

A gentle depilation of the niche: Dicean resource sets in resource hyperspace

Stuart H. Hurlbert
 Department of Biology
 San Diego State University
 San Diego, California

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ABSTRACT: Niche has been and continues to be a label applied to a variety of concepts. There are strong logical and historical grounds, however, for restricting it to mean the set of resources used. It may be so defined for an individual, a species, a multispecific assemblage or for any intermediate level of organization. Three general categories of resources—energy, materials, site—are recognized. Energy, materials, and sites are distributed in space, but space itself, except at the scale of site, is not usefully considered a resource; this important distinction is blurred by use of terms such as 'spatial niche.' If a niche is represented as a hyperspace, the axes of the hyperspace serve to scale the characteristics of these resources.

Resource characteristics include both intrinsic properties of the resources (e.g., prey size) as well as descriptors of the environmental setting of the resources (e.g., temperature). 'Response' can be measured as the probability that a given unit of resource is used. As a consequence of its resource-using activities, an organism has many influences on the surrounding community or ecosystem. If the totality of these influences or impacts is regarded as the 'functional role' of the organism, then 'role' is not equivalent to niche, as many authors would have it, but rather 'role' is a consequence of the niche.

Let's consider the concept of niche—
 If I knew what it meant I'd be rich.
 Its dimensions are n
 But a knowledge of Zen
 Is required to fathom the bitch.

—Grant Cottam and
 David Parkhurst

With your concept of niche I agree
 But there's clearly one hitch I can see.
 You blame the wrong sex
 For the inherent hex,
 For the niche is no she, but a he.

—Joy Zedler

I'm amazed that a smart woman like Joy
 Would believe that a niche is a boy;
 For a niche is elusive,
 Deceitful, confusive—
 It's quite clear it's a feminine ploy.

—Grant Cottam

INTRODUCTION

If the niche concept is still a fuzzy one (Hurlbert 1977), depilation is a reasonable hope for those who prefer the bald truth and a clear view of gender. Gentleness seems possible because the remaining pubescence is loosely rooted: several of the ideas presented in the following pages have been articulated previously and are already accepted by some workers. It is primarily in offering a particular synthesis of these ideas and a critique of others that the following essay pretends originality. My purpose is to develop a framework for the niche and related constructs that is simpler, more operational, and more internally consistent than existing ones.

At present, the term ecological niche is one of uncertain utility. Its value as a concise label for a concept is diminished both by the multiplicity of concepts to which it has been applied and by the vagueness of most of these. I suggest that *niche* (*sensu* realized niche) be defined as the *set of resources used* and that it can be defined relative to an individual, a population, a taxocene, a species, a supraspecific taxon or indeed any set of individuals. Essentially the same definition has been proposed before but it is not

widely accepted, at least not by authors of textbooks or review articles. The present essay attempts to demonstrate the virtues of this definition and, necessarily, the inadequacies of alternative ones. A historical approach is adopted for the first part of the essay. This permits an analysis of the origins of the present confusion and delineation of the historical and logical grounds for accepting the resource set definition. The consequences of accepting this definition are discussed in subsequent sections.

HISTORY

It is convenient to consider the development of the niche concept as having consisted of five phases. These may be called the Grinnellian-Eltonian, Hutchinsonian, Hundred Flowers, Despairing, and Distillation phases. These phases overlap. Some might be regarded as diffuse schools of thought. For each, I list a few characteristic definitions and then briefly discuss the issues raised.

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Grinnellian-Eltonian Phase

1. "The status of an animal in its community . . . its place in the biotic environment, its relations to food and enemies" (Elton 1927, p. 63).
2. "The niche means the mode of life, and especially the mode of feeding of an animal" (Elton 1950, p. 28).
3. "The ultimate distributional unit within which each species is held by its structural and instinctive limitations" (Grinnell 1928).
4. "A niche indicates what place the given species occupies in a community, i.e., what are its habits, food and mode of life" (Gause 1934, p. 27).
5. "The ecological niche of an organism depends not only on where it lives but also on what it does. By analogy it may be said that the habitat is the organism's 'address,' and the niche is its 'profession" (Odum 1959, p. 27).

The early history of the niche concept has been discussed by Udvardy (1959), Vandermeer (1972), and Hutchinson (1978). Birth of the concept was gradual and attended by vague and shifting usage, a pattern hardly unusual in the evolution of ideas. Neither Grinnell nor Elton nor Gause offered very specific formal definitions. Only by referring to their examples and by assuming these to represent the full breadth of their concepts, can one get even a partially clear view of their intents. Udvardy (1959) concluded that "There seems no essential difference between the niche concept of Grinnell and that of Elton ... they both refer to the essential elements of the environment utilized by the animal." I do not agree with that conclusion. I here treat the two men together only because they apparently developed their concepts independently (Hutchinson 1978) and introduced them into the ecological literature during roughly the same period of time.

