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The 'niche' in niche-based theorizing: much ado about nothing

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Abstract

The niche is allegedly the conceptual bedrock underpinning the most prominent, and some would say most important, theorizing in ecology. We argue this point of view is more aspirational than veridical. Rather than critically dissect existing definitions of the concept, the supposedly significant work it is thought to have done in ecology is our evaluative target. There is no denying the impressive mathematical sophistication and theoretical ingenuity of the ecological modeling that invokes 'niche' terminology. But despite the pervasive labeling, we demonstrate that niche talk is nothing more than a gloss on theory developed without it, that doesn't need it, and that doesn't benefit from it.

Keywords Niche · Limiting similarity · Niche construction · Neutral theory · Conceptual engineering · Hutchinson

Introduction

Like currencies, function and demand determine the utility of scientific concepts. Instead of exchange rates, treasury notes, and foreign reserves, cognitive factors such as explanatory power, theoretical unification, and—above all—empirically adequate predictions determine the value of concepts in science. Evaluating scientific concepts, and how (and whether) they facilitate theoretical and other kinds of progress, can only be appraised against these criteria. And just as monetary value fluctuates subject to various economic forces, the cognitive value of theoretical concepts

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evolve as sciences emerge, develop, and mature, and their theories precisify, mathematicize, and their conceptual underpinnings are clarified. The emergence of ecology as a discipline distinct from evolutionary biology at the turn of the twentieth century naturally created new conceptual and methodological demands. And within biology, any new subdiscipline post *The Origin* had much to prove. Darwin's crowning achievement set the benchmark by which any future biological science would be judged. Early ecologists aspired to develop concepts that would generate deep theoretical insights and provide practical tools, and that could be operationalized in a formal theory, arguably akin to the concept of fitness. One concept in particular is widely thought to have delivered this result: the niche.[1]

Beginning with Grinnell (1917), the niche has been defined in a variety of ways against a variety of objectives. Grinnell's habitat-focused conception characterized niches as physical units of the (primarily abiotic) environment, units that exist independently of the animal species occupying them. Elton (1927), in contrast, proposed a functional concept that emphasized biotic interactions, especially trophic relations that determine animals' "place in the community" (63–64). Despite their differences, on both approaches niches are components of broader patterns, either abstracted from the functional interactions that drive community dynamics, or causal structures in the physical environment. But "pattern" is quite imprecise, and intractable vagueness is the general and incessant problem. As numerous criticisms have made clear, the divergent content Grinnell and Elton attached to 'niche' is simply too amorphous to supply definite niche individuation criteria (see Hurlbert 1981; Patten and Auble 1981; Peters 1991; Justus 2019 and references therein). Without these criteria, for instance, no cogent basis for the idea of "vacant" niches, which Grinnell and Elton both countenanced, is possible.

The widely extolled breakthrough supposedly came with G. E. Hutchinson's unscintillatingly titled "Concluding Remarks." Hutchinson (1957) proposed a "revolutionary" niche concept that attempted to integrate the abiotic conditions from Grinnell with the biotic relations from Elton (see Schoener 1989; Chase and Leibold 2003). Hutchinson defined the niche as a "hypervolume" in an n-dimensional abstract space, with dimensions representing ranges of environmental factors affecting species persistence. He further distinguished *fundamental* from *realized* niches. The fundamental niche is that portion of the hypervolume for which species can persist indefinitely, but on the crucial assumption that competitive interactions are left unrepresented. The realized niche is that portion of the fundamental niche actually occupied by species when competitive dynamics *are* represented. The sharp conceptual contrast between Grinnell, Elton, and Hutchinson's niches is the latter's explicit definitional dependence on specific species. Since species persistence determines fundamental niche boundaries—each species S_i generating a unique fundamental

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[1] Chase and Leibold (2003, 2), for instance, claim the niche "can help to solidify the conceptual synthesis that ecology so desperately needs." And other champions of the concept claim its role in *niche construction* is on a par with natural selection (Scott-Phillips et al. 2014, 1232). Laland et al. (2009, 195) similarly assert that neglecting the niche would pose a "major conceptual barrier" to evolutionary and ecological theory, and Vandermeer (2004, 474) states that "niche-based" theorizing may constitute "a major breakthrough."

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niche FN_i—individuating them is straightforward on Hutchinson's concept. Of course, actually demarcating the bounds of persistence is empirically difficult, but in principle it is conceptually clear how they could be.[2] For many ecologists, Hutchinson successfully consummated the definitional deed:

> 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. (Real and Levin 1991, 181)
> [t]he niche has provided and can continue to provide the central conceptual foundation for ecological studies (Chase and Leibold 2003, 17).

But these celebratory judgments were premature.

Justus (2019) documents the definition's significant conceptual costs. Although Hutchinson sidestepped the niche demarcation problem, conceptually indexing niches to specific species precludes the concept of vacant niches. Because Hutchinsonian niches definitionally depend on (the persistence of) particular species, niches *cannot* exist if species are absent. A species-dependent niche concept simply "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" (Justus 2019, 120). In short, Hutchinson's account does not live up to its scientific cachet. This criticism complements and amplifies the persistent worries of a skeptical minority in ecology (besides the citations above, see Gotelli and Graves 1996, Ch. 4; McInerny and Etienne 2012; Scott-Phillips et al. 2014; Pocheville 2015, §1.4 and references therein).

Concepts perform various epistemic functions in science. They are indispensable to reliable inference and progress in constructing successful scientific theories. Given how thoroughly conceptual content permeates scientific practice—and the fact that traditional conceptual analysis has utterly failed to deliver necessary and sufficient conditions aggregatable into successful explicit definitions for the vast majority of concepts (Murphy 2004; Machery 2009)—perhaps it's unsurprising that proposed characterizations of the niche weren't up to definitional snuff. The content of concepts and the work they in turn facilitate, especially for scientifically "foundational" ones, may outrun any attempt to pin it down in explicit definitions. Rather than add to the critical literature documenting the deficiencies of the latter, the seminal work the niche concept has supposedly done in theoretical ecology is our evaluative target.

