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Philosophical Topics, Volume 47, Number 1, Spring 2019, pp. 105-123 (Article)

Published by University of Arkansas Press



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Ecological Theory and the Superfluous Niche

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ABSTRACT: Perhaps no concept has been thought more important to ecological theorizing than the niche. Without it, technically sophisticated and well-regarded accounts of character displacement, ecological equivalence, limiting similarity, and others would seemingly never have been developed. The niche is also widely considered the centerpiece of the best candidate for a distinctively ecological law, the competitive exclusion principle. But the incongruous array and imprecise character of proposed definitions of the concept square poorly with its apparent scientific centrality. I argue this definitional diversity and imprecision reflects a problematic conceptual indeterminacy that challenges its putative indispensability in ecology.

Perhaps no concept has been thought more important to ecological theorizing than the niche. Without it, technically sophisticated and well-regarded accounts of character displacement, ecological equivalence, limiting similarity, and others would seemingly never have been developed. The niche is also widely considered the centerpiece of the best candidate for a distinctively ecological law, the competitive exclusion principle. The received view in ecology has therefore been that the niche is indispensable, despite occasionally vocal protests from a small minority. After all, the concept is often said to simply precisify the idea that species make their biological livelihoods in different ways, and what could be more central to ecology? Many (if not most) influential analyses in the 1960s and 1970s bore the

‘niche’ label, often paying homage to Hutchinson’s (1957) highly abstract definition in particular. Mechanistic models of resource consumption that predominated subsequent decades (e.g., Tilman 1982) are taken to extend and refine the same approach, the niche similarly at their core. More recently, Hubbell’s (2001) unified neutral theory certainly perturbed the prevailing assessment, but it fell far short of upending it (see Odenbaugh forthcoming). A prominent book responding to neutralist theories in favor of niche-based theorizing, for instance, proclaims “the niche has provided and can continue to provide the central conceptual foundation for ecological studies” (Chase and Leibold 2003, 17).

In this case, however, the naysayers were right. The incongruous array and imprecise character of proposed definitions of the concept square poorly with its apparent scientific centrality. Rather than reflect innocuous semantic differences or a potentially useful integrative pluralism, this definitional diversity and imprecision reflects a problematic conceptual indeterminacy that challenges its putative indispensability in ecology. The niche has not and cannot—at least as it has been characterized thus far—do the substantive, foundational work it is claimed to do in ecology. The conceptual content tethered to the term ‘niche’ is just too problematically disjoint and amorphous to play that role.

The gap between conceptual aspiration and scientific practice permeates appraisals of ecological theorizing to the present in many different, multifaceted ways. This analysis focuses specifically on the concept’s origins in the work leading up to, and in many ways culminating in, Hutchinson’s highly abstract n -dimensional hypervolume definition. Section 1 describes the emergence of the ecological niche in Joseph Grinnell and Charles Elton’s work. From the very beginning, the concept’s content was unmistakably disjoint: environments and how they impact species was one focus; how species function in communities, particularly via trophic interactions, was the other. Beyond the bivalent focus, the concept was also problematically imprecise. This point is illustrated by considering the contentious idea of “vacant” niches and the significant indeterminacy about their possibility.

Despite a widespread view it is, section 2 argues the niche concept is not the centerpiece of perhaps the best candidate for a distinctively ecological law, the competitive exclusion principle. Gause’s (1934) *Paramecium* experiments and putatively mechanistic explanation of competitive dynamics with Lotka-Volterra equations are widely taken to supply the first compelling grounds for a niche-based version of the exclusion principle (see Hutchinson 1978). But the evidence for this judgment is pretty thin. Gause’s explanation in *The Struggle for Existence* actually makes little use of niche ideas. His semantically suggestive—but thoroughly non-niche—term ‘vacant places’ may have led many later commentators astray. And what little he did say about niches provides little guidance about how niche considerations might be brought to bear on models of competitive dynamics, via competition coefficients for instance. This serious deficiency is a quite general problem, one shared by later attempts to characterize the concept, including its most influential definition in ecology.

That definition is Hutchinson's n -dimensional hypervolume characterization of the niche, the focus of section 3. As judged by the attention it received, his definition had an enormous impact on ecology. But judged by the content conveyed, the impact seems disproportionate. Hutchinson made highly questionable and significantly limiting assumptions in characterizing the concept. The most serious deficiency, however, is the same kind of conceptual impoverishment exhibited by earlier attempts to pinpoint the concept. Section 4 concludes by arguing that Chase and Leibold's (2003) more recent revival of the niche is problematic in the same way. Rather than convey information about community dynamics, information that helps represent and analyze those dynamics, the niche superfluously supervenes on them on their account of the concept.

1. GRINNELL AND ELTON'S NICHES

The first director of the Museum of Vertebrate Zoology at the University of California at Berkeley, Joseph Grinnell, wasn't the first to use 'niche' in an ecological sense,¹ but he was the first to do so with any significance. His most well-known paper doing so—the first ecological publication with 'niche' in the title—contains three instances all in the penultimate paragraph:

These various circumstances, which emphasize dependence upon cover, and adaptation in physical structure and temperament thereto, go to demonstrate the nature of the ultimate associational niche occupied by the California Thrasher. This is one of the minor niches which with their occupants all together make up the chaparral association. It is, of course, axiomatic that no two species regularly established in a single fauna have precisely the same niche relationships. (Grinnell 1917, 433)²

The "circumstances" are the chaparral habitat's physical characteristics, for which the Thrasher's phenotypic properties are especially well suited. Its dense undercanopy foliage prevents all but short bursts of flight, complementing the Thrasher's small, compact wings. Its inconspicuous drab-brown plumage also enhances predator-evasion in that foliage.

