell and Futuyma the relationship between niche overlap and

competition is not at all clear. I will discuss this matter further in the section on the utilization of niche theory to estimate interaction coefficients. But for now it suffices to say that niche overlap merely represents the degree to which two OTUs co-occupy a habitat in E.

At this point I wish to present a dynamic theoretical framework which will be the basis for all that follows. This underlying framework is actually a formalization of the basic notions of ecological succession, an important topic which has never been really subjected to theoretical analysis. The major features of succession which are of importance here are: 1. interactions among populations are mediated by the environment, and 2. environment is modified by the changing populations. Thus, the determination of interactions by the environment and the reciprocal determination of the environment by the products of the interactions is the driving process of succession. The following is a formal presentation of the above simple concepts.

Begin by assuming that there exists a collection of OTUs called C. Assume that the environment (E) is composed of H discrete operational habitats. If X_{ih} refers to the population density (or biomass) of the ith OTU in the hth habitat, let the following set of equations describe the dynamical behaviour of the system C in habitat h locally in time (over a short time span).

$$\frac{dX_{ih}}{X_{ih}dt} = r_{ih} - \sum_{j=1}^{m} a_{ijh}X_{jh} \qquad\qquad 1.$$

Where r_{ih} and a_{ijh} are constants (to be explained further below) and m is the number of OTUs in C. Note that equations 1 almost certainly are good approximations to nature since it is only necessary to apply them during very short time spans. Note also that if we rearrange equations 1 such that α_{ijh} appears instead of a_{ijh} (where $\alpha_{ijh} = a_{ijh}/a_{ijh}$), the well known Gause-Volterra equations of competition are obtained. However, in the present context let α_{ijh} be positive or negative so that the theory will generally encompass all possible types of biological interaction. From this initial theoretical framework (equations 1) we make three fundamental assumptions: 1. There exists a matrix $\mathbf{G}$ (or set of matrices $\mathbf{G}_i$), called the "grain matrix," the elements of which indicate rates of migration from habitat to habitat. An element of $\mathbf{G}_i$, g_{kh}, gives the likelihood that if an individual was found in habitat h at time t, it will be found in habitat k at time $t + \Delta t$. For the sake of generality the elements of the grain matrix are defined as general functions of the X_{ih}, even though in the rest of the paper they are treated as constants. Thus, we have, in general

$$g_{hk} = f_1(X_{1h}, X_{2h}, \cdots, X_{mh}, X_{1k}, X_{2k}, \cdots, X_{mk}) \qquad\qquad 2.$$

2. There exists a matrix $\mathbf{E}$ (or set of matrices $\mathbf{E}_i$), called the environmental similarity matrix, the elements of which (e_{ij}) specify the relationship between the hth and kth habitats of the environment. In general we have

$$e_{hk} = f_2(X_{1h}, X_{2h}, \cdots, X_{mh}, X_{1k}, X_{2k}, \cdots, X_{mk}) \qquad 3.$$

3. Given a set of matrices $\mathbf{E}_i$ and $\mathbf{G}_i$, there exist the functions f_3 and f_4 such that

$$\alpha_{ijh} = a_{ijh}/a_{iih} = f_3(\mathbf{E}_i, \mathbf{G}_i)$$
$$r_{ih} = f_4(\mathbf{E}_i, \mathbf{G}_i)$$
$$\qquad 4.$$

The above three assumptions, coupled with the initial assumptions of equations 1, represent one possible formalized statement that interactions are functions of environmental patterns, which in turn are functions of the results of the interactions. These formalized notions are presented so as to have a rather general framework upon which recent explorations into niche theory can be placed.

ENVIRONMENTAL GRAIN

The idea of environmental grain was first presented by Levins & Mac-Arthur (24) and has been used in various contexts subsequently (23, 26). Qualitatively, most workers share the view that a population whose members move infrequently from habitat to habitat is basically coarse grained, whereas a population whose members move readily from habitat to habitat is basically fine grained. However, the fine points of environmental grain are difficult to analyze.

The notion of the grain matrix has been introduced in a previous section. The grain matrix is an $\mathbf{H} \times \mathbf{H}$ matrix, the elements of which indicate the probability of transition from one habitat to another. That is, g_{ij} is equal to the probability that an individual found in habitat i at time t will be found in habitat j at time $t + \Delta t$. The notions of coarseness and fineness are notions which apply to individual habitats. As g_{ii} approaches the value of unity we say that the ith habitat becomes coarser. To the extent that all of the habitats in E are fine grained we may speak of the environment E as being a fine-grained environment, and to the extent that all of the habitats in E are coarse grained we can speak of the total environment being coarse grained. It may in fact be more important in some contexts to consider the variance in the grain of the environment, ranging from the situation with high variance, in which some habitats are fine grained while others are coarse grained, to a low variance situation in which all habitats are either fine or coarse.