Both his quoted definition and his other statements strongly suggest that Grinnell viewed the niche as the physical space or habitat (or microhabitat) utilized by a species, *albeit with habitat characterized very specifically in terms of the physical conditions, food resources, etc., required by the species*. For example, he refers to a song sparrow seeking out "its own 'natural' type of habitat, the streamside thicket—the ecologic niche of its species" (Grinnell 1928, p. 442). In another spot (p. 437), Grinnell describes the ground squirrel's "particular habitat, its ecologic niche" and characterizes this in terms of topography, soil type, food supplies, and soon. Similar statements by Grinnell on the niche of the pocket gopher (p. 435) led Udvardy (1959) to claim that "Grinnell emphasized food and enemies as two critical factors in comprising . . . [its] niche." That interpretation seems inaccurate. Grinnell's niche is defined in part by food and enemies, but there is no evidence that he regarded these as *components* of it: they are not the physical space itself.

If Grinnell emphasized the habitat, Elton emphasized diet. However, contrary to Udvardy's implication, it is not clear that Elton intended niche to refer solely to resources (food or otherwise) used. Phrases such as "status," "mode of life," and "relations . . . to enemies" suggest a more inclusive concept, as do also Odum's "profession" (1959) and "role" (1971; see definition #11) metaphors. But one must largely guess what these terms meant to their authors. Is the niche of a deer partly determined by the coprophagous insects that utilize its excrement, by the toads and vegetation that it inadvertently tramples? Such relationships would seem to contribute to the defining of "place in the biotic environment," but, on the other hand, they were not mentioned by these early workers.

Hutchinsonian Phase

6. "an n -dimensional hypervolume . . . defined on axes

representing] all of the ecological factors relative to [the species] . . . [and] every point in which corresponds to a state of the environment which (permits) . . . the species . . . to exist indefinitely' (Hutchinson 1958).

7. "[The niche is] a set of habitats . . ." Vandermeer 1972).
8. "The set of all environmental variables (essentially the habitat) and all organism responses, and both the habitat and total response are subsets of the niche" (Wuenscher 1974).
9. "The niche of a population is a hypervolume in a space defined by axes representing the biotic and abiotic factors to which populations in the community respond differentially. . . . The response of organisms to different environments (different points in niche space) is an essential component of the niche" (Colwell and Fuentes 1975).

Hutchinson's appealing geometric formalization greatly stimulated a quantitative approach to the niche and related phenomena. It does not diminish his contribution to note, however, that *biologically* his concept is essentially identical to that developed but never concisely articulated by Grinnell.

Hutchinson defines the niche as a hypervolume, every point in which corresponds to one or more real physical locations in the environment. The spectrum of environmental conditions available is represented as a larger hypervolume or hyperspace defined on axes that scale those physical (including temporal) and biotic properties of the environment that are considered relevant to the species under study.

Confusion has existed as to whether the so-called 'Hutchinsonian niche' is a subset of real space or a subset of an abstract space. The fact is that both characterizations are correct, for the term is employed in two ways. Most often it is used as a shorthand for 'Hutchinsonian geometric representation of the niche,' and that clearly is an abstract space. However, when used in reference to a particular organism, 'Hutchinsonian niche' often means *the niche itself* (as opposed to a geometrical representation of it), that is, 'the set of all environmental states that permit that species to exist indefinitely'; and that "set" corresponds to a subset of real space, essentially the Grinnellian niche. At least this seems the only interpretation completely consistent with Hutchinson's (1958) definition. And it is the interpretation explicitly adopted by recent reviewers of the Hutchinsonian niche (see definitions #7 and #9).

Confusion also has resulted, I believe, from an inconsistency between Hutchinson's formal definition and his manner of representing food size on niche axes in his hypothetical examples (1958, Fig. 1; 1967, Fig. 71). His definition and his figures of 'niche space' taken together imply that, at any one point or environmental 'state' in the niche, there will be present only a single size of food particle. This is unrealistic. Food particle size would have been represented more appropriately by employing several axes. One axis might scale mean particle size, another might scale variance of particle size, and others might scale other parameters of food particle size-frequency distributions. In that way, at each point in the niche there *would* be a particle size *distribution* capable of sustaining the species. I am not recommending this procedure but only suggesting that it is the one called for by Hutchinson's definition.

It is apparent that the hypervolume concept can be applied in two ways. In one approach the hyperspace axes serve to scale environmental variables and the niche is that subset of environmental states *wherein all requirements of the species are met*. Resources constitute a subset of the relevant environmental variables and therefore contribute to the defining of the niche. In a second approach, the hyperspace axes serve to scale the characteristics of the resources available or present, and the niche is the set of resources used. This approach requires axes to characterize both the intrinsic properties of the resources (e.g., particle

size, palatability, etc.) and their location in the environment relative to temperature, predators, and other variables that determine the real availability of the resources to a species with finite capacities for dealing with such potentially hostile factors.