The allusions to occupation are important. Grinnell's primary focus was animal species; the vegetation they inhabit was conceptualized as part of their physical environments. Niches are then units of that physical, partly biotic environment for Grinnell, units species can occupy. With evolutionary history in mind, relationships between occupants and what's occupied can therefore be explanatory: properties of

1. Apparently, Roswell Johnson was in a 1910 study of ladybug color patterns (see Hutchinson 1978, 155–56).

2. Note the last sentence's close similarity with what was later labeled the 'competitive exclusion principle' (see §2).

niches, as actual bits of physical space, can account for why organisms residing in them possess the (adaptive) phenotypic properties they do.

Although a minority view, there are contrasting readings of Grinnell. Hutchinson (1978, 157) claimed, “it is evident that [for Grinnell] the space occupied by ‘just one species’ is an abstract space that cannot be a subdivision of the ordinary habitat space.” But such abstraction coheres poorly with Grinnell’s extensive descriptions of actual portions of environments as niches. The emphasis on the actual is quite clear in later papers:

Habitats have been variously classified by students of geographical distribution. Some of us have concluded that we can usefully recognize, as measures of distributional behavior, the realm, the region, the life-zone, the fauna, the subfauna, the association, and the ecologic or environmental niche. The latter, ultimate unit, is occupied by just one species or subspecies; if a new ecologic niche arises, or if a niche is vacated, nature hastens to supply an occupant, from whatever material may be available. Nature abhors a vacuum in the animate world as well as in the inanimate world. (Grinnell 1924, 227)

Note that *habitats* are being classified with different measures of *geographical distribution*, the unit of finest resolution being the “ecologic or environmental” niche (synonymy implied).³ The idea an abstraction is really what’s being invoked therefore appears implausible. That Hutchinson favored and developed an abstract-space approach himself may be relevant.

In one of ecology’s founding works, *Animal Ecology*, Charles Elton (1927, 63–64) described a very different concept:

Animals have all manner of external factors acting upon them—chemical, physical, and biotic—and the “niche” of an animal means its place in the biotic environment, *its relations to food and enemies*. The ecologist should cultivate the habit of looking at animals from this point of view as well as from the ordinary standpoints of appearance, names, affinities, and past history. When an ecologist says “there goes a badger” he should include in his thoughts some definite idea of the animal’s place in the community to which it belongs, just as if he had said “there goes the vicar.”

Elton recognized the impacts of abiotic (“chemical,” “physical”) factors, but unlike Grinnell his niche focuses on biotic interactions. The one diagram presented in the ‘Niches’ section, for example, illustrates the “niche occupied by small sap-suckers, of which one of the biggest groups is the plant-lice or aphids” (1927, 66) with a ‘food-cycle’—‘food-web’ in current terminology—comprised solely of biological nodes:

3. ‘Fauna,’ ‘subfauna,’ and ‘association’ were not categories of biological composition for Grinnell. Rather, they were hierarchical units of geography—determined primarily by abiotic factors such as humidity and temperature—within which species distributions could be classified and hypothesis about their causes evaluated (Griesemer 1990).

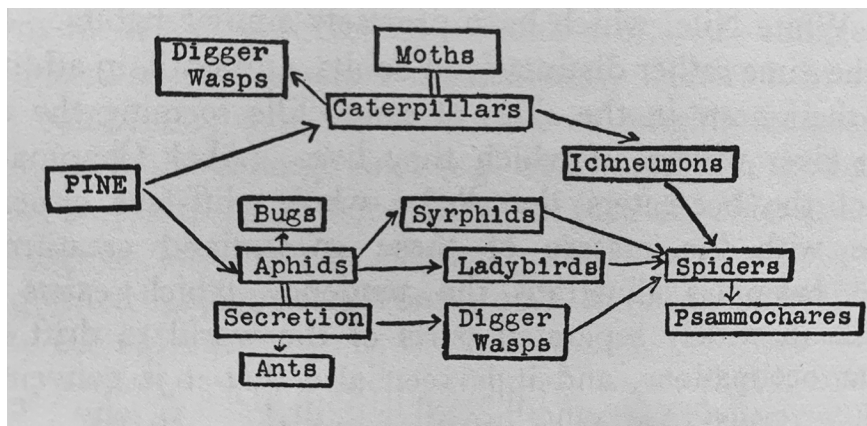


Figure 1. Food-cycle on young pine-trees on Oxshott Common.

This figure and reference to a “small sapsuckers” niche (note the plural) reveals an interesting aspect of Elton’s concept absent from Grinnell’s. For Elton, what individuates niches partially depends on how fine-grained the relations between organisms comprising a biological community are conceptualized. On this point Elton (1927, 64) was quite explicit:

[W]e might take as a niche all the carnivores which prey upon small mammals, and distinguish them from those which prey upon insects. When we do this it is immediately seen that the niches about which we have been speaking are only smaller subdivisions of the old conceptions of carnivore, herbivore, insectivore, etc., and that we are only attempting to give more accurate and detailed definitions of the food habits of animals.

