The Individualized Niche: A Case Study in Scientific Conceptual Change

Katie H. Morrow & Marie I. Kaiser

Morrow: Department of Philosophy, Bielefeld University, Postfach 100131, 33501 Bielefeld, Germany
ORCID: 0000-0002-4126-8121
Correspondence: katherine.morrow@uni-bielefeld.de

Kaiser: Department of Philosophy, Bielefeld University, Postfach 100131, 33501 Bielefeld, Germany and Joint Institute for Individualisation in a Changing Environment (JICE), University of Münster and Bielefeld University, Bielefeld, Germany
ORCID: 0000-0002-9307-7474

Abstract
We explore the causes and outcomes of scientific conceptual change using a case study of the development of the individualized niche concept. We outline a framework for characterizing conceptual change that distinguishes between epistemically adaptive and neutral processes and outcomes of conceptual change. We then apply this framework in tracing how the individualized niche concept arose historically out of population niche thinking and how it exhibits plurality within a contemporary biological research program. While the individualized niche concept was developed adaptively to suit new research goals and empirical findings, some of its pluralistic aspects in contemporary research may have arisen neutrally, that is for non-epistemic reasons. We suggest reasons for thinking that this plurality is unproblematic and may become useful, e.g., when it allows for the concept to be applied across differing research contexts.

Keywords: Ecological Niche, Conceptual Change, Pluralism, Niche Partitioning, Niche Dimension, Individual-Based Research

1. Introduction

Scientific concepts change over time, often in ways that result in complex and pluralistic conceptual structures. Central scientific terms such as ‘species,’ ‘gene,’ ‘temperature,’ ‘planet,’ ‘element,’ and ‘niche’ (our focus) have shifted in both their meanings and extensions. Philosophers have taken the whole range of attitudes toward this phenomenon. First, some philosophers have seen intractable conceptual plurality as a problem threatening reference, realism, generalization, or clear communication (Ereshefsky 1998; Machery 2005; Santana 2018; Justus 2019). In contrast, other philosophers have emphasized that conceptual plurality can contribute to successful scientific practices (Brigandt 2010; Feest 2010; Feest and Steinle 2012; Chang 2012; Neto 2020; Haueis 2024), for example, by allowing established concepts to survive theoretical shifts. Finally, it has recently been proposed that conceptual complexity

could be neutral, arising and persisting simply due to a lack of overt harmfulness (Novick 2023).

We consider the development of the ecological niche concept over time, and in particular, how this concept was expanded to individuals and how it later fragmented into different conceptions. In mid-century ecology, the niche was thought of as an attribute of a population (Hutchinson 1957). However, around the 1980s, early *individualized* niche concepts began developing, attributing niches to individual organisms (e.g., MacMahon et al. 1981). Since the turn of the century, there has been increasing research interest in individualized niches, driven by the general move toward individual-level and integrated ecological-evolutionary research (e.g., Bolnick et al. 2003; Carlson et al. 2021; Takola and Schielzeth 2022; Trappes et al. 2022).

In this paper, we trace the research questions that led to the development of the individualized niche concept and show that this change occurred in order to expand on the explanatory potential and improve the empirical adequacy of niche-related thought. We conclude that the development of the individualized niche concept is an example of scientific conceptual change that occurred adaptively according to epistemic aims of scientists.[1]

We analyze a second conceptual change process that took place after the expansion of the niche concept to individuals. The individualized niche concept fragmented into a plurality of conceptions. We are part of a large interdisciplinary Transregio Collaborative Research Center, SFB-TRR 212, "A Novel Synthesis of Individualisation across Behaviour, Ecology and Evolution: Niche Choice, Niche Conformance, Niche Construction (NC^3)" (CRC for short), whose members are mostly biologists studying individual differences and individualization processes in animals. As philosophers in the CRC, we have identified multiple related yet nonequivalent conceptions of the individualized niche. There are several ways in which the concept is pluralistic: first, it permits multiple views of what counts as a niche dimension (Section 4.1); second, it can be represented as either temporally extended or time-sliced (Section 4.2); and third, it can be attributed to individuals or groups (Section 4.3). We argue that this plurality may have arisen through neutral or non-epistemic processes, though this does not entail that the plurality is harmful.

[1] It should be noted that our analysis is primarily descriptive, as opposed to normative or prescriptive. We reconstruct the actual processes, outcomes, and scientific aims leading to the contemporary structure of the individualized niche concept.

This paper serves two general purposes. First, we characterize the emergence and structure of the individualized niche concept, thus extending the philosophical literature on the population-level ecological niche (Griesemer 1992; Sterelny and Griffiths 1999, chap. 11; Pocheville 2015; Justus 2019; Trappes 2021; Dussault 2022a; 2022b; Wakil and Justus 2022; Morrow 2024). Second, we contribute to debates about the change of scientific concepts by presenting a revealing case study and by applying a framework for characterizing conceptual change, drawing attention to the difference between processes and outcomes of conceptual change, both of which can be adaptive or neutral.

In the next section, we review some philosophical accounts of how to evaluate scientific conceptual change and explain the framework we apply. In Section 3, we give a historical overview of the development of the individualized niche concept, arguing that it arose in an epistemically-driven manner. In Section 4, we present three respects in which the individualized niche concept is pluralistic and explore reasons for the plurality.

2. Characterizing conceptual change in science

Scientific concepts are known to change over time in various ways (e.g., Brigandt 2010). Moreover, scientific concepts are thought to commonly have multiple related meanings (i.e., be polysemous) in contemporary usage (e.g., Taylor and Vickers 2017; Haueis 2024). Processes of conceptual change and dissemination in science need not, but often do, lead to polysemy and complex conceptual structures.

The concept of a niche is no exception. While retaining some core features, the general term ‘niche’ has expanded and been repeatedly redefined over the past century (Griesemer 1992; Pocheville 2015), resulting in a plurality of conceptions at both the population and individual level. This paper analyzes the processes of conceptual change leading to the contemporary structure of the individualized niche concept. First, we document how and why the term ‘niche’ was expanded to include individual-level in addition to population-level phenomena. Second, we reveal that the contemporary concept of an individualized niche has already fragmented and admits of different sorts of plurality. We characterize the reasons for these changes according to the framework developed in this section.

Rose Novick has recently cautioned against “adaptationist” investigations of conceptual complexity (Novick 2023). Adaptationists about scientific conceptual complexity assume that observed conceptual complexity is epistemically beneficial (adaptive outcome), and, moreover, that the conceptual complexity must have come about for those epistemic

benefits (adaptive process). By analogy with insights about neutral evolution, she argues that conceptual complexity should not be *presumed* to have arisen in an adaptive manner, since complexity or polysemy might come about and persist due to neutral mechanisms. We take neutral mechanisms to include linguistic and sociological processes of term dissemination that are not sensitive to local epistemic needs. While Novick's discussion focuses on complex (e.g., pluralistic) concepts, we propose that the framework can be extended to any case of conceptual change and the resulting outcome of that change (Table 1). Thus, conceptual changes – including those that do not increase conceptual complexity – can occur either because of epistemic benefits (adaptive) or in a manner independent of epistemic benefits (neutral). Moreover, the resulting conceptual structure (outcome) can later be evaluated as being suitable, neutral or unsuitable with respect to present epistemic aims. Either of the types of process can be connected to any of the types of outcome: for instance, a conceptual structure that is developed due to perceived epistemic benefits may later turn out not to be comparatively well-suited to changing research aims; and a conceptual structure that arises due to neutral mechanisms might later turn out to have epistemic benefits.

Table 1. Ways of evaluating conceptual changes (framework modified from Novick 2023).

Explanation of conceptual change (process)		**Evaluation of conceptual structure (outcome)**		
Adaptive	*Neutral*	*Suitable*	*Neutral*	*Unsuitable*
Conceptual change occurred on account of epistemic benefits	Conceptual change occurred independently of epistemic benefits	Conceptual structure is comparatively well-suited to epistemic aims	Conceptual structure is neutral with respect to epistemic aims; potential variations in conceptual structure do not make an epistemic difference	Conceptual structure is comparatively ill-suited to epistemic aims

In the next sections, we first trace the research contexts that led to the development and proliferation of the individualized niche concept (Section 3). We argue that the individualized niche concept did arise in an adaptive manner, i.e., it was developed by researchers as an expansion of the population niche concept in view of their epistemic goals and theoretical and empirical findings. An expanded niche concept was expected to generate new and better explanations and to better account for observed individual variation. Moreover, this conceptual expansion opens the door to new research avenues. We then, in

Section 4, turn to a second conceptual change process and its outcome. We document pluralism within the individualized niche concept as it is used in contemporary biological practice. Some aspects of this pluralism may have come about in a neutral manner. However, this cannot be taken to imply that the plurality is problematic. We suggest that conceptual plurality is not a problem in general, and that plurality in the individualized niche case may be beneficial as it allows for the concept to be applied to a greater diversity of research contexts.

