

# **On the Epistemic Roles of the Individualized Niche Concept in Ecology, Behavioral and Evolutionary Biology**

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## **Abstract**

We characterize four fruitful and underappreciated epistemic roles played by the concept of an individualized niche in contemporary biology, utilizing results of a qualitative empirical study conducted within an interdisciplinary biological research center. We argue that the individualized niche concept (1) shapes the research agenda of the center, (2) facilitates explaining core phenomena related to inter-individual differences, (3) helps with managing individual-level causal complexity, and (4) promotes integrating local knowledge from ecology, evolutionary biology, behavioral biology and other biological fields. We thereby also challenge arguments that the niche concept is superfluous in ecology.

## **1. Introduction**

This paper argues that the concept of an individualized niche plays central epistemic roles within a contemporary biological research field at the intersection of ecology, animal behavior and evolution. With this, we challenge claims that the concept of the niche—one of the most recognizable and celebrated ideas associated with ecological science—is explanatorily superfluous and can even be eliminated from theoretical ecology (e.g., McNerny and Etienne 2012; Angilletta et al. 2019; Wakil and Justus 2022). Authors including Wakil and Justus (2022) argue that “niche” has been subject to a history of inconsistent definitions and that it fails to capture what does the causal and explanatory work in theoretical ecology and ecological modeling. While we agree with some of their points about particular models, we hold that it is also important to consider the wide variety of epistemic roles that the niche concept plays in contemporary biology, not only in theoretical ecology.

Scientific concepts can play various epistemic and non-epistemic roles in scientific practice: contributing to the self-conception of a research program (Bausman 2019, 2022) or setting a research agenda (Love 2013, Brigandt 2012, 2020); classifying entities and making precise distinctions (Brigandt 2012); guiding the investigation of phenomena and the design of empirical studies (Feest 2010; Feest and Steinle 2012); providing or facilitating explanation

(Brigandt 2010, 2012; Villegas et al. 2023); and motivating interdisciplinary research and integrating findings across disciplines (Love 2013, Brigandt 2020).

We use the term “epistemic role” to refer to the diverse ways in which scientists can use scientific concepts to pursue a scientific aim. The notion of epistemic roles is similar to the notion of functions that concepts serve in scientific practices (e.g., Novick 2023). The assumption that concepts are used by scientists to pursue specific, local scientific aims is widespread in the literature (e.g., Brigandt 2010; Chang 2012; Brigandt and Rosario 2020). In this paper, we focus on epistemic aims, that is, aims that are related to scientific knowledge formation. Revealing the epistemic roles of scientific concepts requires analyzing how concepts are used in scientific practice and how they contribute to epistemic aims (similar to Feest and Steinle 2012). We analyze the “forward-looking nature” (Brigandt 2020; Bloch-Mullins 2020) of the individualized niche concept, that is, how it guides ongoing scientific practice.

Because concepts play epistemic roles at many stages of a research practice, it would be limiting to only examine scientific publications. Given this, we adopted a partly empirical methodology. As philosophers in residence in the interdisciplinary Transregio Collaborative Research Center (TRR-CRC) 212 “A Novel Synthesis of Individualisation across Behaviour, Ecology and Evolution: Niche Choice, Niche Conformance, Niche Construction (NC<sup>3</sup>)” (hereafter “CRC”), we undertook an empirical study of the biologists’ use of concepts in their research. This paper illustrates the detailed epistemic findings that can be achieved by adopting an empirical methodology as philosophers of science (e.g., Andersen et al. 2015; Hangel and ChoGlueck 2023; Ivanova et al. 2024). Our arguments also bring into contact the growing philosophical literature on the niche (e.g., Justus 2013, 2019, 2021; Trappes 2021; Dussault 2022a, 2022b; Takola and Schielzeth 2022; Aaby and Ramsey 2022; Wakil and Justus 2022; Coninx 2023; Morrow 2024) with the literature on the structures and epistemic roles of scientific concepts (e.g., Brigandt 2010, 2012, 2020; Feest 2010; Feest and Steinle 2012; Haueis 2023, 2024; Novick 2023).

In section 2, we explain the relevant concepts in the CRC, especially the concept of the individualized niche. In section 3, we introduce the methodology of our empirical study. Sections 4-8 present our main positive findings about epistemic roles of the individualized niche concept. We argue that the individualized niche concept shapes the research agenda of the CRC (section 5), facilitates explaining core phenomena in the field (section 6), helps manage individual-level causal complexity (section 7), and promotes integrating knowledge from ecology, evolutionary and behavioral biology (section 8). Section 9 further addresses criticisms of the niche concept.

## 2. Studying Individualized Niches

Philosophers of science will be familiar with the niche as a concept usually applied to populations or species. “Niche” is a pluralistic term that has been defined in a series of distinct ways throughout the history of ecology, with different definitions often playing slightly different epistemic roles (Griesemer 1992; Pocheville 2015; Trappes 2021; Morrow 2024). Following G. E. Hutchinson, the population-level ecological niche is often thought of as the range of environmental conditions tolerated by a population (Hutchinson 1957). In the CRC, researchers are investigating niches at the individual level. Individualized niches are roughly the set of environmental conditions that affect an individual’s fitness.<sup>1</sup> Individuals often utilize different portions of a population’s niche space (e.g., Bolnick et al. 2003; Dall et al. 2012; Layman et al. 2015; Schirmer et al. 2020) – a phenomenon called intrapopulation specialization. This phenomenon is shown to have important ecological and evolutionary consequences.