Degree of representational resolution therefore determines what counts as a niche. And since that degree differs across scientific contexts, species are constituents of many distinct niches with different extensions. The claim that coexisting species cannot have the same niche—one gloss on the competitive exclusion principle that Grinnell expressed in the first quote above—would thus sound foreign to Elton. It relies on a much narrower niche conception. This greater generality may account for the fact, noted by Hutchinson (1978, 152), that Elton never used the niche concept to explain competition. It likely also explains why he was never tempted to elevate competitive exclusion to axiomatic or principle status.

Dependence on representational resolution therefore marks an important contrast between Grinnell and Elton’s understandings of niche. But the contrast also seems to stem from a much deeper and more significant divergence of habitat vs. functional conceptions. Unlike Grinnell’s markedly physical conception, Elton’s vicar analogy manifests the latter. Just as vicars are identified by functional roles in

religious institutions, an animal's "place in the community" is similarly functionally individuated by its role in networks of biotic interactions.

Some resist this bipartite judgment (e.g., Griesemer 1992; Schoener 1989). Griesemer rightly stresses that Grinnell and Elton had different research foci—primarily, how evolutionary dynamics influence species distributions vs. how trophic interactions determine community structure—and that that probably partially explains their divergent uses of "niche." He also correctly highlights that each recognized the importance of biotic *and* abiotic factors, while obviously believing one was more salient than the other. The claim Elton and Grinnell possessed distinct biotic and abiotic concepts should therefore be rejected. These differences, though nontrivial, only indicate different conceptual emphases for Griesemer, not different concepts: "Grinnell and Elton both identified the niche as the place/role a species happens to occupy in an environment" (1992, 235).

Correctly judging when differences in conceptual emphasis signify distinct concepts requires a theory of concept individuation, which is beyond the purview of Griesemer's analysis (or this one). But some of the dissimilarities seem to make concept-individuating differences. For instance, the clause 'occupy in an environment' in Griesemer's characterization is problematic in Elton's case. Elton did mention an animal's place in the 'biotic environment'—though just once in *Animal Ecology* (see above)—but the immediate, emphasized paraphrase ("*its relations to food and enemies*") strongly suggests the functional sense given explicitly two sentences later in the vicar analogy with the very similar phrase "animal's place in the community."

Elton's recognition of a small-mammal-consuming-carnivore niche and carnivore niche *in toto* reinforces this conclusion. These classes are not characterized in relation to environments their members occupy, but rather by their functional role in communities: consuming fleshy prey. On this issue Elton was unambiguous. The 'Niches' section begins, "[A]lthough the actual species of animals are different in different habitats, the ground plan of every animal community is much the same. In every community we should find herbivorous and carnivorous and scavenging animals." After giving specific examples the paragraph continues, "It is therefore convenient to have some term to describe the status of an animal in its community, to indicate what it is *doing* and not merely what it looks like, and the term used is 'niche'" (1927, 63). Niches are thereby characterized in terms of this common 'ground plan': an abstract pattern of basic functional relations underlying all communities according to Elton. But that plan is contrasted with the different habitats species inhabit. Irrespective of whether niches are 'places' or 'roles'—two terms that often have very different connotations—for Elton they are not parts of environments. This concept, unlike Grinnell's, is thoroughly functional.⁴

4. Elton himself sharply distinguished his concept from Grinnell's. He criticized Odum's *Fundamentals of Ecology* for failing to distinguish the two (Elton 1954).

There is, however, a more general perspective from which this difference can appear artifactual. Both Grinnell and Elton describe niches as components of broader patterns, be they structures in physical environments or networks of functional interactions. If these patterns derive from or simply are causal relations, then both ecologists are giving causal representations, the only difference being the nature of the causal relata. This difference would then just reflect Grinnell and Elton's different investigative priorities and explanatory commitments; the underlying content of the niche concept would be the same. The unified characterization would then be:

Niche—a node in a nexus of causal interactions with abiotic and biotic factors occupied by a species.

In a fine-grained species-specific way, 'niche' would then simply convey causal information about ecological systems.

Despite the theoretical allure of unification, this proposal clearly fails. The problem is that Grinnell and Elton both countenanced the possibility of *empty* or *vacant* niches: unoccupied parts of environments (see Grinnell 1924, 227, quoted above), or biologically uninstantiated constituents of food webs (see Elton 1927, 27). The causally focused, species-specific characterization above seems unable to capture this broader notion; tracking the causal habits of nonexistent species is quite difficult. And this wasn't a superfluous conceptual aside. The idea was thought to do important work. Vacant niches feature prominently in Grinnell's explanations of the adaptiveness of species' phenotypes for specific environments, and Elton's explanations of putative ecological equivalents in distinct biological communities.⁵

One might think there is an easy fix, simply add "or not" to the characterization above. But the vacant disjunct is not so conceptually innocuous. Its addition seems to abandon the very causal information upon which the unified characterization is based. If it is the web of causal relations a species realizes that indicates the contours of the niche it occupies, no indication occurs in empty cases (from nonexistent species). Yet Grinnell and Elton were committed to the idea that niches endure rather than expire when those causal relations cease to exist (niches are vacated). So they presumably cannot be (part of?) what constitutes a niche. But what, then, is the relationship between the causal relations species participate in when they occupy a niche and whatever it is that characterizes that niche? Far from being "formalized by Grinnell" (Chase and Leibold 2003, 8), without an answer to this question the niche concept in its Grinnellian, Eltonian, or causal-unificatory guises is problematically vague.

