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Niches and Niche Models

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Abstract

The niche has been central to ecology for most of the discipline's history, yet there have been few attempts by philosophers to work out the ontology of the niche. A challenge is that there is a plurality of seemingly inconsistent definitions of the niche in ecology. This paper characterizes the population-level ecological niche by distinguishing among niche concepts, niche models, and the niche as a phenomenon. I argue that "niche concepts" should be interpreted as theoretical frameworks or modelling strategies. I also argue that there is a unified niche phenomenon underlying the seemingly heterogeneous models and definitions. The plurality of niche concepts in ecology should be seen as an expected consequence of the nature of modelling complex systems.

1. Introduction

The ecological niche refers to the position of a species within its community. The term "niche" seems to have first appeared in ecological publications in the 1910s (Griesemer [1992]), making it one of the earliest distinctly ecological concepts—for example, it predates "ecosystem" by a couple of decades. The niche, and phenomena thought to be explained by niche-related processes, remain important targets of biological research programs to the present. Biologists in fields as diverse as wildlife ecology (Frey *et al.* [2017]; Mori *et al.* [2019]), invasion biology (Dlugosch *et al.* [2015]), chemical ecology (Müller and Junker [2022]), theoretical ecology (Hutchinson 1957; MacArthur and Levins 1967; Blonder 2018; Gauzere et al. 2020), and evolutionary biology (Brockhurst *et al.* [2007]) study explicitly niche-related phenomena.

The niche may be the direct target of such research, as when theoretical ecologists model the characteristics of niche space (Blonder *et al.* [2018]; Gauzere *et al.* [2020]), and when field ecologists empirically investigate the niches occupied by particular populations (Frey *et al.* [2017];

Pianka *et al.* [2017]; Mori *et al.* [2019]). Alternatively, the occurrence of niche-related processes may be investigated as explanations of other phenomena biologists study, such as evolutionary patterns and outcomes (Brockhurst *et al.* [2007]; Hawkins *et al.* [2011]), the structure of ecological communities (Chase and Leibold [2003]; Finegan *et al.* [2015]), and even individual-level behaviors and responses (Jakobs *et al.* [2019]; Hahn *et al.* [2023]). In addition, the niche can function as a framing concept that is used to signal the aims and assumptions of these research programs (see Bausman [2019]). Even critics acknowledge: "Perhaps no concept has been thought more important to ecological theorizing than the niche" (Justus [2019], p. 105, [2021], p. 14).

In the context of community ecology, niche-based thinking supposes that the way species allocate and compete for available habitat, resources, or roles in a community is an important driver of community structure. The niche concept is therefore central to thinking about the assembly of ecological communities, which is not only of theoretical interest, but may also be vital to successful conservation efforts.

An issue is that throughout the history of ecology, ecologists have given many distinct and seemingly inconsistent definitions of the niche. This has led to concerns that the concept of a niche is unclear or confused, even leading some to argue that "niche" should be eliminated from ecological practices (Wakil and Justus [2022]). Despite this concern, the niche remains a central concept in much contemporary ecological, behavioral and evolutionary science. This paper illuminates the resulting puzzles: how does a seemingly ill-defined concept centrally inform so much scientific research? And, how can we understand the nature of the niche, given that it lacks a unified description within scientific practices?

I will argue that the differing so-called niche concepts in ecology are modelling strategies, and that features of modelling as such partly explain the plurality of niche concepts. I also argue that distinct types of niche model emphasize different aspects of the niche, and should be interpreted as partial and perspectival representations rather than as inconsistent definitions.

In the next section, I give some contextualizing information about this project. Then, I develop my position about niche concepts, models, and the niche as a phenomenon or phenomena. I explain in particular how environmental and functional niche concepts are related, and address their relationship to the Hutchinsonian hypervolume model. In the final section, a view of niche ontology will emerge on which there is a core niche phenomenon underlying the diverse models. This phenomenon is a sum of ecologically relevant factors characterizing a population-environment interaction.