In evaluating what concepts contribute to science, a distinction is often drawn between first-order criteria—theory construction, experimental design, techniques of statistical analysis, measurement and standardization procedures, etc.—and higher-order considerations, such as cultural, communicative, heuristic, technological and

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[2] Although Schoener (1989) lauded Hutchinson's niche definition as "revolutionary," he also detailed many of its serious empirical shortcomings. Contra his positive evaluation, but prefiguring the critical line in the next section, he also observed that the "concept of the niche nearly always used in the body of concepts known as 'niche theory' … is not Hutchinson's" (Schoener 1989, 91).

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other influences on scientific practice.[3] In this analysis, our entire critical focus is the former, which is what distinguishes science from other kinds of intellectual inquiry. It's possible that the niche concept shines in higher-order domains, but given the deficiencies this analysis exposes, we're thoroughly skeptical of the prospect. But that possibility falls outside our purview.

Given the impact Hutchinson's (1957) hypervolume definition had, our story begins in "“Niche theory”: the broken-stick, theory of limiting similarity, and their successors" section with the "niche theory" it is thought to have inspired in the 1960s and 70s. During these theoretically fertile decades, influential developments such as the broken stick model, theory of limiting similarity, and optimal foraging theory emerged and enthusiastically referred to Hutchinson's account. But it's a history of scientific reality frustrating inflated expectations about the contribution of the niche. "Neutral theory and the “niche” don't actually compete" section considers whether the rise of a supposedly formidable competitor to niche theory, neutral theory, actually poses a serious conceptual challenge, and whether responding to that challenge offers any real prospects for strengthening the case for the niche. "The niche evolving: niche construction theory" section examines the proposed integration of evolutionary and ecological theorizing with what's called niche construction theory (NCT) and argues the evolutionary perspective does not improve the niche's scientific standing. The last section concludes by comparing the niche to another abstract and quite general scientific concept, fitness, and explores the broader philosophical issue of concept determination and revision in epistemic inquiry.

"Niche theory": the broken-stick, theory of limiting similarity, and their successors

In the eyes of many commentators (McIntosh 1985; Worster 1994; Kingsland 1995) the 1960s and 70s witnessed an explosion of mathematically sophisticated theorizing in ecology rivaled only by the "Golden Age" of the 20s and 30s (Scudo and Ziegler 1978). These commentators also largely agree the prime progenitor of this theoretical surge was G. E. Hutchinson and his cadre of influential students and collaborators, Robert MacArthur being first among equals.[4] With the notable exception of the theory of island biogeography, and with Hutchinson's hypervolume niche definition in the background, "niche theory" later became the rubric under which much of this work was loosely amalgamated. The desire to pay homage to Hutchinson in this literature is clear (see Pedruski et al. 2016). The question is whether the homage reflects something deeper than the veneration and gratitude that inspiring

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[3] On the latter in philosophy of science, see Wilson (2006), Thagard (2012), and Sohlberg and Leiulfsrud (2016). Within the literature on concepts and conceptual engineering, see Burgess et al. (2020).

[4] According to Worster (1994, 374), MacArthur was "an ecologist who had the kind of 'superbrain' charisma commonly enjoyed by celebrities in physics."

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and admirable mentors rightly merit. Specifically, does his definition and the niche concept in general contribute significantly to the theory?[5]

However numerous and serious its flaws, much of niche theory was built upon or at least catalyzed by MacArthur's (1957, 1960) original "broken-stick" model. Hutchinson (1957, 231–232) prominently discussed it, after all, in the course of proposing his influential hypervolume definition. In an effort to understand the forces that might explain patterns of relative abundance and generate community structure, MacArthur represented "the environment" (1957, 293) as a stick. Different hypotheses about community structure were then visualized as different processes, such as randomly breaking the stick into non-overlapping independent segments, or randomly selecting two points on the stick and measuring their distances. The first is intended to correspond to dynamics in which, say, competition leads species to partition "the environment"; in the second species are independent and their portions of "the environment" overlap. Assuming stick segment sizes are positively correlated with (and determine) species abundances, each hypothesis leads to different relative abundance predictions. MacArthur briefly discussed their fit with existing data.

As critics later revealed and MacArthur himself came to appreciate,[6] the broken-stick model was fatally flawed. Retracing the nuances of those criticisms is orthogonal to our analysis. Rather, our question is what, if anything, the niche concept adds to MacArthur's model. The textual evidence suggests little or nothing. MacArthur did label the three hypotheses he considered "Nonoverlapping Niches," "Overlapping Niches," and "Niches Particulate, Not Continuous," which together with another mention of the first hypothesis in the conclusion (1957, 295) account for four of the five paper's uses of 'niche'.[7] But simply relabeling the ecological platitude that there are parts of "the environment" in which species are abundant with another word obviously doesn't break new conceptual ground, nor does it seem that any other content from the concept contributes to MacArthur's analysis. Nowhere was any independent meaning for 'niche' presented; Elton and Grinnell's earlier work, and Hutchinson's hypervolume definition were not discussed or even referenced.

The absence of any mention of Hutchinson's definition is understandable. The conference in which Hutchinson presented it occurred almost 5 months after he communicated MacArthur's (1957) paper to the *Proceedings of the National Academy of*

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[5] The history of the niche in ecology is vast, intricate, and very difficult to address comprehensively. Our objective is supplying compelling evidence for a strong inductive argument against the scientific utility of the niche concept. Careful examination of the text and key equations from the first and most influential publications propelling the development of niche-theorizing therefore yields a weighty evidentiary basis for our induction. Other works adopt a wider scope of analysis, and although we don't have the space to present it here, what those works uncover complements and enhances, rather than diminishes, the strong evidence driving our critical induction (see Schoener 1989, 2009; Pocheville 2015).

[6] See especially Kingsland's (1995, 203–204) discussion of the work of Nelson Hairston among other critics.

[7] The fifth occurs in the last sentence: "The failure of Hypotheses II and III suggests that, at least as a rough approximation, niches do not overlap much and are more continuous than discrete." As with its role labeling hypotheses, 'niche' was given no independent sense.