Vagueness is not always problematic in science. Imprecision can accurately represent appropriate uncertainty about how a phenomenon is best described, or capture precisely the right level of generality when explaining it. It is problematic

5. A more recent example is Lawton's (1982) influential analysis of bracken herbivores in North American and Britain, and conclusion that the American communities were comparatively "unsaturated"—containing many more empty niches—and were therefore more susceptible to invasion.

here because vagueness precludes clarity about what individuates niches. And clear individuation standards are certainly necessary if the concept is to perform the substantive function it is thought to in ecological theorizing. This kind of criticism has a well-established track record in biology. It is the same kind of charge made against adaptationism in an evolutionary context:

The niche is a multidimensional description of all the relations entered into by an organism with the surrounding world . . . To maintain that organisms adapt to the environment is to maintain that such ecological niches exist in the absence of organisms and that evolution consists in filling these empty and preexistent niches. But the external world can be divided up in an uncountable infinity of ways, so there is an uncountable infinity of conceivable ecological niches. Unless there is a preferred or correct way in which to partition the world, the idea of an ecological niche without an organism filling it loses all meaning. (Levins and Lewontin 1985, 68)

Allusion to uncountable infinities aside, it certainly doesn't seem that Grinnell or Elton's accounts provide much guidance about how to affect the required partitioning.

For the kind of purpose Grinnell and Elton often seemed to have in mind, however, the inability to partition might be only marginally problematic, if at all. Rather than attempting to ecologically carve nature at some joint—one strictly inhabitable by a single species—they were often concerned with analogical inferences across dynamically and structurally similar communities. Communities in geographically and evolutionarily remote areas often seem to exhibit similar dynamics. If this African grassland community has a large species guild performing this critical ecosystem function, then that seemingly analogous American grassland community likely has a similarly large guild performing that same kind of function. This type of inference is particularly clear in Elton's allusion to a basic 'ground plan' underlying all animal communities. But the same idea underlies Grinnell's descriptions of how species are adapted to properties of their physical environments, and how at very distant geographical locations one still often finds similar kinds of species if their environments are similar. Lawton's (1982) bracken study is another example of the same kind of inference.

These analogical inferences depend on recognizing broad causal patterns that indicate similarities of structure or dynamics: the similarities make the analogies apt. But analogy aptness doesn't require isomorphism, homomorphism, or any other fine-grained correspondence of dynamics or structure, the kind of precise correspondence a niche concept that partitioned the environment (Grinnell) or functional community relations (Elton) would afford. Of course, analogical inferences are notoriously difficult to assess. But when they are fruitful it's characteristically not because such a high degree of correspondence precision can be established. Such precision in fact cuts against the less constrained connections analogies trade upon. Biologically informed pattern recognition, not a foundational and systematic niche concept, seems to underpin the cross-community, cross-environment inferences Elton and Grinnell were making.

2. THE STRUGGLE FOR EXISTENCE AND COMPETITIVE EXCLUSION

The shortcoming discussed above squares poorly with the prevalent view of the niche's role in perhaps the best candidate for a distinctively ecological law, the competitive exclusion principle (CEP). Simply put, it says *complete competitors cannot coexist* (Hardin 1960) or, in niche-theoretic terms, *species with identical niches cannot coexist*. This principle has a long history in ecology. Grinnell, for instance, arrived at an exclusionary principle early in the twentieth century, perhaps drawing upon suggestive passages from Darwin (see Hardin 1960).⁶ But the CEP's most compelling development and elevation to 'principle' status is largely credited to Georgii Gause, his influential *The Struggle for Existence* in particular.

Despite its pedigree and pretensions to lawhood, the CEP is controversial. With Popperian flare, Peters (1991) deemed it tautologous. Even more methodologically tolerant ecologists have called it "untestable" and "of little scientific utility" (Pianka 2000, 248). The present task isn't to render judgment on these claims. Rather, it's to evaluate what could be considered the received view about the contribution the niche concept makes to CEP, which Griesemer (1992, 237) captures: "Gause's and Park's experiments showed that the concept of niche, in the guise of determinants of relations of competitive exclusion, was central to an understanding of population dynamics and the evolutionary structuring of communities." But if the concept is as problematically imprecise as indicated in section 1, such centrality would be perplexing. No concept that indeterminate can do that much heavy theoretical lifting. Fortunately, a close reading of Gause's reasoning shows that although he used the term, the concept actually contributes little.

In several ingenious experiments Gause (1934) studied competitive dynamics in *Paramecium* and yeast species. In constant ecological conditions (e.g., nutrient levels, medium temperature, turbidity, etc.), and absent refugia that might mitigate interspecific competition effects, one species inevitably outcompeted the other to extinction. This result matches what classical Lotka-Volterra competition equations predict (exclusion), and Gause believed this furnished a compelling case for CEP. The key question is what the niche concept contributes to this case.

Gause (1934, 19) first mentioned 'niche' in a context-setting discussion of "general principles" zoologists had developed in connection with competition. After citing Elton's (1927) "place in a community" definition referencing "habits, food, and mode of life," Gause then stated, "It is admitted that as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has an advantage over its competitor."⁷ The clause "It

6. "[T]wo species of approximately the same food habits are not likely to remain long evenly balanced in numbers in the same region. One will crowd out the other" (Grinnell 1904, 377).

7. Gause (1934) did not cite and was apparently unaware of Grinnell's work.

is admitted” reflects Gause’s awareness that Lotka, Volterra, and J. B. S. Haldane (1924) had already demonstrated exclusion with mathematical models of competition, models in which ‘niche’ is absent (see below). The CEP was definitely “in the air” well before *The Struggle*.