3. The individualization of the niche

This section analyzes the origin and development of the individualized niche concept. This is not meant to be a comprehensive history, but rather we describe major relevant research developments. We begin with a short overview of the population-level ecological niche concept, highlighting one way in which the received concept of a niche was pluralistic. We then discuss the research questions that led to expanding the niche to individuals and explain why it makes sense to expand what is typically thought of as a population-level attribute to individuals. We argue that this expansion process was adaptive, i.e., it was driven by epistemic aims and resulted in epistemic benefits.

3.1. Population-level ecological niches

The niche was initially characterized as either the habitat (Grinnell 1917; 1924) or trophic role of a species (Elton 1927). In contemporary language, these are known as *environmental* and *functional* definitions of the niche, respectively (Griesemer 1992; Leibold 1995; Morrow 2024). Thus, researchers in the Grinnellian tradition conceive of the niche in terms of environmental conditions under which populations are found, while those in the Eltonian tradition conceive of the niche with respect to functional traits exhibited by members of the population.

Both environmental and functional conceptions of the population niche have persisted to the present (e.g., Soberón 2007; Junker et al. 2019). More recently, some ecologists—most notably Jonathan Chase and Mathew Leibold—have developed integrated definitions of the niche that include both environmental states and species' effects on those states (Chase and Leibold 2003). As a descriptive matter, this work has not led to a single unified meaning of 'niche' being adopted within the ecological literature. Instead, at least three distinct conceptions of the ecological population niche (environmental, functional, and integrated) remain, and ideally papers clearly state which definition(s) they apply or at least what *niche*

dimensions[2] they investigate (e.g., Sanz-Aguilar et al. 2015; Pianka et al. 2017; Junker et al. 2019; De La Riva et al. 2023). As we will explain, a similar type of conceptual plurality has also arisen with respect to 'individualized niche' (Section 4.1).

While a plurality of concepts or definitions of the niche remain in use (a matter that is well-recognized among ecologists), Hutchinson's definition is the most influential on how many contemporary ecologists think about niches. Hutchinson thought of the niche as a multidimensional hypervolume, or abstract geometric space. This space represents the combinations of environmental conditions that would allow a population to persist indefinitely, assuming the absence of competition (Hutchinson 1957). Hutchinsonian niches have an interesting modal character. Hutchinson refers to the space of conditions under which a population *could* persist as the fundamental niche. He distinguishes this from the realized niche, or the set of conditions actually experienced by a population. Because of this modal character of Hutchinsonian fundamental niches, they are widely thought to be characteristics of populations, rather than, for instance, independently existing "slots" in the environment (Whittaker, Levin, and Root 1973; Sterelny and Griffiths 1999, chap. 11; Justus 2019). In the following section, we explain how the Hutchinsonian understanding of 'niche' was modified to develop the concept of an individualized niche.

3.2. From niche partitioning to individualized niches

As stated, Hutchinsonian niches have been widely considered as attributes of populations. In particular, the Hutchinsonian fundamental niche is delimited by conditions that would permit a population as a whole to persist, which does not translate directly to individual-level attributes (since population persistence does not rely upon the reproductive success of any members considered individually). In view of this, it may be surprising that individualized niche researchers have often specifically cited Hutchinson and characterized the individualized niche as a modification of the Hutchinsonian conception (Takola and Schielzeth 2022; Trappes et al. 2022). To achieve this, contemporary researchers delimit the boundaries of the individualized niche in terms of individual fitness rather than population persistence (Section 4). In what follows, we show that the individualized niche is a natural expansion of the Hutchinsonian approach to modeling population niches that developed out of

[2] In traditional hypervolume models (see below), niche dimensions correspond to the axis labels, i.e., environmental variables or variable functional traits. In concrete terms, environmental examples include conditions such as water depth and resources such as prey species abundance.

theoretical work on niche *width* and *partitioning* in the 1960s-70s (e.g., Van Valen 1965; Roughgarden 1972). We characterize this conceptual change as an adaptive conceptual expansion (Table 2, Case I).

Table 2. Processes in the development of the individualized niche concept.

Case	Concept	Process of conceptual change	Explanation for conceptual change	Outcome of conceptual change
I	Ecological niche concept	Expansion (to individuals)	Adaptive	Broader concept (larger domain of applicability)
II	Individualized niche concept	Fragmentation* (of individual-level concept)	Neutral	Conceptual plurality (multiple conceptions)

*Term from Taylor and Vickers (2017)

We lead with a few terminological clarifications. Niche width refers to the breadth or variability along a niche dimension for a given population. For environmental niches, populations with a wider niche use a greater variety of resources or tolerate a wider range of environmental conditions. Populations with a narrower niche are more specialized and require more specific conditions. Niche partitioning refers to the dividing up of niche space among populations within a community (e.g., Albrecht and Gotelli 2001; Cardinale 2011; Frey et al. 2017). One hypothesis investigated in this research on population niches is whether niche partitioning, resulting in narrower (realized) niches, promotes the coexistence of greater numbers of similar species (e.g., Michalko and Pekár 2015; Lear et al. 2021).

A natural continuation of this line of thought is to consider how niche space is partitioned *within* populations. When a population's realized niche width changes, it does so in virtue of its individual members interacting with the environment differently. In addition, biologists have always known that populations are not homogeneous but are made up of individuals that specialize in different ways. In principle, populations could be made up of individuals that all utilize the same range of environmental conditions, or they could be made up of small groups of highly specialized individuals that each utilize a small segment of the population's niche space (Fig. 1).

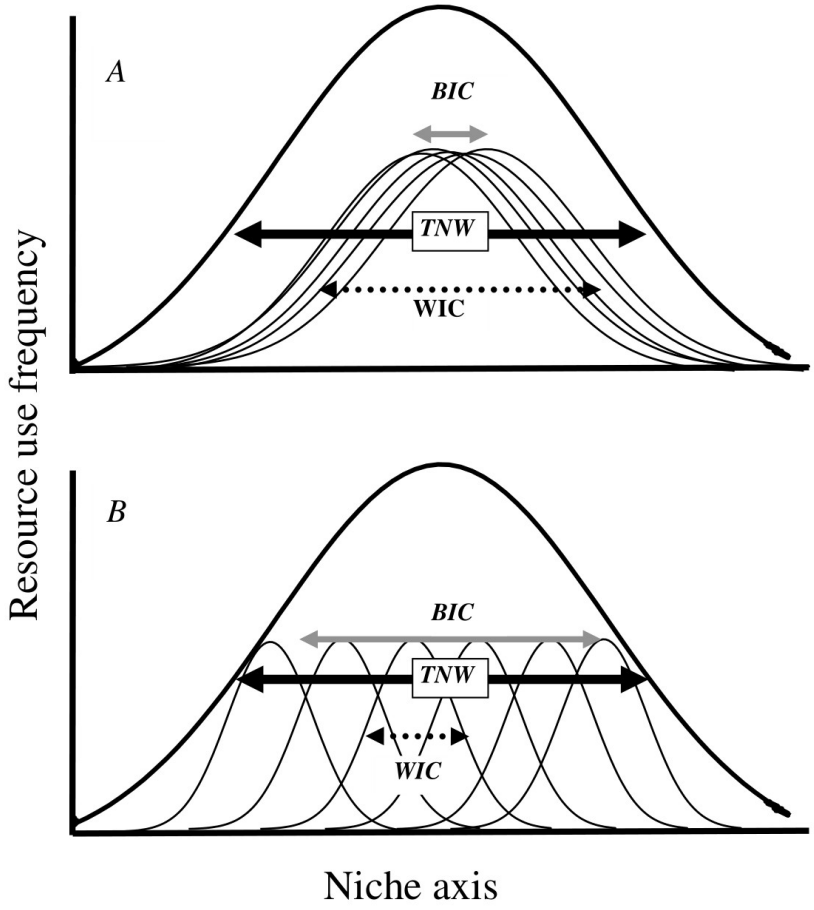

Figure 1. An abstracted depiction of a population consisting of niche generalists (top) and a population consisting of niche specialists (bottom). The thick curves depict population niche width for a particular niche dimension (x-axis), which is a type of resource here, while the thin curves depict niche specialization by individuals (i.e., differing preferential use of the resource). The y-axis in this figure is resource use frequency, but this could be replaced by environmental condition tolerance or by fitness. Contemporary individualized niche researchers often use fitness as the y-axis variable, such that the individualized niche is represented as an individuals' fitness function over environmental conditions. TNW refers to the total niche width of a population, and WIC and BIC are measures of individual-level niche partitioning. The individual curves within population B are naturally interpreted as (depicting one dimension of) individualized niches. While this figure is reprinted from a 2003 article, the authors present it to illustrate Joan Roughgarden's work on niche width from the 1970s. Reproduced with permission from Bolnick et al. (2003, Fig. 1).

