



Niche, Habitat, and Ecotope

R. H. Whittaker; S. A. Levin; R. B. Root

The American Naturalist, Vol. 107, No. 955. (May - Jun., 1973), pp. 321-338.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0147%28197305%2F06%29107%3A955%3C321%3ANHAE%3E2.0.CO%3B2-O>

The American Naturalist is currently published by The University of Chicago Press.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ucpress.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

NICHE, HABITAT, AND ECOTOPE

R. H. WHITTAKER,* S. A. LEVIN,† AND R. B. ROOT‡

Cornell University, Ithaca, New York 14850

It is a maxim of the civil law that definitions are dangerous.

[SAMUEL JOHNSON, *The Rambler*]

It is regrettable that two of the most important terms in ecology, “niche” and “habitat,” are now among the most confused in usage. To the extent that use of these is confused, use of other terms and concepts which depend on them will be confused as well. It is the purpose of this paper to sort out these concepts and to suggest a clear assignment of terms.

HISTORY OF NICHE CONCEPTS

The confusion comes from use of the same word, “niche,” for different concepts. We shall distinguish three senses of the word as: (a) the niche as the position or role of a species within a given community—the functional concept of niche; (b) the niche as the distributional relation of a species to a range of environments and communities—the niche as habitat, or the place niche concept; and (c) the niche as an amalgam of both these ideas, and thus defined by both intracommunity and intercommunity factors. Of these (b) makes “niche” synonymous with “habitat”; for the present, we term (c) the “habitat + niche” concept.

Grinnell (1917, p. 433) first proposed “niche” to designate the place in an association occupied by a single species, emphasizing for the California thrasher not only food relations but dependence on cover, and adaptation thereto in physical structure and temperament. The thrasher’s “ultimate associational niche . . . is one of the minor niches which with their occupants all together make the chaparral association.” Grinnell (1924, p. 227) later called the ecologic niche the ultimate unit of habitat, and still later (1928, p. 435) defined it as the “ultimate distributional unit, within which each species is held by its structural and functional limitations.” Grinnell’s intention was probably closest to concept (c) of the habitat

* Section of Ecology and Systematics.

† Department of Theoretical and Applied Mechanics, Section of Ecology and Systematics, and Center for Applied Mathematics.

‡ Department of Entomology and Section of Ecology and Systematics.

+ niche, but from these statements stems use of "niche" in sense (b), as undistinguished from "habitat" (e.g., Hesse, Allee, and Schmidt 1937, p. 135; Allee et al. 1949, p. 234).

The functional concept of niche (a) was developed by Elton (1927) and others. For Elton (1927, p. 63) the niche is "the status of an animal in its community," its place in its biotic environment, particularly its relations to food and enemies. Elton's concept was adopted by Gause (1934, p. 19) as a basis for his development of the idea now termed the principle of Gause and Volterra or of competitive exclusion. "A niche indicates what place the given species occupies in a community, i.e. what are its habits, food, and mode of life." Similar statements were made in other books (Andrewartha and Birch 1954, p. 3; Bodenheimer 1958, p. 166; Kendeigh 1961, p. 16; Andrewartha 1961, p. 4; Whittaker 1970, p. 16; see also articles by Savage 1958; Udvardy 1959; DeBach 1966). Dice (1952, p. 227) summarized changing statements of the concept and defined niche as "the ecological position that a species occupies in a particular ecosystem." For Odum (1953, p. 15; 1959, p. 27), "the ecological niche, . . . is the position or status of an organism within its community and ecosystem resulting from the organism's structural adaptations, physiological responses, and specific behavior (inherited and/or learned)." Clarke (1954, p. 468) indicates that "niche" stresses "the function of the species in the community rather than its physical place in the habitat." "This 'functional niche' is more fundamental than the 'place niche,' but both concepts exist and should eventually be given different names." The uses by Dice (1952), Odum (1953), and Clarke (1954) might well have stabilized the term as the functional role in the community, but this stabilization did not occur.

The current difficulty derives primarily from different interpretations of a single, seminal paper by Hutchinson (1958). Hutchinson (1958, 1965, 1967) proposed that the environmental variables affecting a species be conceived as a set of n coordinates. For each of these coordinates limiting values exist, within which the species can survive and reproduce. The ranges of the coordinates within the limiting values define an n -dimensional hypervolume, at every point within which environmental conditions would permit the species to exist indefinitely. This hypervolume may be called the species' "fundamental niche." If both physical and biological variables (e.g., temperature difference with depth and food-size difference affecting a zooplankton community) are considered, the fundamental niche will completely define the species' ecological properties. The fundamental niche defined in this way is an abstract formalization of what is usually meant by ecological niche. If, within the ordinary physical space of a given biotope, there are points at which the conditions of this fundamental niche are fully realized, then the biotope is "complete" relative to that species. Because of competition and other interactions the species may be excluded from some parts of the fundamental niche. The reduced hypervolume in which a species then exists is termed its "realized niche." Hutchinson (1958) further observes: (1) Though the formulation suggests equal

probability of survival of a species at all points up to the boundaries of its niche hypervolume, there will ordinarily be an optimum part of the niche and suboptimum conditions near the boundaries. (2) Linear ordering of all environmental variables is assumed, though this is not in practice possible. (3) The formulation refers to an instant in time, but time must also be considered a variable: A nocturnal and a diurnal species, with the same food and temperature ranges, etc., will occupy quite separate niches. Similarly, species that are motile in the biotope in different ways occupy different niches, even though they compete for food.