But what is most striking about Gause’s claim is how little Elton (1927) actually tied the niche concept to competition, and that he didn’t entertain anything resembling the CEP. In fact, Elton allowed that two species might occupy one niche (see §1). While many ecologists at the time were seeing competition as the prime driver of community structure (Kingsland 1995), Elton never shared this confidence. Elton was also quite skeptical of the ecological salience of mathematical approaches to studying natural systems; he thought they typically oversimplified their subject (Crowcroft 1991). Gause’s effort to situate his project within the influential work of the day—*Animal Ecology* having had an immense impact on the incipient science—therefore seems to run a bit roughshod over the actual content of Elton’s niche concept.

Immediately after mentioning Elton’s niche, Gause (1927, 19–20) illustrated the idea of closely related species with different niches with an example of phylogenetically close sympatric tern species. They appeared to minimize competition by having distinct food sources. But the importance of differential feeding behaviors on communities composed of related species was well known long before Elton (or Grinnell) ecologically coined ‘niche,’ at least since Darwin’s discussion of Galapagos finches. Moreover, modeling work bereft of niche considerations Gause knew well demonstrated the same result. Gause (1934) cited Lotka’s (1932) analysis of competitive equations, which showed competitors could coexist by utilizing different food sources. The analysis never mentioned ‘niche’ and Elton and Grinnell are not referenced. Without something beyond the mere fact that Elton’s niche includes food, it therefore appears the concept contributes little in this part of *The Struggle* to Gause’s case for CEP.

The aim of Gause’s initial discussion was context-setting, however. And at the section’s end Gause (1934, 19) emphasized, “we shall endeavor to express all these relations [food sources on competition] in a quantitative form.” His explanation of how Lotka-Volterra differential equations represent competitive dynamics 25 pages later supplies that quantification, and it contains the next ‘niche’ reference. If the niche concept is to make a significant contribution to the CEP, this is the place.

At first glance, the intended contribution seems clear. ‘Niche’ first occurs in this section in Gause’s (1934, 45–46) discussion of α , a coefficient of interspecific competition in the equations:

if the interests of the different species do not clash and if in the microcosm they occupy places of a different type or different “niches” then the degree of influence of one species on the opportunity for growth of another, or the coefficient α , will be equal to zero. But if the species lay claim to the very same “niche,” and are more or less equivalent as concerns the utilization of the medium, then the coefficient α will approach unity.

Putting the potential significance of scare quotes aside, niches—via ‘places’—then seem to factor explicitly into Gause’s (1934, 47) word-equation-explanation of the equations given one page later:

$$\left\{ \begin{array}{l} \text{Rate of growth} \\ \text{of the first spe-} \\ \text{cies in a mixed} \\ \text{population} \end{array} \right\} = \left\{ \begin{array}{l} \text{Potential in-} \\ \text{crease of the} \\ \text{population of} \\ \text{the first species} \end{array} \right\} \times \left\{ \begin{array}{l} \text{Degree of reali-} \\ \text{zation of the po-} \\ \text{tential increase.} \\ \text{Depends on the} \\ \text{number of still} \\ \text{vacant places.} \end{array} \right\}$$

$$\left\{ \begin{array}{l} \text{Rate of growth} \\ \text{of the second} \\ \text{species in a} \\ \text{mixed popula-} \\ \text{tion} \end{array} \right\} = \left\{ \begin{array}{l} \text{Potential in-} \\ \text{crease of the} \\ \text{population of} \\ \text{the second spe-} \\ \text{cies} \end{array} \right\} \times \left\{ \begin{array}{l} \text{Degree of reali-} \\ \text{zation of the po-} \\ \text{tential increase.} \\ \text{Depends on the} \\ \text{number of still} \\ \text{vacant places.} \end{array} \right\}$$

Immediately after this verbal description, Gause (1934, 47) gave their mathematical representation:

$$(1a) \quad \frac{dN_1}{dt} = b_1 N_1 \frac{K_1 - (N_1 + \alpha N_2)}{K_1}$$

$$(1b) \quad \frac{dN_2}{dt} = b_2 N_2 \frac{K_2 - (N_2 + \beta N_1)}{K_2}$$

where $N_{1,2}$ represent competing species; $b_{1,2}$ represent birth rates; $K_{1,2}$ represent “maximally possible” carrying capacity population sizes; and α, β are competition coefficients representing the effect of N_1 individuals on N_2 individuals, and *vice versa*. These equations for the “struggle for existence,” Gause (1934, 48) clarified, “express quantitatively the process of competition between two species for the possession of a certain common place in the microcosm.” Note ‘place’ here and in the word-equation.

“Degree of realization of the potential increase” in the far right term designates the “drag” factors represented in competition equations. (1) shows there are two: intraspecific density-dependent drag captured by the logistic element (the

second term: $-\frac{b_{1,2} N_{1,2} N_{1,2}}{K_{1,2}}$) and interspecific density-dependent drag captured

by the competition element (the third term: $-\frac{(\alpha, \beta) b_{1,2} N_{2,1} N_{1,2}}{K_{1,2}}$). These factors,

the word-equation tells us, depend upon the “number of still vacant places.” What else could those places be but the same “places” Gause considered when discussing α and “niches” a single page before, or the “place” in Elton’s niche characterization Gause referred to explicitly? The first chapter of *The Struggle* pays Darwin

significant tribute for largely founding its scientific subject matter; perhaps Gause was harkening back to his niche-like use of ‘place’ (see Pearce 2010).⁸