Early works highlighting niche differentiation among individual members of a population came out in the 1980s, setting the stage for an explicit individualized niche concept. We focus on just one important early presentation of the concept, which occurs in a paper by James MacMahon and coauthors (1981), who develop an organism-centered framework for various ecological concepts. Their move to the organism level was also clearly influenced by the mid-century trend toward individual-based ecological models and studies. This paper includes a view of the "individual niche" (MacMahon et al. 1981, 289), which they argue is partly determined by genetics, can be restricted by physiological and acclimation processes, and changes over the course of an organism's development. MacMahon and coauthors distinguish between the potential individual niche, reflecting the range of environmental tolerance of an individual, and the actual individual niche, which is the point in the abstract depiction of environmental space actually occupied by an individual at a moment in time. This distinction clearly follows Hutchinson's fundamental-realized niche distinction. Interestingly, they explicitly incorporate a temporal dimension in their representation of the individualized niche (Fig. 2), which highlights that individualized niches, actual as well as potential, change over the lifetime of the individuals.

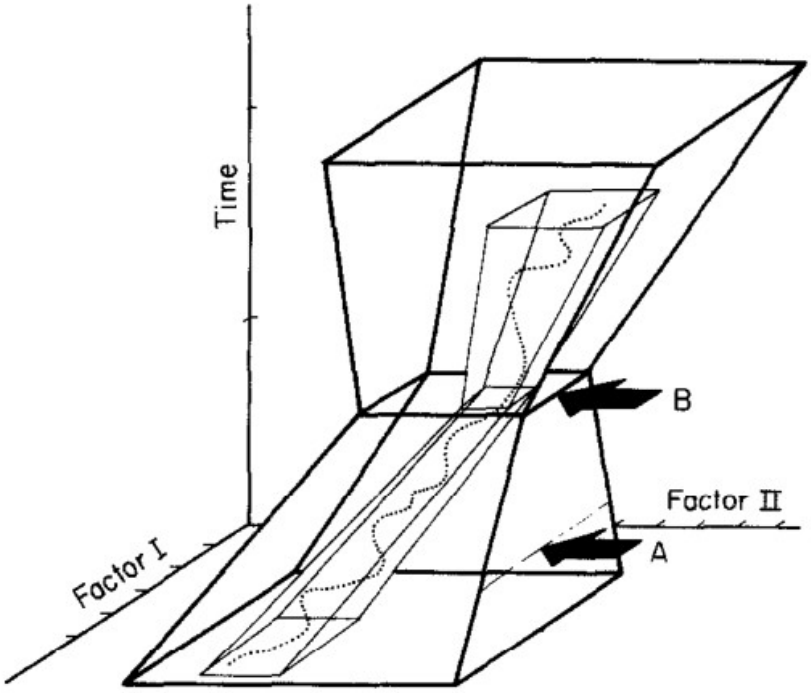

Figure 2. An early depiction of a temporally extended individualized niche. Factors I and II are environmental dimensions, and the dotted line shows the realized individualized niche (actual individual niche, in their terminology) at each point in time. The largest volume depicts the "prospective" or "potential" individualized niche, or the range of conditions tolerated by the individual. In addition, MacMahon et al. distinguish between the potential niche for the genotype (the larger volume) and the potential niche for the developed phenotype, which they term the "acclimatized niche" (the inner volume). The latter distinction has not often been made in subsequent literature, but it might usefully be merged with thought about developmental canalization and plasticity. Reproduced with permission from MacMahon et al. (1981, Fig. 8).

To conclude, there were a couple of major theoretical developments in the period of around 1960-2000. First, the idea of niche partitioning was extended from between-population partitioning to within-population partitioning. This gave rise to the idea that individuals within populations might utilize only portions of the population's overall niche width. In these cases, studying only the population's niche width as a whole might mask important ecological processes. For example, whether a population consists of generalists or specialists is theoretically expected to influence how the population responds to environmental changes.

At the same time, ecologists were increasingly tracking individuals in long-term field studies, allowing for more detailed findings about both populations and individual behavior (Clutton-Brock and Sheldon 2010). Proponents of the move to individual-based research, such as MacMahon and coauthors, were led to consider whether traditionally population-level concepts such as the niche could be specified at the individual level. Moreover, the theoretical-conceptual work of Richard Levins and Richard Lewontin (1985), drawing attention to the reciprocal interaction between individual organisms and their environment, also encouraged research focusing on the individual level. In the coming subsections, we develop the argument that this ongoing conceptual expansion of 'niche' is adaptive because it brings the concept of a niche better in line with emerging empirical evidence and allows for new explanatory directions.

3.3. From theory to empirical evidence

Prior to around 1990, the importance of individual niche-related specialization was largely theoretical. Diagrammatic depictions of individual niche partitioning may seem intuitively compelling, but empirical evidence is needed to confirm whether intrapopulation niche specialization is common in nature. This subsection reviews the empirical research that led ecologists to think of intrapopulation niche partitioning as a ubiquitous natural phenomenon rather than an exceptional theoretical possibility, evidence that contributed to the development and growing popularity of the individualized niche concept. Thus, we will argue that this expansion of niche thinking reflected new empirical evidence and developed in view of emerging explanatory goals.

In a paper published in *Nature*, Thomas Bates Smith (1987) empirically documents "intraspecific niche utilization" differences in feeding in black-bellied seedcracker (*Pyrenestes ostrinus*), thought to be due to bill size polymorphism. Interestingly, Smith remarks that "[d]ietary differences between morphs [of *P. ostrinus*] are similar to those found

between congeneric, sympatric species of Darwin's finches and *appear to be one of the few examples among vertebrates* where a polymorphism is associated with differential niche utilization" (718, emphasis added). This illustrates that as recently as the 1980s, working ecologists thought of intraspecific niche partitioning as exceptional or poorly-documented. As we will go on to discuss, since the publication of Smith's article, a great number of niche-related polymorphisms have been documented among not just vertebrates but also many invertebrate and non-animal species. Thus, there was a major change in the ecological evidence base partly driving the conceptual change. Biologists were concerned not only that their conceptualization of the niche be able to account for the empirically documented variation within communities, but moreover the emergence of the individualized niche concept allowed for novel explanatory aims and research directions.

Studies in the late 1980s and 90s continued to document ecologically important intraspecific variation. An important development in the individualized niche literature (and the study of individual specialization within ecology more generally) was the publication of a review by Daniel Bolnick and coauthors (2003), which surveys documented individual specialization within populations and its potential biological implications. In their words, "[t]he primary goal of this article is to challenge [received] views by showing that individual specialization is widespread and that it can profoundly affect a population's ecological and evolutionary dynamics" (Bolnick et al. 2003, 2). The authors argue that between-individual variation or specialization can be a major component of population niche width, though they summarize evidence for and against this hypothesis. As of the time of writing, the Bolnick et al. article has been cited more than 3000 times.[3] While the cited review focuses on animals, subsequent reviews of plants have also confirmed that intraspecies ecological variation is common (Siefert et al. 2015).

The empirical study of individualized niches accelerated in the 2010s (e.g., Dall et al. 2012; Layman, Newsome, and Gancos Crawford 2015b (special feature)), with some important new theoretical developments being published since 2020. So, while the individualized niche is not a brand-new concept, it is still the subject of novel and developing research programs and is actively changing in relevant ways.

3.4. New applications of individualized niches

[3] According to the Google Scholar "cited by" function, accessed 22 February 2024.

Having outlined the historical emergence of the individualized niche concept and reasons for thinking this conceptual change was adaptive, we now turn to some of its major uses in contemporary research. Individualized niches and (changes to) individual niche width are being studied as both causes and consequences of other biological phenomena to be discussed below. In the literature, standard terminology for individualized niches has not crystallized, which suggests that the concept is still undergoing changes. Some papers use 'individual niche' rather than 'individualized niche.' In addition, some studies about individualized niches do not use the phrase but instead refer to (intraspecific) niche specialization, intraspecific niche variation, or (individual) niche width. Nevertheless, these studies target similar phenomena. Some aims of the biologists in the CRC are to further popularize the individualized niche concept and contribute to the elaboration and standardization of this conceptual-theoretical framework.