2. Background

To contextualize this project, some philosophical literature related to the niche is recently developing, though so far the focus has been on a few particular controversies. As mentioned, some philosophers have criticized the concept of the niche, arguing that it is superfluous within ecological practice (Justus [2013], [2019]; Wakil and Justus [2022]). There is also a growing philosophical literature on the controversy about ecological neutral models, which are thought to be an explanatory alternative to niche models of community assembly (Wennekes *et al.* [2012]; Bausman [2018], [2019]; Bausman and Halina [2018]; Odenbaugh [forthcoming]). Neutralists hold that the structure of communities is explained by chance events and ecological drift, in contrast to niche theorists who traditionally hold that the structure of communities is explained by the distinct fitness-related ecological characteristics of populations and their competition for resources. The above cited literature focuses primarily on mathematical modelling practices in ecology. Less has been written by philosophers about niche-related concepts as they influence experimental practices (though see Dussault [2022]; Kaiser and Trappes [2023]).

The majority of philosophical literature using the term "niche" is about niche construction, which is thought to be a potential evolutionary mechanism. It should be noted that "niche" in this context has a somewhat different meaning from its meaning in ecology proper. The *evolutionary* niche is often defined by niche construction theorists as the sum of selective pressures experienced by a population (Odling-Smee *et al.* [1996]; Laland *et al.* [2016]). It remains an open question in the philosophy and theory of biology how exactly niche construction and the evolutionary niche relate to the ecological niche, though it seems clear that the evolutionary and ecological niche are non-equivalent (Trappes [2021]). This paper focuses on developing an account of the population-level ecological niche, leaving further consideration of its relationship to the evolutionary niche for other work.

Few prior attempts have been made by philosophers to work out what niches are, in a general ontological sense (an exception being Smith and Varzi [1999]). Having a better grasp on the nature of the niche will help with future assessments of the issues cited above, e.g., the eliminativist arguments of Justus and Wakil, the controversies about neutralism, and the relationship between the ecological niche and niche construction as an evolutionary process. This paper addresses one problem surrounding the niche (namely, the seeming plurality of inconsistent definitions), leaving consideration of other eliminativist arguments to future work. A better understanding of niche concepts will also help to address some longstanding puzzles within niche theorizing. For example, the questions whether the niche is an attribute of a species or of the environment, and whether niches can be vacant (Whittaker *et al.* [1973]; Lewontin [1978]; Sterelny and Griffiths [1999], Chapter 11; Lekevičius [2009]; Justus [2019]). There are also various special cases that raise interesting philosophical questions, such as temporal niches (Hut *et al.* [2012]) and social niches (Kaiser *et al.* [2024]). This paper addresses the question whether the niche is a property of a species or the environment, and aims to scaffold future work on these other theoretical questions.

A short methodological note before I proceed. I will not attempt a detailed textual or historiographical evaluation of niche concepts in this paper. Rather, I will focus on the niche concepts that occur in contemporary ecology, citing their historical origins as appropriate. It should be kept in mind that contemporary niche-related research practices have moved beyond the well-known niche models developed around the 1960s (e.g., MacArthur and Levins [1967]), which are still of interest but not representative of the current state of ecological theory.

Lastly, a terminological caution. I have adopted the language of "niche concepts" from the ecological literature. There are at least three related senses of the term "concept" that should be distinguished. First, in the colloquial sense, "concept" refers to our general notion of something. Second, in some philosophical contexts, "concept" may be taken to refer to a particular kind of mental entity. Third, in some biological contexts, "concept" is used to refer to a scientific definition or theoretical approach. This will be familiar from the case of so-called species concepts, which are approaches to the individuation of species. For example, "biological species concept" refers to an approach of individuating species based on populations' interbreeding patterns, where reproductive isolation is the main criterion for individuating species. The term "concept" as used here refers to a scientific framework or definition (Ereshefsky [1998]) rather than to a concept in the colloquial sense, i.e., to the general notion of a species.

Similarly, I will argue that what ecologists refer to as "niche concepts" are theoretical frameworks for representing population-environment interactions. If you take "concept" to refer to a general notion or to a mental entity, then my claim that a niche concept is a modelling strategy might sound like a category mistake. So, it should be kept in mind that I have adopted biologists' usage of the term "concept," which I argue should be interpreted here as meaning modelling strategy rather than general notion or the like.