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Sciences, and MacArthur apparently didn't attend anyway.[8] But it remains a bit curious. MacArthur had been Hutchinson's student since 1953, they worked closely and collaborated together, and Hutchinson had conceived of and published the rudiments of the definition more than a decade before (see Hutchinson 1944).[9] MacArthur, in fact, coined the term 'fundamental niche' for Hutchinson (see 1957, ff. 2). And if Hutchinson (1957, 421) was correct that, "MacArthur (1957) has advanced the [study of relative abundances] by deducing the consequences of certain alternative hypotheses *which can be developed in terms of a formal theory of niches*" (emphasis added), it's somewhat puzzling why no allusion to those developments and Hutchinson's "formal" theory occurred, not even a footnote or citation. Moreover, what Hutchinson offered immediately after this teaser (421–422) merely redescribes MacArthur's original analysis with niche-theoretic terminology. "Biotops" from Hutchinson's definition, for example, just replace "the environment" and segments thereof. Of course, better understanding the environment by attempting to characterize and compartmentalize it exactly has a long history in ecology, and within which MacArthur's mathematically sophisticated analysis was an exciting development (Worster 1994). But doing nothing beyond relabeling terms of that analysis (of the environment) and then assuming that it yields insights into the niche *without ever substantiating any real link from the latter to the former* doesn't validate the niche. The suspicion that niche talk is a gloss on theory developed without it, that doesn't need it, and that doesn't benefit from it is there right at the beginning of the supposed niche-centered theoretical turn in ecology.

Three years later, MacArthur (1960) presented the broken-stick model a second time, but with more explicit details about its ecological interpretation and the equilibrium and competitive exclusion dynamics he believed favored the "nonoverlapping niches" hypothesis. As it did 3 years earlier, the niche concept received scant attention. 'Niche' is first mentioned on page four of the eight-page paper, and again almost all instances of the term refer to hypothesis labels (seven of the nine). The remaining two quote occurrences are in the passage: "Hutchinson (1957) defined 'niche' in very elegant terms and was able to show that his 'niche' and the non-overlapping segments of [hypothesis 1] are closely related. It is thus appropriate to refer to [hypothesis 1] as 'niches non-overlapping' and [hypothesis 2] as 'niches overlapping.'" But elegance aside, the only discernible demonstration of close relations was the simple replacement of terms and phrasing discussed above. The contribution the niche supposedly makes to understanding community structure and explaining relative abundance patterns would have to await further work.

Collaborations between MacArthur and Levins (1964, 1967) propelled the next theoretical advance with shrewd analyses attempting to ascertain how species coexist in biological communities, and particularly what factors limit the total number of species that may. They labeled this approach the "theory of limiting similarity." Their first step was to analyze several standard Lotka-Volterra equations of

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[8] See https://library.cshl.edu/symposia/1957/participants.html, accessed January 3, 2021.

[9] And in 1960 MacArthur thanked Hutchinson for providing "a continuous stream of good ideas on the subject for 7 years since he first drew the author's attention to it" (1960, 33).

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competitive dynamics involving two, three, and n species to determine the conditions under which species can coexist. These conditions are expressed in terms of the carrying capacity K_i and the interspecific competition coefficients α_{ij}, and were well-known at the time. More importantly, they provided the grist for their second ingenious step: attempting to account for α_{ij} and thus the conditions permitting species coexistence in more fundamental terms. And it's here the niche concept might appear to come into its own: "how the α's [sic] are specified," MacArthur and Levins claimed, "will reflect the structure of the niche" (1967, 378). But as we argue below, that reflection was rash.

As they (1967, 379) observed, "[α_{ij}] measures the relative depression of [species i's growth], caused by an individual of species [j] compared to another of species [i]." Standard competition models typically leave α's interpretation at that. MacArthur and Levins' masterful innovation was pushing one analytic step deeper and developing an explicit account of α in terms of species' underlying resource utilization and habitat selection dynamics. Let the probability a resource item R is consumed in a unit of time by a species i individual be $U_i(R)$ (see Fig. 1 from MacArthur and Levins 1967, 379).[10]

The probability two species try for the same R unit is then, they suggested, $U_1(R)U_2(R)$. With these clarifications, a "houristic [sic] justification" for an explicit characterization of α_{12} was proposed (1967, 380):

> Basically, to compete for space individuals of species 1 and 2 must confront one another and hence be present simultaneously. Similarly, when resources are rapidly renewed, individuals only compete if they are present within a short time of each other. In either case $\frac{\int U_1(R)U_2(R)dR}{\int \left[U_1(R)\right]^2 dR}$ measures the relative probability of the simultaneous presence of species 1 and species 2 compared to species 1 and species 1. Hence it measures α_{12}.

MacArthur and Levins (ibid.) noted that if resources are discrete, summations replace integrations, and if resources aren't rapidly renewed, the formula for α is more complicated. Despite the potential complexities, MacArthur and Levins deftly showed how insights about α can be derived by analyzing different resource utilization scenarios represented by different $U(R)$ curves.

This analysis raises subtle methodological and theoretical issues, and praise was not universal among commentators (see Schoener 1989, section "Criticism of Modern Niche Theory" for a review). But wading into those complexities isn't required to broach our fundamental question: what work does the niche concept do in this analysis? Besides perhaps introducing new terminology, the answer *nothing* is difficult to resist. Undoubtedly, patterns of resources in environments and their utilization do feature prominently in the niches of Grinnell, Elton, and Hutchinson. But that doesn't demonstrate niche thinking contributed to MacArthur and Levins' analysis any more than ideas about unicorns illuminate properties of horned animals. A

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[10] The scale of the independent variable R can represent any properties of resources that affect their utilization, such as location or size.