A number of other writers (including two authors of this paper) have considered that Hutchinson's fundamental niche formulated concept (*c*) of the habitat + niche. However, it should be emphasized that Hutchinson (1958) was concerned with the ecological requirements of individual species and competing species within biotopes, that is, within the environments of particular communities. The direction of his argument was toward interpretation of the principle of Gause and Volterra, and toward MacArthur's (1957) approach to niche space division by the birds of a "homogeneously diverse" biotope (that is, of a given community) and the question of the implication of niche specificity for the number of species that a given biotope can support. His formulation was of niche concept (*a*), with the niche defined purely *intensively*—that is, by variables as they apply within the biotope (Hutchinson 1967, p. 232). Factors of habitat, in contrast, have spatial extension. Hutchinson was not defining habitat; other authors (Ramenski 1924, 1930; Ellenberg 1950, 1952; Whittaker 1951, 1952, 1956; Bray and Curtis 1957) had used multidimensional treatments of habitat relations and had, moreover, sought to characterize species habitats through population measures. The multidimensional concept of habitat thus did not originate with Hutchinson and was not his concern in statement of the fundamental niche, although some other authors have approached species distributional or habitat relations through the multidimensional concept and termed the result "niche" analysis. That which was most original with Hutchinson and of profound significance was the application of the multidimensional concept of niche relationships to the coexistence of species in biotopes and the richness in species of communities.

Odum's (1971, p. 234) new edition has sought clarification, but we feel it has not succeeded. Odum accepts Grinnell's later (habitat + niche) position as the general concept of "ecological niche," and three aspects of this are distinguished as the "spatial or habitat niche," Hutchinson's "multidimensional or hypervolume niche," and for the Eltonian concept the "trophic niche." This division of the concept, however, leaves us with several difficulties. Elton, as an animal ecologist, indeed emphasized trophic relations in his discussions of the niche (cf. Weatherly 1963). However, the niche, as the species' place in the community, involves not only food, but also shelter and substrate, vertical position, relation to patchiness or grain, diurnal and seasonal timing, control by predation, competition, allelochemic relations, etc. Also, the niche concept must apply to plants and saprobes as

well as to animals, and the nutritional definition has little utility for discussing plants (Wuenschel 1969). Moreover, the critical dimensions of the niche may be not food resources but other limiting factors; it is the latter which, when a resource shared by two species is superabundant, may operate to permit their coexistence (Levin 1970). "Trophic niche" is not at all the same as *niche* in the functional or Eltonian sense (*a*), by which we mean the fully characterized position of the species in relation to intensive or intracommunity variables and other species within the community.

CONSEQUENCES OF CONFUSION OF CONCEPTS

Clearly the multiple usage of the term "niche" is confusing, and some narrowing of application for the sake of clarity is needed. If one were to discard the functional concept (*a*) in favor of either the niche as habitat (*b*) or as involving both habitat and niche factors (*c*), then one would have to accept certain undesirable consequences:

1. With either concept (*b*) or (*c*) application of the niche concept to community organization is obscured. The attributes of niche most relevant to a given community are those of the species' role in that community, not the species' distributional response to environmental gradients (*b*), or these plus different functional niche relationships in other biotopes (*c*).

2. Either of these concepts alters statements of the principle of Gause (1934). His conception was that two species could not persist in the same niche—that is, in direct competition in the same community. The central point that many niche differences are adaptive responses to competition in the community is altered if two species with "different niches" may either have different habitats (*b*) and hence not meet in competition in the same community, or differ in habitat + niche (*c*) but do not persist in the same community because their functional niches in that community are the same.

3. When the habitat + niche concept (*c*) is used, different (but equally important) evolutionary relationships are being compacted in the same terms. Niche difference within the community involves genetic characteristics evolved in relation to other species in the community. Habitat difference involves evolutionary response to gradients of environmental factors external to (though often modified by) the community. A product of niche differentiation among species is within-habitat or α diversity; the corresponding product of habitat differentiation is between-habitat or β diversity. Breadth of resources used or other coordinates occupied within the community is niche breadth and expresses intrapopulation genetic characteristics. Range of habitat gradients occupied is habitat amplitude or width, and this amplitude may express interpopulation differentiation based on mechanisms (ecotypic and subspecific differentiation, apomictic clone selection, etc.) different from those responsible for niche breadth.

4. Beyond this, if the use is not restricted to that of the functional concept (*a*), it may be unclear to which concept or to what combination of niche and habitat factors the word "niche" applies. For example, Levins

(1968) suggests as measurements of "niche breadth" both distribution of species over environments, and relation to such intracommunity variables as food source and season. Having measured niche breadth by concept (c), Levins (1968) goes on to discuss niche relationships within a community and thus applies, without indicating the change of perspective and measurements appropriate, concept (a). McNaughton and Wolf (1970) also sought a correlation between dominance (which may be considered an expression of resource use and hence of niche breadth) and "niche width" (for which they use a measure of habitat width). Green (1971) applied multiple discriminant analysis to bivalve mollusc species, and the physical and chemical characteristics of samples from lakes in which they occur, to ordinate the species and the lakes. The species were shown to differ in the ranges of environmental characteristics over which they occur, with the exception of one pair of *Pisidium* species with closely similar distributions in one lake; at least partial trophic separation was suggested for this pair. The study, though termed an analysis of "niche," is an analysis of habitat; and in relation to this the point of the *Pisidium* pair may be that species can have closely similar habitats if they differ in niche. No criticism of such studies as research is intended in the observation that their uses of the term "niche" do not facilitate communication of the significance of their research.

In summary, use of "niche" in sense (b) or (c) both leaves nameless the concept of most significance for community theory and fails to distinguish between intracommunity and intercommunity relationships. The crucial question for usage is whether clarity is served when "niche" and "habitat" are overlapping terms, with habitat attributes either identical with, or a subset of, niche attributes. For us, clarity is better served by a usage in which "niche" and "habitat" are complementary terms for different sets of attributes—respectively, intra- and intercommunity. However, if the term "niche" is assigned to the functional sense, a term is also needed for another concept, that of the habitat + niche.