3. Niche Concepts as Theoretical Frameworks

All niche concepts share the following idea: they recognize that species occupy certain "spaces" within ecological systems. An oak tree and a bird occupy very different spaces in their ecosystems, while an American robin and a Eurasian blackbird occupy similar ecological spaces in different ecosystems. This idea recognizes that species often have stable ecological roles within communities, and that the way species divide up activities and resources is a meaningful way to represent the structure of an ecological community (Elton [1927]).

Ecologists have supplied various definitions in order to precisify this intuitive notion of a species' place or role. For clarity, it will be important to distinguish among concepts, models, and the niche as a putative phenomenon or entity "in the world."

A niche concept is a certain way of thinking about and representing the niche: as stated, I will argue that particular niche concepts should be characterized as theoretical frameworks. While existing niche concepts are seemingly heterogeneous, I will argue that they largely represent the same core phenomenon from different angles or perspectives. I will return to models and phenomena after surveying the main niche concepts.

3.1. Population-level niche concepts in ecology

There are three main population-level niche concepts in contemporary biology: the environmental niche, the functional niche, and the evolutionary niche. The environmental and functional niche concepts belong to ecology proper, and will be the focus of the following discussion. As stated, the evolutionary niche is a seemingly distinct idea that forms the basis for defining the proposed evolutionary mechanism of niche construction (Odling-Smee *et al.* [1996]; Laland *et al.* [2016]; Trappes [2021]).

The environmental niche encompasses features of the environmental context that a species interacts with—including habitat features, resources, and climatic conditions. This encompasses, for example, temperature and precipitation, the availability of certain types of food, and the presence of structures needed for cover or nesting. This idea has historical roots in the work of Grinnell ([1917], [1924]) and was adopted in somewhat modified form by Hutchinson ([1957]). It is also (anecdotally) the default conception of the niche in contemporary ecology.

A contrast is often drawn between two ways of thinking about the environmental niche. Theorists can focus on the environmental conditions tolerated by a population (Hutchinson [1957]), or on the resources and conditions that are actually utilized by a population (MacArthur and Levins [1967]). Generally, work that aims to measure niche factors in the field adopts a utilization approach, due to the difficulty of empirically assessing the whole range of conditions a population would tolerate. It seems ambiguous whether the toleration and utilization conceptions of the environmental niche should be considered distinct niche concepts, or whether the latter should be thought of as an operationalization of the former (see Griesemer [1992]). Regardless, the plurality is not accidental; it was designed to serve epistemic purposes. Hutchinson's characterization of the niche as a species' range of permissive environmental states was developed to do theoretical work, e.g., to (attempt to) explain the circumstances under which species can coexist, while the resource utilization approach was developed to permit direct measurement of niche factors in the field.

The best-known niche concept is Hutchinson's proposal that the niche is an *n*-dimensional hypervolume plotted on a space whose axes are environmental factors (Hutchinson [1957]). The hypervolume represents, roughly, the range of environmental states that would enable a population to persist. This formal characterization of the niche is widely regarded by ecologists as a key moment in the history of ecological theorizing (see Chase and Leibold [2003], pp. 9–10).

The Hutchinsonian niche is sometimes characterized as a mathematization of the environmental niche concept, but also sometimes presented as contrasting with received understandings of the niche (e.g., Justus [2019]). I will show below that both of these interpretations are partly correct. The hypervolume approach should be interpreted as a modelling strategy that in practice can cross-cut the distinction between environmental and functional niche models.

Turn now to the functional niche concept. The functional niche of a species is the sum of its ecologically-relevant functional traits and behaviors, including what researchers term "strategies." Throughout this paper, "functions" refers to species' functions (i.e., explanatorily relevant biological activities) rather than to mathematical functions. A species' functional traits include traits that support certain responses to surrounding conditions (response traits) or that affect the surrounding ecological system in relevant ways (effect traits) (Suding *et al.* [2008]).[1] An important functional trait of plants is their leaf breadth, since this trait influences a variety of ecological processes and interactions including drought response and palatability to herbivores. Examples of strategies include foraging at a particular time of day or ocean depth, and depositing a large number of small

[1] Those effects and responses are examples of role functions, which is why this is termed a functional niche concept. Regrettably, functional traits and role functions are not equivalent, but the distinction is not important in the present context.

offspring versus a smaller number of large offspring. The functional niche concept has historical roots in Elton's characterization of the niche in terms of trophic (feeding) relationships (Elton [1927]).