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confusion about conceptual priority besets that claim. On Hutchinson's account, the niche's definition concerns environmental impacts on species persistence, the latter being some complicated function of the (presumably usually positive) absolute fitnesses of the genotypes comprising a species. So understood, species persistence is therefore obviously dependent on what resources are available, how they're distributed and used, how they affect fitnesses, and other causal facts. The definition leaves the multifarious details of these dependencies problematically underdetermined and unstated, and the reason is transparent. Given the definition, resource dynamics have clear epistemic and ontological primacy over niche attributions (and arguably conceptual as well): the latter *at best* supervenes on the former and other basic facts about species' relationships with environments. But MacArthur and Levins' breakthrough stemmed directly from insights about the former, not the latter. They grasped that the physical co-occurrence of organisms that competition for resources requires can be captured probabilistically, and in so doing provides an explicit characterization of α. Niche thinking nowhere appears in the reasoning. The already tenuous thread linking their incisive observation about α and the niche now appears dubious indeed. Unlike other cases of supervenience where the legitimacy of what supervenes is arguably retained, the kind of vacuity James (1879) charged against epiphenomenalism bites against the niche.

This critical point is illustrated particularly clearly in MacArthur and Levins' examination of Gaussian function $U(R)$. If $U_i(R)$ are Gaussian functions, e.g. $U_i(R) = e^{-\frac{R^2}{H^2}}$, separated by some specific distance as in Fig. 1, explicit characterizations of α can be derived.[11] For one kind of separation and when D designates the distances between $U_i(R)$ means, for instance:

$$\alpha = e^{-\frac{D^2}{2H^2}}. \tag{1}$$

Especially given the significance of normal distributions in the natural world and arguably in this context, that a mathematically precise quantity for α is derivable from more causally basic resource dynamics is quite an achievement. Much more importantly for our purposes—and foreshadowed by "form of the niche" in their Fig. 1 caption—MacArthur and Levins embedded niche-centric assertions in their reasoning. Seemingly auspiciously, they equate H in the α formula above with "niche breadth" (1967, 380). If sound, such an equation would put flesh on the enticing prospect of connecting standard competition models and niche thinking.

The antecedent ("If sound") is, unfortunately, false. Nowhere before H was equated with niche breadth, and nowhere after in the paper, was the notion independently characterized, with one exception. Not in the main text, but in the caption of their Fig. 2, MacArthur and Levins (1967, 382) disclosed, without any clarifying explanation, that "H is the standard deviation." Now, the probative power of statistics is not to be questioned, but why exactly standard deviation has special niche relevance is entirely unclear. Equation (1) shows how α can be small enough to reduce competition and thereby permit species coexistence. And resource utilization

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[11] This is a specific Gaussian function centered at $R = 0$ and peaking at $U = 1$.

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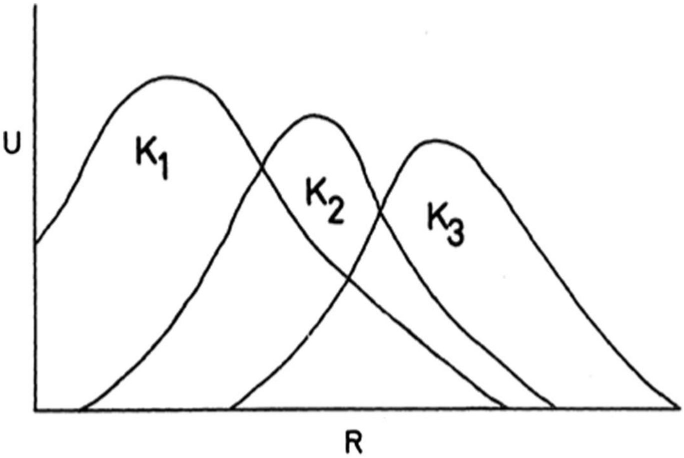

Fig. 1 The form of the niche. For each resource r, U is the probability of its utilization in a unit time by an individual. The area under each curve, therefore, is the total resource utilization K_i for species i

patterns represented as $U_i(R)$ distributions can obviously decrease the exponent $-\frac{D^2}{2H^2}$ in numerous ways. What's missing is *any* rationale for elevating H within that multiplicity as the unique determinate of niche breadth: there is nothing distinctively compelling about H in this regard. Why, specifically, is standard deviation niche-privileged? Statistically, standard deviation possesses many attractive properties—it exhibits a certain formal simplicity, is easy to calculate, and is expressible in the same units as the data—to highlight a few. But as desirable attributes *of a mathematical measure of distributional dispersion*, it remains mysterious (and unexplained) why those features are cognitively compelling, or even relevant, for evaluating putative niche properties.[12] Of course, none of this arbitrariness is surprising given that these ostensible niche attributions are entirely derivative on the causal relationships being represented with the $U_i(R)$.[13] Given the conceptual and epistemic priority of the latter over the former, there is simply no fact of the matter about whether any (all? some?) of this medley of unconstrained statistical choices corresponds to the "niche."

The history recounted thus far suggests a troubling induction for the niche concept. Despite pretenses otherwise, it has not—and seemingly cannot if future

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[12] There are, moreover, many other measures of variation displaying similarly appealing statistical properties, such as the interquartile range and mean absolute deviation measures. But if resource use is more accurately represented with curves other than Gaussian functions, even these closely related measures can diverge. We thank an anonymous reviewer for highlighting this important fact.

[13] Even some niche loyalists seem to concede this priority. Schoener (2009, 5), for example, says, "Indeed, the resource-utilization niche *is nothing more* than a precisely formulated description of the natural history of a species: its habitat, food types, and activity times, among other things … Thus, we have a niche concept that precisely encapsulates *what ecologists measure anyway*" (italics added). The superfluous supervience couldn't be clearer.

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characterizations of the concept share the sins of their ancestors—do the significant theoretical work it's claimed to in the ecological modeling invoking 'niche' terminology. Its supposedly central role in extensions and successors to the broken stick model and "theory of limiting similarity" (e.g. MacArthur 1968; Levins 1968; Colwell and Futuyma 1971; Sugihara 1980), optimal foraging theory (MacArthur and Pianka 1966), and others are also casualties to our criticism. This general theoretical orientation in many ways culminated with David Tilman's resource-based approach to understanding community structure and dynamics developed in the 1980s. But what Tilman (impressively) accomplished is orthogonal to and doesn't in any way resurrect the concept (see Justus 2019, §4 for the criticism).[14]

Although models that focus on resources don't thereby redeem the niche, so-called niche-based ecological theorizing has risen to prominence in response to a perceived theoretical competitor, "neutral" theory. Faced with a formidable scientific foe, perhaps niche advocates have honed their arguments. The next section considers whether there is a genuine conflict, and debunks the idea that the case for the niche has improved for having been tested against a challenger.