The terminological convergence here, however, is highly misleading. By ‘place’ in “vacant places” and “common place in the microcosm” Gause meant something very specific, and entirely distinct from ‘place’ in Elton’s “place in a community.” The former sense is made clear in Gause’s earlier discussion of the logistic equation’s representation of intraspecific density-dependence. For species N in a specific environment at a particular time, “The difference between the maximally possible and the already accumulated population ($K - N$), taken in a relative form, i.e., divided by the maximal population $\left(\frac{K-N}{K}\right)$, shows the relative number of ‘still

vacant places’” (Gause 1934, 34–35). That is, ‘vacant places’ simply numerically measure how much more populations can grow given intraspecific density-dependence and—when competing with another species—interspecific density-dependence. ‘Common places’ are then actually arithmetic units of population size, realized or potential (vacant), that species “compete” for according to Gause.⁹ Function-laden Eltonian notions of habit, feeding behavior, and mode of life are orthogonal to this numeric ‘place’ notion. The former therefore doesn’t help make the case for CEP via the latter.

But this portion of *The Struggle*—the mathematically rich explanation of competition—is arguably its most compelling core: “Gause’s great achievement was to give a clear exposition of the way that competitive exclusion, so often previously noted, actually worked” (Hutchinson 1978, 152). The ostensibly mechanistic detail of the account of competitive dynamics made it so convincing. If niche-considerations contribute little if anything to that account, what real work is the concept doing in Gause’s case for CEP?

The remaining five ‘niche’ references in *The Struggle* bolster this judgment. They occur (with occasional scare quotes again) 50 pages later in Gause’s discussion of several *Paramecium* experiments that resulted in competitive exclusion. All those references appear in one passage questioning the result’s relevance to real-world biological systems:

However, there is in nature a great diversity of “niches” with different conditions, and in one niche the first competitor possessing advantages over the second will displace him, but in another niche with different conditions the advantages will belong to the second species which will completely displace the first. Therefore side by side in one community, but occupying somewhat different niches, two or more nearly related

8. In fact, adding to the terminological congruence, Gause (1934) seemingly used it in precisely this sense on page 1: “Darwin considered the struggle for existence in a wide sense, including the competition of organisms for a possession of common places in nature, as well as their destruction of one another.”

9. This language is very strained. Cheetahs and lions compete for food, territory, and other resources. Saying they compete to “occupy” possible numerical population sizes is idiosyncratic at best.

species . . . will continue to live in a certain state of equilibrium. (Gause 1934, 98)

But nowhere did Gause explain how different niches must be to ensure coexistence, how niches could be individuated, or, most importantly, how niche considerations could help determine the competition coefficients required by the Lotka-Volterra competition equations. That different species typically utilize different food sources was well known well before Darwin, and existing models of competition had already captured the resulting interspecific dynamics with mathematical precision (e.g., Lotka 1932). Rather than constitute the indispensable conceptual core of Gause's work supporting CEP, his allusions to the niche seem more gloss than grist.

3. HUTCHINSON'S *N*-DIMENSIONAL HYPERVOLUME

For many ecologists, Hutchinson's definition in "Concluding Remarks" (1957) was a watershed moment:

it was not until Hutchinson's "Concluding Remarks" that the niche concept was rigorously defined and its relationship to competition and species diversity rigorously explored . . . Hutchinson succeeded in combining both the Eltonian and Grinnellian concepts of niche into one model. (Real and Levin 1991, 180–81)

This "revolutionary" account (Chase and Liebold 2003; Schoener 1989) set the trajectory of niche-based theorizing in ecology for several decades.

Hutchinson's definition, which first appeared in a footnote of an earlier limnological paper (Hutchinson 1944),¹⁰ characterizes two concepts, a species' *fundamental* and *realized niche*. For a specific species S_1 , consider all the environmental variables x_1, x_2, \dots, x_n that affect S_1 , which Hutchinson (1957, 416) emphasized includes both biological and (nonbiological) physical factors. If these variables are conceptualized as axes, they define an abstract n -dimensional space. The subset of this space in which S_1 can persist indefinitely (i.e., have positive fitness) is the fundamental niche of S_1 , with an important qualification: persistence is assessed in the absence of all *competing* species. Not all other species are excluded in this assessment, as is sometimes incorrectly claimed, because some of the environmental variables that define the space are in fact species (e.g., S_1 's food resources, or obligate symbionts). Of course, species often do face competitors that constrict their range. The subset of the fundamental niche actually realized by S_1 given competitive dynamics is its realized niche.

10. "The term niche (in Gause's sense, rather than Elton's) is here defined as the sum of all the environmental factors acting on the organism; the niche thus defined is a region of an n -dimensional hyper-space" (Hutchinson 1944, 20, n. 5).

In significant ways, Hutchinson's account breaks sharply with earlier work. Unlike Grinnell's niche but similar to Elton's, the fundamental and realized niches are abstractions, not portions of real-world environments. Any Hutchinsonian niche might correspond to highly disjoint sets of areas in the real world. The sole figure in "Concluding Remarks" illustrates this relationship, 'biotope space' being the actual environment of the two species (see Fig. 1).