It is obvious from the above that the process of migrating from habitat to habitat in the absence of population growth may be viewed as a Markov process in which the grain matrix is a matrix of transition probabilities. To simplify the ensuing discussion we make the further restriction that G, the grain matrix, is both positive and stochastic. That is, $g_{ij} > 0$ and $\Sigma_j g_{ij} = 1$. Let $X_{ih}(t)$ be the number of individuals of the ith OTU present in the hth habitat at time t. Then, evidently we have

$$X(t)G = X(t + \Delta t)$$

and in general

$$X(t)G^n = X(t + n\Delta t)$$

where X is a row vector. As n approaches infinity, $X(t + n)$ approaches u—meaning that whatever distribution is started with, u is the distribution that ultimately is reached. It is a well-known theorem in matrix algebra that when a transition process, such as the above, results in a stable vector, that vector (in this case u) is the eigenvector associated with the dominant eigenvalue of the transition matrix. In the case of a stochastic matrix the dominant eigenvalue is always equal to unity. Thus, u satisfies the equation

$$uG = u$$

As the environment as a whole approaches an extremely coarse-grained situation, the eigenvalues of G all approach unity. On the other hand, as the environment as a whole tends towards a situation where it is perfectly fine-grained, the variability in eigenvalues necessarily increases, since the dominant eigenvalue is always equal to one. The rate at which an arbitrary distribution will settle down to the stable distribution u is roughly proportional to the difference between the dominant and the subdominant eigenvalues. Therefore, we have the general conclusion that a highly coarse grained environment will settle down to the stable form of the distribution much less rapidly than will an environment which is less highly coarse grained. This result is fairly obvious if we look at the elements of the grain matrix from a biological point of view. As the elements on the diagonal approach a value of one (the totally coarse-grained state), they tend to approach what is commonly called *absorbing state*. That is, once an individual finds itself in an environment from which the probability of transition to some other environment is near zero, the individual will remain in that environment. Thus, those habitats which have interhabitat transition probabilities approaching zero will tend to "absorb" individuals, preventing them from moving to other habitats. It will take a relatively long time for the individuals to get out of the habitats they occupy initially and be reapportioned in the other habitats in proportion to the elements in the vector u. The fine-grained situation operates conversely.

The above conceptual development of environmental grain totally ignores a relatively important point, which is the time an organism spends in one habitat. In the above analysis is was merely necessary to choose some arbitrary time unit, Δt, stipulating that Δt is small relative to generation time. In the original utilization of the grain notion the interest was in application to adaptive strategies (23, 24), and it became important to define habitat in such a way that a fitness differential existed for the population between two

different habitats. In this paper the concern is not with adaptive strategies per se, and therefore it is probably not of major significance to link up the determination of an appropriate time unit (Δt) and the manner in which a population responds to natural selection vis-a-vis these two different habitats. A further analysis of this problem can be found elsewhere (34) and is beyond the scope of this brief review.

THE BREADTH DENSITY PROFILE

Hairston was perhaps the first to emphasize the ecological importance of the manner in which spatial distributions related to population densities of different populations (17). His analysis showed a highly significant relationship between the degree of clumping in a two-dimensional plane and the population density of various populations of soil arthropods. In a recent paper (35) the relationship between population density and niche breadth is examined in considerable detail.

Recalling the earlier definitions and notational scheme for niche breadth we have, in general, $B_i(j, k, \ldots, m)$, which refers to the niche breadth of the ith OTU in the presence of density dependent effects felt by the j, k, . . . , m OTUs in the community. As the population density changes from small to large, the niche breadth of an OTU must go from $B_i(0)$, the fundamental niche, to $B_i(i)$, the breadth of the first partial niche with respect to i (i.e., in the presence of intraspecific density dependence). All of this assumes an absence of density dependent effects from any of the other OTUs in C. Thus, if niche breadth is plotted against population density, we obtain a graph in which three zones are evident. First is a zone of population densities in which density dependence is nonoperative (fundamental niche); second, a transition zone in which the effects of density dependence are being felt but have not yet reached completion (transition zone); third, a zone in which the density dependent effects have reached completion (first partial with respect to i). In Figure 1 the above notions are presented in graphical form.

Assume for the moment a population which is nonreproducing and merely mobile from habitat to habitat; then conceive of a situation in which test runs are made in which a number of individuals are experimentally introduced into the environment and at some later time their occupation of the habitats which make up that environment is examined. Suppose that the habitats are chosen by the individuals in the population on the basis of their desirability to those individuals and that the habitats are unequally desirable; then there exists a preferred habitat, a second-best habitat, a third-best habitat, etc. At extremely low population densities the individuals in the population will tend to occupy the favored habitat first. Presume here that there are specific probabilities associated with individuals being found in specific habitats when density dependent effects are totally absent. Depending on the abundance or availability of the habitat types themselves, there may be a wide range of population densities in which negative feedback resulting from density depen-
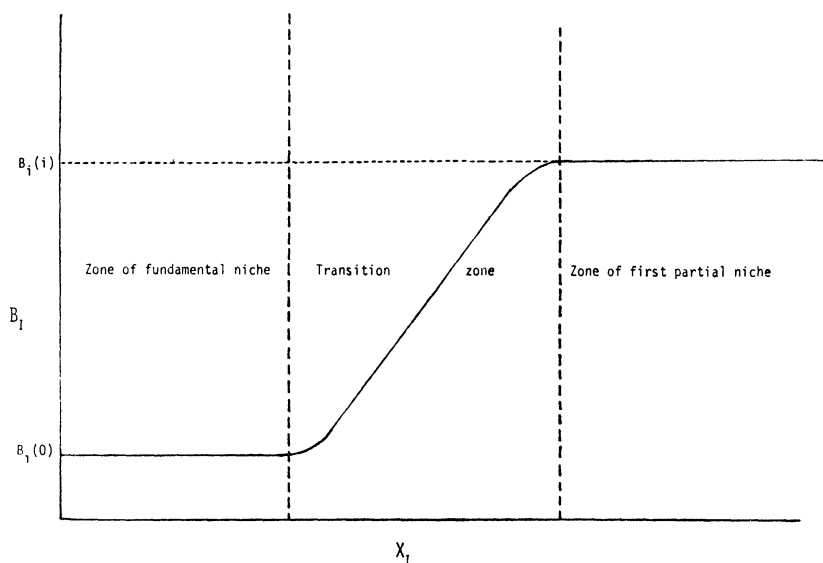
FIGURE 1. The niche-breadth–population density profile
(after Vandermeer, Bauman & Williamson 35).