Individualized niches arise from individuals interacting in specialized ways with their environments. Researchers in the CRC characterize individual-environment interactions according to three niche-altering mechanisms, which are referred to as niche choice, niche conformance, and niche construction – in short NC<sup>3</sup> mechanisms (Trappes et al. 2022; Kaiser and Trappes 2023). While several of these terms refer to existing notions, the CRC has assigned them specific definitions for the context of individual-based research. First, niche construction refers to actions of individuals that modify their environment, making the environment more suitable for their phenotype. Second, niche choice refers to instances of dispersal in which individuals select an environment better suited to their phenotype, and also selective interaction of an individual with certain parts of an environment. Third, niche conformance refers to the alteration of an individual’s phenotype to make it more suited to the surrounding environment.

We identify several epistemic roles that the individualized niche concept plays in the CRC’s research practice. While our focus is on developing these positive roles, this paper draws two additional conclusions: First, our analysis of the epistemic roles of the individualized niche concept shows that some critical assessments of niche concepts in ecology have focused too narrowly on theoretical and definitional problems (e.g., McInerney and Etienne 2012; Angilletta et al. 2019; Justus 2013, 2019, 2021; Wakil and Justus 2022) and not addressed other roles of niche concepts within biological practice. Second, we more generally

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<sup>1</sup> For expository simplicity we assume an environmental individualized niche conception in this paper. Other individualized niche conceptions also include behaviors, traits and internal states of the individual as niche dimensions.

conclude that philosophical analysis of scientific concepts should not be limited to the practices of theorizing and modeling, but also take into account the variety of roles that scientific concepts play in regard to, for instance, research agenda formation, study design, explanation, integrating knowledge, and causal selection.

### 3. Methods

This paper arose from our work as philosophers within an interdisciplinary research center. The CRC has around 50 researchers from multiple disciplines, mainly from ecology, evolutionary biology, and behavioral biology. It has been running since 2018 and includes members mainly from Bielefeld University and the University of Münster. The 21 research projects are organized in four research areas: empirical projects studying primarily niche choice (A), niche conformance (B), or niche construction (C) as well as the theoretical research area (D), connecting theory and empiricism (containing projects on philosophy, modeling, meta-analysis and statistics). The diverse projects within the CRC all investigate individual differences, individualized niches, and NC<sup>3</sup> mechanisms leading to changes of individualized niches.

In 2023 we performed a qualitative empirical study consisting mainly of a questionnaire and semi-structured interviews with CRC biologists.<sup>2</sup> The study was approved by the Ethics Review Board of Bielefeld University (application number 2023-069). The aims of our study were to investigate how the biologists in the CRC study and conceptualize individualized niches, the prospects and challenges of individual-based research, and how epistemic integration happens in their biological research. In this paper we often make claims about the CRC in general. However, our claims about epistemic roles of concepts concern the biologists and biological research in the CRC. Since we are members of the CRC, our interpretation of the results also draws on our personal expertise and acquaintance with the biologists.

The questionnaire was conducted in the summer of 2023. We had 23 responses, a 51% response rate out of scientists currently employed by the CRC (the 6 philosophers were excluded from the study). We asked participants short-answer questions about the individualized niche concept, individual-based research, and integration practices in interdisciplinary science (Appendix 1).

The semi-structured interviews with the CRC members were conducted in the summer 2023. We did a total of 12 interviews (42% women; 75% native speakers of German; 25% native speakers of other languages). Interviewees included 9 project leaders, 1 postdoctoral

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<sup>2</sup> A detailed description of the qualitative empirical study, including our methodology and (coding) results is published as an Open Science Framework project (Morrow et al. 2024).

researcher and 2 PhD students, in total 27% of non-philosopher members of the CRC. The sample was chosen mainly for breadth: we selected interviewees to cover a range of disciplinary backgrounds, animal species and research topics. For instance, 1 interviewee is a theoretical biologist, 4 interviewees are studying vertebrates, and 7 interviewees are studying invertebrates.

Interviews were between 30 and 55 minutes long, with two interviewers and a single interviewee, usually conducted in the interviewee's work office. The interviews had two parts: questions about individual-based research and questions about the individualized niche concept (Appendix 2). This paper only reports findings about individualized niches. Interviews were recorded and later transcribed to permit analysis.

We analyzed the results of the questionnaire responses and transcribed interviews by assigning codes to the text, short phrases that condense content and "tag" important and often repeated ideas. We developed an initial codebook (MacQueen et al. 1998) in a theory-driven, top-down manner with the goal of identifying claims relevant to answering our research questions. The final codebook was iteratively revised based on our close reading of the transcripts.

Given the selection of interviewees for breadth together with our personal acquaintance with the CRC members, we expect our sample to reflect the range of perspectives among the biological project leaders in the CRC. We do not take our data to reflect the views of "biologists in general."