Distinguishing environmental and functional niche concepts has been standard in commentary on ecological practice, although the labels used sometimes differ, e.g., one sometimes finds the phrase "habitat niche" in place of "environmental niche" (Leibold [1995]; Justus [2019]). This language should not be taken to imply that contemporary ecologists think a niche is equivalent to a habitat or environment; rather, "habitat niche" models represent some features of the habitat or environment. Conventionally, a habitat is thought to be a concrete place, while a niche is an abstract entity. (One reason for thinking this is that two species must be in the same location to share a habitat, while two species in different locations can occupy or realize[2] the same niche. You can find some ecologists who seem to equate habitat and niche, but this is a minority view.)

In section 3.3, I will return to the question of how the environmental and functional niche concepts are related. Notably, the environmental and functional perspectives have been integrated by some ecologists, including Chase and Leibold ([2003]), which remains an influential work on niche theory. Their initial, qualitative explanation of how they model the niche is: "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" (p. 15). So, this is a toleration conception of the niche that includes both environmental and functional factors. The authors also provide a more precise definition that states how the niche in this sense is to be mathematically represented: "the joint description of the zero net growth isocline (ZNGI) of an organism along with the impact vectors on that ZNGI in the multivariate space defined by the set of environmental factors that are present" (p. 16).

This example should make it plausible that a niche concept is a theoretical framework or modelling strategy. The Chase-Leibold niche concept specifies that niche models are to represent tolerated environmental conditions plus species' effects on the environment in terms of a ZNGI. The Hutchinsonian niche concept specifies that niche models are to represent certain environmental factors by means of a geometric hypervolume. The functional niche concept specifies that niche

[2] Whether someone prefers to speak of species realizing or occupying niches will depend on whether they think of niches primarily as attributes of species or environments. This question will be addressed later in this paper.

models are to represent functional components of population-environment interactions, while the environmental niche concept specifies that niche models are to represent environmental components of population-environment interactions. Now it should be apparent that some of these frameworks place formal constraints on models, while some of the frameworks have only content-related constraints. To illustrate, the Hutchinsonian niche concept states that niches should be represented as having a certain geometric form (though there are multiple means of implementing such a model mathematically or computationally). In contrast, a functional niche concept states that the niche dimensions should be species' functions or strategies, without placing any further constraints on the form of the model. This shows how some of the distinctions among modelling approaches can be cross-cutting. For instance, one can apply hypervolume modelling to represent functional niche dimensions (Soberón [2007]; Pianka *et al.* [2017]; Gauzere *et al.* [2020]). Hutchinson himself discussed environmental niche dimensions, but this is not required by the formal characterization of hypervolumes. (Indeed, using geometric volumes to represent state spaces is a highly generic modelling strategy that can be applied to many phenomena across the sciences.)

3.2. Models and theories

At this point, I should address how I understand models. While I won't take a position about how models should be characterized in general, in the present context I presume that niche models have important representational functions (Giere [2004]; Weisberg [2013]). Niche models are mathematical, computational, and/or visual representations of some ecologically relevant characteristics of functional or environmental feature space or their effects on population assembly and other relevant biological outcomes. Niche models may represent parts of the niche(s) of particular populations or species, or they may represent niche space and its partitioning among real or hypothetical species or populations. Niche space is the (abstract) space of available conditions or traits in a real or idealized ecosystem. Partitioning is the process or phenomenon whereby niche space is divided among species or individuals (e.g., MacArthur 1958; Roughgarden 1972; Cardinale 2011). In many cases, partitioning is thought to be a means of reducing inter- or intraspecific competition (e.g., Mujic *et al.* [2016]), which is hypothesized to permit species coexistence (in the interspecific case) and to improve individual fitness (in the intraspecific case).[3] Models of niche

[3] Whether niche partitioning is in fact what explains species coexistence is an empirical question. As mentioned in section 2, neutralists have argued that species coexistence can be explained by ecological drift

partitioning can have highly general or particular aims, e.g., to better understand the conditions under which species can coexist, or to document how a particular community of lizards is differentiated in terms of feeding strategies.