The first approach is that implicit in Hutchinson's definition, while the second approach is the one most in accord with his examples, with most of those provided by subsequent workers, and with the 'resource set' definition of niche. Both approaches are reasonable but they do not hybridize well. Confusion will be avoided if niche is applied to only one of them. The second, with its emphasis on resources, seems more useful to the study of competition and, perhaps, of ecological phenomena generally. Also, as discussed above, the second approach permits resource characteristics (e.g., food particle size) to be scaled in a simpler and more direct manner.

Hundred Flowers Phase

"Let a hundred flowers bloom, let a hundred schools of thought contend."

—Mao Zedong (1956)

10. "The nutritional role of the animal in its ecosystem, that is, its relations to all the foods available to it" (Weatherly 1963).
11. "The niche includes not only the physical space occupied by an organism, but also its functional role in the community (as, for example, its trophic position) and its position in environmental gradients of temperature, moisture, pH, soil and other conditions of existence" (Odum 1971).
12. "The places where a species feeds within its habitat are called its 'ecological niche'" (Lack 1974).
13. "The niche comprises all the bonds between the population and the community and ecosystem in which it is found" (Clapham 1973).
14. "The niche is the genetically (evolutionarily) determined capacity (range of tolerance) and pattern of biological response of an individual, a species population, or the whole species to environmental conditions" (Maguire 1973).
15. "The sum total of the adaptations of an organismic unit . . . [all of the various ways in which a given organismic unit conforms to its environment]" (Pianka 1974).
16. "The set of conditions that a particular species . . . [experience[s]] . . ." (Pielou 1975).
17. "The complete functional role a species within a given community" (Whittaker and Levin 1976).

The Hundred Flowers phase was the result of renewed interest in the niche following Hutchinson's (1958) geometric formulation. Many attempts were made to restate or redefine the niche. The ideas of Elton, Grinnell, Hutchinson, and others were variously combined, reinterpreted, misinterpreted, and rejected. The eight definitions listed above are among the resultant 'flowers.' Weatherly defines niche as a concept pertaining to trophic relations only, in keeping with a narrow interpretation of Elton. Odum's definition represents an amalgamation, actually developed much earlier, of the ideas of Elton and Grinnell (Vandermeer 1972). Lack's definition is clear but idiosyncratic. Clapham's and Maguire's niches are too inclusive, being essentially synonymous with 'ecology of the population.' Likewise, Pianka's definition is too abstract to be useful and, in any case, has since been abandoned by him (cf. Pianka 1976, p. 116). Pielou's definition is Hutchinsonian, if "conditions" may be taken to refer to the locations and their characteristics. Whittaker and Levin (cf. Whittaker et al. 1973, also) claim that their definition is an accurate restatement of Hutchinson's concept; use of the term 'role,' however, leaves their definition as vague and open to variable interpretation as was Elton's (1927) phrase "place in the biotic environment."

The Hundred Flowers phase is still in progress. The divergence of opinion seems much greater among writers of books and review articles, however, than among the practitioners in the field and laboratory. Most articles which report research results in niche terminology do not bother to define *niche* formally and thus avoid the fray. It appears that those few aspects of niche that are readily quantified and frequently studied are exactly those aspects common to many definitions. Nevertheless, inconsistent use of the term does decrease the intelligibility of much literature.

Despairing Phase

18. "niche . . . I doubt that it would be valuable to try to define it rigorously" (Lack 1971).
19. "I think it good practice to avoid the term niche whenever possible" (Williamson 1972).
20. "The term is probably unnecessary" (Margalef 1974).
21. "The niche concept is a very useful addition to the ecologist's tool kit because it combines the best properties of both bailing wire and putty; it holds ill-fitting pieces together that would otherwise fall apart and at the same time fills the gaps between them so that poor workmanship may go undetected" (D. Reilloc in Hurlbert 1977).

The above authors apparently feel that further attempts to refine the niche concept are unwarranted. Lack's pessimism at least is closer to the mark than was his later definition (#12 above). Margalef's opinion is substantiated by the existence of two modern textbooks (Collier et al. 1973, Ricklefs 1976) which present the full spectrum of ecology without once using the term niche. Margalef (1974) feels that niche, defined as the "functional role" of a species, has been a useful vehicle for ideas in the past; he leaves open the question of its future utility. Reilloc's comment represents the nadir of this phase, implying that the concept has served as the tool of charlatans.