#### **4. General Empirical Results**

This section presents some general results from our coding analysis. The codes that we used are in italics. Eight of 12 interviewees (67%) indicated that the *individualized niche concept is important or useful for their research*; four interviewees (33%) stated this about the NC<sup>3</sup> concepts (even if we did not mention these concepts in our questions). Three interviewees (25%) suggested that the *individualized niche concept is not important for their research* and one interviewee (8%) was *unclear whether the individualized niche concept is important*. Since the interviewees were asked about the concept in their own research project, the answers reflect the fact that a minority of the biologists run empirical studies for which they feel the individualized niche concept is not central (often those studies focus more directly on the NC<sup>3</sup> concepts). In addition, all of the interviewees identified at least one epistemic role of the individualized niche concept within the CRC or their work conceived more broadly (table 1).

Four interviewees mentioned that there are barriers to utilizing the individualized niche concept in their research. All four stated that the *individualized niche concept is not*

*common* in their research field, so that referees and talk audiences might not understand the concept or even evaluate its usage negatively. This reflects the fact that the individualized niche concept is more recent and less well-known than the population-level niche concept, although the former is growing in popularity as a research target. In response to this, some biologists alternate between foregrounding or downplaying individualized niche-related terms depending on their audience.

**Table 1:** Codes assigned to the responses to the interview question “What roles does the individualized niche concept play in your research?” (including responses to follow-up questions)

Code	Number of Interviewees	Percentage of Interviewees (%)
Promotes studying individual variation	7	58
Influences research agenda	6	50
Important for communication with externals	6	50
Important for communication within the CRC	4	33
Allows integrating different biological perspectives	2	17
Influences measurement/experiment	2	17
Important for applications (animal welfare, conservation)	1	8

In our questionnaire, we asked the biologists how they would explain the importance of the niche concept within their research. Of the 23 responses, 18 agreed that the *individualized niche concept is important or useful* (78%) while four responses were *unclear whether the individualized niche concept is important* (17%) and one response could not be coded. Due to the different format, the different questions, and the different people being asked, the epistemic roles mentioned in the questionnaire (table 2) and interviews diverge from each other. In general, the responses to the questions in the questionnaire were much shorter and the respondents rarely referred to more than one epistemic role.

**Table 2:** Codes assigned to the responses (in total 23) to the questionnaire question “How would you explain... the importance of the niche concept within your research?”

Code	Number of Questionnaire Respondents	Percentage of Questionnaire Respondents (%)
Promotes studying individual variation	12	52
Facilitates understanding/explanation	8	35
Influences research agenda	2	9
Important for applications (animal welfare, conservation)	2	9
Allows integrating different biological perspectives	1	4
Influences measurement/experiment	1	4

One will notice that the codes assigned to the interview and questionnaire responses do not map identically to the four roles that we argue for in this paper (to be summarized just below). This is because the four roles represent our interpretation of the overall coding results together with specific important passages from the interviews, our personal experience from our collaborations, and relevant biological and philosophical literature.

The coding results represented in tables 1 and 2 provide initial empirical support for the four epistemic roles identified in this paper. The first epistemic role “shaping the research agenda” (section 5) is mentioned by half of the interviewees and by two questionnaire respondents (9%). One way in which the individualized niche concept shapes the research agenda is by drawing research attention to individual variation, which is among the most frequently assigned codes in the interviews (58%)<sup>3</sup> and questionnaire (52%). Another way is by shaping experiments and measurement, mentioned by some interviewees (17%) and by one questionnaire respondent. The second epistemic role “facilitating explanation” (section 6) is among the most frequently assigned codes in the questionnaire (35%). The third epistemic role “managing causal complexity” (section 7) is supported by our close reading of certain interview passages and other sources rather than by coding results. The fourth epistemic role “fostering integration” (section 8) is mentioned in some interviews (17%) and in one questionnaire. It was more often stated in the interviews that the individualized niche concept is important for communication *within* and *outside* of the CRC (respectively, 33% and 50%).

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<sup>3</sup> The percentages in this paragraph are percentages of interviewees or questionnaire respondents, so they do not “double count” responses that mention an idea twice.

Since epistemic integration requires that biologists across different fields can communicate ideas, we argue that the communicative role of the individualized niche concept contributes to its integrative role (section 8). So much for the general results from our empirical study. In the following sections we will explain the four epistemic roles in more detail and provide further empirical support.

## **5. First Epistemic Role: Shaping the Research Agenda**

The individualized niche concept (and the closely related NC<sup>3</sup> concepts) shape the research agenda or “research program” (Bausman 2019) of the biologists in the CRC. We consider four major aspects that characterize a research agenda: phenomena, research questions, study design, and data analysis. The individualized niche concept shapes the CRC’s research agenda in regard to all four of these aspects. The following quotes point to the first epistemic role of the individualized niche concept:<sup>4</sup>

“It’s really, I would say, it [the individualized niche concept] has changed my whole research agenda... I have different things in mind when I conceptualize my research. I have different things in mind when I analyze research and how I write about it.” (Interviewee 08)

“I think it [the individualized niche concept] is a concept that is, I mean, not radically new or different or unseen before, but I think it opens a particular perspective. And of course, this changes whatever categories you see the world with, influences what you see.” (Interviewee 09)