Niches include an enormous, potentially indeterminate number of variables; in most studies and models only a small selection of variables can be considered. Thus, you may often see models representing just one or two niche dimensions, where a niche dimension is a niche-related variable included in a model of a niche. Ecologists sometimes also refer to niche dimensions as "niche axes" due to the popularity of graphical representations.

Philosophers of science have previously characterized theories as families of models (e.g., Suppes [1960]; van Fraassen [1980]; Lloyd [1984]). You might wonder whether niche concepts, which I have characterized as modelling strategies, should be considered theories (full stop).[4] This move will depend partly on whether you endorse the model-family (semantic) account of theories, and partly on whether you view philosophical accounts of theories as descriptive or prescriptive. Characterizing families of niche models as theories would depart somewhat from ecologists' usual language. Ecologists do use the phrase "niche theory," but often this refers to niche modelling in general, rather than to a particular family of niche models. However, it may be that philosophers are warranted in interpreting at least some of ecologists' niche concepts as theories on a semantic view of theories. Put differently, what ecologists call concepts might just be what philosophers of science call theories on a certain conception of theories. I am not ready to endorse this interpretation, partly because I have not defended a semantic account of theories here, but I think it represents an interesting target of further consideration.

Recently, Jun Otsuka developed a similar conclusion regarding species concepts (Otsuka [2019]). Otsuka argues that species are representational models of biological organisms, and that distinct species concepts should be interpreted as different kinds of models. Moreover, he argues that the debate over species concepts should be understood as a debate over theory choice, with some features of the conflict created by the nature of modelling as such—e.g., trade-offs between empirical nuance and operability.

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and chance events rather than by competitive processes. The current consensus among many ecologists, and the author's view, is that both drift and competition are relevant to structuring many communities. In addition, ecologists increasingly appreciate that cooperative processes and not only competition may be relevant to niche dynamics.

[4] Thanks to Alkistis Elliott-Graves and also Marie Kaiser for raising this question.

Without fully endorsing this interpretation of species concepts,[5] Otsuka's view has clear similarities to my own interpretation of niche concepts. I have interpreted niche concepts as modelling strategies, and niche models as functioning in part as representations of (some features of) population-environment interactions. My position similarly implies that debates over niche concepts should be reframed partly as debates over model-family selection. We can expect constraints of modelling practice as such to influence niche concept selection. It is likely impossible in principle to represent all the dimensions of a niche. Moreover, it is computationally expensive to represent, for instance, hypervolumes with multiple axes. Because of issues like these, we can expect niche models to leave out a lot of detail. This will result in very dissimilar-appearing models of similar niche-related phenomena. In addition, there are multiple mathematical frameworks for modelling niches (in this paper I've mentioned the Hutchinsonian hypervolume and Chase-Leibold ZNGI approaches, but of course there are plenty of others) and these will experience trade-offs in terms of tractability, computational expense, understandability to humans, ability to capture different kinds of detail, and so forth. Since models are never intended to be fully complete and accurate pictures of the world, the occurrence of differences among niche models need not alarm us; modelling practice engenders plurality.

I also mention Otsuka's work because the convergence between our views may lend support to the suggestion that what biologists call "concepts" should be interpreted as theories. However, you don't need to accept Otsuka's arguments in order to accept this paper's arguments. In particular, there is a more direct case for interpreting niche concepts as model families, because many niche concepts are explicitly developed as mathematical frameworks. As Otsuka allows, the connection between species concepts and mathematical practices is sometimes more indirect. However, we should we should also remember that models need not be mathematical.

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[5] A question is why Otsuka thinks that species models represent organisms rather than species. He seems to think that species just are models. He compares this approach with views about, e.g., the plurality of models of atoms. But the conventional view is that atoms are something distinct from models of atoms. I think it is a coherent view that atoms, species or niches just are models, or that scientific entities are "models all the way down." However, this is not a view I can defend in the present paper, and I don't think Otsuka's arguments do enough to support this interpretation either. Put differently, one may seemingly accept Otsuka's arguments that species *concepts* are theories-as-model families while holding that *species* are some type of entity distinct from models.

I have now described niche concepts and models, arguing that niche concepts are theoretical frameworks. In the next section, I investigate the relationship between environmental and functional niche concepts, from which I will develop a unified view of niche ontology.