dence will not affect the probabilities of being found in these habitats. There-fore, over a relatively broad range of population densities, on the lower end of the scale of population densities niche breadth will remain constant. This results in a lower plateau on the breadth density profile. (The plateau repre-sents the fundamental niche breadth.) On the other hand, when the popula-tion becomes extremely large, density dependence will be of greater impor-tance in specific habitats, and an individual will choose to occupy a particular habitat partially on the basis of the extent to which the habitat is preferred and partially on the basis of the extent to which negative interaction from the other individuals in that habitat affect it. Thus, we expect another plateau on the breadth density profile. This plateau is to be called the first partial niche breadth with respect to i. In between these two plateaus there must be a tran-sition zone, a zone in which the originally preferred habitat is saturated with individuals (whereas the other habitats are not occupied completely), imme-diately followed by a zone in which the somewhat less desirable habitats are slowly being filled up, but have not yet reached the point where density de-pendence within any one habitat is completely operative. This zone on the breadth density profile is termed the *transition zone*.

    Generalizing the above, imagine B_i plotted against the population density of OTU j (where OTU j could be the same OTU as that of the niche breadth which is being computed, or it could be another OTU in the community). We can then speak of intra- and interspecific breadth density profiles, and ultimately of multidimensional breadth density profiles, in which the depen-

dent variable is B_i and the independent variables are the population densities of all the other OTUs in the community. However, a more important direction in which this concept must be generalized is that of reproduction and survivorship and how it affects the breadth density profile. It is possible to imagine a breadth density profile resulting from organisms which did not, in a strict sense, select habitats, but rather had their population densities within habitats specified by differential survivorship across those habitats and/or differential reproduction within those habitats. These components would be interrelated by migration among the habitats, which relates the entire problem to the notion of environmental grain as pursued in the previous section. At present I shall only note that it is easiest to conceive of the breadth density profile in terms of habitat selections; however, the notion is of much more general importance and must be analyzed with respect to survivorship, reproduction, and interhabitat migration.

It has been pointed out (Allen Wolf, personal communication) that the transition zone of the breadth density profile is not likely to appear as a smooth increasing function, as it is drawn in Figure 1. In fact, as less preferred habitats become saturated with individuals, small plateaus will appear and will continue over a range of population densities corresponding to the next point of critical-population density at which the next least preferred habitat begins to feel the negative effects of density. The smooth, increasing transition zone in Figure 1 refers to a rather idealized case in which density dependence in a particular habitat is just beginning to be felt at the same population density for which the next most preferred habitat has completely felt population density effects.

A somewhat more practical consideration should be mentioned, that is, the pattern with which the operational habitats occur in the environment and the way that pattern affects the qualitative nature of the breadth density profile. Suppose that a breadth density profile had been calculated by observing habitat selection of individuals in a population over four operational habitats and that each of the habitats occurred in the environment with a relative density of one. Suppose on the other hand that the profile was determined again, this time making each operational habitat ten times more available. The probable change in the breadth density profile would be an increase in the range of densities in which the fundamental niche breadth could be observed. That is, the probability of being found in any particular habitat type will be unaffected for a larger range of densities since there is more of an abundance of each of the habitat types. This notion is diagramed qualitatively in Figure 2. The principal conclusion to be drawn is that there exists the possibility of experimentally determining a breadth density profile with such a low habitat availability that the fundamental niche is in some sense on the imaginary part of the graph, to the left of the zero ordinate (see leftmost curve in Figure 2).

ENVIRONMENTAL ANALYSIS

Thus far, everything has followed somewhat logically from an original set of arbitrary definitions. Of the original definitions the one which most obvi-

ously needs further examination is that of operational habitat. That it is possible for an ecologist to recognize distinct habitats or positions along an environmental gradient does not necessarily mean that organisms living in that environment are capable of distinguishing those habitats one from another, or that they see the differences among those habitats as being equivalent, in one sense or another, to the differences that the ecologist sees. This notion was discussed earlier in a very abstract way when the theoretical foundations of this paper were presented. It has always been assumed that underlying everything there has been a matrix, the elements of which represent the way in which habitats are related to each other—the environmental similarity matrix ($\mathbf{E}$).