SUGGESTED USAGE

On use of these terms we suggest:

1. The term "niche" should apply exclusively to the intracommunity role of the species.
2. When the broader concept entailing both intercommunity and intracommunity variables, hence habitat + niche, is used, a different term is appropriate; and for this we suggest "ecotope" (Schmithüsen 1968, p. 128; Troll 1968). The term is currently variously used as equivalent to habitat, biotope, microlandscape, or biogeocenose, but is not needed as a synonym of one of these. We suggest that henceforth it represent the species' relation to the full range of environmental and biotic variables affecting it. It should be pointed out that this concept is still useful when the distinction between inter- and intracommunity variables is not feasible or not desired; the concepts of "niche" and "habitat" in contrast require this distinction.

3. The terms "habitat" and "biotope" have been used almost interchangeably (the former more in English and the latter more in other European languages) for environment in its physical and chemical aspects. Two concepts are being covered by these terms, for they apply to the environment of the community at a given place, and to the environment of a species including the range of situations in which it occurs. No serious confusion seems to result from use in English of "habitat" for the environments of both communities and species. When distinction is desired, however, "biotope" should apply to the community's environment; "habitat," to the species' environment (Udvardy 1959). In the next section we shall define habitat by environmental gradients that may be considered in some sense external to (even though modified by) communities, but it is common informal practice to specify a kind of community as a habitat (for example, the habitat of the red crossbill in North Carolina is the spruce-fir forest). Such a statement is not inconsistent with our treatment, for it also implies specification of a species' habitat in terms of a range of environments occupied by a community type. James (1971) ordines bird species by their relations to characteristics of plant communities; the result is properly termed an ordination by habitat, since it relates the distribution of the bird populations to intercommunity gradients of vegetation structure that express differences in environment of the vegetation.

FORMULATION

a) Interrelation of Concepts

While we think meaning of niche, habitat, and ecotope should normally be clear in practice, a formal statement of their relations to one another (and Hutchinson's "fundamental niche") is not simple. Three kinds of variables are to be considered in the definitions: (1) intercommunity or habitat variables, that is, environmental variables with an extensive spatial component (e.g., elevation, slope exposure, soil moisture from valley bottom to open south slope, soil fertility as affected by parent materials, etc., and community gradients consequent on these); (2) intracommunity or niche variables, that is, intensive or local environmental variables (height above ground, relation to intracommunity pattern, seasonal time, diurnal time, prey size, ratio of animal to plant food, etc.); and (3) population response variables (density, coverage, frequency of utilization, reproductive success, fitness, etc.). Though distinctions among these are important, they are not discontinuous with one another. When intercommunity and intracommunity variables are difficult to separate, they may be grouped as "environmental variables."

A habitat gradient may be treated for discussion as if external to or independent of species' population responses to it, but primary habitat gradients are to varying degrees modified or determined by the species and communities that occur along them. Thus a gradient of decreasing elevation

and soil moisture in California mountains may be occupied by a spectrum of intergrading communities (pine forest, pine-oak woodland, chaparral, desert). Presence of the communities modifies or produces additional environmental factor gradients (of vegetation height and cover, exposure to sunlight, microclimatic humidity, soil organic-matter content, etc.) to which some species populations respond. Species populations are then distributed along a gradient we may conceive as a complex gradient (Whittaker 1967), or an assemblage of environmental factor gradients that change together through space along this elevation gradient (but may be quite differently related to one another along other primary habitat gradients). Each species is distributed along the complex gradient on the basis of its own environmental requirements and population dynamics, and the population response of a given species may have a significant effect on the environments of its own members (as needle litter of and transpiration of soil water by the pines affect the root environments of those pines). The response of a population to the gradient may affect other species, and consequently the niche and habitat relationships to these, as well.

For example, the niche of the California thrasher as described by Grinnell (1917) includes its nesting in dense masses of foliage 2-6 feet above the ground. Along the California mountain gradient this requirement is met only by the shrubs in that part of the community spectrum we term "chaparral." The habitat of the thrasher may consequently be determined by its population response to niche requirements, as these, in turn are affected by population responses of the shrub species that dominate the chaparral to the habitat gradient. Thus habitat, niche, and population variables are variously interlinked in the thrasher's total relationship to environment, which we term its "ecotope." This interlinkage of variables makes no less significant the distinction between the California thrasher's niche within the chaparral (in which it differs from other bird species occurring there), and its habitat in the middle elevations occupied by chaparral (in which it differs from the Crissal thrasher of the deserts at lower elevations). Further complications involve the migrations and movements in feeding of animal populations; the ecotope of a bird population may include population movement between two different habitats occupied (with different niche behaviors) at different times.

Troublesome as these interrelations may be for our definitions, the problems of definition are much like those encountered in other areas where terms are found to be interlinked in clusters, as observed by Dewey and Bentley (1949). We seek to order our cluster of terms, and the concepts they stand for, as parts of a conceptual system, a system including other concepts we shall relate to niche, habitat, and ecotope (see Whittaker 1967). The system may well be thought of as occupying a hyperspace defined by the three kinds of variables—of habitat, niche, and population measure—as axes. We shall deal with our conceptual axes two at a time—first habitat and population variables, then niche and population variables—before drawing them together in the concept of ecotope.

b) Habitat

Consider a landscape, locations or sites in which may be characterized by m environmental variables (extensive variables in the sense of Hutchinson [1967], such as, elevation, slope exposure, soil fertility, etc.). These variables may be conceived as axes of an m -dimensional coordinate system defining an environmental or *habitat hyperspace* (Goodall 1963; Whittaker 1967). Communities occur at locations in the landscape pattern, to which correspond points in the habitat hyperspace. (In this usage we understand by "community" an entity defined in the neighborhood of a point location in the landscape. Thus the landscape need not be viewed as dotted with a collection of discrete communities, but may often be conceived as a continuum of communities blending into one another.) The location of the community is its community habitat or *biotope*, characteristics of which are specified by a point or set of points in the hyperspace. (The combination of the variables bearing upon a particular organism or species within a biotope is referred to as an *environmental complex* [Billings 1952].) Each species in the landscape occurs over some range of the environmental variables, the limits of which for the species outline a habitat hypervolume as a fraction of the habitat hyperspace.