3.3. Uniting environmental and functional niche concepts

As mentioned, a key point of criticism against niche concepts has been the apparent incompatibility of different conceptions, particularly the Grinnell-inspired habitat conception versus the Elton-inspired functional conception. Although contemporary conceptions of the niche have expanded on the specific focuses of Grinnell and Elton, one can still identify a contrast between niche-related research focused on environmental variables and research focused on organisms' strategies, functional traits or actions on their environments. The apparent disunity has been one key complaint about the niche, e.g., James Justus objects to the "incongruous array and imprecise character of proposed definitions" (Justus [2019], p. 106).

It should be noted that Justus and others have raised a range of challenges about the use of the term "niche" in ecology, and this paper is not primarily meant as a response to all of these challenges. For example, in addition to his concerns about the inconsistent definitions of "niche," Justus has raised questions about whether the niche continues to serve its original theoretical purposes within ecology, and about whether certain competition models are best interpreted as models of niches. These are reasonable concerns about niche-related theorizing which are not immediately addressed in this paper. As a matter of descriptive fact, there is ongoing research in biology that purports to be about niches, and this paper aims mainly to give a positive characterization of the entity this research purports to be about. Addressing the criticisms of niche-related research in adequate detail would require a separate discussion.

That said, one of the conclusions of this paper is that biologists' conceptions of the niche are less disunified than has been thought. This does suggest a response to one part of Justus' critique, having to do with disunity and definition problems. In this section I argue that despite appearances, environmental and functional niche concepts circle around a core phenomenon and highlight different facets of that same phenomenon.

On the surface, the environmental and functional niche seem like very different ideas. Resources and functional traits appear to be different in kind. In addition, when species compete for similar resources, dividing up the resources versus adopting different behavioral strategies represent distinct ways to mitigate competition. To illustrate, if two coexisting bird species eat similar kinds of seeds, they can reduce competition either by eating seeds of different sizes (resource partitioning), by foraging at different times of day (temporal partitioning[6]), or by adopting different methods of foraging (strategy/functional partitioning).

Despite appearances, notice an interesting feature of the bird foraging example. When species eat seeds of different sizes, this can equally be described as a functional difference—the species have somewhat different roles in the (fine-grained) trophic organization of the ecosystem, and perhaps also serve to spread the seeds of different plant types. Similarly, when birds adopt different foraging strategies, this presumably results in a partitioning of environmental conditions—e.g., as a consequence of foraging behaviors, the birds either eat different types of seed or feed in different locations. Thus, the functional and environmental perspectives are often inter-translatable.

In some cases, it is clearly more felicitous to describe a niche dimension or an instance of partitioning as environmental versus functional. For example, species that occupy different habitat types are often most felicitously described as partitioning environmental conditions—temperature, precipitation, irradiation, presence of cover. At the same time, it is important to recognize that populations are not only passive or accidental recipients of these environmental conditions. Instead, organisms often choose (i.e., disperse to, or successfully recruit within) environments with those characteristics that are suited to their needs and habits; on the flip side, populations will not persist in habitats unsuitable to their needs and habits.

Despite their seeming differences, both the environmental and functional perspectives have to do with the relationship of a population to its surrounding biotic and abiotic environment. In contemporary practice, the first concept emphasizes the resources supplied to a population by its surroundings, while the second concept emphasizes the way populations act on and within their surroundings. Both of these ideas are parts of the larger picture, which is that species and their environments reciprocally act on each other, with important ecological and evolutionary consequences of this interaction.

A key point is that both a resource or condition and a functional trait or strategy are entities picked out relationally within the context of niche thinking. Not just any property of the

[6] Temporal partitioning could be seen as either environmental partitioning (considering time of day as an environmental condition that is divided among species) or as behavioral partitioning (characterizing circadian rhythms as a kind of behavioral strategy). Because of this ambiguity, and because ecologists often characterize temporal partitioning as a special phenomenon of its own (Kronfeld-Schor and Dayan [2003]; Valeix *et al.* [2007]; Lear *et al.* [2021]), I have listed it separately.

surrounding environment counts as a potential niche dimension. Only those features that act on, are relevant to, or are utilized by organisms count as niche-related. For example, the price of bread is not a niche dimension for most nonhumans, while percent tree cover or presence of artificial illumination at night might be. Similarly, not every property or behavior of an organism counts as a potential functional dimension. Only those traits that generate ecologically relevant interactions with the environment count (construing the environment broadly to include other biotic factors). Thus, describing either an environmental or functional niche dimension implies a population-environment relationship.