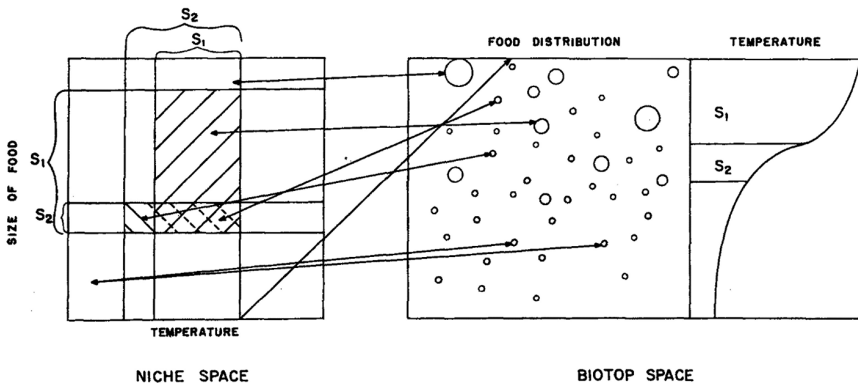


Figure 3. Two fundamental niches defined by a pair of variables in a two-dimensional niche space. Only one species is supposed to be able to persist in the intersection subset region.

The lines joining equivalent points in the niche space and biotope space indicate the relationship of the two spaces. The distribution of the two species involved is shown on the right hand panel with a temperature depth curve of the kind usual in a lake in summer.

Abstraction can make empirical concepts less tractable, and Elton's concept is often contrasted unfavorably with Grinnell's in this regard (Griesemer 1992). But Hutchinson's abstract definition is coupled with a significant conceptual shift that greatly enhances tractability: niches are strictly defined *in relation to species*, persistence of the latter determining the boundaries of the former (for fundamental niches). By definitionally tethering niches to species, Hutchinson's account is much clearer about how niches are individuated: positive fitness delimits the niche-relevant portion of a species' causal nexus. Concerns about how niches are delineable that plagued Grinnell and Elton's conceptions don't gain nearly the same purchase. It may be exceedingly empirically difficult to ascertain, but in principle at least it is clear how species' niches can be delimited.¹¹

11. Note that what allows determination of niche boundaries is the focus on a particular species property affected by its environment, positive fitness. That focus precisifies but it also narrows scope. If members of a species stray from their domain of nonnegative fitness and have significant impacts on other species or the abiotic environment, the source of those causal impacts would seem to fall outside the purview of Hutchinsonian niche considerations.

Gains in precision and tractability, however, came with significant costs. Hutchinson himself highlighted some shortcomings. The definition assumes all points comprising the hypervolume entail equal probability of persistence (1957, 417). In reality, (absolute) fitness will vary markedly in any plausibly realistic assessment. Capturing these important differences requires explicit representation of the relevant ecological dynamics; i.e., the more fine-grained causal details that determine whether and how species persist. The definition also assumes all the environmental variables characterizing the space can be linearly ordered, which Hutchinson admitted, “In the present state of knowledge this is obviously not possible” (1957, 417). It is not entirely clear what precisely the difficulty is, and Hutchinson did not elaborate. Schoener (1989, 90) mentioned prey species and vegetation type as examples of not linearly orderable environmental variables, without further explanation. It seems, however, that prey species can be ordered by their abundance, or frequency of encounter. If particular vegetation types are required for species persistence, and their existence is binary and not a matter of degree, then these environmental variables would not be linearly orderable. But such bivalence seems quite unrealistic. As habitats, patches of vegetation of different types presumably come in different degrees of suitability for different species. Suitably then seems to impose an ordering, from the optimally fitness enhancing to the barely positive-fitness maintaining. But again, this task faces the necessity of representing fine-grained causal details discussed immediately above.

Hutchinson also stipulated, but apparently did not perceive as problematic, that the environmental variables were independent and thus determined spaces with orthogonal axes. But this assumption is false in most cases. In the limnological systems for which Hutchinson first formulated the definition, for example, temperature, nutrient availability, light penetration, and other variables impacting species are all dependent on depth. Temperature and precipitation are interrelated for most if not all ecological systems. Nonindependence does not prevent construction of an abstract niche space, but it necessitates nonorthogonal, skewed axes and coordinate systems to do so. Besides making visualization much more difficult, it also renders some techniques used to analyze the detailed dynamics upon which niche spaces depend inapplicable (e.g., the Fourier method for partial differential equations representing those dynamics).

These are nontrivial problems, but they pale in comparison with the limitation imposed by the significant conceptual shift away from Grinnell and Elton’s account: defining niches *in terms of species persistence*. That relativization, for instance, makes the notion of a vacant niche conceptually incoherent.¹² A niche absent an occupying species is impossible because the former is definitionally dependent on the latter. And without the notion of a vacant niche—and in general a substantive, species-independent niche concept—Hutchinson’s account is explanatorily

12. Hutchinson sometimes failed to recognize this implication of his definition (e.g. 1957, 424; 1959, 150; 1978, 161).

impoverished. It does not have the resources to explain phenomena such as ecological equivalents, adaptive radiation into novel environments, similarities of different communities' structure, and others that were squarely in Grinnell and Elton's purview. The idea that "the Grinnellian niche and the Eltonian niche are united through correspondence between points in N [the abstract niche space] and points in B [the biotop space]" (Real and Levin 1991, 181) in Hutchinson's definition just fails to recognize how dramatically his concept diverges from theirs, and how that divergence impacts its explanatory capabilities.