Neutral theory and the "niche" don't actually compete

Given the prolific—and pioneering—theoretical output it was (mistakenly) thought to have catalyzed, the niche's fanbase steadily grew. Each new modeling innovation promised profound insights about the processes driving the dynamics of ecological systems. But the positive fanfare was abruptly challenged by the debut of a radically new theory with a very different conceptual core: neutrality.

The watershed moment came in 2001. Hubbell's *Unified Neutral Theory of Biodiversity and Biogeography* was widely considered an iconoclastic attempt to overturn the overriding niche-based paradigm. Contrary to so-called niche-assembly theories, his neutral theory—what Hubbell dubbed the 'dispersal-assembly perspective'—assumes random stochastic processes like ecological drift and migration determine species abundances. Importantly, the theory does not ignore ecological interaction rules governing communities and their dynamics, rather it postulates identical rules for all organisms comprising them. This homogeneity assumption seems incompatible with the differences between species that make competition possible. It is therefore the main target of critics who believe neutral theory conflicts with core principles of niche-assembly (Bausman 2019; Odenbaugh forthcoming).

The apparent rivalry is due, at least in part, to Hubbell's provocative introductory remarks:

> ... it may be hard for many ecologists to accept that ecological drift might actually be important in natural populations and communities ... There are

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[14] For example, Tilman's (1982) impressive manuscript, which integrated and expanded on several prior papers, contains exactly four instances of 'niche' and in each case the word is simply being used to refer to labels chosen by others. We thank an anonymous reviewer for stressing this point.

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> those who seek and find deterministic order and meaning, if not purpose, in every event. And then there are those who believe events to be influenced, if not dominated, by intrinsically inscrutable, and meaningless, random chance. (Hubbell 2001, 7)
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> ... the lack of neutral theory in ecology is also due in no small measure to widespread and, in my opinion, counterproductive resistance to such theories among ecologists ... As I will repeatedly demonstrate in this book, however, niche differences are not essential to coexistence. (Hubbell 2001, 9)

The controversy has several complex dimensions, which the coarse label 'niche versus neutrality' papers over (Vergnon et al. 2009; Wennekes et al. 2012; Kalyuzhny et al. 2014). But even this uninformative characterization of the dispute is misleading. Hubbell's theory is not itself an attack on niche-based theorizing, and the niche concept itself is not his critical target. In fact, Hubbell conforms to the overwhelming consensus about the legitimacy of the niche concept and even commends the contribution it supposedly made in the history of ecology's development as a science. He is explicit that neutral theory, "does not deny the obvious existence of niche differentiation," but just "ascribes much less importance to [the] niche" (2001, 15).

Despite the facile niche versus neutrality narrative, Hubbell is little concerned with the niche's conceptual underpinning, and he concedes that "actual ecological communities are undoubtedly governed by both niche-assembly and dispersal-assembly rules" (2001, 24). This recognition forms the basis of his belief that both perspectives are ultimately needed:

> I am convinced that a truly synthetic theory for ecology must ultimately reconcile these divergent perspectives. Applied ecology and conservation biology and policy critically depend on which perspective is closer to the truth, a fact that is not as widely appreciated as it should be. A major motivation for writing this book has been the search for the grail of reconciliation. Reconciling these perspectives is the underlying, if often unstated, theme running through this book. I believe I have made some significant theoretical progress on this question ... (2001, 26)

So, the putatively epic neutral-niche battle is mostly a mirage. And that clarity helps dispel a tempting presumption that there is a genuine rivalry between two substantive research programs for studying the biological world, one prioritizing nonequilibrium states and stochastic processes and the other built upon the niche concept. Rather, there are two competing hypotheses about the specific causal drivers of ecological dynamics.[15] However ecologically implausible it sounded at the time,

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[15] Alternative explanations have been promulgated and Hubbell's remark above about getting "closer to the truth" indicates there are philosophical undercurrents to the debate. Beyond his speculation that deterministic dispositions might underwrite ecologists' "resistance" towards neutral theorizing, the last quote broaches another potential philosophical divide: realism versus instrumentalism. Wennekes et al. (2012, 259), for instance, argue that the "niche-based" vs. neutral theory feud ultimately boils down to fundamental disagreements between realists and instrumentalists, respectively, which they strangely claim correspond to "philosophical preference[s] for either general but vague versus specific and detailed models." Scientific judgments are obviously shaped by folk metaphysical beliefs and tacit assumptions about the limits of epistemic inquiry, but Wennekes et al.'s specific assessment squares poorly with

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Hubbell's radical theory challenged the pervasive certitude that species being different actually makes an ecological difference. But this challenge is just an instance of the age-old scientific question: which of two causal models does the evidence favor? And on that point of causal inference, "“Niche theory”: the broken-stick, theory of limiting similarity, and their successors" section showed that the niche concept is null and void. The label sounds important, but when so-called niche-based theorizing is contrasted with neutral theory in this debate, the 'niche' captures nothing more than the ecological platitude that species are different.

Of course, differences between species amount to different things in different biological contexts. Saying species have distinct Hutchinsonian niches is an oblique way of trying to say that environments shape the boundaries between positive and negative absolute fitnesses differently for different species, i.e. different species are different. But Hubbell (2001, 20) describes the niche in a more expansive, evolutionary, and specifically adaptationist way:

> Most proponents of niche assembly come out of a strong neoDarwinian tradition, which focuses on the lives of interacting individuals and their fitness consequences. The concept of niche follows naturally and logically as the population-level summation of the individual adaptations of organisms to their biotic and abiotic environments. Indeed, most ecologists after Grinnell (1917) explicitly grounded niche formalism in the language of fitness and intrinsic rates of increase (Whittaker and Levin 1975). One consequence of a focus on adaptation and niche assembly has been a tendency to accept an equilibrium and a relatively static view of niches and ecological communities.