In this section we argue that the individualized niche concept contributes to explanatory goals by encouraging subpopulation variation to be incorporated into niche-related explanations, further suggesting that its development and proliferation is driven by epistemic aims. The present-day explanatory goals related to the individualized niche concept have arisen from those in the past, shaping the expansion of the niche concept to individuals. There is some overlap in explanatory goals, but also a general trend from explaining that there are differences in individualized niches to focusing on how these differences change over time and what their ecological-evolutionary consequences are.

A major reason for the development and popularization of the individualized niche concept is some biologists' concern that ecological and evolutionary models that ignore intraspecific variation cannot adequately explain certain biological outcomes. Niche models that treat populations as if they were homogeneous neglect the real variation that occurs within populations. This variation is thought to affect how populations interact, evolve, respond to environmental change, and so forth.

As a *cause*, niche individualization has been proposed as a mechanism for mitigating intraspecific competition. One illustration is that niche utilization often varies between age classes, likely to reduce competition between adults and young of the same species (Zhao et al. 2014; Székely et al. 2020). Individual niche specialization has also been suggested to contribute to the coexistence of functionally similar species at the community level (Schirmer et al. 2020). In addition, intraspecific phenotypic variation has been proposed as a key driver of both adaptation and evolutionary diversification (following, e.g., West-Eberhard 2005). A

major aim of the CRC is to move toward integrating ecological and evolutionary insights at the individual level.

While the individualized niche concept arose out of concerns to better explain certain ecological-evolutionary phenomena, individualized niches are now being studied as research targets in their own right (Layman, Newsome, and Gancos Crawford 2015a). As *explananda* or *effects*, (changes to) individualized niches can be linked to various factors including genetics, phenotypic and behavioral differences, dispersal, environmental heterogeneity, resource availability, and social interactions, including both cooperative and competitive interactions (Layman, Newsome, and Gancos Crawford 2015a; Newsome et al. 2015; Robertson et al. 2015; Trappes et al. 2022; Kaiser et al. 2024). Individual niche width—one way of representing the extent to which an individual is a specialist or generalist—is thought to be an evolvable and plastic trait. Intriguingly, competition has been hypothesized to either increase or decrease individualized niche width (Sheppard et al. 2018), so clarifying this relationship has been a target of both theoretical and empirical research (Svanbäck and Bolnick 2005; Costa et al. 2008).

One recent study did not detect individual niche variation related to foraging in three Antarctic seabirds: Antarctic petrel (*Thalassoica antarctica*), cape petrel (*Daption capense*), and southern fulmar (*Fulmarus glacialoides*) (Dehnhard et al. 2020). The authors suggest that generalism is favored in this system due to a combination of high productivity and environmental heterogeneity. The discussion in the cited paper illustrates a shift in perspective that we argue is occurring in biology. Rather than seeing individual ecological specialization as a departure from the norm that requires explanation, many biologists now see the absence of specialization as something that also requires explanation.

Lastly, directing greater research attention to individualized niches allows for new research and explanatory directions that are not supported by population-level niche research. As we argued, individualized niches are inspired by thought about niche partitioning, and they have sometimes been characterized as segments of population niches (Müller et al. 2020; Müller and Junker 2022). However, strictly speaking individualized niches are not segments of population niches because they are thought to have some dimensions that cannot be dimensions of population niches. Two examples are population density and social relationships (Takola and Schielzeth 2022; Kaiser et al. 2024). These cannot be population niche dimensions since they are not in the population's environment nor are they population-level functional roles, yet they are considered important dimensions of individualized niches.

Thus, research focusing on the individualized niche opens up new explanatory directions such as characterizing the relevance of social contexts to ecological-evolutionary outcomes.

In summary, the individualized niche concept grew out of ecological theory regarding niche width and partitioning, combined with increasing empirical evidence of the ecological relevance of intraspecific specialization. The individualized niche concept is thought by biologists to do explanatory work not captured by the population-level niche concept alone since it incorporates the consideration of individual specialization and its effects on population, community, and evolutionary outcomes. In addition, this research interest is situated within the broader move toward greater integration of ecological and evolutionary research, a goal that may be advanced by moving to the individual level.

This concludes our argument that the individualized niche concept both arose and proliferated in a manner that was driven by specific explanatory goals and changing empirical evidence, and moreover that expanding the niche concept to the individual level has permitted new research directions and perspectives. In the next section, we turn to current conceptual issues in research on individualized niches. We discuss ways in which 'individualized niche' has fragmented into a polysemous term. We argue that some aspects of the plurality may have arisen due to neutral mechanisms, although this plurality is likely to permit benefits.

4. Fragmentation of the individualized niche concept within contemporary research

In contemporary studies of ecology, behavior and evolution the term 'individualized niche' is pluralistic in the sense of having multiple meanings. Interestingly, researchers are only starting to become aware of this polysemy. As philosophers in residence in the CRC, one of our contributions has been to detect implicit conceptual similarities and differences among the diverse research projects of the CRC. This research center has been running since 2018 and consists of empirical biologists working in behavior, ecology and evolution along with some theoretical biologists, statisticians and philosophers. The projects in the CRC use diverse study organisms and methodology but all study how individual organisms differ from each other (e.g., by realizing different individualized niches), how differences in individualized niches arise and change over time (e.g., via niche construction: Odling-Smee, Laland, and Feldman 2003; Aaby and Ramsey 2022; Trappes et al. 2022), and what ecological-evolutionary consequences these differences have.

In order to clarify and evaluate differing conceptions of the individualized niche within the CRC, we have conducted collaborative work with the biologists as well as a

qualitative empirical study of concepts and practices in the CRC.[4] In this paper, we focus on summarizing some respects in which 'individualized niche' has been found to display interesting polysemy.

The distinct conceptions of the individualized niche within the CRC do share five key features (Kaiser and Morrow 2025a). *First*, in line with Hutchinson's general idea (1957), it is assumed that individualized niches are *n*-dimensional spaces. This means that individualized niches have many different niche dimensions, such as temperature of the water that an individual lives in and the species that the individual feeds on. Individualized niches are not conceptualized as concrete spaces or locations (like habitats), even though space often matters because, for instance, different environmental conditions exist in different locations.[5] *Second*, the concept of an individualized niche arises from applying a population-level niche concept to individuals, an assumption corroborated by the historical discussion of this paper. *Third*, only those dimensions that affect an individual's fitness are niche dimensions of its individualized niche. Another way to put this is that individualized niches are characterized by individual fitness functions over the *n*-dimensional space, where the boundaries of the niche are set by a fitness cutoff, such as replacement-level fitness of the individual. *Fourth*, individualized niches arise from the interactions of an individual with its environment. The behaviors and other phenotypic traits of an individual shape how it interacts with its environment, how well the individual's phenotype and behaviors match the environment, and which fitness consequences that has. Without individual-environment interactions there would be no fitness consequences and thus no individualized niche. CRC biologists study several mechanisms by which individuals interact with their environments in ways thought to enhance phenotype-environment match (Müller et al. 2020; Trappes et al. 2022; Kaiser and Trappes 2023). *Fifth*, it follows from the second and third assumption that there can be no pre-existing, vacant or empty individualized niches because individualized niches depend for their existence on the individuals. Individualized niches are thus realized by individuals, in contrast with the view that niches are recesses in the environment that can be empty (Smith and Varzi 1999).

In the next three subsections, we highlight three ways in which the individualized niche concept is pluralistic within contemporary research: it permits multiple views of what

[4] Details of this study's methods and summarized findings may be found at Morrow et al. 2024.

[5] For some individualized niches, such as social niches (Kaiser et al. 2024), space might be completely irrelevant.

counts as a niche dimension (Section 4.1), it can be represented as either temporally extended or time-sliced (Section 4.2), and it can be attributed to individuals or types of individuals (Section 4.3). The combination of shared key features and differing specific meanings might indicate that the individualized niche is an interesting example of a "boundary object," that is, an object that is "plastic enough to adapt to local needs, … yet robust enough to maintain a common identity across sites" (Star and Griesemer 1989, 393). We argue that some of the conceptual changes leading to pluralism may have arisen via neutral processes (Table 2; Case II), although this should not be taken to suggest that the plurality serves no beneficial epistemic roles (see Kaiser and Morrow 2025b), since this can permit application of concepts to a greater number of research designs. Following Novick (2023), we hold that conceptual complexity in general is not harmful and that the costs of attempting to revise conceptual structures are often likely to outweigh any epistemic costs associated with working with complex terms.