One major way in which the individualized niche concept shapes the CRC’s research agenda is by focusing research attention on the ubiquity and explanatory importance of individual variation. In regard to phenomena and research questions, thinking about individualized niches implies focusing on how the individuals in a population differ in their phenotypic traits and behaviors and, consequently, how they differently interact with the environment. The different ways in which individuals interact with their environment is what gives rise to individualized niches. The biologists in the CRC seek to understand which individual differences exist, how they arise and change (a process called individualization; Kaiser et al. 2024b), what their underlying molecular mechanisms are, and what evolutionary and

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<sup>4</sup> In the interviews we asked the biologists what roles the individualized niche concept plays in their research (Appendix 2). If not indicated otherwise, the quotes are answers to this question. Most of the quotes represent repeated ideas, but for the sake of length we present only a selection of relevant quotes.



ecological consequences they have (Kaiser and Trappes 2023). The following quotes illustrate how the individualized niche concept draws attention to individual variation:

“It [the individualized niche concept] has helped me to reshape my thinking tremendously. I think the focus on individuals is the biggest thing that I have gained.... I want to understand the individualization process. I want to understand what makes individuals different from each other. And I think individualized niches are a very great concept to understand how that comes into being, because essentially, it's an interactive process between individual and environment.” (Interviewee 08)

“I think the only thing that has changed since working on this project... is that we became aware to look more into individual variation. And when before we saw that as annoying and making it more difficult to find differences between treatment groups, now we're excited by it because we see that this is maybe what we are looking for, an individualization going on. So, I think this is what has changed and what is the important role of this concept.” (Interviewee 10)

The last quote illustrates the role of the individualized niche concept in changing how biological phenomena are studied. Before joining the CRC, the interviewee regarded individual variation as problematic, yet now it is the center of their research interest.

The concept of an individualized niche also shapes study design and data analysis. Many biologists in the CRC aim at collecting individual-level data, for instance by tracking individuals in space and time or performing experiments in which single individuals are identified:

“I would say, [the individualized niche concept influences] also how we design studies, that we always try to take individual data... is already something that differs from what most people do. So, it would be much easier to... [treat] the whole group, for example.... [But] we probably bring out the animals, we individualize them or mark them or take samples so that we know in the end which individuals have survived... and so on. And most studies wouldn't do that, I think. [They] would be more interested in the effect on a group, on a population level.” (Interviewee 04)

One interviewee explained how data analysis in the CRC differs from other group- or population-based research:

“So, at least in my case, there are a lot of... differences. As I said, first of all, I do have concern in using average to describe my data, because many times it happens that the average does not represent the individuality that they see... So, if I have position data, and I do the mean of the position data, that doesn't really tell me anything about the variability that I see... Calculation-wise, comparing mean, you use the standard statistical data, that could be t-test or ANOVA and so on. When you compare variance or variability, you need to use other tests. The two-sided F-test, Ansari test, Mood test, and so on.” (Interviewee 01)

This interviewee indicated that some of these statistical tests are less well-known but better suited to capturing individual variability, requiring the CRC members to learn new statistical methods.

A closely related way in which the individualized niche concept influences the research agenda of the CRC, is by focusing research attention on individual-environment interactions. Population-level conceptions of the niche have to do with how populations interact with their environments (Hutchinson 1957; Chase and Leibold 2003). Similarly, *individualized* niches are thought to arise from individual-environment interactions (e.g., Takola and Schielzeth 2022; Carlson et al. 2021). Individuals differ not only in their phenotypes but also in how they interact with their environments (Fokkema et al. 2021). For example, individual Galápagos sea lions (*Zalophus wolfebaeki*) have several individualized niches because they pursue distinct foraging strategies: some are benthic divers, others are pelagic or night divers (Schwarz et al. 2021). This affects, for instance, which prey species they feed on.

The individualized niche concept plays the role of foregrounding individual-environment interactions together with the concepts of niche choice, conformance and construction (NC<sup>3</sup>), as the following quotes show. The first quote refers to the interactions of an individual with its social environment.

“I think... it’s more like these mechanisms, how we get individualized, like this niche construction, conformance, and choice. I think that was really, I think, quite interesting for me in the sense of interpreting the interaction between the [individuals].” (Interviewee 03)

“I would say I could do some of the things we do without this [individualized niche] concept, but not everything. [...] it’s not that we do a completely different type of research. We are still interested in host-parasite interaction, how evolution is, or as an example how fast the evolutionary process is. But the interest in niche construction and how different individuals influence niche construction is certainly only possible with the individualized niche concept.” (Interviewee 04)

As introduced in section 2, NC<sup>3</sup> concepts enable biologists to study how individuals interact (differently) with their environments and how this gives rise to changes of individualized niches (Trappes et al. 2022; Kaiser and Trappes 2023). Since NC<sup>3</sup> processes consist of individual-environment interactions it is clear that they draw research attention to individual-environment interactions. Moreover, NC<sup>3</sup> concepts facilitate studying individual-environment interactions because they provide the biologists with specific interpretations of individual-environment interactions (section 6).

To conclude, the first epistemic role of the individualized niche concept is that it shapes the CRC’s research agenda by focusing research attention on individual variation and

on individual-environment interactions. We now turn to the role that the concept plays in the context of explanation.