Distillation Phase

22. "The ecologic position that a species occupies in a particular ecosystem . . . [includes] a consideration of the habitat that the species concerned occupies for shelter, for breeding sites, and for other activities, the food that it eats, and all the other features of the ecosystem that it *utilizes* [my emphasis]. The term does not include, except indirectly, any consideration of the functions that the species serves in the community" (Dice 1952).
23. "The niche may be thought of as composed of several dimensions . . . each corresponding to some requisite for a species" (Root 1967).
24. "An adaptive zone is the niche of any taxon, especially a supraspecific one . . . [and has] two more or less independent components. One involves use of resources (which are part of a lower trophic level); the other involves resistance to predation and parasitism . . ." (Van Valen 1971).
25. "Recently . . . the niche has become increasingly identified with resource utilization spectra through both theoretical and empirical work of a growing school of population biologists [dating from the later 1960s]" (Pianka 1976).
26. "Niche is one of those concepts that should not be defined too rigidly, but, roughly, a niche consists of the resources a species uses, where it finds them, and the strategy by which it harvests them" (Diamond 1978).

Dice's definition has two great virtues. First is its clarity and specificity. No refuge is sought in "status," "mode of life," "profession," "role," "bonds," "etc.," or other convenient evasions. Second, it defines the niche as consisting, in effect, of the set of resources used by a species. This for some time has been the

meaning implicitly assigned to niche in much of the literature reporting empirical studies. It is close to the meanings assigned the term by some early reviewers of the concept (e.g., DeBach 1966, Van Valen 1960). It is also the sense, as was argued earlier, most consistent with Hutchinson's (1958, 1967) manner of defining the hyperspace axes. And, finally, the resource set definition of niche will facilitate clarification of some related issues.

It may be argued that Dice's definition is little more than a restatement of the Grinnellian concept. My interpretation, however, is that for Dice all resources utilized had equal standing with each other as components of the niche, whereas for Grinnell the habitat resource was the niche and other resources served only to characterize it. In this sense, Dice's definition represents a fusion and distillation of the ideas of Grinnell and Elton rather than a simple summing of them as exemplified, for example, by definition #11.

For the most part, Dice's contribution has been overlooked by recent ecologists or, when noticed, misrepresented. Whittaker et al. (1973) quote only the first ten words, which say little, of Dice's full definition (#22). Pianka (1974) claimed that Dice defined niche as "a subdivision of the habitat," a clear error, and later (Pianka 1976; cf. definition #25) gave primary credit for the resource set concept to the post-1968 MacArthurian young turks. Root (1967; #23 above) formulated the resource set definition rather clearly, at least if we take "requisite" to mean resource. However, I would suggest that each hyperspace dimension corresponds not to a resource but rather to a single characteristic of the resource. Subsequently Root subscribed to a definition of the niche as "the intracommunity role of the species" (Whittaker et al. 1973), but he now favors something closer to his earlier conception (R. B. Root, pers. comm.).

For discussion of the evolutionary history of major taxa, Van Valen (1971) prefers Simpson's term 'adaptive zone,' which Van Valen regards as less ambiguous than, but essentially synonymous with, 'niche.' Except for the fact that it seems to consider only food resources (neglecting space and non-food materials), Van Valen's definition of niche is effectively 'the resource set utilized.' Predation and parasitism are not really a second "independent component." They are regarded as pertinent only because "They may . . . prevent full or even any use of part of the resource space that the species would otherwise use . . ."

Diamond's caveat (cf. definition #26) would seem to place him in the "Despairing Phase" along with Lack (definition #18) and several anonymous reviewers of this paper who feel that it is inappropriate to advocate that a single precise definition be assigned 'ecological niche.' On the other hand, the tentative definition he puts forward coincides exactly with the resource set definition if "where" and "strategy" are viewed not as niche components having equal standing with "resources used" but rather as factors that serve to define "resources used."

THE NICHE AS A RESOURCE SET

The preceding section presented several arguments for defining the niche as 'the set of resources used by an organism.' The principal ones are that many workers have used it implicitly in that sense; and that 'resources used' is the area of intersection of most explicit definitions—and often "truth is the intersection of independent lies" (Levins 1966). I now elaborate on this definition by specifying what these resources are and what resource characteristics must be considered for the full definition of a niche.

Kinds of Resources

The resources used by organisms are of three sorts: energy, materials and sites. Energy resources include, principally, solar radiation, utilized by green plants for photosynthesis and by many

organisms as a direct source of heat, and the energy content of food or organic matter. Material resources include chemicals such as oxygen, mineral nutrients, vitamins, etc., and a heterogeneous assemblage of materials such as those used in construction of nests or protective shelters, those used in the capture or processing of food (e.g., the stone on which a sea otter cracks shellfish, the gravel in the crop of a dove), and others.