4.1. What are the dimensions of the individualized niche?

In our work as philosophers in residence in the CRC, we have distinguished three conceptions of the individualized niche: the environmental individualized niche, the inclusive individualized niche, and the strategy-based individualized niche (Kaiser and Morrow 2025a). All of them share the assumptions specified above and, hence, all are different conceptions of the same core concept of an individualized niche.

According to the *environmental* individualized niche conception, only environmental factors are niche dimensions (loosely following Grinnellian views of the population niche: Section 3.1). Environmental factors or conditions include, for instance, abiotic conditions (e.g., temperature, salinity, pH value) and parts of the social environment (e.g., mating partners, aggressive conspecifics). Specific examples of environmental niche dimensions include parasite density; population density; the green-up date in an area; water depth; abiotic water parameters; water flow speed; and time of day at which an individual is active.[6] An example of a non-CRC study that we interpret as applying the environmental conception of the individualized niche is Carlson et al. (2021), titled "Individual environmental niches in

[6] The examples are due to a workshop on the individualized niche concept for the CRC biologists held in December, 2023. For more information about the workshop (data) see Morrow et al. 2024 (File 7).

mobile organisms," which uses environmental variables characterizing foraging habitat as niche axes.

The *inclusive* conception recognizes not only environmental factors as niche dimensions but also behaviors and other phenotypic traits of the individual whose niche is at stake (compare to the integrated view of population niches: Section 3.1). Even more, it encompasses internal states of the individual as niche dimensions. These can be hormonal states, immune states, or other physiological states. The CRC biologists have identified some important niche dimensions as especially apt for an inclusive niche concept, in some cases because it is unclear whether the dimension should be attributed to the environment or to the individual. Examples like this include daily or seasonal activity patterns, compounds on the cuticle or skin, and behavioral responses to external stimuli. They also mentioned that niche dimensions on this conception could include internal states, such as cortisol level and immune state, and environmental states, such as green-up date.[7] While some CRC biologists expressed reasons for favoring this conception (e.g., being able to focus on the interdependencies between phenotypic traits/behaviors and environmental conditions because both are niche dimensions), we are not aware of any already-published studies that clearly apply it, so it remains to be seen how widely it will be utilized.

The *strategy-based* conception locates the niche entirely on the side of the individual and not the environment. According to this conception, individualized niches are combinations of phenotypic traits of individuals, or spaces of alternative (behavioral) strategies that individuals employ, including trophic strategies. This roughly aligns with Eltonian (functional) conceptions of the population niche (Section 3.1). Environmental conditions are thus not niche dimensions but only constrain or shape these (behavioral) strategies. Examples of strategy-based niche dimensions include individual color (when fitness-relevant, e.g., in organisms that use camouflage), activity budgets, anti-predator traits, habitat use preferences, immune responses, and foraging strategy.[8] An example of a non-CRC study that we interpret as applying the strategy-based conception is Zhao et al. (2014), titled "High intraspecific variability in the functional niche[9] of a predator is associated with

[7] Workshop results: see note 6.

[8] Workshop results: see note 6.

[9] The label 'strategy-based niche' was developed internally to the CRC, so other groups employing a similar conception may use different terms, including 'functional niche' or 'individualized Eltonian niche.'

ontogenetic shift and individual specialization," which investigates functional traits related to feeding to characterize niche variation.

Each of the three conceptions has advocates among the senior CRC biologists, and at least two of them also appear in literature not associated with the CRC. It may seem surprising that individualized niche researchers hold conflicting views about what count as niche dimensions, but we argue that this should be expected in view of the history of 'niche' in ecology.

Earlier in the paper, we briefly outlined the history of functional, environmental and integrated conceptions of the population niche. The three conceptions of the individualized niche we identify within the CRC closely reflect these three conceptions of the population niche. The environmental individualized niche reflects environmental conceptions of the population niche, on which niche dimensions are exclusively features of the environment. The strategy-based individualized niche is similar to the functional population niche, since both focus on behaviors and trophic roles. Finally, the inclusive individualized niche reflects integrated conceptions of the population niche, although the individual-level notion is more encompassing, since it also includes factors internal to the individual.

This neat correspondence did not occur by our design. We have identified the three conceptions of the individualized niche in collaboration with working biologists in the CRC, and we did not have a prior expectation that we would find the conceptual correspondence noted here. However, we are also not the first researchers to note a connection between conceptions of population and individualized niches. For example, Devictor et al. (2010) distinguish Grinnellian and Eltonian (Section 3.1) conceptions of individualized niches. Given that individualized niches have been thought to arise from the partitioning of population niches, it is unsurprising to find that conceptual plurality at the level of individualized niches reflects that at the population level.

Given the correspondence between conceptions of the population and individualized niche, it is possible that the polysemy of 'individualized niche' arose due to biologists differentially inheriting distinct population niche concepts. A neutral hypothesis would be that biologists who have been educated in a theoretical framework favoring the Eltonian niche concept may have gravitated toward the strategy-based individualized niche, while biologists who have been brought up on a Grinnellian niche concept may have gravitated toward an environmental individualized niche, perhaps only implicitly. The dissemination of preexisting niche concepts may serve as an epistemic constraint on the development of new concepts,

where epistemic constraints limit potential conceptual variation in a way that is not directly linked to considerations of epistemic suitability. On this hypothesis, while each of the existing conceptions may have epistemic benefits, the plurality may have arisen independently of epistemic advantages of polysemy per se, and thus the fragmentation has persisted through neutral mechanisms. There are also potential adaptive hypotheses explaining this conceptual structure, for instance, that biologists have deliberately generated multiple conceptions based on the better perceived suitability of a fragmented conceptual structure for investigating diverse research questions. Importantly, one can evaluate the suitability of an existing conceptual structure independently of its origins (Table 1). Even if the structure of the individualized niche concept arose in a neutral manner, this is compatible with particular conceptions having epistemic benefits and does not directly suggest that the conceptual structure ought to be revised.

4.2. Are individualized niches temporally extended?

A second way in which the individualized niche concept is pluralistic has to do with the role of time. Individualized niches (both fundamental and realized) potentially change over the lifetime of individuals. In this regard they differ from population fundamental niches, which change only if a population evolves, and do not otherwise change over ontogenetic timescales. There are currently two lines of thought about how to deal with this change of individualized niches over lifetimes (Takola and Schielzeth 2022). One approach (following MacMahon et al. 1981) is to represent individualized niches as temporally extended. The second is to index individualized niches to life stages.

For empirical studies that cannot follow organisms over their lifetimes, indexing individualized niches to life stages is most practical. For example, field studies of organisms that undergo a metamorphosis, such as various amphibians or insects, are generally not able to re-identify individuals post-metamorphosis. These studies distinguish the individualized niches of life classes, such as the individualized niches of fire salamander adults and larvae (Schulte et al. 2024). In studies this is often done implicitly, and diagrammatic representations of individualized niches do not always clearly signal that they are connected to particular time periods of development. However, defining the focal individual(s) of a study, such as adult and larval fire salamanders, inherently attributes individualized niches to particular life stages.

By contrast, empirical studies that can reliably re-identify individuals and follow them over long time periods are able to study temporally extended individualized niches of

individual organisms (Trappes 2023). This is being done for several animal species, particularly large birds and mammals, for example by fitting them with a transmitter device or by tracking them with video. This allows for researchers to investigate how individualized niches change over time, for instance how the neonatal environment affects movement patterns and activity levels of Antarctic fur seals (*Arctocephalus gazella*) later in life (Nagel et al. 2021).

To sum up, the individualized niche concept is pluralistic in the respect that niches can be conceived of as either temporally extended or as indexed to life stages. This flexibility appears beneficial because it permits a greater number of study designs. However, this does not mean that the plurality came about for this reason (Section 2). Contemporary works most often include depictions of individualized niches that are time-sliced or that do not explicitly incorporate temporal extension (see Carlson et al. 2021, fig. 1; Trappes et al. 2022, fig. 2; Kaiser et al. 2024, fig. 3). An exception is Takola and Schielzeth (2022, figs. 3–5) which includes figures of both types. In general, while researchers are aware that individualized niches change over organisms' lifetimes, there may be less familiarity with works presenting temporally-extended depictions of individualized niches. For instance, recent papers on individualized niches have not cited the MacMahon et al. (1981) paper or other publications utilizing temporally-extended representations. Because niches are often represented by visual figures, and because new figures are often modeled on or adapted from prior ones, the citation and dissemination patterns of works containing well-known figures representing the niche may serve as another epistemic constraint on how niches are conceptualized. The current dominance of time-sliced representations of the niche modeled after figures such as the one reproduced in Fig. 1 may explain why there have not been many attempts to comparatively assess or integrate the two time-related conceptions. These considerations suggest that the process generating this conceptual structure was neutral. Again, it is plausible that each of the temporal views of the individualized niche can contribute to achieving epistemic goals even if the plurality itself is epistemically neutral or arose due to neutral mechanisms.