## **6. Second Epistemic Role: Facilitating Explaining Individual Variation**

In our questionnaire (Appendix 1), we asked the biologists in the CRC to specify why they think the individualized niche concept is important to their research. In their answers, many biologists referred to the role that the concept plays in developing explanations:

“It is now very clear that animals differ individually in behavioral tendencies - how these individual differences arise, could be explained via the individualized niche concept.” (Respondent 8)

“It is very well known that individuals differ in their phenotypes and interact differently with their environment. Thus, to understand how individuals can adapt to changing environments we not only need to study this question at the species or population level but also at the level of the individual. This understanding is crucial for profound insights into both ecological adjustment and evolutionary adaptation in response to a rapidly changing world.” (Respondent 12)

“it [the individualized niche concept] helps to envision evolutionary and ecological consequences of individual differences in behavioral traits.” (Respondent 20)

These quotes point to two major epistemic roles of the individualized niche concept in regard to explanation: First, it facilitates explaining how individual differences in phenotypes arise, e.g., different behavioral tendencies (first quote); second, the individualized niche concept facilitates explaining the ecological-evolutionary consequences of individual differences (last two quotes).

Consider the first of these explanatory roles. The individualized niche concept helps to develop explanations of how individual differences in phenotypes arise because it requires the biologists to look at how individuals interact differently with their environments (and what fitness consequences this has). For instance, biologists hypothesize that some zebra finch males (*Taeniopygia guttata*) react to a high number of zebra finch males in their social environment by adjusting their social behavior in two different ways (both are cases of niche conformance): some invest into parental care, while others show aggressive behavior and increase the competitiveness of their sperm (Lilie et al. 2022). Both behavioral strategies seem to have positive consequences for the fitness of the individuals in an environment with a high density of zebra finch males. The individuals adopting the different behavioral strategies thus realize different individualized niches. This example shows that the individualized niche concept, together with the NC<sup>3</sup> concepts, facilitates explaining how individual differences arise and change.

We are not claiming that the individualized niche concept is part of the explanation of how the specific differences in behavioral strategies of zebra finch males arise: the individualized niche concept is far too general to be a part of such a specific explanation. Rather, utilizing the concept promotes developing the explanation. Thus, it serves a scaffolding or schematic role in explanatory contexts. This is one of the types of roles of scientific concepts that has not been a focus in the critical discussions of niche concepts so far.

A second explanatory role of the individualized niche concept is that it facilitates explaining ecological-evolutionary consequences of individual differences. In the zebra finch case, the ecological consequences of individual differences are the consequences that the different behavioral adjustments have for their “phenotype-environment match” (Trappes et al. 2022; Kaiser and Trappes 2023), or for how well their social behavior matches the social environment. The evolutionary consequences arise, for instance, from the consequences that the different behavioral adjustments have for the inclusive fitness of the individual zebra finch males.

The individualized niche concept facilitates explanation by enabling the biologists to identify the different niche dimensions of a specific individualized niche and by drawing their attention to the fitness consequences of these niche dimensions. The concept also helps to pick out salient phenomena to be explained. The NC<sup>3</sup> concepts – in the example the concept of niche conformance – facilitate explanation by providing a general mechanistic schema (Machamer et al. 2000; Craver and Darden 2013) that guides how the biologists interpret individual-environment interactions (section 5) and that provides the biologists with a general explanatory sketch that can be filled with specific information about the case in question. In the zebra finch case, the explanatory sketch is something like “Individuals of species X conform to their environment Y by adjusting their phenotype/behavior Z. This improves phenotype-environment match and fitness because...”. The mechanistic schema of niche conformance tells the biologists studying the zebra finches to look for individuals adjusting their own social behavior in ways that improve match to the social environment.

In sum, the second epistemic role of the individualized niche concept is that it facilitates explanation of how individual differences arise and what ecological-evolutionary consequences they have. More precisely, it serves a scaffolding explanatory role by specifying the explanandum and possible explanatory factors, and by providing explanatory sketches. We now turn to the role that the concept plays in managing complexity.

### 7. Third Epistemic Role: Managing Individual-level Causal Complexity

The CRC researchers focus on individual variation as an important object of study. This is in contrast to ignoring variation, focusing on the population or species level, and working with averages. Biologists have good reasons for highlighting individual differences because many individual differences turn out to be biologically important. However, this creates complications about how to manage heterogeneity and causal complexity (Elliott-Graves 2023).

Biologists studying individual differences need ways of dealing with individual-level causal complexity. In particular, they need reasons to focus on certain causal factors, while ignoring others, when designing empirical studies, drawing conclusions from empirical results, and developing explanations. The individualized niche concept is one tool that the CRC biologists use to manage individual-level causal complexity. The following quotes illustrate the challenges arising from individual-level complexity (first quote) and the role that the individualized niche concept plays in overcoming them (second quote):

“So, in many aspects that we study, we study certain interactions or responses with the environment. But it's not always the focus to have the entire niche in view or the individualized niche. Particularly also for the reason because I think that if we want to describe the niche, we would need to study all the main factors.” (Interviewee 07)

“It [the individualized niche concept] is a very useful term to describe how the many different factors interface with each other to form the individual.” (Respondent 2)

The individualized niche concept helps to manage this individual-level causal complexity in two different ways: it requires identifying one focal individual whose individualized niche is at stake, and it provides the biologists with good reasons to focus on certain types of causal factors; namely on fitness-relevant, direct causal interactions.