The site of an organism is, at the most fundamental level, simply the physical space occupied by an individual, the ultimate microhabitat. This space may be relatively undifferentiated from immediately surrounding space, e.g., the space occupied by a phytoplankton, or it may correspond to a more or less discrete physical configuration such as a crevice in a rock. Sites may provide shelter from enemies and the physical environment or they may simply permit access to energy and materials.

Many organisms lay claim behaviorally or allelochemically to sites slightly to very much larger than themselves. These are usually called territories and may serve to assure adequate supplies of energy or materials. Although clearly distinct from the 'standing room' site in important ways, territories are also similar to them: each represents the physical space an organism appropriates to itself, to the exclusion of other individuals (of certain types).

This simple classification of the kinds of resources required by organisms does not imply that each item used is necessarily assignable to only a single category. A green leaf, for example, can provide energy, materials, and a site to an aphid.

Resource Characteristics

If the niche is defined as the set of resources used then its representation in a resource hyperspace requires that the axes of the hyperspace serve to scale the characteristics of the resources. Full characterization of a resource includes consideration of (1) its intrinsic characteristics and (2) its environmental characteristics or context. This classification is slightly arbitrary but nevertheless useful.

a) Intrinsic Characteristics

Intrinsic characteristics of resources (energy, materials, sites) include features such as prey size, behavior and palatability, chemical form of a nutrient, wavelength (solar radiation), texture of a substrate, soil porosity, size of a crevice, and so on. At a slightly different level, the abundance (concentration, intensity) of a resource and certain spatiotemporal patterns to its abundance may also be considered intrinsic properties. An axis representing resource abundance can account for a large proportion of the total ecological separation between organisms; many species have 'carved out' niches for themselves by evolving to have very low requirements for food, water, mineral nutrients, oxygen, or light. Whether a resource is uniformly, randomly or patchily distributed over an area will also influence its effective availability, as Reichman and Oberstein (1977) have demonstrated for seed-eating kangaroo rats. More than one axis may be required to represent those characteristics of resource dispersion critical to the species in question.

The frequency, magnitude and regularity of fluctuations in abundance of a resource determine its availability to an organism, in accordance with the organism's dispersal and reproductive capabilities, its ability to withstand periods of resource shortage, and so on. Temporal patterns of resource abundance may be due to intrinsic properties of the resource itself (e.g., the physiology of a prey organism) or to influence on the resource of the fluctuations in the physical and biotic environment. A 'calendar' axis often can be employed to scale the

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phenological component of temporal variation. Did, lunar and other periodicities can also be scaled. Some successional aspects of temporal variation in resource abundance can be represented by an axis scaling 'time since last disturbance.' This is an important characteristic of site. Areas that have been cleared by fire or some other catastrophe are subject to rapid colonization by opportunistic species. But, for opportunistic species the effective quality of such sites declines with time as more slowly invading but competitively superior species gradually occupy the sites. The above are only examples of the temporal characteristics of resources pertinent to user species.

b) Environmental Characteristics

The characteristics of the space or environment about a resource define the effective availability of that resource just as much as do the intrinsic characteristics of the resource. This is my rationale for representing temperature, salinity, and other physical environmental factors on hyperspace axes. It is not simply that they are environmental factors, but rather that they are environmental factors that *constrain the utilization of resources*. For exactly the same reason, competitors, predators, parasites, and pathogens are also determinants of the environmental context of resources and are logically represented by resource hyperspace axes. They can exclude an organism from an area or reduce its abundance and thereby reduce the effective availability or 'quality' of whatever resources may be present in that area.

Obligate or facultative cooperative relationships often permit greater abundance and wider distribution of one or both partners to such relationships. Each such 'friend' should be represented by a hyperspace axis scaling its abundance. Whether, for example, the bull's-horn acacia (*Acacia cornigera*) can survive to utilize the solar radiation, water, and nutrients present in a given location is determined in large part by whether the ant *Pseudomyrmex ferruginea* is present to protect it from vines and herbivores (Janzen 1967). The density of the *P. ferruginea* population is an environmental property which partially defines the niche of *A. cornigera*.

A final consideration in the characterization of environmental context is the spatial distribution of the resources in relation to one another. The resources required by a given organism have distributions that are non-coextensive in various degrees, and the availability of one resource is effectively diminished if another requisite is lacking or is available only at a great distance. The permissible distance between the different resources can be great for highly mobile organisms. These may feed in one location, drink at a second, and find shelter in a third, without utilizing resources in intervening areas. A sessile organism naturally requires a sufficiency of all resources at a single location.

Response Surface

In his original characterization of the multidimensional niche, Hutchinson (1958) recognized that the various "states of the environment" comprising a niche were not equally favorable to the persistence of the population or species. Thus complete specification of the niche required that an axis scaling probability of survival be included among those defining the hyperspace. This probability when plotted over all environmental states would form, in essence, a response surface in hyperspace. This idea has been widely accepted and has been elaborated upon (see especially, Maguire 1973), but usually it has proved operational only when the physiological response of individuals (e.g., Wuenschel 1969) has been substituted for probability of population survival as the variable to be scaled on the response axis.