4.3. Are individualized niches attributed to individuals or groups of individuals?

In addition to the questions about the niche dimensions and temporal extension of an individualized niche, there is a question about whether individualized niches can be attributed to groups of individuals or only to single individuals. We argue that attributing them to both single individuals and types or groups of individuals is legitimate.

Proposed definitions of individualized niches refer to (token) individuals rather than to groups or types of individuals (e.g., Carlson et al. 2021; Trappes et al. 2022). Thinking about a particular organism is often most useful for diagrammatic and pedagogical representations of individualized niches. In addition, many studies of individualized niches collect data at the level of individual organisms, which in principle allows for attribution of realized niches to single individuals. However, in practice, niches of types or groups of individuals are often investigated under the description of individualized niches. Since individualization is a process, multiple individuals can realize the same individualized niche. The term 'individualized niche' does not imply that only a single individual can realize a given individualized niche.

There are several methodological reasons why biologists often focus on groups, even within individual-based studies. For studies that cannot track individuals at all (e.g., laboratory or field studies of very small insects), it is necessary to attribute individualized niches to groups of individuals sharing relevant characteristics. However, many studies can re-identify individuals but still consider individualized niches at the level of types of individuals. One reason is that it is difficult to empirically study the fundamental niche of a single individual, since this would require (on an environmental niche conception) estimating the fitness effects on one individual of a variety of non-actual environmental conditions (see Takola and Schielzeth 2022). Instead, research groups often investigate the niches of salient types of individuals, such as fire salamander larvae (*Salamandra salamandra*) deposited in ponds versus streams (Schulte et al. 2024), female Galápagos sea lions (*Zalophus wollebaeki*) that forage at different ocean depths (Schwarz et al. 2021), or California harvester ant (*Pogonomyrmex californicus*) queens that do or do not tolerate the presence of other queens in their colony (Errbii et al. 2021). A second reason is that the statistical methods used in biological studies generally preclude the possibility of separately analyzing data for individual organisms. While it is now feasible for many behavioral-ecological niche studies to track individuals, the resulting data are always analyzed in groups (e.g., Carlson et al. 2021; Schwarz et al. 2021; Heinze et al. 2022). Moreover, most biologists aim at drawing general conclusions from their empirical findings. Developing generalizations about the ecological and evolutionary consequences of individual differences requires classifying individuals into types. The key feature of individual-based ecological research is not that studies report findings at the level of single individuals, but rather that they investigate within-population variation and the consequences of individual variability (see Trappes 2022).

In this section we have argued that individualized niches can be attributed to groups of individuals of the same type and not only to particular individuals. This flexibility is useful because it allows individualized niches to be investigated within a greater number of study systems and with various methodologies. As we have discussed, however, the fact that conceptual plurality is useful does not necessarily entail that it came about for that purpose. In this case, a potential neutral hypothesis is that the fragmentation occurred because biologists did not notice the difference between attributing individualized niches to token individuals versus groups of similar individuals, since they are accustomed to study designs that utilize replicates. Thus, an adaptive explanation cannot be assumed, although this form of plurality now contributes to epistemic goals.

5. Conclusions

This paper characterizes the origins and structure of the individualized niche concept. We show that the expansion of the population-level concept of a niche to individuals occurred in an adaptive manner, while some aspects of the fragmentation of the individualized niche concept likely occurred via neutral mechanisms. We also illustrate that a neutral origin for a complex conceptual structure (Novick 2023) is compatible with the conceptual structure permitting beneficial uses. In the case of the individualized niche concept, for instance, we argue that the respects in which it is pluralistic permit the concept to be applied to a greater variety of study designs. In closing, we expect this concept to continue undergoing change within currently developing biological research programs, making it a fruitful ongoing case study.

Author contributions statement
KHM drafted most of sections 1, 2, 3, and 4.2-4.3. MIK drafted the beginning of section 4 and section 4.1. Both authors contributed to conceptualizing the paper's arguments and intensively revised all sections.

Acknowledgments
We thank all of the members of the CRC, especially participants in the Individualized Niche Concepts Workshop in December, 2023, which was run by the authors together with Alkistis Elliott-Graves. Thanks to Marlene van den Bos for contributing to the workshop design. We also thank the members of the Philosophy of the Life Sciences work-in-progress group at Bielefeld University for their feedback on this paper and the two anonymous referees.

Funding statement
This research was funded by the German Research Foundation (DFG) as part of the project D02 "Individual-Based Research: Concepts, Epistemology and Integration" (project number:

396781820) in the CRC TRR 212 “A Novel Synthesis of Individualisation across Behaviour, Ecology and Evolution: Niche Choice, Niche Conformance, Niche Construction (NC³)” (project number: 316099922). Research for this paper also profited from the research project “Individualisation in Changing Environments (InChangE)” funded as a part of the programme “Profilbildung 2020”, an initiative of the Ministry of Culture and Science of the State of North-Rhine Westphalia. The sole responsibility for the content of this publication lies with the authors.

References

Aaby, Bendik Hellem, and Grant Ramsey. 2022. “Three Kinds of Niche Construction.” *The British Journal for the Philosophy of Science* 73 (2): 351–72. https://doi.org/10.1093/bjps/axz054.

Albrecht, M., and N.J. Gotelli. 2001. “Spatial and Temporal Niche Partitioning in Grassland Ants.” *Oecologia* 126 (1): 134–41. https://doi.org/10.1007/s004420000494.

Bolnick, Daniel I., Richard Svanbäck, James A. Fordyce, Louie H. Yang, Jeremy M. Davis, C. Darrin Hulsey, and Matthew L. Forister. 2003. “The Ecology of Individuals: Incidence and Implications of Individual Specialization.” *The American Naturalist* 161 (1): 1–28. https://doi.org/10.1086/343878.

Brigandt, Ingo. 2010. “The Epistemic Goal of a Concept: Accounting for the Rationality of Semantic Change and Variation.” *Synthese* 177 (1): 19–40. https://doi.org/10.1007/s11229-009-9623-8.

Cardinale, Bradley J. 2011. “Biodiversity Improves Water Quality through Niche Partitioning.” *Nature* 472 (7341): 86–89. https://doi.org/10.1038/nature09904.

Carlson, Ben S., Shay Rotics, Ran Nathan, Martin Wikelski, and Walter Jetz. 2021. “Individual Environmental Niches in Mobile Organisms.” *Nature Communications* 12 (1): 4572. https://doi.org/10.1038/s41467-021-24826-x.

Chang, Hasok. 2012. “Acidity: The Persistence of the Everyday in the Scientific.” *Philosophy of Science* 79 (5): 690–700. https://doi.org/10.1086/667900.

Chase, Jonathan M., and Mathew A. Leibold. 2003. *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press. https://doi.org/10.7208/chicago/9780226101811.001.0001.

Clutton-Brock, Tim, and Ben C Sheldon. 2010. “Individuals and Populations: The Role of Long-Term, Individual-Based Studies of Animals in Ecology and Evolutionary Biology.” *Trends in Ecology & Evolution* 25 (10): 562–73. https://doi.org/10.1016/j.tree.2010.08.002.

Costa, Gabriel C., Daniel O. Mesquita, Guarino R. Colli, and Laurie J. Vitt. 2008. “Niche Expansion and the Niche Variation Hypothesis: Does the Degree of Individual Variation Increase in Depauperate Assemblages?” *The American Naturalist* 172 (6): 868–77. https://doi.org/10.1086/592998.

Dall, Sasha R. X., Alison M. Bell, Daniel I. Bolnick, and Francis L. W. Ratnieks. 2012. “An Evolutionary Ecology of Individual Differences.” *Ecology Letters* 15 (10): 1189–98. https://doi.org/10.1111/j.1461-0248.2012.01846.x.

De La Riva, Enrique G, Iván Prieto, Sergio De Tomás Marín, Jesús Rodríguez-Calcerrada, Pardis Golabvand, and Javier Galán Díaz. 2023. “Living at the Edge: The Functional Niche Occupation of Woody Plant Communities in the Submediterranean Ecotone.” *Annals of Botany* 132 (3): 471–84. https://doi.org/10.1093/aob/mcad138.