Recognizing the degree of similarity of one habitat to another has been most commonly accomplished through the measurement of various physical parameters or, less frequently, through the physiological response of organisms to the different habitats. In this paper I prefer to take the approach of utilizing the response of organisms at the population level as a measure of the relationship between habitats. Such an approach is not without historical precedent, probably having been a common intuitive tool of the early naturalists. In fact one of the standard ecology textbooks (1) quotes Grinnell as saying "the animal is more sensitive than any thermometer or atometer." More recently the work of Colwell & Futuyma (6) has presented actual operational procedures for using a bioassay of population level measurements in measuring habitat similarities and has suggested a particular methodology for using these similarities in computing niche breadth. These authors utilized the
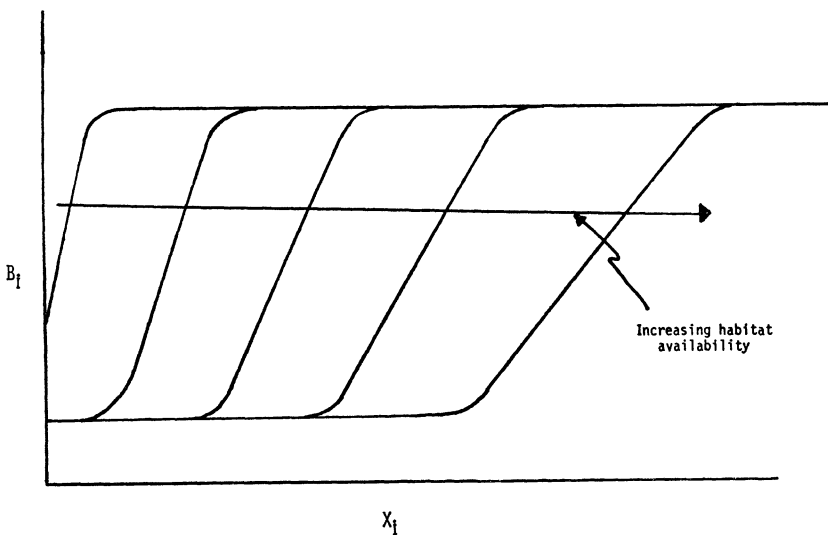

FIGURE 2. Changes in the breadth density profile as a function of the abundances of habitat types.

relative abundance of all of the species in the community to estimate the degree to which a given habitat contributed to the heterogeneity of the distribution of all species over all habitats. Thus, they obtain a measure of the relative distinctness of each habitat. This measure is then utilized to weight the habitat in computing niche breadth. The importance of their work lies in the recognition of the possibilities of using all of the OTUs in the community as a type of bioassay of the environment. In the present context it will be useful to pursue this general notion on a somewhat more abstract level.

The most general assumption I make is the one originally made in association with the environmental similarity matrix—that the relationship of one habitat to some other habitat is a function of the population densities of all the OTUs in the community. This is, in fact, not as general an assumption as it might first appear, in that it is certainly not strictly true that the relationship of one habitat to another habitat can be completely and totally specified by some function of the population densities of the OTUs in the community and only the OTUs in the community. In fact, this is probably too restrictive an assumption for a complete understanding of nature, but unfortunately it is also too general to use in devising specific measurements of habitat similarities. In any real situation it will be necessary to explicitly derive equations which enable us to calculate the similarities of habitat pairs. The approach of Colwell & Futuyma (6) could be expanded quite easily, explicitly to provide equations for this purpose. However, I prefer to take a somewhat simpler approach, at least as a first approximation.

We now stipulate the way in which $e_{hk}(j)$ is to be computed, where $e_{hk}(j)$ is the similarity between habitats h and k, from the point of view of i, in the absence of j. Later development requires that the similarity between habitats h and k be referred to particular OTU's—the view of the environment as OTU i sees it. Thus, it makes sense to define e_{hk} as the amount of overlap experienced by OTU i between habitats h and k, where amount of overlap refers to all OTUs in C. Thus, we have

$$e_{hk}(0) = \sum_n (P_{ih}P_{nh} - P_{ik}P_{nk})$$
$$e_{hk}(j) = \sum_{n \neq j} (P_{ih}P_{nh} - P_{ik}P_{nk})$$

5.

where P_{ih} is the portion of individuals of OTU i which occur in habitat h, as measures of the similarity between habitats h and k from the point of view of OTU i, both in the presence of all OTUs in C ($e_{hk}(0)$) and in the presence of all but OTU j ($e_{hk}(j)$). The intuitive justifications for these equations are perhaps not entirely evident at first glance. Habitats h and k will be similar to each other from the point of view of OTU i if the other OTUs in the system tend to occupy the habitats similarly relative to OTU i—that is, if the population densities of the other OTUs, relative to the population density of OTU i, tend to be high in habitat h when they are

high in habitat k and low in habitat h when they are low in habitat k, the two habitats h and k are similar. Thus, we have stipulated not merely a "bioassay" to estimate the relationship between two habitats but, more specifically, a bioassay that is particularly referable to a specified OTU.

It cannot be emphasized too strongly that the above equations (equations 5) are one specific, explicit set of equations which could be used as estimates of the elements of the environmental similarity matrix. Underlying all of this, we are assuming the existence of some environmental similarity matrix which may not be specified by the above equations, but which exists at least as a theoretical construct.

Given an environmental similarity matrix, a variety of techniques have been used to represent the degree to which the environment is structured in one way or another. For example, a whole school of phytosociologists has utilized clustering techniques and ordination techniques in an attempt to determine similar sets of habitats (37). A number of other approaches may be of more potential significance than a further analysis of the environmental similarity matrix.

To return for a moment to the grain matrix, assume that the grain matrix satisfies all the properties of a transition matrix of a homogeneous Markov process—that is, the sum of all rows is equal to one and the elements are constant. Consider the following graphical model in order to generate a grain matrix which may be manipulated for illustrative purposes. Figure 3 is a series of nine habitats diagramatically presented to show the ease with which organisms can proceed from habitat to habitat. The arrows crossing the lines separating the habitats indicate how difficult it might be for one organism to cross from one habitat to another habitat: one arrow indicates extreme difficulty of passage; five arrows indicate extreme ease in crossing.