Instead of being lead in the ecological theater, Hubbell also conceptualizes the niche as a protagonist in the adaptationist evolutionary play. Given the glaring inadequacies of niche-centric perspectives in ecology we document above, the decisive question addressed in the next section is whether an evolutionary perspective helps the niche concept evade a tragic ending.

The niche evolving: niche construction theory

Despite its exalted scientific billing, in ecology the niche concept failed to deliver any significant theoretical insights or useful content. But perhaps that conceptual expendability is one-off. In evolutionary theorizing, longstanding criticisms of standard accounts of evolution by natural selection (and especially strong adaptationism) have recently matured into a diverse array of sophisticated models. Known

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Footnote 15 (continued)

Hubbell's own words. As the previous quotes manifest, he explicitly endorses the truth-seeking aim of realism. And it's plausible Hubbell's predilection for realism prompted his prediction that the two approaches would be "reconciled" and eventually integrated (2001, 26), a prediction born out by the vast majority of research done on the issue in the last 2 decades (Haegman and Loreau 2011; Fisher and Mehta 2014).

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under the rubric 'niche construction theory,' perhaps 'niche' isn't mere window-dressing in these models, and in evolutionary biology in general.

According to Lewontin (1983), the standard model is deeply flawed. As it is typically portrayed, "[t]he environment 'poses the problem'; the organisms 'posit solutions,' of which the best is finally 'chosen'" (Lewontin 1983, 276). In other words, adaptive features of organisms and environmental factors that select are treated independently of one another. Lewontin represented this formally as a pair of *separable* differential equations:

$$\frac{dO}{dt} = f(O, E), \tag{2}$$

$$\frac{dE}{dt} = g(E). \tag{3}$$

Equation (2) expresses the obvious truth that change in the organism over time depends on its current state and its environment. Equation (3) states that environmental change depends *only* on environmental variables. That, in Lewontin's eyes, is the problem. Lewontin claimed that decoupling environmental selection pressures from organismal adaptations in this way does not accurately reflect evolutionary dynamics in nature: "Organisms do not adapt to their environments; they construct them out of the bits and pieces of the external world" (1983, 280). Putting aside the fact that organisms *do* adapt to their environments, they also modify them, so any realistic evolutionary model must subsume both components into an integrated system of feedbacks. Accordingly, Lewontin proposed a set of *coupled* differential equations in which organisms and their environments are represented as both causes and effects:

$$\frac{\boldsymbol{dO}}{\boldsymbol{dt}} = f(O, E), \tag{4}$$

$$\frac{\boldsymbol{dE}}{\boldsymbol{dt}} = g(O, E). \tag{5}$$

Unlike Eqs. (2) and (3), (4) and (5) describe the *co*-evolution of organisms with their environments (i.e. each co-determines and co-directs changes in the other). This reciprocal causal model caught the attention of ecologists and evolutionary biologists who saw it clearing a path for a new theoretical role the "niche" could play.

Inspired by Lewontin's work, John Odling-Smee conceptually broadened the standard ecological niche into the evolutionary domain with a new theory he first coined "niche construction" in 1988. Importantly and very controversially, he also argued niche construction is an independent, theoretically indispensable and novel

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mechanism of evolution.[16] According to Odling-Smee (1988), organisms construct their niches by modifying their environments to favorably engineer selection pressures as Lewontin's equations describe. This insight was potent. Soon after, there was an explosion in modeling investigating the ecological and evolutionary consequences of niche construction with mathematical precision (see Laland et al. 2016 and references therein). These modeling developments culminated in Odling-Smee et. al's seminal book *Niche Construction: The Neglected Process in Evolution.* It begins by proposing "a more dynamic niche concept, namely an 'evolutionary niche'" (Laland et al. 2016, 192), which was roughly characterized as, "the sum of all the natural selection pressures to which the population is exposed" (Odling-Smee et al. 2003, 40). Crucially, the "evolutionary niche" (minimally) modifies Hutchinson's ecological niche:

> To set the scene for niche construction all we need do is translate this modern ecological concept of a niche into one that is also evolutionary. We will do so by adopting a simple, pragmatic, and minimalist definition. We will treat the niche of any population as the sum of all the natural selection pressures to which the population is exposed … Like Hutchinson's, this definition is strongly relativistic in that selection pressures are only selection pressures relative to specific organisms. It is also consistent with Hutchinson's fundamental niche. It differs only in that the fundamental niche is now treated as a set of "*n*" natural selection pressures relative to its occupant, in addition to being a hypervolume of resources and tolerance limits relative to its occupant, the former being merely the evolutionary aspect of the latter. (2003, 40)

Just as the "evolutionary niche" generalizes the Hutchinsonian niche from ecology, niche construction theory (NCT) also expands the usual gene-focused conception of heredity from the Modern Synthesis to "ecological inheritance," which includes non-genomic environmental factors that similarly help account for extragenetic fitness dynamics that changes in gene frequencies cannot.[17] For Laland et al. (2016, 192), these two conceptual generalizations constitute the fundamental theoretical core of NCT: "[t]he concepts of evolutionary niches and ecological inheritance are central to understanding four key tenets of niche construction theory." Those tenets are:

> (1) Organisms modify environmental states in nonrandom ways, thereby imposing a systematic bias on the selection they generate, and allowing organisms to exert some influence over their own evolution;
> (2) Ecological inheritance strongly affects evolutionary dynamics, and contributes to parent-offspring similarity;

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[16] "Niche construction should be regarded, after natural selection, as a second major participant in evolution" (Odling-Smee et al. 2003, 2), and others claim its role is "*equal* in explanatory importance to natural selection" (see Scott-Phillips et al. 2014, 1232, our italics).

[17] Ecological inheritance is defined as "any case in which organisms encounter a modified feature-factor relationship between themselves and their environment where the change in the selective pressures is a consequence of the prior niche construction by parents or other ancestral organisms" (2003, 42).