To be clear, a particular niche dimension might not be best described as a relational (extrinsic) property. For example, ambient temperature or lighting are probably just properties of the environment, and some functional traits like leaf shape or beak size are just properties of the organism. However, the criteria for something to count as a niche dimension are relational—the proposed dimension must create some relevant population-environment interaction. For example, light often entrains organisms' circadian rhythms and activity patterns, while a bird's beak size is relevant to its ability to consume specific food types from its environment.

As suggested, species' resource needs and functional traits at least sometimes inter-translate in a fairly neat manner. For example, a piscivorous species requires fish of certain sizes and abundances to be present in its environment, and has the functional trait of being a piscivore. A niche dimension representing this species' food needs or trophic role are two ways of representing the same relationship. So, the environmental and the functional conception of the niche both get at the overall species-environment relationship, but emphasize a different perspective.

However, some cautions are in order. In general, the empirical or inferential relationship between distinct niche dimensions is complex. For example, one should not assume a highly simple relationship between climate dimensions and plants' leaf morphology. It is an empirical question to what extent a species' suite of functional traits determines what climate conditions it tolerates (and vice versa, to what extent climate conditions dictate functional traits). Assuming a very simple mapping of these two may represent an adaptationist error—i.e., assuming that each of a species' traits is separately and precisely tuned to a specific environmental condition. From the perspective of evolutionary theory, this is known not to be possible due to barriers such as developmental linkage, allometric constraints, and historical constraints on evolutionary changes (Gould and Lewontin [1979]).

So, when I argue that functional and environmental niche dimensions can often be inter-translated, the claim is not that functional niches can be read off of environmental niches or the reverse. Rather, the claim is that for any *particular* niche dimension, a population-environment relationship is implied, regardless whether that dimension has been characterized functionally or environmentally. For example, precipitation levels (environmental characterization) are often niche dimensions, especially for plants, because organisms require and respond to moisture levels in ways that are ecologically relevant. Species that specialize on habitats with high, low, or seasonal levels of precipitation can also be characterized functionally in terms of their tolerance of wet, dry, or seasonal habitats. So, this particular niche axis is inter-translatable for purely conceptual reasons. As stated before, it may be that not all niche axes behave this way, but all niche axes are relevant to characterizing population-environment interactions.

Functional and environmental perspectives on the niche are not equivalent, but they emphasize different facets of the overall species-environment relationship. The sum of relevant ecological relationships is what I identify below as the core niche phenomenon, or the entity that is partially captured by ecological niche concepts and models.

4. From Niche Models to Ontology

As stated, there have not been too many attempts to work out what, ontologically, niches are as a phenomenon or entity.[7] Put differently, what are niche models models of? I expect this will be a matter of some difficulty, but that thinking about relations is a natural start. As indicated above, the niche is plausibly a sum of all ecological factors relevant to population-environment relationships and interactions.[8] This entity can be characterized from the perspective of a population (e.g., the resources afforded to the population by the environment) or from the perspective of the

[7] One attempt is Smith and Varzi ([1999]). However, their account of the niche seems to reflect the colloquial sense of the term (i.e., a physical space that may be occupied by an object) more than the ecological niche.

[8] A distinction between the realized or actual and fundamental or potential niche is now standard in ecology. To make this distinction, the realized niche is the sum of factors characterizing an actual population-environment interaction, while the fundamental niche is the set or space of possible states characterizing a population-environment interaction in which that population can persist. The distinction is normally credited to Hutchinson ([1957]), but Hutchinson attributes the term "fundamental niche" to MacArthur, as pointed out by Griesemer ([1992]). Classically, competition is thought to be the main mechanism restricting the realized niche as compared to the fundamental niche, though see Colwell and Rangel ([2009], pp. 19653–4).

surrounding community and environment (e.g., the trophic role of the population within its community).