When niche is defined as the set of resources used, every point in its multidimensional representation corresponds to a specific type of resource characterized by both its intrinsic and its environmental properties. The logical variable to represent on the response axis will be intensity of use. Most if not all workers who have considered this aspect have followed the lead of Levins (1968) and Root (1967) and measured intensity as relative frequency of utilization. e.g., percentage of individuals found on each of several substrates, percentage contribution to total diet, etc. An alternative would be to measure intensity of use as the percentage of the resource that is used or as the probability that a given unit of that resource is used during a given period. This approach requires much more information, namely that on the actual abundance of each kind of resource used, but also yields utilization measures of greater ecological interest. They will measure both *the efficiency with which a resource is used* as well as how much remains available to other organisms. They also are the utilization measures required for biologically interpretable indices of niche breadth and niche overlap (Hurlbert 1978).

CONSEQUENCES OF THE 'RESOURCE SET' DEFINITION

Defining the niche as the set of resources used has a number of salutary consequences. It allows clarification of several other terms, permits more intelligible discussion of various issues, and even leads to the defining of some new issues. Some of these consequences are examined in this last section.

'Role' Pinned Down

The resource set definition does not conflict with those definitions phrased in terms of 'role,' 'functional relations,' etc., as much as it suggests a specific interpretation of them: *the 'role' of a species might be defined as the sum of the impacts, direct and indirect, it has on a system as a result of the species' utilization of resources in the system.* Such a definition assigns a definite meaning to role, and perhaps one close to some workers' concept of niche. Acceptance of this definition would not justify equating this sense of role with niche, however. The resource set is more useful and tractable, both conceptually and operationally, than is the 'sum of impacts' and should have more appeal to theoretician and field-worker alike. Role is best regarded as only a consequence of the niche. Dice's (1952; definition #19) astute rejection of the "function" definition of niche perhaps was based on a similar line of reasoning.

Persons who define niche as role may not agree with the above restriction of the meaning of role, and it must be agreed that the word does have more ample connotations. But that has been the problem. Frequently employed and almost never defined, role has come to signify something *like* the sum of the ecological relations of a species or, in short, the ecology of the species. If niche has no more specific meaning than this, then the term is undesirable.

Space, Site and Habitat

Energy, materials and sites are distributed in space, but space itself, except at the scale of site, is not usefully considered a resource. Recognition of the distinction between spatial distribution and site utilization should resolve confusion surrounding the terms 'habitat' and 'spatial niche.' I contend that the first of these terms has no single, specific relationship to niche, and that the second is superfluous.

Habitat has been regarded both as a component of niche and as complementary to niche. Most workers, starting with Johnson (1910, cf. Gaffney 1975) and Grinnell (1924), have considered niche to be or include some aspect of spatial distribution, and usually that aspect has been labeled *habitat*. Dice (1952; #21) formally included habitat as a component of the niche. However, in referring to the particular aspects

of a habitat ("shelter," breeding sites") that an organism "occupies" or "utilizes," Dice was using habitat in a very specific sense, a sense I am calling 'site.' The more general and common sense of habitat is "the place where an organism lives" (Odum 1971, p. 234), with "place" corresponding to a piece of space much larger than the space actually occupied or defended by an organism. Habitat certainly specifies the general location of the resources used by an organism, but it does not indicate their specific locations and characteristics nor does it directly connote their utilization.

Whittaker et al. (1973; 1975) made a major effort to clarify the relationship between niche and habitat. They suggested that niche be defined as the "intracommunity role" of a species and that habitat refers to "the range of environments or communities over which a species occurs." They adopted the term *ecotope* to represent the sum of niche and habitat, that is, "the species response to the full range of environmental variables to which it is exposed." This conceptual-terminological framework seems unsatisfactory in key respects. First, it perpetuates the notion of niche as role, a notion that, as argued earlier, seems too diffuse to be useful. Second, it defines niche as "intracommunity role" despite their admission that "'community' is in many cases an arbitrarily bounded segment of a continuum." Kulesza (1975) also has criticized this aspect. In practice there may be little difficulty in setting boundaries, however arbitrary, to a study area, vegetation type, etc., and calling the included assemblage of organisms an operational 'community.' But that which it is merely operationally feasible to define may not be an adequate foundation for a conceptual scheme—specifically, one that establishes a formal dichotomy between intracommunity and intercommunity variables even though "There is no discontinuity between the two groups of variables" (Whittaker et al. 1975). In this scheme neither niche nor habitat can be defined, formally, for an organism unless one is willing to specify exactly what scale or segment of nature is to be meant by 'community.'