Habitat is usually conceived as the range of environments or communities over which a species occurs; the habitat hypervolume is an abstract formulation of this range in terms of extensive environmental variables and the species' limits in relation to them. The habitat hypervolume will not, however, be delimited simply as a region within which the species could persist indefinitely, as defined by physiological tolerances. Not only may interactions with other species exclude it from some environments in which it is physiologically able to exist, but the species may also occur in environments that are at times unfavorable to it. Organisms regularly confront conditions in their environments that are temporarily beyond their "limits of tolerance," however these limits are defined. If the environment did not change, a population of such organisms would become extinct unless sustained by immigration from more favorable regions. However, environments do change, and a population's survival in a changing environment may depend crucially on its responses to unfavorable periods, during which the best it can do is to "cut its losses," while making up for these during more favorable periods. We thus cannot include only favorable environmental conditions in our discussion of habitat. The hypervolume concept (Hutchinson 1958), when applied to habitat gradients, may not adequately define a species' habitat; and some measure of the species' distribution over its habitat is desirable.

Along a given habitat gradient the species shows response curves for various population measurements that may be applied to it. Population density curves are typically bell-shaped, apparently Gaussian in form (fig. 1), tapering on each side of the mode or population optimum toward ill-defined limits (the asymptotic tails of the curves). (The population

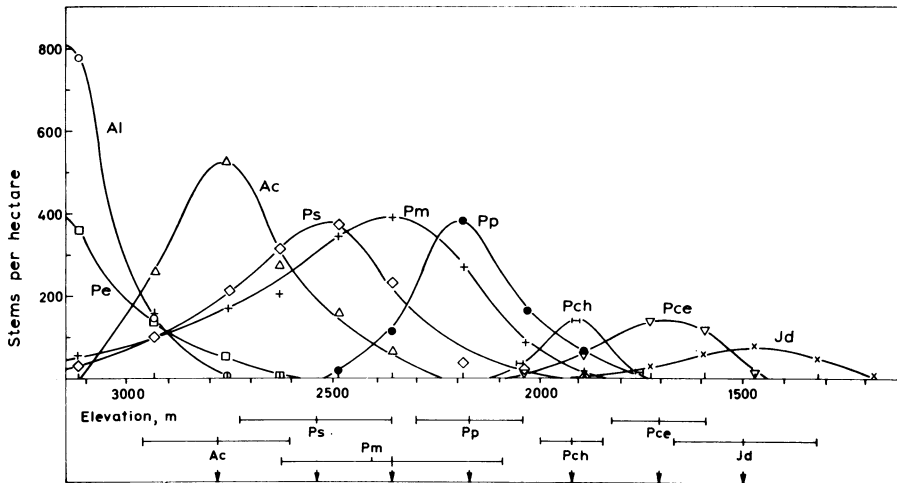


FIG. 1.—Population distributions on a habitat gradient. Coniferous tree species populations are plotted in relation to the elevation gradient on north-facing slopes in the Santa Catalina and Pinaleno Mountains, Arizona (data of Whittaker and Niering 1965). The tree species, competing as community dominants, form a replacement series along the gradient (comparable series formed by oak species along the same gradient are shown by Whittaker [1969]). Whereas the modes of species populations are apparently distributed randomly along the gradient when there are many competing species (Whittaker 1956), the distribution of modes of these competing dominants appears to be regular. Furthermore, in those cases in which the bars for habitat widths overlap, the species of an overlapping pair are differently distributed along the topographic moisture gradient. Species pairs of which the first occupies the more mesic and the second the more xeric topographic position at a given elevation are: Al and Pe, Ac and Ps, Pm and Ps, Pm and Pp, Pce and Jd. Data are numbers of tree stems over 1 cm dbh per hectare, based on sets of five 0.1-hectare samples grouped by elevation intervals and plotted at the mean elevations for the groups. The bars below the abscissa give means and habitat widths expressed as one standard deviation, except for Pm, in which the apparent mode has been used as its center rather than its mean (also indicated). Tree species are indicated by genus and species initials: *Picea engelmanni*, *Abies lasiocarpa*, *Abies concolor*, *Pinus strobiformis*, *Pseudotsuga menziesii*, *Pinus ponderosa*, *Pinus chihuahuana*, *Pinus cembroides*, and *Juniperus deppeana*. These species are dominants of a community gradient from subalpine forest (Pe and Al), through montane forests (Ac, Ps, Pm, and Pp) to submontane woodlands (Pch, Pce, and Jd).

optimum is not the same as the physiological optimum; moreover, some species have more than one local population optimum, for different ecotypes.) Along any two axes of the hyperspace the population densities may form a Gaussian response surface (fig. 2; Whittaker 1956); in response to more than two axes of the hyperspace they form an "atmospheric" distribution (Bray and Curtis 1957). The species in its hypervolume forms not a sharply bounded distribution but a population cloud. Characterization through experiments of the species' habitat hypervolume is a principal goal

of autecology (Billings 1952; Wuenscher 1969), but experiments in the absence of other species cannot adequately describe the population cloud in the habitat hyperspace.