Dehnhard, Nina, Helen Achurch, Judy Clarke, Loïc N. Michel, Colin Southwell, Michael D. Sumner, Marcel Eens, and Louise Emmerson. 2020. “High Inter- and Intraspecific Niche Overlap among Three Sympatrically Breeding, Closely Related Seabird

Species: Generalist Foraging as an Adaptation to a Highly Variable Environment?" *Journal of Animal Ecology* 89 (1): 104–19. https://doi.org/10.1111/1365-2656.13078.
Devictor, Vincent, Joanne Clavel, Romain Julliard, Sébastien Lavergne, David Mouillot, Wilfried Thuiller, Patrick Venail, Sébastien Villéger, and Nicolas Mouquet. 2010. "Defining and Measuring Ecological Specialization." *Journal of Applied Ecology* 47 (1): 15–25. https://doi.org/10.1111/j.1365-2664.2009.01744.x.
Dussault, Antoine C. 2022a. "Does the Study of Facilitation Require a Revision of the Hutchinsonian Niche Concept?" *Biology & Philosophy* 37 (2): 16. https://doi.org/10.1007/s10539-022-09844-3.
———. 2022b. "Functionalism without Selectionism: Charles Elton's 'Functional' Niche and the Concept of Ecological Function." *Biological Theory* 17 (1): 52–67. https://doi.org/10.1007/s13752-020-00360-9.
Elton, Charles. 1927. *Animal Ecology.* New York: The Macmillan Company.
Ereshefsky, Marc. 1998. "Species Pluralism and Anti-Realism." *Philosophy of Science* 65 (1): 103–20.
Errbii, Mohammed, Ulrich R. Ernst, Aparna Lajmi, Eyal Privman, Jürgen Gadau, and Lukas Schrader. 2021. "The *Pogonomyrmex californicus* Social Niche Polymorphism Is a Polygenic Trait Involving a Young Supergene." bioRxiv preprint. https://doi.org/10.1101/2021.03.21.436260.
Feest, Uljana. 2010. "Concepts as Tools in the Experimental Generation of Knowledge in Cognitive Neuropsychology." *Spontaneous Generations: A Journal for the History and Philosophy of Science* 4 (1): 173–90. https://doi.org/10.4245/sponge.v4i1.11938.
Feest, Uljana, and Friedrich Steinle, eds. 2012. *Scientific Concepts and Investigative Practice*. Berlin Studies in Knowledge Research, volume 3. Berlin: De Gruyter.
Frey, Sandra, Jason T. Fisher, A. Cole Burton, and John P. Volpe. 2017. "Investigating Animal Activity Patterns and Temporal Niche Partitioning Using Camera-Trap Data: Challenges and Opportunities." *Remote Sensing in Ecology and Conservation* 3 (3): 123–32. https://doi.org/10.1002/rse2.60.
Griesemer, James R. 1992. "Niche: Historical Perspectives." In *Keywords in Evolutionary Biology*, edited by Evelyn Fox Keller and Elisabeth A. Lloyd, 231–40. Cambridge, MA: Harvard University Press.
Grinnell, Joseph. 1917. "The Niche-Relationships of the California Thrasher." *The Auk* 34 (4): 427–33. https://doi.org/10.2307/4072271.
———. 1924. "Geography and Evolution." *Ecology* 5 (3): 225–29. https://doi.org/10.2307/1929447.
Haueis, Philipp. 2024. "A Generalized Patchwork Approach to Scientific Concepts." *The British Journal for the Philosophy of Science* 75 (3): 741–68. https://doi.org/10.1086/716179.
Heinze, Pauline, Petra Dieker, Hannah M Rowland, and Holger Schielzeth. 2022. "Evidence for Morph-Specific Substrate Choice in a Green-Brown Polymorphic Grasshopper." Edited by Marie Herberstein. *Behavioral Ecology* 33 (1): 17–26. https://doi.org/10.1093/beheco/arab133.
Hutchinson, G. Evelyn. 1957. "Concluding Remarks." *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–17.
Junker, Robert R., Martin H. Lechleitner, Jonas Kuppler, and Lisa-Maria Ohler. 2019. "Interconnectedness of the Grinnellian and Eltonian Niche in Regional and Local Plant-Pollinator Communities." *Frontiers in Plant Science* 10:1371. https://doi.org/10.3389/fpls.2019.01371.

Justus, James. 2019. “Ecological Theory and the Superfluous Niche.” *Philosophical Topics* 47 (1): 105–23. https://doi.org/10.5840/philtopics20194716.
Kaiser, Marie I, Jürgen Gadau, Sylvia Kaiser, Caroline Müller, and S Helene Richter. 2024. “Individualized Social Niches in Animals: Theoretical Clarifications and Processes of Niche Change.” *BioScience* 0:1–13. https://doi.org/10.1093/biosci/biad122.
Kaiser, Marie I., and Katie H. Morrow. 2025a. “How to Balance Conceptual Unity and Plurality: The Case of the Individualized Niche Concept.” EcoEvoRxiv preprint. https://doi.org/10.32942/X2GS7J.
———. 2025b. “On the Epistemic Roles of the Individualized Niche Concept in Ecology, Behavioral Biology, and Evolutionary Biology.” *Philosophy of Science* 92 (1): 162–84. https://doi.org/10.1017/psa.2024.48.
Kaiser, Marie I, and Rose Trappes. 2023. “Individual-Level Mechanisms in Ecology and Evolution.” In *From Biological Practice to Scientific Metaphysics*, edited by William C. Bausman, Janella K. Baxter, and Oliver M. Lean, 116–52. Minnesota Studies in the Philosophy of Science. Minneapolis: University of Minnesota Press.
Layman, Craig A., Seth D. Newsome, and Tara Gancos Crawford. 2015a. “Individual-Level Niche Specialization within Populations: Emerging Areas of Study.” *Oecologia* 178 (1): 1–4. https://doi.org/10.1007/s00442-014-3209-y.
———, eds. 2015b. “Special Feature on Individual-Level Niche Specialization.” *Oecologia* 178 (1).
Lear, Karissa O., Nicholas M. Whitney, John J. Morris, and Adrian C. Gleiss. 2021. “Temporal Niche Partitioning as a Novel Mechanism Promoting Co-Existence of Sympatric Predators in Marine Systems.” *Proceedings of the Royal Society B: Biological Sciences* 288 (20210816). https://doi.org/10.1098/rspb.2021.0816.
Leibold, Matthew A. 1995. “The Niche Concept Revisited: Mechanistic Models and Community Context.” *Ecology* 76 (5): 1371–82. https://doi.org/10.2307/1938141.
Levins, Richard, and Richard C. Lewontin. 1985. *The Dialectical Biologist.* Harvard University Press.
Machery, Edouard. 2005. “Concepts Are Not a Natural Kind.” *Philosophy of Science* 72 (3): 444–67. https://doi.org/10.1086/498473.
MacMahon, James A., David J. Schimpf, Douglas C. Andersen, Kimberly G. Smith, and Robert L. Bayn. 1981. “An Organism-Centered Approach to Some Community and Ecosystem Concepts.” *Journal of Theoretical Biology* 88 (2): 287–307. https://doi.org/10.1016/0022-5193(81)90077-1.
Michalko, Radek, and Stano Pekár. 2015. “Niche Partitioning and Niche Filtering Jointly Mediate the Coexistence of Three Closely Related Spider Species (Araneae, Philodromidae).” *Ecological Entomology* 40 (1): 22–33. https://doi.org/10.1111/een.12149.
Morrow, Katie H. 2024. “Niches and Niche Models.” *The British Journal for the Philosophy of Science*. https://doi.org/10.1086/730329.
Morrow, Katie H., Marlene van den Bos, Alkistis Elliott-Graves, and Marie I. Kaiser. 2024. “Individual-Based Research: Concepts, Epistemology and Integration.” *OSF.* https://doi.org/10.17605/OSF.IO/X3HSJ.
Müller, Caroline, Barbara A. Caspers, Jürgen Gadau, and Sylvia Kaiser. 2020. “The Power of Infochemicals in Mediating Individualized Niches.” *Trends in Ecology & Evolution* 35 (11): 981–89. https://doi.org/10.1016/j.tree.2020.07.001.
Nagel, Rebecca, Sina Mews, Timo Adam, Claire Stainfield, Cameron Fox-Clarke, Camille Toscani, Roland Langrock, Jaume Forcada, and Joseph I. Hoffman. 2021. “Movement Patterns and Activity Levels Are Shaped by the Neonatal Environment in Antarctic