The proposed complementarity of niche and habitat may seem reasonable when these are interpreted as, respectively, 'what it does,' and 'where it lives,' the 'profession' and 'address' metaphors of Odum (1959). However, when a *precise* definition of niche (the resource set definition being only one example of such) is adopted and when the variety of meanings that inevitably will continue to attach to habitat is recognized, the proposed complementarity seems futile.

A related aspect of the scheme of Whittaker et al. (1973,1975) is the formal dichotomy it establishes between habitat and microhabitat, the latter being considered a component of niche. Again this distinction would be very difficult to employ consistently in practice. It also distracts attention from the really fundamental distinction, that between site and the distribution of sites, i.e., between the space resource and the distribution of that resource in the larger spatial frameworks of biotope, geographic region, and so on.

Possibly if Whittaker et al. (1973) had first attacked the imprecision of the 'role' metaphor itself instead of concerning themselves with the secondary problem of the spatial extension of niche, they would have developed a different scheme. Although they gave examples of the variables that define 'role' (e.g., Whittaker et al. 1973, p. 323), they did not specify the criteria by which these variables were judged pertinent. In relation to the 'resource set' definition of niche, the listed variables would all be pertinent because they are either resources, resource characteristics, or determinants of resource availability. But 'resource set' appears not to be what they meant by 'role.'

"Spatial niche" has sometimes been considered a synonym for habitat or habitat niche (Odum 1971, p. 234). If this term means no more than habitat or microhabitat, it is superfluous. If it were given a different and

more specific meaning and if the new definition were generally accepted, the term might be useful. Realistically, however, spatial niche probably would continue to be used in many senses, including habitat, site, and site plus environmental context of energy and materials. The best option seems to be to drop the term completely.

It is necessary to affirm that while the geographical distribution of an organism will be partially specified by a characterization of the resources used by an organism, there is no basis for permitting geographic location per se to contribute to the characterization of a niche. Williamson (1972) misinterprets Hutchinson (1958) in stating that: "Elton's niche allows the comparison of species, say, in Europe and Australia, but this feature is lost with the multidimensional niche simply because the dimension Europe-Australia will inevitably separate all of the species." In no plane does the Hutchinsonian hyperspace correspond to a map of the world!

Unconstrained Niche

Up to this point I have used niche in the sense of the *realized niche*, i.e., the set of resources actually used. If a competing species or a small set of competing species is removed from a system, the species that remains may use a wider range of resources. This expanded resource set constitutes what MacArthur (Hutchinson 1958) termed the *fundamental niche*. Although belying the highly situation-dependent nature of such an expanded niche, this term has been used consistently and merits retention in the new framework proposed here.

It is possible, however, to view the fundamental niche as a special case of a more general construct. Predators and physical factors, as well as competitors, can also constrain the availability of resources and, thus, the realized niche. If we remove a predator or ameliorate a condition of the physical environment, the niche of a species may expand as readily as it will on removal of a competitor. These sorts of relationships have been recognized for some time and are discussed most explicitly by Connell (1975) and Colwell and Fuentes (1975). I suggest *unconstrained niche* as a general term for the set of resources utilized after relaxation of a specific constraint on resource availability, irrespective of the nature of the constraint.

The notion of unconstrained niche, though similar in spirit to those of pre-competitive niche (Levins 1968), virtual niche (Colwell and Futuyma 1971), and pre-interactive niche (Vandermeer 1972), is nevertheless distinct from them in meaning. Perhaps fundamental niche can be used in a broad sense to cover all the ideas involved (Colwell and Fuentes 1975). But if a Dicean rather than the more traditional Grinnellian-Hutchinsonian definition of niche becomes generally adopted, a separate term, unconstrained niche, will minimize ambiguities.

The *unconstrained niche*, like the *fundamental niche*, is not susceptible to much conceptual extension or elaboration. It represents a convenient way of expressing immediate, first order effects. It is incapable of dealing with long-term, second order, or evolutionary consequences of constraint removal. Removal of a competitor or a predator will, at least in principle, cause direct and indirect changes in many components of the system, not merely the availability of a single specific type of resource. Similarly, if temperature conditions ameliorated, all components of the system will be able to respond, not only the species for which we wish to define an unconstrained niche. The conceptual limitations of the unconstrained niche derive from the ecological axiom that it is impossible to do only one thing.

Constraining versus Limiting Factors

It is consistent with the above to speak of resource characteristics

Niche

(intrinsic or environmental) as being either constraining or non-constraining factors. Niche-constraining factors usually are the only ones of interest or importance. The non-constraining factors would be those resource characteristics which do not influence resource use in a given case. For example, the density of microscopic hairs on plant leaves would be a characteristic of the plant, but it may not be a characteristic likely to influence utilization of these plants by deer, with respect to the deer's niche, though perhaps not those of aphids, the density of plant hairs is a non-constraining factor.