Species evolve toward scattering of their population centers in the habitat hyperspace—toward difference in habitat (Whittaker 1956, 1967, 1969). The population clouds of species normally, however, overlap broadly if their centers are close together; only exceptionally are species sharply bounded at discontinuities of exclusion (Whittaker 1956, 1962; Terborgh 1970). In the habitat hyperspace the many species populations consequently form together a complex population continuum. Techniques of gradient analysis

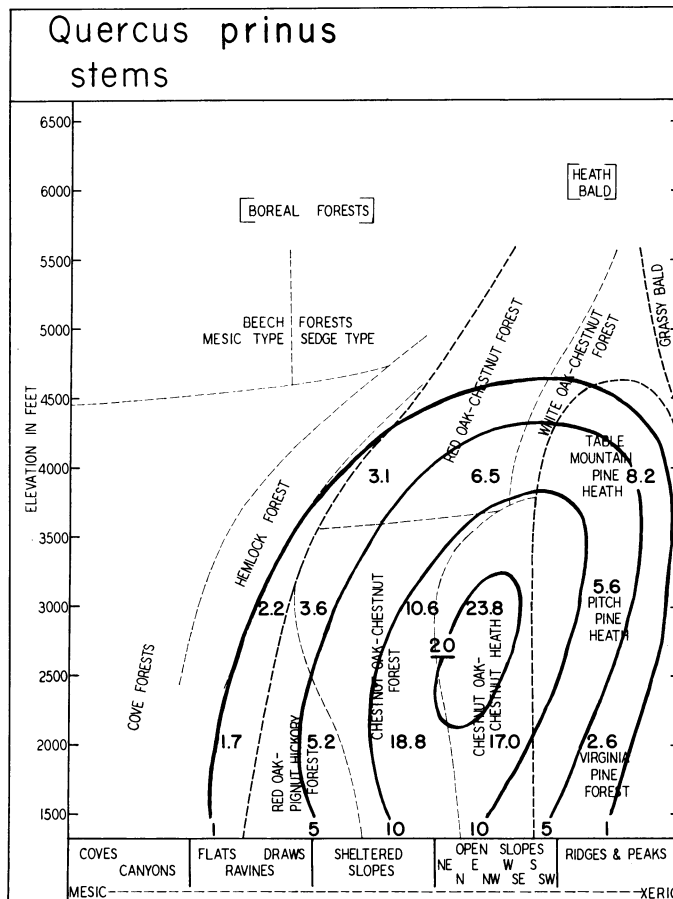


FIG. 2.—A Gaussian response surface or “binomial solid” for the habitat of *Quercus prinus* (chestnut oak) in the Great Smoky Mountains, Tennessee (Whittaker 1956). The population is centered in the chestnut oak heath, at the middle elevations in moderately dry sites, and decreases in all directions away from this, as indicated by the population contour lines. Data points are percentages of stems over 1 cm dbh in composite samples of approximately 1,000 stems each.

seek understanding of this continuum and species habitat relations within it by: (1) reduction of the m -dimensional continuum to a coordinate system of a few major axes (either recognized complex gradients of many correlated environmental factors, e.g., elevation, or compositional axes derived from indirect ordination); major relationships of communities to biotopes in the landscape may then be understood as a pattern in this coordinate system; (2) representation of the distributions of the species populations in this coordinate system (fig. 2), so that relations of species to one another and communities may be observed; (3) ordination of the species by locating in the coordinate system the centers of their hypervolumes or population clouds (fig. 3 and Whittaker 1967; for applications to animal species see Pennak 1951; Whittaker 1952; Bond 1957; Whittaker and Fairbanks 1958; Beals 1960; Fager and McGowan 1963; Terborgh 1970; Green 1971; James 1971).

c) Niche

Consider a community in the landscape; the intracommunity variables to which species respond may be represented by n "niche variables," which

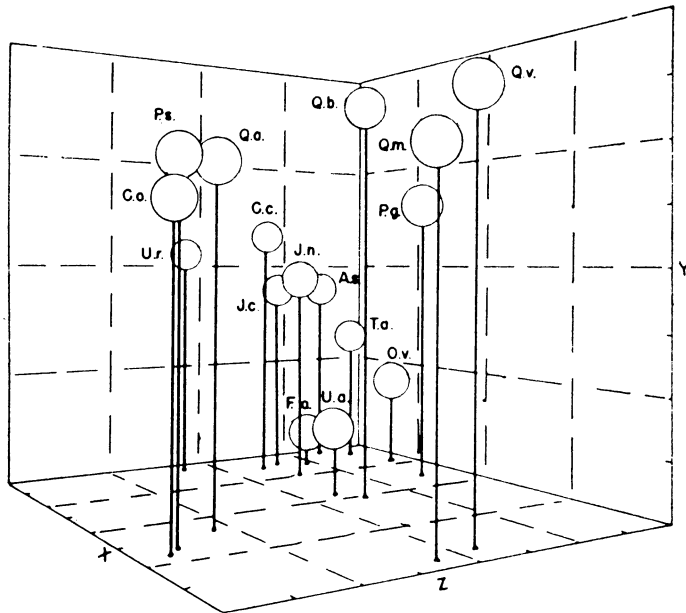


FIG. 3.—A habitat ordination of tree species by the centers of their distributions in a three-dimensional hyperspace (Bray and Curtis 1957). Tree species are indicated by genus and species initials: *Acer saccharum*, *Carya cordiformis*, *C. ovata*, *Fraxinus americana*, *Juglans cinerea*, *J. nigra*, *Ostrya virginiana*, *Populus grandidentata*, *Prunus serotina*, *Quercus alba*, *Q. borealis*, *Q. macrocarpa*, *Q. velutina*, *Tilia americana*, *Ulmus americana*, and *U. rubra*. Successional relations toward increasing mesophytism are significant along the X axis, soil drainage relations along the Y axis, and disturbance effects along the Z axis.

will in general include axes representing other member species of the community as well as more general niche variables such as height above ground, prey size, etc. These variables as axes define a multidimensional niche hyperspace interrelating the species of the community. Each species in the community utilizes, or occurs in, or is affected by, some range of these axes, the limits of which outline its niche hypervolume, or realized niche in the sense of Hutchinson (1958, 1967).