An examination of Figure 3 gives the general impression that there are two rather distinct clusters of habitats, composed of 1, 2, 4, 5, 7, and 8 on the one hand, and of 3, 6, and 9 on the other. Within the first cluster it is obvious that 1, 4, and 7 form some sort of a subcluster which appears to be separate from the habitats 2, 5, and 8. Habitat 2 appears to be a kind of

FIGURE 3. Diagramatic representation of the environment
which gives rise to the grain matrix of Table 1.

TABLE 1. GRAIN MATRIX FOR THE ENVIRONMENT
DIAGRAMED IN FIGURE 3

	1	2	3	4	5	6	7	8	9
1	.22	.11	.00	.18	.14	.06	.15	.11	.03
2	.13	.15	.11	.12	.14	.08	.08	.12	.06
3	.05	.08	.22	.08	.11	.19	.03	.08	.16
4	.15	.11	.06	.17	.13	.07	.15	.11	.05
5	.11	.13	.08	.13	.15	.09	.11	.13	.07
6	.07	.09	.13	.09	.12	.19	.05	.09	.16
7	.14	.09	.04	.16	.12	.05	.18	.14	.08
8	.09	.11	.07	.12	.14	.08	.13	.16	.10
9	.04	.07	.12	.07	.10	.17	.09	.13	.20

passageway, but it does not receive very many individuals from any of the other habitats (a lack of arrows leading into a habitat indicates that passage is not possible). Without going into details, it is possible to construct a grain matrix which approximately represents the model presented in Figure 3. Table 1 presents the grain matrix which represents the environment diagramed in Figure 3.

Given a grain matrix for an environment, we wish to find the procedure by which we can quantify the above statements about the approximate nature of a hierarchy of the habitats in the environment. To do this, it is necessary to introduce the notion of stochastic submatrices. If one takes any transition probability matrix and merely replaces all zero elements with dots and all positive elements with plusses, one frequently sees square submatrices of the original transition matrix which have the property that, once entered, there is no possibility of exit. That is to say, in the present context, that a stochastic submatrix would be a subset of habitats with the property that any organism finding itself in one of the habitats within that subset would never find itself in elements which are not included in that subset. Such subsets are frequently termed *absorbing subsets* because, once the system enters any element in the subset, it never exits from that subset. If we now conceive of a situation in which the organisms begin moving more slowly—or, in terms of the grain matrix itself, any probability less than some arbitrary value is set equal to zero—we can devise a scheme of clustering habitats in a quasihierarchical pattern such that virtually all of the interesting information in the grain matrix is retained. There is no room here to discuss the details of this methodology, and I hope it will suffice to merely present an example and explain in detail exactly what the example means.

Figure 4 presents an environmental dendrogram for the model environment shown in Figure 3, and it is derived from the grain matrix in Table 1. Note that a dendrogram is made on the basis of a grain matrix and not on a physical analogy as I have presented it here. The use of the physical analogy
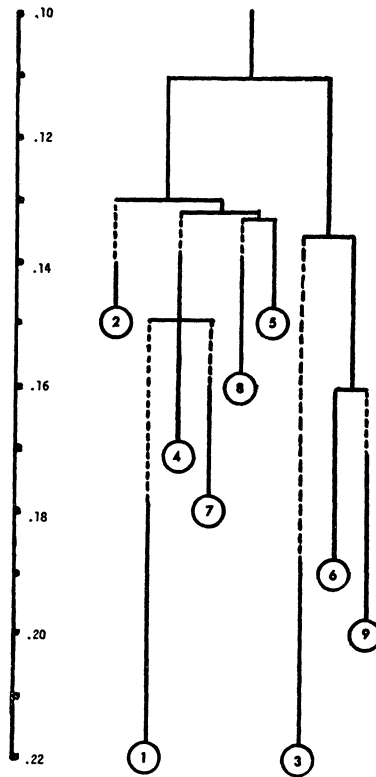
FIGURE 4. Environmental dendrogram for the environment diagramed
in Figure 3 and represented by the grain matrix in Table 1.

is only heuristic. The interpretation of the environmental dendrogram is clari-
fied by the following example. Suppose that we had assumed in the grain
matrix presented in Table 1 that all probabilities equal to or less than .145
were equal to 0. With such an assumption, draw an imaginary horizontal line
across the environmental dendrogram at the level .145. This line intersects six
different vertical lines, five of which are solid, one of which is dotted. A solid
line represents a cluster of habitats which would constitute a stochastic sub-
matrix or an absorbing cluster if probabilities less than or equal to .145 were
set equal to 0. Dotted lines represent clusters which are not absorbing clus-
ters. This example shows that habitat 2 is an absorbing cluster (when one
habitat alone is an absorbing cluster it is frequently referred to as an *absorb-
ing state*); habitats 1, 4, and 7 together constitute one absorbing cluster; habitat
8 is an absorbing state; habitat 5 is an absorbing state; habitat 3 is not an
absorbing state; whereas, habitats 6 and 9 constitute a definite absorbing
cluster. Next, suppose that all probabilities equal to or less than .131 are
set equal to 0. The situation now has changed, and in drawing a horizontal

line at .131, we see that it crosses a dotted line which represents habitat 2; a solid line which defines an absorbing cluster containing habitats 1, 4, 7, 8, and 5; and a solid line which represents an absorbing cluster composed of habitats 3, 6, and 9. Whereas in the former case of setting to 0 all probabilities equal to or less than .145, habitat number 3 was not a member of a stochastic submatrix, here (looking at a lower level of probability) habitat 3 is indeed a member of a stochastic submatrix, the one composed of habitats 3, 6, and 9. Thus, when the critical probability equals .145, habitat 3 is not an absorbing cluster. Due to its membership with 6 and 9 at a higher level of probability, one can say that if an individual is found in habitat 3 there is a greater probability that it will be found later in habitat 6 or 9 than in any of the other habitats.