Fur Seal Pups.” *Scientific Reports* 11 (1): 14323. https://doi.org/10.1038/s41598-021-93253-1.
Neto, Celso. 2020. “When Imprecision Is a Good Thing, or How Imprecise Concepts Facilitate Integration in Biology.” *Biology & Philosophy* 35 (6): 58. https://doi.org/10.1007/s10539-020-09774-y.
Newsome, Seth D., M. Tim Tinker, Verena A. Gill, Zachary N. Hoyt, Angela Doroff, Linda Nichol, and James L. Bodkin. 2015. “The Interaction of Intraspecific Competition and Habitat on Individual Diet Specialization: A near Range-Wide Examination of Sea Otters.” *Oecologia* 178 (1): 45–59. https://doi.org/10.1007/s00442-015-3223-8.
Novick, Rose. 2023. “The Neutral Theory of Conceptual Complexity.” *Philosophy of Science* 90: 1021–1030. https://doi.org/10.1017/psa.2023.25.
Odling-Smee, F. John, Kevin N. Laland, and Marcus W. Feldman. 2003. *Niche Construction: The Neglected Process in Evolution*. Princeton University Press.
Pianka, Eric R., Laurie J. Vitt, Nicolás Pelegrin, Daniel B. Fitzgerald, and Kirk O. Winemiller. 2017. “Toward a Periodic Table of Niches, or Exploring the Lizard Niche Hypervolume.” *The American Naturalist* 190 (5): 601–16. https://doi.org/10.1086/693781.
Pocheville, Arnaud. 2015. “The Ecological Niche: History and Recent Controversies.” In *Handbook of Evolutionary Thinking in the Sciences*, edited by Thomas Heams, Philippe Huneman, Guillaume Lecointre, and Marc Silberstein, 547–86. Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-94-017-9014-7_26.
Robertson, Andrew, Robbie A. McDonald, Richard J. Delahay, Simon D. Kelly, and Stuart Bearhop. 2015. “Resource Availability Affects Individual Niche Variation and Its Consequences in Group-Living European Badgers *Meles meles*.” *Oecologia* 178 (1): 31–43. https://doi.org/10.1007/s00442-014-3202-5.
Roughgarden, Jonathan. 1972. “Evolution of Niche Width.” *The American Naturalist* 106 (952): 683–718.
Santana, Carlos. 2018. “Biodiversity Is a Chimera, and Chimeras Aren’t Real.” *Biology & Philosophy* 33:15. https://doi.org/10.1007/s10539-018-9626-2.
Sanz-Aguilar, Ana, Martina Carrete, Pim Edelaar, Jaime Potti, and José L. Tella. 2015. “The Empty Temporal Niche: Breeding Phenology Differs between Coexisting Native and Invasive Birds.” *Biological Invasions* 17 (11): 3275–88. https://doi.org/10.1007/s10530-015-0952-x.
Schirmer, Annika, Julia Hoffmann, Jana A. Eccard, and Melanie Dammhahn. 2020. “My Niche: Individual Spatial Niche Specialization Affects within- and between-Species Interactions.” *Proceedings of the Royal Society B: Biological Sciences* 287 (1918): 20192211. https://doi.org/10.1098/rspb.2019.2211.
Schulte, Laura, Pia Oswald, Max Mühlenhaupt, Edith Ossendorf, Sabine Kruse, Sylvia Kaiser, and Barbara A. Caspers. 2024. “Stress Response of Fire Salamander Larvae Differs between Habitat Types.” *Royal Society Open Science* 11 (4): 231304. https://doi.org/10.1098/rsos.231304.
Schwarz, Jonas F. L., Sina Mews, Eugene J. DeRango, Roland Langrock, Paolo Piedrahita, Diego Páez-Rosas, and Oliver Krüger. 2021. “Individuality Counts: A New Comprehensive Approach to Foraging Strategies of a Tropical Marine Predator.” *Oecologia* 195:313–25. https://doi.org/10.1007/s00442-021-04850-w.
Sheppard, Catherine E., Richard Inger, Robbie A. McDonald, Sam Barker, Andrew L. Jackson, Faye J. Thompson, Emma I. K. Vitikainen, Michael A. Cant, and Harry H. Marshall. 2018. “Intragroup Competition Predicts Individual Foraging Specialisation

in a Group-Living Mammal.” *Ecology Letters* 21 (5): 665–73. https://doi.org/10.1111/ele.12933.
Siefert, Andrew, Cyrille Violle, Loïc Chalmandrier, Cécile H. Albert, Adrien Taudiere, Alex Fajardo, Lonnie W. Aarssen, et al. 2015. “A Global Meta-Analysis of the Relative Extent of Intraspecific Trait Variation in Plant Communities.” *Ecology Letters* 18 (12): 1406–19. https://doi.org/10.1111/ele.12508.
Smith, Barry, and Achille C. Varzi. 1999. “The Niche.” *Noûs* 33 (2): 214–38.
Smith, Thomas Bates. 1987. “Bill Size Polymorphism and Intraspecific Niche Utilization in an African Finch.” *Nature* 329 (6141): 717–19. https://doi.org/10.1038/329717a0.
Soberón, Jorge. 2007. “Grinnellian and Eltonian Niches and Geographic Distributions of Species.” *Ecology Letters* 10 (12): 1115–23. https://doi.org/10.1111/j.1461-0248.2007.01107.x.
Star, Susan Leigh, and James R. Griesemer. 1989. “Institutional Ecology, ‘Translations’ and Boundary Objects: Amateurs and Professionals in Berkeley’s Museum of Vertebrate Zoology, 1907-39.” *Social Studies of Science* 19 (3): 387–420. https://doi.org/10.1177/030631289019003001.
Sterelny, Kim, and Paul Griffiths. 1999. *Sex and Death: An Introduction to Philosophy of Biology*. Chicago: University of Chicago Press.
Svanbäck, Richard, and Daniel Bolnick. 2005. “Intraspecific Competition Affects the Strength of Individual Specialization: An Optimal Diet Theory Method.” *Evolutionary Ecology Research* 7: 993–1012.
Székely, Diana, Dan Cogălniceanu, Paul Székely, and Mathieu Denoël. 2020. “Adult—Juvenile Interactions and Temporal Niche Partitioning between Life-Stages in a Tropical Amphibian.” *PLOS ONE* 15 (9): e0238949. https://doi.org/10.1371/journal.pone.0238949.
Takola, Elina, and Holger Schielzeth. 2022. “Hutchinson’s Ecological Niche for Individuals.” *Biology & Philosophy* 37 (4): 25. https://doi.org/10.1007/s10539-022-09849-y.
Taylor, Henry, and Peter Vickers. 2017. “Conceptual Fragmentation and the Rise of Eliminativism.” *European Journal for Philosophy of Science* 7 (1): 17–40. https://doi.org/10.1007/s13194-016-0136-2.
Trappes, Rose. 2021. “Defining the Niche for Niche Construction: Evolutionary and Ecological Niches.” *Biology & Philosophy* 36 (3): 31. https://doi.org/10.1007/s10539-021-09805-2.
———. 2022. “Individual Differences, Uniqueness, and Individuality in Behavioural Ecology.” *Studies in History and Philosophy of Science* 96:18–26. https://doi.org/10.1016/j.shpsa.2022.08.007.
———. 2023. “How Tracking Technology Is Transforming Animal Ecology: Epistemic Values, Interdisciplinarity, and Technology-Driven Scientific Change.” *Synthese* 201 (4): 128. https://doi.org/10.1007/s11229-023-04122-5.
Trappes, Rose, Behzad Nematipour, Marie I Kaiser, Ulrich Krohs, Koen J van Benthem, Ulrich R Ernst, Jürgen Gadau, et al. 2022. “How Individualized Niches Arise: Defining Mechanisms of Niche Construction, Niche Choice, and Niche Conformance.” *BioScience* 72 (6): 538–48. https://doi.org/10.1093/biosci/biac023.
Van Valen, Leigh. 1965. “Morphological Variation and Width of Ecological Niche.” *The American Naturalist* 99 (908): 377–90. https://doi.org/10.1086/282379.
Wakil, Samantha, and James Justus. 2022. “The ‘Niche’ in Niche-Based Theorizing: Much Ado about Nothing.” *Biology & Philosophy* 37 (2): 10. https://doi.org/10.1007/s10539-022-09839-0.

West-Eberhard, Mary Jane. 2005. “Developmental Plasticity and the Origin of Species Differences.” *Proceedings of the National Academy of Sciences* 102:6543–49. https://doi.org/10.1073/pnas.0501844102.

Whittaker, R. H., S. A. Levin, and R. B. Root. 1973. “Niche, Habitat, and Ecotope.” *The American Naturalist* 107 (955): 321–38.

Zhao, Tian, Sébastien Villéger, Sovan Lek, and Julien Cucherousset. 2014. “High Intraspecific Variability in the Functional Niche of a Predator Is Associated with Ontogenetic Shift and Individual Specialization.” *Ecology and Evolution* 4 (24): 4649–57. https://doi.org/10.1002/ece3.1260.