The limits of this hypervolume do not adequately characterize the species' niche relationships as relative success or concentration of the species population (as expressed in density, fitness, frequency of resource utilization, or other measures) changes along the axes. To complete the definition of the niche, one superimposes on the hypervolume a measure of the population response of the species at each point. These response variables emphasize the functional relationships of the species in the community, and thereby link Hutchinson's realized niche and the functional niche concept of Elton. The *niche* then becomes the species' position in the hyperspace as represented by a response surface or cloudlike population measure within its niche hypervolume. MacArthur (1958; MacArthur, MacArthur, and Preer 1962) has done most to characterize the niche clouds of animal species populations in a community. Figure 4 represents in this form two dimensions of the niche of the blue gray gnatcatcher as studied by Root (1967).

It is no contradiction of the principle of Gause that species clouds may overlap broadly in the niche hyperspace. Species evolve toward scattering of their centers in the hyperspace—toward niche difference. Species may be

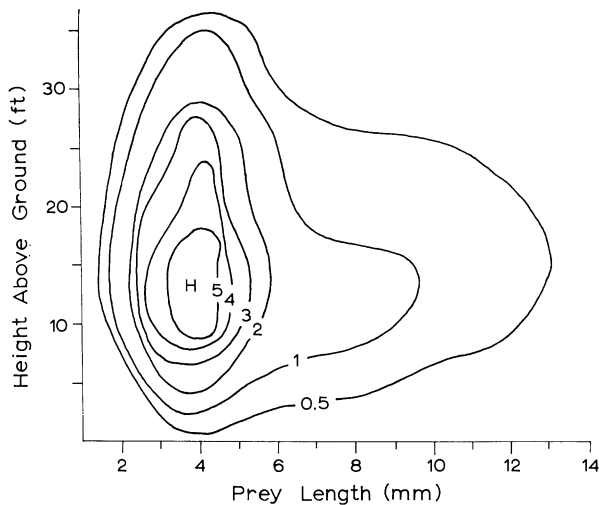


FIG. 4.—A niche response surface, representing capture of prey of different sizes taken at different heights above the ground by the blue gray gnatcatcher (*Poliophtila caerulea*). The contour lines map the feeding frequencies (in terms of percentage of total diet) to these two niche axes for adult gnatcatchers during the incubation period in July and August, in oak woodlands in California (data of Root [1967]).

added to the community; along a given niche or resource gradient the additions may be seen as increased species packing (MacArthur 1970), implying increase in α diversity. It is because species that occur in the same community differ in niche that discontinuities at which species exclude one another are few (and some of these few are recent contacts) among the many broadly overlapping distributions of species that are partial competitors (Whittaker 1965). When major niche relationships in a community can be reduced to a few niche axes, species can be ordinated in a manner analogous to habitat ordination (MacArthur, MacArthur, and Preer 1962; Cody 1968).

A niche is an evolved, multidimensional attribute of a particular species population (see Colwell and Futuyma 1971). The range of an external niche axis for the species (e.g., prey size, or light intensity), and the species' response in that range (pursuit and consumption, plant height and photosynthetic adaptation) are coupled or complementary (Wuenschel 1969). Since a niche is a set of relationships for a particular species population in a given community, there is no need to postulate the existence of empty niches. Much debate on the nature of the niche, its measurement, formulation, and demonstration independent of the species can be resolved by recognizing the nature of the concept. It is a construct, one of a class of concepts not subject to direct observation but postulated to explain a range of observations. A niche is as much an attribute of a species as a personality (as expressed in interaction with others) is of a person, but this fact does not deprive of their interest efforts at quantitative formulation, grouping of species' niches into guilds (Root 1967; Price 1971), and comparison of niche relationships in different communities (Cody 1968).

A niche hyperspace is an evolved, multidimensional attribute of a particular community. The niche hyperspace also is a construct, postulated as a basis for interpreting community organization, species packing, and α diversity. The "structure" of the hyperspace is inseparable from the community of which this structure is an abstraction. There is no vacant niche awaiting the arrival of spider monkeys on the pampas; the pampas have not evolved a niche hyperspace including a potential hypervolume for the monkeys. There was no niche awaiting deer in New Zealand. The deer, when added to a community, laid claim to resources that had been otherwise used (by saprobe species, if not by animals) and altered the niche hyperspace of the community; the altered hyperspace includes a hypervolume occupied by the deer.

d) Ecotope

Consider, finally, the landscape of communities. A species in the landscape has its "place" in relation to $m + n'$ variables of habitat and niche. (The n' is used to indicate that the n niche axes as formulated above for a particular community have been extended to apply to the full range of communities in the landscape. The transformed niche hypervolume thereby defined we shall not distinguish further from the hypervolume discussed in the preceding

section.) Niche and habitat variables may be combined to form an $(m + n')$ -dimensional compound hyperspace, representing the full range of external circumstances to which species in the landscape are adapted (Whittaker 1969). In accordance with suggested usage (2), above, the compound hyperspace may be termed an "ecotope hyperspace." Each species in the landscape is adapted to some range of the environmental factors that are axes of the hyperspace. The limits of that range for the species outline its ecotope hypervolume. When a population measure is superimposed on the $m + n'$ hypervolume, the resulting cloud describes the species' relation to both habitat and niche; this we call the ecotope. The ecotope hypervolume provides a more formal statement of the habitat + niche concept.

It is critical to note that the ecotope as herein developed describes the species' response to the full range of environmental variables to which it is exposed. As such, the ecotope definition can be made independent of the notions of niche and habitat, and is unaffected if the notions of intercommunity and intracommunity variables are indistinct. The ecotope indeed is the ultimate evolutionary context of a species, even if the niche is the proximate one. Species' distributions over ranges of habitats, and migrations between communities as evolutionary responses, are to be understood in terms of the ecotope. The niche may moreover be regarded as the restriction of the ecotope to a particular community, however that community is defined.