I have referred to the environmental dendrogram as representing a quasi-hierarchical system since the dotted connecting lines actually represent habitats which are not members of absorbing clusters. It might be interesting to utilize environmental dendrograms in deciding whether or not habitats in a particular environment are arranged in a hierarchical way—a state which would exist if the environmental dendrogram were composed only of solid connecting lines, and if for all levels of probability, all habitats were members of some absorbing cluster. However, it is not my intent here to discuss whether or not habitats are ordered hierarchically: it is obvious that they are ordered in at least a quasihierarchical fashion and can be forced into a hierarchy if one should so desire. The environmental dendrogram affords a natural procedure for redefining habitat in a way which might be more meaningful for computing niche breadth or perhaps some other measurement of the ecological niche. For example, review of the dendrogram in Figure 4 might cause us to contend that the level of probability of .145 is somehow the smallest probability that has any chance of actually showing a transition from one habitat to another habitat, and therefore we set all probabilities less than .145 equal to 0. This is equivalent to drawing a horizontal line across the dendrogram at the level of .145, indicating that instead of nine operational habitats as originally recognized, the organisms of concern here recognize only six habitats—namely 2; 1, 4, 7; 8; 5; 3; 6, 9. Thus, it might make more sense to compute niche breadth based on these six habitats, as opposed to the original nine habitats which admittedly were chosen arbitrarily.

Environments viewed through the vehicle of the environmental dendrogram lend insight into what the basic structure of environments must be, at least from the point of view of the way in which organisms move from habitat to habitat. It would thus seem important, when making any sort of measurement that relies on a distinction among habitats, that if comparisons are to be made between organisms one must be assured that the position on the probability axis of the environmental dendrogram is the same for both organisms. Perhaps what should be done is to look at a graph of the measurement (say niche breadth) plotted against the probability axis on the environmental dendrogram. Further discussion of the environmental dendrogram may be found elsewhere (34).

DYNAMIC INTERACTIONS AND NICHE THEORY

It is commonplace for biologists to examine data gathered from a single point in time and then to attempt to deduce something about the dynamic rules which operated in the past, forcing those data into the particular form in which they are found; for example, see the well-known reconstruction of phylogenetic trees from only a knowledge of recent specimens or the inferences about competitive exclusion from distributional records (4, 16, 21). In the past, such attempts have been aimed at the qualitative nature of the dynamic processes and have been surprisingly successful. It would appear that if it is possible to infer qualitative aspects of dynamic processes from an examination only of static data, one might be able to extend those principles and then infer quantitative aspects of those dynamic processes from static data. There are many who would deny this in principle, and they are probably right. It is important, however, to examine the nature of the problem more closely. Given that a model of nature exists, we cannot in principle determine the values of the parameters in that dynamic model from an examination of the system at any one point in time. Exactly how much perturbation of the system is needed to gain an estimate of the desired parameters at a given level of precision? This is a problem wholly separable from the problem of what model should be used initially. Assume that a model which is a realistic analog of nature has been found and that we wish to utilize data from natural communities to estimate the parameters of that model. The important question is: to what extent must one tamper with nature to observe the actual dynamic process itself and thereby estimate the values of the parameters in the model. Clearly, extremes exist in this matter. At one end is the contention that estimates of dynamic parameters may be obtained only through the most voluminous reseach program in which all possible combinations of variables are set against each other in all possible interactive sequences, while at the other end is the examination of what exists presently without making any perturbations or making any attempt at observing the behavior of the system through time. It is obvious to me that somewhere in between these two extremes lies the optimal approach to the problem.

We shall be concerned in this section with deriving an estimate of α_{ij} which is equal to a_{ij}/a_{ii}, where the a's come from Equation 1. Levins' (23) is the best-known attempt to derive an indirect measure of α, and he was one of the first to actually extend the notion of dynamic conclusions from static observations from the qualitative to the quantitative phase. Levins' method rests on the rather shaky suppositions that if two OTUs are found together they most likely compete, and that the intensity of that competition is proportional to the relative numbers that occur together. Specifically, if we randomly pick from the habitats in the environment one individual from each of two OTUs, the probability that these two individuals came from the same habitat is given by $\Sigma_n P_{ih} P_{jh}$, where P_{ih} is the proportion of the ith OTU that occurs in the hth habitat. Since the coefficient under consideration refers to the effect of OTU j on OTU i relative to the effect of

OTU i on itself, the above probability should be compared to the probability that two individuals of the same OTU chosen at random will have come from the same habitat. This probability is given by $\Sigma_n P_{ih}{}^2$, in which case we obtain as the final estimate of competition