This idea that the important niche axes are those which scale constraining factors may be compared with Levin's (1970; Whittaker and Levin 1976) idea that the important axes are those which serve to define *limiting factors*. The main distinction hinges on the question: important for what? Levins was concerned with 'those aspects of the niche crucial in the determination of whether species coexist' and consequently considered as limiting factors only those which operated with density-dependent effects. My concern has been to define the niche in terms of all factors which define and constrain resource utilization, irrespective of their bearing on problems of coexistence. Thus, constraining factors, in my usage, include limiting factors *sensu* Levins and other factors, such as various aspects of temperature, salinity, etc., which can constrain resource use via density-independent effects.

It is apparent that full specification of the niche of a population requires information on all factors that, at one time or another, affect the size of that population. To my knowledge, only Van Valen (1973) has explicitly discussed population regulation in terms of "how much of the resource space is used."

Empty versus Expropriable Niches

The term *empty niche* has often been used in referring to the invisibility or openness of a system to a particular type of potential colonist. Two ideas have been embraced by the term, and the resource set definition of niche allows these to be distinguished. A given species can invade and colonize a system only if it can obtain sufficient resources there. If the resources obtained were not being utilized by other organisms prior to its arrival, the new species may be said to have occupied an *empty niche*. However, if the resources were being used by other species and the new species obtains them only by preempting or expropriating other species, then the new species may be said to have taken over an *expropriable niche*: the niche was occupied but nevertheless available to the new species by virtue of the new species' particular abilities.

Minimal Niche

Instead of removing a constraint, it is possible to increase a constraint and determine how far a niche can be compressed along a given axis before it no longer can sustain the population (or other unit). For example, one might slowly decrease a species' range of temperature tolerance or the range of prey sizes that it can utilize (which, in this context, would be equivalent to decreasing the range of temperature conditions or prey sizes available). This may be done until percent utilization or probability of utilization (the response axis) drops to zero for all points in the niche hyperspace—or, alternatively, until the probability is greater than a specified level, e.g., 95 percent. That resource utilization is nowhere greater than zero in the hyperspace. Such a set of 'barely adequate' resources

may be termed the *minimal niche*.

This concept has most of the limitations of the fundamental and unconstrained niche concepts, such as neglect of second order effects. In addition, the nature of a minimal niche will depend not only on the columbarium axis along which compression takes place but also on whether the upper limit (e.g., of prey size utilizable) is compressed toward the lower limit, the lower toward the upper, or both toward the center. Also the degree of compressibility along one axis will depend not only on the distribution of resource along that axis but also on the distribution of resources along other axes.

Nevertheless the term may be a useful vehicle for several ideas. For example, most populations utilize more kinds of resources than those required for bare survival—that is, realized niches exceed minimal niches. The magnitude of the difference between realized and minimal niches, however, must vary greatly among species and among populations of the same species. It is also the availability of a minimal niche (empty, expropriable or a mixture of these) which determines whether a species can invade a new system. And the number of species that can coexist in equilibrium, i.e., the answer to the species-packing problem, will be determined, in part, by the sizes of the minimal niches of the species that are potentially members of the assemblage (Pielou 1975, p. 113).

Breadth of Application

Most commonly niche has been considered an attribute of a population or a species, but it can also apply to an individual (Pianka 1974, p.190) and also to any intermediate level of organization, such as a breeding pair, an age class, an ecotype and soon. Moreover, the concept is perfectly extendable to various types of multispecific assemblages such as guilds (Root 1967), taxocenes (Chodorowski 1959), and entire supraspecific taxa (Van Valen 1971). For example, the total lizard niche may be greater in Australian deserts than in the Kalahari desert, because in the former there are fewer birds, mammals, and snakes competing with the lizards for resources (Pianka 1975). Extinction of a higher taxon often is best interpreted as the result of expropriation of its collective niche (or adaptive zone) by one or more new taxa - it is simply outcompeted (Van Valen 1971). The multispecific niche is a concept of some heuristic value for ecological biogeography and paleobiology.

If the resource set definition is accepted, no confusion should result from allowing niche such wide applicability. The resources used by any given biologic unit are simply the sum of the resources used by its component subunits. Confusion would be fostered, if a new term for 'set of resources utilized' had to be used every time that discussion shifted from one level of organization to another. Use of the single term niche also serves the positive function of spotlighting the centrality of resource use phenomena at all levels of ecological organization.

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Post-publication epilogue

"The landlady's daughter seemed to be much amused that a depilatory could take the place of literary and scientific accomplishments; she wanted me to print the piece, so that she might send a copy of it to her cousin in Mizzourah.. ." -Oliver Wendell Holmes, The Autocrat of the Breakfast-Table, Ch. VI.