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> (3) Acquired characters and byproducts become evolutionarily significant by affecting selective environments in systematic ways, and
> (4) The complementarity of organisms and their environments (traditionally described as 'adaptation') can be achieved through evolution by niche construction. (Laland et al. 2016, 192)

These concepts and NCT in general have arguably changed the theoretical landscape of biology. It's opened the door to integrative and unificatory aspirations. NCT "provides additional conceptual tools with which to integrate evolution and ecology more effectively" (Laland et al. 2016, 197); it "provides useful theoretical insights and practical tools that contribute to the integration of ecosystem ecology and evolutionary theory" (Odling-Smee et al. 2013, 4); and, finally, "has generated a body of conceptual and formal theory that explores the ramifications of niche construction for evolutionary biology" (ibid. 5). Stronger still, niche construction "is an important missing element of niche theory" (Kylafis and Loreau 2011, 82). And worse, neglecting NCT poses "major conceptual barriers" (Laland et al. 2009, 195) to future evolutionary theorizing because of its conceptually impoverished neo-Darwinian legacy. That legacy is claimed to be "built on inappropriate metaphysical foundations" (ibid, 195), and in turn "fails to recognize a fundamental cause of evolutionary change, 'niche construction'" (ibid, 195).

The modeling conducted under the NCT framework is unquestionably fruitful and is challenging conventional biological assumptions about evolutionary dynamics; it may even merit being judged a distinct evolutionary force. Our (rhetorical) question, again, is what the revamped "evolutionary niche" concept contributes to this work? Nothing about the expansionary shift from the ecological to the evolutionary perspective evades our deflationary criticism. The "simple, pragmatic, and minimalist" modifications of Hutchinson's original definition fail to safeguard the evolutionary niche from the exact same conceptual deficiencies described before: "what this niche definition offers seems largely to be a superfluous gloss on the causal details" (Justus 2019, 121).

To be sure, NCT can be formalized in terms of a so-called "niche function,"$N(t)$. Building upon Lewontin's coupled Eqs. (4) and (5), $N(t)$:

> represents the niche of the population of organisms O at time t, and that
>
> $$N(t) = h(O, E), \tag{6}$$
>
> where the dynamics of (t), which we can regard as 'niche evolution,' are driven according to equations [4] and [5], by both O's prior niche-constructing acts and natural selection, including selection stemming from sources that have previously been modified by O's niche-constructing activities, and sources that are independent of O's niche construction and that may change for independent reasons. (Odling-Smee et al. 2003, 42)

But these details and the "niche function" label don't resuscitate the concept; the "niche" contributes nothing to the broader synthesis of eco-evolutionary dynamics being proposed. As it was in the ecological context, in the evolutionary context it

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functions as at most a heuristic placeholder for what's doing the real scientific work: the complex causal processes the models represent with sophisticated differential equations. Niche construction just is a form of causation, and as such, it just adds an important new wrinkle in the vast and extraordinary causal story that is evolution.[18]

After reviewing how NCT might rehabilitate the niche concept, the future continues to look bleak. The evolutionary niche inherits the sins of its ecological progenitor. No new *conceptual* underpinning for the niche has been supplied. Given the repeated frustrated attempts to find such moorings, there is ample evidence for a strong negative inductive inference.

Conclusion

Concepts are tools for understanding and navigating the world. In science, concepts inform and enable methods of discovery, inference, and they underwrite the content of knowledge claims. If our analysis is correct, the niche concept does none of these.[19] What does do significant scientific work in the sophisticated modeling described above is clarity about—and analytic ingenuity mathematically representing—the causal complexities of how species make their ecological living: what and where they eat, how they compete, and how they construct favorable environments. Rather than seed and cultivate this work with essential conceptual content, the term 'niche' seems to be a free-riding epiphenomenon.

Finding supposedly essential concepts are actually far from it, and the issue of appraising conceptual utility in general, has recently garnered considerable philosophical attention under the rubric "conceptual engineering" (Cappelen 2018; Prinzing 2018; Plunkett and Cappelen 2020). Within that literature debating how concepts *should* be evaluated, the issue of how to respond to conceptual deficiency has generated four possibilities:

> **Revise**—attempt to improve the concept to remedy the specific defects;
> **Replace**—with another concept for particular purposes in certain contexts;
> **Resign**—do nothing. The concept cannot be improved but its content is indispensable and cannot be abandoned; or,
> **Abandon** (or Retire)—the concept entirely, its deficiencies cannot be remedied and its content is inessential.

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[18] In fact, NCT advocates are quite explicit about the narrow focus on causality. Despite the proclaimed centrality of the concepts of "environmental niche" and "ecological inheritance" for NCT, in an unobtrusive footnote of *Niche Construction* within the section "A Definition of Niche Construction" Odling-Smee et al. (2003, 41) disclose, "[o]ur use of the term *construction* refers to a physical modification of the selective environment or actual movement in physical space." Intricate conceptual machinery is conspicuously absent.

[19] Moreover, if our critical line is correct, it's implausible there is such a role even when evaluating higher-order ways concepts can influence scientific practice, but we're not making that case here. See footnote 3 above.

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Compared with **R**^{3}, conceptual engineers have paid little attention to **Abandon**, which is unsurprising given that abandoning leaves nothing to engineer. At least since the turn of the twentieth century, complete concept abandonment also appears to be a rarity in science.[20] The high degree of mathematical and methodological rigor, and theoretical systematicity of contemporary science, might partly explain this phenomenon. But as Kuhn persuasively demonstrated, powerful institutional and socio-politico-cultural forces might also encourage concepts (that favor a reigning "paradigm").

For the niche concept, one of the forces that was surely operative was the influential institutional impact and patronage of G. E. Hutchinson. After all, "G. Evelyn Hutchinson was, according to Stephen Jay Gould, the most important ecologist of the twentieth century and, according to newspaper accounts, the 'Father of Ecology'" (Slack 2010, xi). To deny that that eminence had (and has) any role in the pervasive homage to the niche concept, especially among his students and collaborators that would go on to become the leading figures in ecology (Edmondson 1971; Kingsland 1995), defies credulity.

Another force undoubtedly driving the niche's perceived stature is the psychological satisfaction of theory-seeking. As numerous studies have strongly suggested, scientists (and children much more than non-scientist adults, interestingly) are motivated by a so-called 'theory drive' to uncover—and understand—the underlying causal structure of the world (Gopnik 1998; Trout 2017; Kon and Lombrozo 2019). This activity also precipitates pleasurable excitations when those *Eureka!* moments occur (Gopnik 1998). Ecologists are humans, so this deep biological disposition to unify ecology in a comprehensive theory might account for their evaluative shortcoming recognizing that the niche concept cannot fulfill this aspiration and in fact contributes nothing to the impressive theoretical insights their innovative modeling achieved.