Species of a landscape (or area or island) evolve toward different positions in the ecotope hyperspace; they may evolve simultaneously toward niche and habitat difference from one another (Whittaker 1969). From different aspects of this evolution result niche packing, α diversity, and dominance-diversity structure within the community; and habitat packing, β diversity, and community distribution along habitat gradients. For the landscape as a whole these processes in evolutionary time are expressed in biotic richness, area, or gamma diversity.

SUMMATION

The confusion affecting use of "niche" and related terms can be resolved as follows:

1. The m variables of physical and chemical environment that form spatial gradients in a landscape or area define as axes a habitat hyperspace. The part of this hyperspace a given species occupies is its habitat hypervolume. The species' population response to habitat variables within this hypervolume, as expressed in a population measure, describes its *habitat*. The environment of a particular community in the landscape is a community habitat or biotope.
2. The n variables by which species in a given community are adaptively related define as axes a niche hyperspace. The part of this hyperspace in which a species exists is its niche hypervolume, or realized niche in the sense of Hutchinson. The species' population response within its niche hypervolume describes its *niche*.

3. The variables of habitats and niches may be combined to define as axes an $(m + n')$ -dimensional ecotope hyperspace. The part of this hyperspace to which a given species is adapted is its ecotope hypervolume. When a population measure is superimposed on this hypervolume, the *ecotope* of the species is described.

4. Niche and niche hyperspace are complementary constructs important for the interpretation of community organization. Clarity in the use of these and other terms is served by applying "niche" to the role of the species within the community, "habitat" to its distributional response to inter-community environmental factors, and "ecotope" to its full range of adaptations to external factors of both niche and habitat.

Figure 5 is an abstract representation of the relations of these concepts in a conceptual hyperspace with habitat, niche, and population variables as axes. Habitat variables are described along an "axis" perpendicular to the page. In general there will, of course, be more than one habitat variable, but for idealized representation the m -dimensional *habitat hyperspace* is reduced to a single axis. Similarly, niche variables are described along an axis parallel to this line of print, though in truth this axis stands for an n' -dimensional *niche hyperspace* (for each set of values of the habitat variables). One can then visualize these n' -dimensional niche hyperspaces, built or fibered upon the m -dimensional habitat hyperspace as a base space, to form an $(m + n')$ -dimensional *ecotope hyperspace* (reduced for illustration to a plane defined by habitat and niche variables). Finally, the population measures superimposed on the $(m + n')$ -dimensional hyperspace unite to form the $(m + n' + k)$ -dimensional surface pictured, the species *ecotope*. (We have for this representation reduced to one the various possible population measures.)

The vertical projection of this ecotope onto the ecotope hyperspace "floor" of the figure defines the *ecotope hypervolume*. Projection of the ecotope hypervolume onto habitat hyperspace defines the *habitat hypervolume*;

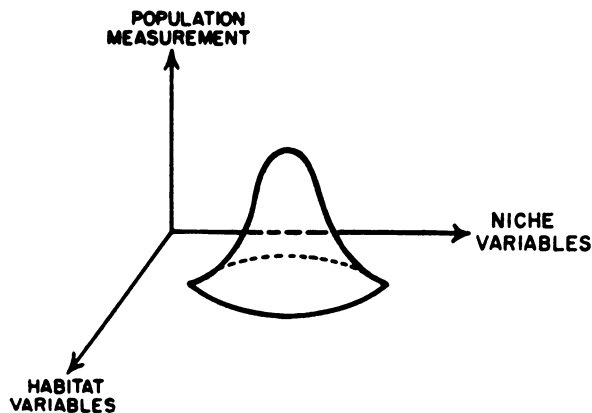


FIG. 5.—A diagrammatic representation of the relations to one another of a system of concepts including niche, habitat, and ecotope. See text.

projection of the ecotope hypervolume onto the niche hyperspace defines the *niche hypervolume*. Horizontal projection of the ecotope onto the "wall" of the habitat and population variables describes the species' range of habitat response. A cross section through the ecotope with an $(n' + k)$ -dimensional hyperplane parallel to the page (i.e., for fixed values of the habitat variables) describes the niche of the species (for those habitat variables).

ACKNOWLEDGMENTS

For comments on the manuscript we thank P. F. Brussard, W. L. Brown, Jr., L. C. Cole, H. G. Gauch, Jr., D. C. Lewin, P. L. Marks, R. K. Peet, D. Pimentel, O. Sexton, and, especially, G. E. Hutchinson and the late R. H. MacArthur. The contributions of the first two authors were supported by National Science Foundation grants and that of the third author by Hatch funds.

LITERATURE CITED

- Allee, W. C., O. Park, A. E. Emerson, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology. Saunders, Philadelphia. 837 p.
- Andrewartha, H. G. 1961. Introduction to the study of animal populations. Methuen, London. 281 p.
- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. Univ. Chicago Press, Chicago. 782 p.
- Beals, E. W. 1960. Forest bird communities in the Apostle Islands of Wisconsin. *Wilson Bull.* 72:156-181.
- Billings, W. D. 1952. The environmental complex in relation to plant growth and distribution. *Quart. Rev. Biol.* 27:251-265.
- Bodenheimer, F. S. 1958. Animal ecology today. Junk, Den Haag. 276 p.
- Bond, R. R. 1957. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. *Ecol. Monogr.* 27:351-384.
- Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27:325-349.
- Clarke, G. L. 1954. Elements of ecology. Wiley, New York. 534 p.
- Cody, M. L. 1968. On the methods of resource division in grassland bird communities. *Amer. Natur.* 102:107-147.
- Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. *Ecology* 52:567-576.
- DeBach, P. 1966. The competitive displacement and coexistence principles. *Annu. Rev. Entomol.* 11:183-212.
- Dewey, J., and A. F. Bentley. 1949. Knowing and the known. Beacon, Boston. 334 p.
- Dice, L. R. 1952. Natural communities. Univ. Michigan, Ann Arbor. 547 p.
- Ellenberg, H. 1950. Landwirtschaftliche Pflanzensoziologie. I. Unkrautgemeinschaften als Zeiger für Klima und Boden. Ulmer, Stuttgart. 141 p.
- . 1952. Landwirtschaftliche Pflanzensoziologie. II. Wiesen und Weiden und ihre standörtliche Bewertung. Ulmer, Stuttgart. 143 p.
- Elton, C. 1927. Animal ecology. Sidgwick & Jackson, London. 209 p.
- Fager, E. W., and J. A. McGowan. 1963. Zooplankton species groups in the North Pacific. *Science* 140:453-460.
- Gause, G. F. 1934. The struggle for existence. Reprint ed., Hafner, New York, 1964. 163 p.
- Goodall, D. W. 1963. The continuum and the individualistic association [French summary]. *Vegetatio* 11:297-316.