For the same reason, the Hutchinsonian niche cannot ground or otherwise be the basis of the competitive exclusion principle. As indicated above, competitive dynamics are excluded from the fundamental niche's characterization. The realized niche, on the other hand, *assumes* the principle: "we should expect that, in the part of the hyperspace where the overlap occurred, competitive exclusion would take place and the overlap would either be incorporated into the niche of one or the other species or be divided between the two, producing the *realized* or *post-interactive* niches of the two species" (Hutchinson 1978, 159).¹³ Hutchinson, along with many ecologists at the time, thought competition was the primary driver of community structure; he called the CEP "a principle of fundamental importance" (1957, 417). Hutchinson's niche concepts reflect this commitment, they don't independently support it.¹⁴

Niches as defined by Hutchinson therefore convey very little information about community dynamics. Hutchinsonian niche considerations cannot, for example, determine which of two competitors will outcompete the other, and to what degree. In fact, answering most questions that ecologists find important—that competitive exclusion will occur at all when fundamental niches overlap (without simply assuming it will), how it occurs, the dimension size n of the hyperspace, the identity

13. There are technical complications in assessing the relevant "overlap" that expose further challenges of Hutchinson's hypervolume approach. First, if such overlap could be assessed in niche space, it would require determining the intersection of two subspaces in a more expansive space defined by the total set of environmental variables for both species. The fundamental niches of different species will almost always be defined with nonidentical sets of environmental variables, hence the need for the more expansive superspace. Although different species are sometimes similar in specific ways, which can generate competition, they almost always have significantly different ecological requirements and tolerances in other ways. But, second, and more importantly, it is unclear overlap can even be assessed in that abstract space. When competition occurs, it occurs in the real-world space species physically occupy (the "biotop" space). Trees compete for light and soil nutrients in geographically coincident portions of the rainforest; pelagic birds compete for nesting sites in specific cliffs of remote ocean islands. Competitive exclusion in the biotop space would then translate into exclusion in portions of the abstract (nonspatially explicit) niche space (see Fig. 1) that do not intersect in any set-theoretic or geometric sense. Simply talking of overlap in an abstract hyperspace is therefore not an adequate representation of (spatially explicit) competitive dynamics.

14. That commitment, furthermore, reflects but one view of what primarily governs the structure of biological communities. Fundamental and realized niches could be defined, for instance, with predation, mutualism, or other ecological interactions at the forefront. If competition is not the main driver of patterns and processes in the ecological world, Hutchinson's approach will miss much of what does.

of those dimensions, etc.—requires an explicit representation of species dynamics. As a tool for representing and thereby understanding the dynamics responsible for community structure and species properties, the Hutchinsonian niche is hardly the epoch-making innovation it is often heralded as.

4. CONCLUSION

These shortcomings of past accounts are not a historical curiosity. In a recent effort to reinvigorate niche-based ecological theorizing after Hubbell's (2001) influential neutral theory, Chase and Leibold review past characterizations of the concept and propose a definition aiming at synthesis:

NICHE DEFINITION #1: the joint description of the environmental conditions that allow a species to satisfy its minimum requirements so that the birth rate of a local population is equal to or greater than its death rate along with the set of per capita effects of that species on these environmental conditions. (2003, 15)

The next sentence clarifies the definition is “a simple joining of the two concepts that we have outlined in our historical review,” by which they mean a Grinnellian-Hutchinsonian concept and Eltonian one.¹⁵ In effect, then, this is a bipartite notion:

NICHE =_{df} (i) all factors causally relevant to a species' persistence;
(ii) all the species' causal impacts on those factors.

But this characterization's sweeping generality raises serious concerns about its scientific utility. Rather than yielding something fruitful—that would, say, provide guidance in representing and analyzing community dynamics—this niche definition simply seems to acknowledge such dynamics exist. It's as if, in a chemistry context, one were told that the matter concept—with zero information about what specific forms it can take, its compositional building blocks, or its connections with other properties or lawful regularities—is nevertheless the key to chemical analysis. What this niche definition offers seems largely to be a superfluous gloss on the causal details actually required to assess species persistence.

Chase and Leibold don't explicitly recognize this deficiency, of course, but they may suspect something is amiss about the first definition because a page later they offer a second they claim is more precise:

NICHE DEFINITION #2: the joint description of the zero net growth isocline (ZNGI) of an organism along with the impact vectors on that

15. That's inaccurate. Any partitioning of environments independent of species persistence considerations, Grinnell's conception, is absent. Species' functional properties that cannot be characterized relative to environments in any straightforward way, Elton's conception, are also absent. Rather, this seems largely to be a recasting of Hutchinson's notion.

ZNGI in the multivariate space defined by the set of environmental factors that are present. (2003, 16)

‘Zero net growth isocline’ is short for the population values where $\frac{dN}{dt} = 0$.

Revealingly, just before DEFINITION 2 Chase and Leibold (2003) say, “we will use simple population dynamics models to justify a second more precise version of this definition [#1].” In other words, niches are only determinable, and this definition is only justifiable, once species interactions have already been represented in those models. That is, this niche concept itself contributes little or nothing to determining that representation.

In the rest of their book this prioritization is never upended. It contains interesting extensions of resource utilization models first developed by Tilman (1982) and sophisticated analyses of how empirical data might bear on them. But one despairs of finding any nonredundant contribution the niche concept, as they define it, makes to these analyses. The absence isn’t surprising. Tilman’s (1982) highly influential book mentions ‘niche’ exactly four times, and in each case it refers to a label used by others.

The shortcomings described above don’t impugn the sophisticated modeling and empirical studies done under a ‘niche’ rubric. But they do indicate there isn’t some insightful and foundational concept at the base of this work, in some way guiding and shaping it all. That work stands alone.

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