Given how nugatory the niche concept is—and contrary to the non-cognitive factors that may account for its conceptual entrenchment—**Abandon** seems to be the appropriate option. A large part of the niche's perceived potency as a unifying foundation for ecological theory was its generality. Contours of niches would carve *any* physical environment into determinate units that illuminate what species are where, how they interact, and explain why species inhabiting them possess the adaptive properties they do. The auspicious expectation was that the niche would be the fulcrum for an imminent theoretical breakthrough like those achieved with core concepts such as inertial frame, atomic number, and fitness. The sincere prospect of a "periodic table of niches," for example, betrays the perceived inferiority and eagerness to emulate the preeminent sciences (Real and Levin 1991; Pianka et al. 2017). Although its modeling is highly mathematized, ecology did not (and does not) have an overarching and extraordinarily well-confirmed theory like Einstein's relativity theory, Mendeleev's periodic table, or Darwin's theory of evolution by natural selection. The conceptual indeterminacy and problematic vagueness Justus (2019)

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[20] Prominent examples can probably be counted on two hands: e.g. absolute simultaneity, entelechy, ether, and phlogiston.

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uncovered in the original characterizations of the niche demonstrates that the belief in the concept's promise was misjudged. This analysis augments that conclusion by showing the "niche-based" theorizing the concept supposedly catalyzed never overcame that failing and burgeoned in spite of—rather than because of—it.

On the continuum of conceptual utility between **Abandon** and **Preserve Perfectly**, the niche is clearly at the former extreme. But there's a potential worry here: what's ultimately responsible for the clarity in this case? Perhaps the extreme generality of the niche concept begets its downfall and other general scientific concepts might face similar ruin. Take the concept of fitness. There are many mathematical measures of fitness (absolute and relative) and it can be modeled at different levels of biological organization (trait, phenotype, genotype, individual, even population or species). Abstracting away from fine-grained details, in the broadest sense fitness represents the ability to reproduce and survive in specific environments. But in this case the extreme generality does not portend vacuity.

Unlike the niche, fitness has an explicit and indispensable designation in the relevant population models. For alleles and genotypes, for example, abundance changes caused by selection measure absolute or "Darwinian" fitness. These changes then determine frequency changes that measure relative fitnesses. Consider a very simple one-locus, two-allele (A_1A_2) model of a diploid population. When populations are sufficiently large (and drift therefore negligible), mutation is inconsequential, and other complexities involving development and mating behavior can be ignored, then equations governing the dynamics of allele and genotype frequencies can be directly stated. Let p and q designate the frequencies of A_1 and A_2, respectively, in a single generation. The change in allele frequency (due entirely to selection: subscript s) for A_1 is captured by:

$$\Delta_s p = \frac{pq\left[p\left(w_{11} - w_{12}\right) + q\left(w_{12} - w_{22}\right)\right]}{\overline{w}} \tag{7}$$

where w_{ij} are the respective Darwinian genotype fitnesses and $\overline{w}$ is mean population fitness. As Gillespie's (1998, 52) exposition makes clear (and any population genetics textbook confirms), "this equation easily reveals a great deal of the dynamics of natural selection," and by adding more realistic components to the model, insights about a great variety of genetic systems can be acquired.[21] For this reason, Gillespie is only faintly flirting with hyperbole by saying: "This is probably the single most important equation in all of population genetics and evolution!" (52). Without belaboring the obvious, the most important ingredient in that all important equation is: fitness.

As this rudimentary but representative example reveals, fitness is obviously what's doing the heavy scientific lifting. If the niche played a similarly important role—if it featured explicitly in the building block models of theoretical ecology as fitness does in population genetics, or at a minimum gestured towards such a contribution—it would no longer reside at the empty end of the continuum.

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[21] Darwinian (and relative) fitnesses of genotypes can also be derived from Eq. (7).

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Note that this scientific fecundity obtains despite the issue of defining and measuring fitness being unbelievably contentious and complex (Sober 2001; Ariew and Lewontin 2004; Pence and Ramsey 2013). Rather than expose problematic conceptual indeterminacy, the multiplicity of fitness measures demonstrates how the concept is fruitful in distinct ways in different modeling contexts.[22] Perhaps counterintuitively, fitness therefore shows successful definition and scientific merit can come apart. Fitness is a successful scientific concept given its overt function in the mathematical models and what that affords, *despite* its proper definition being elusive. Of course, many successful concepts in science *are* adequately definable *and* play important theoretical roles. The niche fails on ***both*** counts.[23]

Justus (2019) documented the niche’s definitional deficiencies. This analysis completes the negative case by uprooting its exalted scientific status in the work it supposedly supported. Part of what fueled this status was surely a misguided philosophical tendency to think one spectacular definition could supply the key to an entire domain: that a single concept generalizing over all ecological dynamics could unlock our understanding of it, provide a “central conceptual foundation” for it.[24] But definitions in science are expendable and malleable; what’s really important is the work concepts do as tools of epistemic inquiry. Beyond verbiage, the niche is a tool that hasn’t outlived its uselessness.

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[22] See Justus (2012) for another example of this kind of pluralistic fruitfulness in theoretical ecology, and Wakil (2020) for an example in evolutionary biology.

[23] It’s worth stressing that this critical judgment carries with it no reductionistic pretensions. As the fitness concept indicates, the utility of a concept in science doesn’t depend upon it being reducible to something more fundamental, such as causal relations. A concept may be fruitful because it can be so reduced, or its utility might be clearly ascertainable independent of any reductionistic commitments, such as for fitness or the concept of force in physics, at least since Newton (see Smith 2002).

[24] Chase and Leibold (2003, 19), for example, claim their niche concept successfully combines various definitions into “a single organized conceptual framework” that is “probably valid for almost any situation of ecological interest” (ibid, 2).

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