- Green, R. H. 1971. A multivariate statistical approach to the Hutchinsonian niche: bivalve molluscs of central Canada. *Ecology* 52:225-229.
- Grinnell, J. 1917. The niche-relationships of the California thrasher. *Auk* 34:427-433.
- . 1924. Geography and evolution. *Ecology* 5:225-229.
- . 1928. Presence and absence of animals. *Univ. California Chron.* 30:429-450.
- Hesse, R., W. C. Allee, and K. P. Schmidt. 1937. *Ecological animal geography*. Wiley, New York. 597 p.
- Hutchinson, G. E. 1958. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* 22:415-427.
- . 1965. *The ecological theater and the evolutionary play*. Yale Univ. Press, New Haven, Conn. 139 p.
- . 1967. A treatise on limnology. Vol. 2. Introduction to lake biology and the limnoplankton. Wiley, New York. 1,115 p.
- James, F. C. 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bull.* 83:215-236.
- Kendeigh, S. C. 1961. *Animal ecology*. Prentice-Hall, Englewood Cliffs, N.J. 468 p.
- Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *Amer. Natur.* 104:413-423.
- Levins, R. 1968. *Evolution in changing environments*. Princeton Univ. Press, Princeton, N.J. 120 p.
- MacArthur, R. H. 1957. On the relative abundance of bird species. *Nat. Acad. Sci., Proc.* 45:293-295.
- . 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599-619.
- . 1970. Species packing and competitive equilibrium for many species. *Theoret. Pop. Biol.* 1:1-11.
- MacArthur, R. H., J. W. MacArthur, and J. Preer. 1962. On bird species diversity. II. Prediction of bird census from habitat measurements. *Amer. Natur.* 96:167-174.
- McNaughton, S. J., and L. L. Wolf. 1970. Dominance and the niche in ecological systems. *Science* 167:131-139.
- Odum, E. P. 1953. *Fundamentals of ecology*. Saunders, Philadelphia. 384 p. 2d ed., 1959, 546 p. 3d ed., 1971, 574 p.
- Pennak, R. W. 1951. Comparative ecology of the interstitial fauna of fresh-water and marine beaches. *Année Biol., ser. 3*, 27:449-480.
- Price, P. W. 1971. Niche breadth and dominance of parasitic insects sharing the same host species. *Ecology* 52:587-596.
- Ramensky, L. G. 1924. Die Grundgesetzmässigkeiten im Aufbau der Vegetationsdecke [in Russian]. *Věstnik Opytnogo Dëla, Voronezh*, p. 37-73. (Abstr. in *Bot. Centralblatt*, n.s. 7:453-455, 1926.)
- . 1930. Zur Methodik der vergleichenden Bearbeitung und Ordnung von Pflanzenlisten und anderen Objekten, die durch mehrere, verschiedenartig wirkende Faktoren bestimmt werden. *Beitr. Biol. Pflanzen* 18:269-304.
- Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Monogr.* 37:317-350.
- Savage, J. M. 1958. The concept of ecologic niche, with reference to the theory of natural coexistence. *Evolution* 12:111-112.
- Schmithüsen, J. 1968. Allgemeine Vegetationsgeographie. In E. Obst and J. Schmithüsen [ed.], *Lehrbuch der allgemeinen Geographie*, pt. 4. 3d ed. De Gruyter, Berlin. 463 p.
- Terborgh, J. 1970. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology* 52:22-40.
- Troll, C. 1968. Landschaftsökologie [English summary]. In R. Tüxen [ed.], *Pflanzensoziologie und Landschaftsökologie*. Ber. Symp. Int. Vergl. Vegetationskunde, Stolzenau/Weser 1963, 7:1-21.

- Udvardy, M. F. D. 1959. Notes on the ecological concepts of habitat, biotope and niche. *Ecology* 40:725-728.
- Weatherley, A. H. 1963. Notions of niche and competition among animals with special reference to freshwater fish. *Nature* 197:14-17.
- Whittaker, R. H. 1951. A criticism of the plant association and climatic climax concepts. *Northwest Sci.* 25:17-31.
- . 1952. A study of summer foliage insect communities in the Great Smoky Mountains. *Ecol. Monogr.* 22:1-44.
- . 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* 26:1-80.
- . 1962. Classification of natural communities. *Bot. Rev.* 28:1-239.
- . 1965. Dominance and diversity in land plant communities. *Science* 147:250-260.
- . 1967. Gradient analysis of vegetation. *Biol. Rev.* 42:207-264.
- . 1969. Evolution of diversity in plant communities. *Brookhaven Symp. Biol.* 22:178-196.
- . 1970. *Communities and ecosystems*. Macmillan, New York. 162 p.
- Whittaker, R. H., and C. W. Fairbanks. 1958. A study of plankton copepod communities in the Columbia Basin, southeastern Washington. *Ecology* 39:46-65.
- Whittaker, R. H., and W. A. Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona. II. A gradient analysis of the south slope. *Ecology* 45:429-452.
- Wuenschel, J. E. 1969. Niche specification and competition modeling. *J. Theoret. Biol.* 25:436-443.