First, the individualized niche concept guides biologists to focus on one (type of) individual and to investigate the niche of this individual. This (type of) individual is referred to as the focal individual (e.g., Trappes et al. 2022).<sup>5</sup> Without having identified the focal individual, we cannot characterize its individualized niche. For example, some biologists study how female Antarctic fur seals (*Arctocephalus gazella*) choose their breeding site, what fitness consequences for the offspring this has (Nagel et al. 2021a), and how fur seal pups conform to the social environment into which they are born (Nagel et al. 2021b). Despite the complexity of

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<sup>5</sup> The focal individual is often, but not necessarily, a type of individual (e.g., beetles bolder than average or optimistic rats), rather than a single individual. For reasons of simplicity, in what follows we will leave out “(types of)” and only speak of focal individuals.

social interactions, they are clear that they study adult female niche choice (of breeding sites) and pup niche conformance. One way to navigate through the causal complexity on the individual level is to make explicit *whose* individualized niche (adult female fur seal or fur seal pup) they are studying.

Second, the individualized niche concept guides biologists to focus on direct causal interactions with the focal individual because indirect interactions (e.g., between conspecifics of the focal individual) are rarely components of an individualized niche (Kaiser et al. 2024a). This is not to say that empirical studies should not also investigate indirect interactions. However, the individualized niche concept provides a reason to prioritize direct interactions. For example, adult sawflies (*Athalia rosae*) acquire certain chemical compounds from a conspecific by mating or fighting with them (Paul and Müller 2022). For the focal individual, only its contacts with other individuals (with or without these compounds) are relevant. Mating or fighting among other conspecifics may indirectly affect its own opportunities but are not directly part of its individualized social niche.

In sum, the third epistemic role of the individualized niche concept is that it helps to manage individual-level causal complexity by providing criteria that allow the biologists to focus on certain types of causal factors while ignoring others. We now turn to the role that the concept plays in integrating knowledge from different biological fields.

## **8. Fourth Epistemic Role: Fostering Epistemic Integration**

The individualized niche concept fosters the integration of local knowledge from various biological fields, most importantly from ecology, behavioral biology, and evolutionary biology, but also from genetics, physiology, developmental biology and microbiology. What joins together biologists from these different fields is their common research interest in studying individual differences and individualized niches.

Accordingly, the individualized niche concept is important for communicating between the members of the CRC and for promoting the CRC's research to external reviewers and colleagues, as our interview results show (section 4). This communicative role of the individualized niche concept is closely tied to its role of fostering epistemic integration, since integrating local knowledge from different biological fields requires that the researchers can communicate with each other and find a common basis to collaborate. Hence, the communicative role of the individualized niche concept is at least a precondition, if not an element of its role to promote epistemic integration.

Even more, the individualized niche concept is integrative because it combines ideas from different biological fields. So, using this concept requires integrating local knowledge (e.g., parts of theories, ideas, explanations, data, approaches, methods, etc.) from different biological fields. In our questionnaire, we asked the biologists in the CRC to explain how knowledge from different biological fields is synthesized in their research. The following two quotes answer this question.

“The niche concept is not a behavioral biology concept, including it is already a synthesis, evolutionary thinking is also included” (Respondent 2)

“The interaction of an individual with its environment as a classic ecological process plays a crucial role for this project. Moreover, how these interactions shape the evolution of individuals of certain populations in the form of adaptations is a central point of this project. We therefore combine classical concepts of ecological and evolutionary biology.” (Respondent 22)

Later in the questionnaire, we asked more specifically how the NC<sup>3</sup> concepts contribute to integrating different biological fields. The following quote is a response to this question.

“In our research we investigate differences between individuals with different personality traits... in their niche choice and niche conformance, to reveal potentially ecologically relevant fitness consequences and to understand how these different phenotypes evolved and are maintained within a population. Thereby we link the fields of animal welfare, animal personality, behavioral ecology and evolution.” (Respondent 6)

The individualized niche concept has its roots in ecology because it is derived from the concept of an ecological niche, most importantly from Hutchinson’s niche concept (Hutchinson 1957; see also Takola and Schielzeth 2022). How individuals interact with their environments is central to the individualized niche concept but also to ecology in general. The concept of the phenotype-environment match used is related to that of fitness, so it has both ecological and evolutionary implications (Trappes et al. 2022; Kaiser and Trappes 2023).

Furthermore, the individualized niche concept (together with the NC<sup>3</sup> concepts) facilitates explaining the ecological and evolutionary consequences of individual differences (section 6). The individualized niche concept adds an explicit evolutionary perspective to the ecological niche because it states that individualized niches consist of only those dimensions that affect the fitness of the individual. Hence, individualized niches are often represented by individual fitness functions (e.g., Kaiser et al. 2024a) and estimating an individual’s fitness is an integral part of empirical studies of individualized niches in the CRC.