This kind of duality is a normal feature of how relational structures work. For example, if you ask a child to describe their family, they may describe having grandparents, parents and a sibling, while an adult might describe the same family as consisting of their partner and children. These are distinct but compatible ways of describing a family structure from different perspectives. There is no perspective-independent answer about what is the "correct" angle from which to describe a family structure. Similarly, there is no perspective-independent answer about whether niches ought to be described from the perspective of populations or environments. However, one perspective or the other may be more apt for answering particular questions. Moreover, once a perspective is fixed, there may be objectively accurate and inaccurate ways to describe the observed relationships.

My position about the nature of the niche as a core phenomenon illuminates the question whether the niche is a property of an environment or a species (see Griesemer [1992]). It is frequently claimed in contemporary work that niches should be thought of as properties of species. A common reason stated in support of this position is that species alter their environments, so niches cannot be thought of as static, pre-existing "slots" in the environment. I agree with this reason, but not the conclusion. To the extent that niches are properties of species, they are relational and extrinsic properties—they rely on the existence of certain organism-environment relationships. The niche cannot be a property of a species considered fully in isolation, since it depends on what conditions and factors are actually or potentially present in the environment for a species to interact with.[9] Thinking of the niche as relational shows that the question whether they are properties of environments or species is probably an ill-formulated question, since relations "belong" to all of their relata.

So, following such biologists as Lewontin ([1978]) and Chase and Leibold ([2003]), I propose that the core ecological niche phenomenon encompasses both environmental and functional characterizations of a population-environment interaction. Thus, the niche encompasses environmental conditions and resources afforded to organisms; and organisms' behaviors, responses

[9] Even characterizing the fundamental niche (see previous note) depends on what suites of conditions are available, or plausibly could be available, in real ecosystems on earth. Ecologists are concerned with explaining what happens in real ecosystems, not with what could happen in unlikely, imaginary, or distantly counterfactual scenarios.

to and effects on those states, where environmental states should be understood broadly to include both abiotic and biotic conditions (including other species that are part of a community).

This paper will remain officially neutral about whether this niche phenomenon is a natural entity "out there in the world" or whether it is best seen as a theoretical construct. However, if niches are thought to be real, this core phenomenon may be the best candidate for that real entity. One reason in support of this view is that, as argued above, it unifies and explains the plurality of niche concepts in ecology—one might develop a convergence argument for the reality this entity. (I would not endorse this argument but this is, in brief, because I am not a realist in general, not because I think there is some special problem about the niche.)

Some may hold that we should think about the niche primarily as a metaphor that guides ecological research but does not have a unique ontological characterization, or as an ontologically pluralistic term that captures multiple distinct phenomena. It is likely, for instance, that the evolutionary niche and the individualized niche (Takola and Schielzeth [2022]) are distinct kinds of phenomena from the ecological population niche. However, my arguments above suggest that there is a unified core underlying the conceptions of at least the ecological population niche. While this position is ontologically monistic, it is consistent with pluralism about niche concepts and representations in scientific applications. Because ecological communities are highly complex (sensu Elliott-Graves [2023]) and because generally, niches are too large to model more than a few of their dimensions at once, we should expect the persistence of a diverse plurality of model types representing different facets of niches.

In closing, some theorists in both ecology and philosophy have complained about the proliferation of inconsistent definitions of the niche, yet many such "definitions" are merely explanations of the type of model that a group of researchers will be using. In contrast with Justus' picture of an "incongruous array," I have argued that the existing plurality of ecological niche concepts all circle around a core phenomenon, and new modelling strategies have been developed often with specific theoretical or practical applications in mind. The complexity of niche-related processes will create modelling trade-offs (e.g., among ease of implementation, representational accuracy, and generality), which will result in a plurality of models in practice (Levins [1966]; Weisberg [2006]; Elliott-Graves [2023]). Considering hypervolume models, an example of this kind of trade-off is that including more niche dimensions in a particular model will enhance the ecological accuracy of the model while reducing its ease of implementation[10] and likely its generality. Very multidimensional hypervolumes may allow for novel ecological and evolutionary predictions, but are computationally expensive, difficult for humans to visualize, and not suited to simulating dynamical processes. This suggests that the variety of niche modelling strategies in contemporary ecology is not only expected but beneficial.

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[10] In multiple respects: the model will require more empirical data for validation, it will require more computational power, and it will be more difficult to represent visually on a page.

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