$$\alpha_{ij} = \frac{\sum_n P_{ih}P_{jh}}{\sum_n P_{ih}{}^2} \qquad 6.$$

This derivation is based on the proposition that the probability of occurrence of two individuals of different OTUs relative to the occurrence of two individuals of the same OTU equals the competition coefficient. That the probability of joint occurrence has anything whatsoever to do with competition is not at all obvious. Recently, it has been shown (8) that in a two-species situation the only case in which Levins' measure of competition is equal to the true competition coefficient occurs when the coefficients are both equal to one; but in this case the system is degenerate anyway and therefore not of interest. Even so, Levins' equation has been rather indiscriminately applied to natural distributions of a large variety of organisms. The widespread use of this equation is unfortunate since there are fairly obvious reasons why it could never work in real situations. There are two quite different reasons why the occurrence of two OTUs could be correlated. If the two are physically distinct from one another such that they are incapable of living in the same habitat (for example a fish and a bird), application of this measure would rightly yield the competition coefficient of zero. However, if we imagine two OTUs which potentially occupy exactly the same set of habitats but through the action of competition displace each other completely from any one habitat, application of Levins' measure would once again give the competition coefficient of zero, which is exactly the opposite of what it should be. Clearly, it is necessary to look at the difference between the potential occupation of habitats and the actual occupation of habitats and how that difference relates to the presence or absence of other OTUs. In the terminology of this paper, it is necessary to look at the occupation of habitats in the fundamental niche and to the occupation of habitats in the first partial interspecific niche and then to compare the difference thereof to the difference between the occupation of habitats in the fundamental niche and the occupation in the intraspecific first partial niche. More generally we can say that the estimate of competition should be in some sense the ratio of the difference between i performing alone and i performing in the presence of j, divided by the difference between i performing alone and i performing in the presence of itself (the effect of j on i divided by the effect of i on itself).

All of the above leads to the general problem of estimating interaction coefficients from the distribution of individuals in habitats. In other words, returning to the original theoretical framework of this paper, we are now interested in explicitly stating the form of f_3 as it appears in Equation 4, so

that data from natural communities may be manipulated in such a way as to quantitatively determine dynamic interactions. This paper is not concerned with whether or not there exists a relationship as expressed in Equation 4, but presumes that this relationship does exist. (Indeed, it is an interesting and important question whether or not such an existence can be proved.) We shall be concerned with the possible forms that f_3 may take and how those forms relate to estimating interaction coefficients in natural communities.

There are two quite distinct points of view regarding the estimation of interaction coefficients (MacArthur, personal communication). The first point of view is basically as presented in the introduction to this section: namely, to conceive of an experiment whereby various OTUs will be eliminated from the community and in which the remaining OTU will be allowed to expand into its "fundamental niche." This notion of estimation will be called *expansion estimation*. We may conceive of a momentary interaction coefficient which is determined by the pattern of the environment: specifically, looking at the grain matrices and environmental similarity matrices, we may ask to what extent the pattern of the elements in those two matrices is affected by the presence or absence of the OTUs in question. This instantaneous measure of the interaction coefficient is called *point estimation*. On the one hand, the operational procedure which determines interaction is one in which an experiment is assumed whereby OTUs have their population densities altered; and, on the other hand, the operational procedure is an observational one in which one compares the view of the environment which must accrue to a pair of OTUs to that of a single OTU. If linear or log-linear equations truly describe the underlying behavior of the system, both of these methods should yield the same result. The problem arises when, as probably is usually the case in nature, a large number of nonlinearities are in fact the rule. In this case, the experiment in which various OTUs have their numbers altered will result in an averaging of the various values that the linear approximation will have in going from the state which is intended for study to the state which is the experimental starting point. The strong point of the expansion estimation is that one need not make assumptions about the way a particular environmental variable is fed into the interactive process, since, at least in principle, an experiment is performed in which one looks at the difference between the performance of an OTU in the presence and in the absence of some density dependent factor. The second method, point estimation, has the distinct advantage of being applicable within the neighborhood of an equilibrium point within which a linear approximation undoubtedly applies, but the disadvantage that one must stipulate the way in which an environmental pattern is related to the dynamic process of interaction. In the following discussion I shall present methods of estimating interaction coefficients appropriate to both of these points of view.

The first method (35) is based on the notion of the breadth density profile. At this point it is necessary to generate a new notational scheme which is very similar to the notational scheme used for niche breadths. In-

stead of having $B_i(j, k, \ldots, m)$ we replace the B with a P and we have $P_{ih}(j, k, \ldots, m)$, where the P refers to the proportion of individuals in the ith OTU which appears in the hth habitat under the density dependent effects of OTU $j, k, \ldots, m$. Thus, $P_{ih}(j)$ refers to the probability (loosely speaking) that the ith OTU will be found in the hth habitat under the influence of a population density within the range of those population densities in which the first partial niche breadth of i with respect to j is realized. Presuming that the relative changes in niche breadth in the presence of density dependence of various kinds is reflective of the true dynamic processes which happen in the community, we can then write approximately

$$\bar{\alpha}_{ij} = \frac{\sum (P_{ih}(0) - P_{ih}(j))^2}{\sum (P_{ih}(0) - P_{ih}(i))^2}$$

The numerator of the above equation, or the effect of j on i, is most intuitively obvious when thought of as the decrease in "self-overlap" between fundamental niche and first partial niche. That is, one must ask what part of the fundamental niche has been eliminated through the action of the other OTU. Thus, we look at the area under the fundamental niche curve plus the area under the first partial niche curve and subtract from those the area of overlap between them. This more or less gives us the change perpetrated on i by the presence of j—both the change in the shape of the niche curve and in its effective displacement in one direction or another along a particular environmental axis. The same general notion applies to the density dependent effect of OTU i on itself—the ratio between the two naturally making the measure a relative measure which is what is needed to fit into equations 1. The equation in general satisfies the intuitive notions one might have about relative changes in niche breadth (both intra- and interspecifically) as they relate to the process of competition. Extending the equation to include other types of interactions is problematical and will not be treated here.