The individualized niche concept also includes behavioral biological perspectives. Behavior is one major phenotypic trait that shapes how an individual interacts with its

environment. The same is true for animal personality traits (e.g., sociability, boldness), which are temporally stable and contextually consistent behaviors (Wolf and Weissing 2012; Dingemanse et al. 2020; Kaiser and Müller 2021). The individualized niche concept also recognizes the importance of social environments (i.e., other individuals) and social interactions (i.e., interactions with other individuals), which are centrally studied in behavioral biology. Since the social environment of individuals and how individuals interact with each other varies strongly between individuals, most social niches cannot be studied on the species or population level. Hence, the individualized niche concept can accommodate behavioral biological perspectives better.

The individualized niche concept also allows for integrating knowledge from other biological fields, such as from genetics, epigenetics and population genetics. Studying the genetic (and epigenetic) differences between individuals allows biologists to identify the genetic components of individual differences in the phenotype and in behavior. For example, some biologists study how genes and the environment shape intraspecific phenotypic and life-history variation.

In our questionnaire, we asked the biologists how knowledge from the different biological fields is synthesized in their research. The first quote is a response to this question. The second and third quotes are taken from the interviews, where we asked the interviewees what role the individualized niche concept plays in their research.

“We will have reproductive behavior data, which will be linked to individual genetics. This will allow to gain a better understanding of the species ecology in terms of lifetime reproductive success trajectory. By studying its genetic determinants, we can also interpret that in a broader evolutionary way.” (Respondent 5)

“Certainly, my perspective is broader. But what I do outside the CRC is quite defined... Population genetics is quite a tight subject... So, I think within the CRC we've got this behavioral component which is not something that is a general feature of my research. So, it's all quite new... Maybe I have a broader context. Certainly, I'm very fond of trying to link different types of data and insights, which is something that I've become, that's become more a theme of my research since the CRC.” (Interviewee 05)

“I mean, behavioral ecologists are usually more [of] the evolutionary ecology type, right, so... qualitative population genetics. With the individualized niche, I became more, I think, animal behavior type... So, but now, I think there's this individualized niche, and these processes... because they also include development in the end – right, individualization – so now evo-devo, behavioral ecology, ecology, all this comes together.” (Interviewee 03)



As the last quote mentions, development comes into play because the CRC studies the processes of how individual differences arise and change (i.e., individualization; Kaiser et al. 2024b). This prominently includes developmental processes.

Individual differences are often studied on several different levels, not only on the behavioral level. In addition to genetics and epigenetics, this includes individual differences in hormones and hormone concentrations, in the microbiome, in the immune system, and in parasites. Most of these additional kinds of individual differences are also conceptualized as being phenotypic differences. Accordingly, biologists speak, for instance, about hormonal phenotypes (Mutwill et al. 2020) and about immune phenotypes. Most of these additional kinds of individual differences can be conceptualized as “internal states” of individuals (Kaiser et al. 2024a), but some of them might be external or include external factors (e.g., skin microbiome, external immune system, ectoparasites). Furthermore, all of these additional kinds of individual differences affect how individuals interact with their environments and which individualized niches individuals realize. Some of them, such as hormones, affect the realization of individualized niches by mediating information and shaping interactions within and between individuals (Müller et al. 2020).

To conclude, the fourth epistemic role of the individualized niche concept is that it fosters the integration of local knowledge from ecology, evolutionary and behavioral biology. Moreover, the individual niche concept promotes studying individual differences on multiple levels, which requires drawing knowledge from genetics, physiology, developmental biology, and microbiology.

## **9. Why the Niche Concept Is Not Superfluous**

Some philosophers and biologists have raised serious concerns about niche concept(s) (McInerny and Etienne 2012; Angilletta et al. 2019; Justus 2013, 2019, 2021; Sales et al. 2021; Wakil and Justus 2022). These include concerns that “niche” lacks a unified definition in biology, that the concept fails to capture what is doing the causal work in ecological models, and that it is superfluous from the perspective of ecological theory. There have even been several calls to abandon the term “niche” or particular conceptions of the niche within ecological modeling practice (McInerny and Etienne 2012; Angilletta et al. 2019; Wakil and Justus 2022). For instance, Angilletta et al. state that “we should ask whether Hutchinson's concept of the fundamental niche has outlived its use to ecologists.” They conclude that “[c]learly, we believe it has done so” (2019, 1045). Similarly, Wakil and Justus argue: “Concepts are tools for understanding and navigating the world. In science, concepts inform and enable methods

of discovery, inference, and they underwrite the content of knowledge claims. If our analysis is correct, the niche concept does none of these” (2022, 16).

We do not necessarily disagree with some of these authors’ arguments about modeling. However, we argue that this modeling- and theory-oriented approach to evaluating the niche concept overlooks other positive contributions that the concept makes to gaining knowledge about the biological world. We have argued that a niche concept contributes to major epistemic practices such as explanation, study design, data analysis, causal selection, and integration in at least one research area in biology. Positive evaluations of the niche concept, such as ours, do not necessarily challenge the existing negative ones but they complement the picture and broaden the existing focus on modeling and theory.

There is a possible objection to our arguments that the individualized niche concept plays crucial epistemic roles. One might argue that it is instead the finer-grained descriptions of causal processes giving rise to individual differences that play these epistemic roles. Along these lines, Wakil and Justus argue that it is the complex causal processes represented in ecological models, not the niche concept, doing the “real scientific work” (2022, 16).