The second approach of measuring interaction coefficients has been termed *point estimation*. Suppose that the environment (the collection of habitats) has a particular configuration which uniquely determines the interaction coefficients for any pair of OTUs. In all of what follows in this section it is presumed that the community is within the neighborhood of a particular equilibrium point, such that a linear approximation (equations 1) is applicable. The entire underlying theory behind point estimation merely states that there is a function which maps the environment, possibly defined specifically for each OTU, into an interaction coefficient which represents the mean value of the interaction coefficient represented in equations 1. This function is f_3 of Equation 4, where it is assumed that the state of the environment which appears in the function f_3 is as that environment appears at the present time.

Stipulating the nature of the function f remains a difficult task. Included

here is an example which brings together several levels of approximation.

In the spirit of the definition given under expansion estimation, we define an estimate of $\bar{\alpha}_{ij}$ as the change in OTU i's perception of E due to the removal of j, relative to i's perception of E due to the removal of i. In general we may write

$$\bar{\alpha}_{ij} = \frac{\Delta_j E_i}{\Delta_i E_i} \qquad\qquad 7.$$

where the subscript on Δ refers to the OTU which is eliminated, and the subscript on E refers to the OTU through which the environment is perceived. Equation 7 is probably the most general form for point estimation, but it is hardly practical. Sacrificing some generality, we conceive of the environment as a similarity matrix, the elements of which indicate the degree to which habitat pairs are related to each other from the point of view of a particular OTU. That is, if E_i is a similarity matrix, an element of E_i, e_{hk}, is equal to the degree to which habitats h and k are related to each other from the point of view of OTU i. Furthermore, if the habitat similarities are determined solely by the OTUs in the community, the environmental similarity matrix may be computed from the population densities of any subset of OTUs in C. We are concerned with two similarity matrices: $E_i(0)$, the environmental similarity matrix computed from all OTUs in C; and $E_i(j)$, the environmental similarity matrix computed from all OTUs in C except OTU j. That is, whatever procedure is used to compute $e_{hk}(j)$, when it is being computed for the matrix $E_i(j)$, OTU j is eliminated from the calculations.

With the notion of environmental similarity matrix in the absence of a particular OTU in mind, we rewrite Equation 3 as

$$\bar{\alpha}_{ij} = \frac{\theta(E_i(0) - E_i(j))}{\theta(E_i(0) - E_i(i))} \qquad\qquad 8.$$

where θ represents the operation of summing all elements in a matrix ($\theta E = \Sigma_h \Sigma_k e_{hk}$). Equation 8 is similar to Equation 3 in that the numerator represents the change in i's view of the environment resulting from the removal of OTU i, while the denominator is the change in i's view of the environment resulting from the removal of OTU j. Without detailing the steps, it is true that Equation 8 reduces to Equation 6, the estimate of interaction originally proposed by Levins.

Thus, there are two philosophically distinct points of view regarding the estimation of interaction coefficients in natural communities. The first method is termed *expansion* and conceptually relies on a perturbation of the environment and an observation of the system as it returns to some other state. The second procedure, that of *point estimation,* is dependent on a

knowledge of the way in which an environmental configuration feeds back onto the dynamic process of interaction. In both cases we conceive of inter- action as being in essence a ratio of "the change imposed upon a potential of i through the presence of j" and "change imposed upon potential of i through presence of i." Defining the words *change, potential,* and *presence* in specific ways dictates whether it is appropriate to use a point estimation or an estima- tion through expansion.

<div align="center">DISCUSSION</div>

The previous analysis has been a sequence of statements about how niche theory fits into the basic theoretical framework which was presented earlier. The attempt to set everything into a coherent pattern has probably led to a rather restricted treatment of the subject. A few of the more obvious omis- sions are discussed presently.

Levins (23) and MacArthur & Levins (25) introduced the concept of the dimensionality of the niche. In the Hutchinsonian sense of the niche we may conceive of a very large number of environmental gradients, each of which will be called a *dimension.* It is true that a given species exists at some point along an environmental gradient in the world. The question of dimensionality is one of how many dimensions are important to a particular OTU for sepa- rating that OTU from other OTUs in the community. The concept has been dealt with elsewhere at a somewhat more statistical level (10) and, in point of fact, the entire notion of ordination (11) is an attempt at getting at this fundamental concept of niche dimensionality. However, in order for the con- cept of niche dimensionality to fit into a coherent body of theory, it must first be tied in, at least on an abstract level, with the dynamic processes which operate in that theory.

The question of niche shape has been considered by some ecologists in recent years (18, 36). Returning momentarily to the concept of the Hutchin- sonian niche, it is obvious that if there are no interactions between two envi- ronmental gradients, the niche of an organism will appear as a rectangular object in the environment space. However, if there are interactions, this rec- tangle can be deformed in many ways. It is perhaps most useful to distinguish between two extremes, a circular niche and an ellipsoidal niche. A circular niche simply means that if an OTU is broad niched on one dimension it is likely that the OTU is broad niched on the second dimension. An ellipsoidal niche means that if an OTU is broad on one dimension it will be narrow on some other dimension.

There are yet other approaches to the study of the ecological niche. Limi- tations on space mitigate against their inclusion here. I have only included those approaches that seem to be related to one another in such a way that a rather general theoretical framework emerges. I have attempted to set up a formal theoretical framework upon which much of the work relative to niche theory can be placed. Much of the initial framework is so abstract that it is of little value except as a vehicle to organize ideas relative to niche theory. It

is hoped that the importance of any one study, relative to other studies, may be more easily seen due to its position in this framework.

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