We argue that this case cannot be made for the epistemic roles of the niche concept identified in this paper. Consider the role of shaping the research agenda first. There are many individual-level processes and phenomena that are biologically meaningful and could be studied. The individualized niche concept guides the biologists in the CRC to focus on those phenotypic traits and behaviors that vary between individuals and to investigate how this variation affects individual-environment interactions. These decisions about research focus cannot be guided by representations of the causal processes themselves because they are so many and they do not provide a selection criterion.

A similar point can be made in regard to the roles of the individualized niche concept to facilitate explanation and to manage causal complexity. Both epistemic roles concern the selection of explanatorily relevant causal factors. The individualized niche concept guides this activity because the concept’s content provides the biologists with clear selection criteria (e.g., identify causal interactions that affect the focal individual’s fitness, focus on direct causal interactions with the focal individual). Similarly, the meaning of the individualized niche concept brings together theoretical elements and ideas from ecology, behavioral and evolutionary biology and thereby promotes epistemic integration. This includes bringing together causes and mechanisms often studied in different disciplines (e.g., population genetics and behavior differences). This integrative role is not played by the finer-grained causal processes that this concept refers to.

We grant that there are further challenges about the niche, including the issue that it lacks a unified definition across biology, which we have not addressed in this paper. However, its elimination would cause a disruption to the organization and research program of the CRC and similar groups, requiring the development of a novel conceptual-theoretical framework for structuring their investigation of individual-environment interactions. Therefore, we suggest a more fruitful approach is to continue work classifying the plurality of niche concepts (e.g., Sales et al. 2021) and evaluating the suitability of different definitions for particular epistemic practices.

## 10. Conclusion

This paper contributes to the lively debate about scientific concepts and how they are used and evaluated in scientific practice. We present a case study that shows how a niche concept guides ongoing scientific practice. We argue that the concept of an individualized niche plays central epistemic roles: it shapes the research agenda of the CRC, facilitates explaining core phenomena in the field, helps with managing individual-level causal complexity, and fosters integrating local knowledge from ecology, behavioral, and evolutionary biology. Our practice-based and empirical analysis shows that some philosophers and biologists have been too quick to argue that the niche concept is superfluous. Philosophical analyses of scientific concepts should not be limited to the practices of theorizing and modeling, but rather take into account the variety of epistemic practices and roles that scientific concepts play. For instance, we advocate for centering the rich features of empirical practices in biology and roles of concepts related to driving research agenda formation and interdisciplinary synthesis.

## Appendix 1: Questionnaire Questions

### Part I: Niche Concept

1. Please provide an example of an individualized niche that you study in your project.
2. What question(s) *related to individualized niches* is your research trying to answer?
3. Regarding your example of an individualized niche, please specify which focal individual, niche dimensions, behaviors, and phenotypic traits you study:
  - 3.1 focal individual:
  - 3.2 niche dimensions:
  - 3.3 behaviors/behavioral traits:
  - 3.4 (non-behavioral) phenotypic traits:
  - 3.5 other:

- 4 How do you distinguish between environmental fluctuations that are just noise and environmental differences that count as individualized niche dimensions?
- 5 Which internal or non-environmental conditions (e.g., behaviors, genes, immunological factors, hormonal states, etc.) can be part of individualized niches? Please briefly explain why you include/exclude certain conditions.
- 6 Imagine you are speaking to someone who worries that the concept of individualized niches is not very useful. How would you explain to them the importance of the niche concept within your research?
- 7 In the CRC grant application, the individualized niche is defined as follows: “The individualized niche is a subset of the species’ niche that arises from the interaction of the individual with its environment. ... it constitutes an n-dimensional space that describes how abiotic and biotic variables affect individual-specific fitness functions.”
  - 7.1 Are you aware of alternative concepts/understandings of individualized niches?  yes  no
  - 7.2 If yes, can you specify an alternative niche concept?
  - 7.3 What kind of advantages or disadvantages does the alternative niche concept have compared to the CRC’s main niche concept?

## Part II: Methods

8. What is your unit of research? Check all that apply  genes  individuals  groups  populations  (ecological) communities  ecosystems  other: ...
9. In your research, does the unit of research ever change?  yes  no
10. Why does or doesn’t the unit of research change?
11. What type(s) of data do you collect? (e.g., response times, tracking data, temperature data, model variables, etc.)
12. In your research, what are the main difficulties in data collection? (Please give 1 or 2 examples)
13. How do you measure individual variation?
14. What are the difficulties for measuring individual variation?
15. How do you distinguish between individual variation and noise?
16. Are your results applicable to individuals or groups?  individuals  groups  both
17. Please explain why.
18. *Individual-based research (i.e., research about individuals and their interactions with the environment)*. Would you describe your research as individual-based research in this sense?  yes  no

19. Please explain why your research is or isn't individual-based.

### **Part III: Integration**

20. The CRC brings together different biological fields: ecology, behavioral biology and evolutionary biology (and theoretical biology). What do you think is the relation between these different fields?

21. The goal of the CRC is to develop a "Novel Synthesis of Individualization..." Please explain how knowledge from the different biological fields is synthesized in your research? (We mean 'knowledge' broadly to include concepts, models, findings, methods, theories, explanations, etc.)

22. How does synthesis or integration of knowledge from different biological fields happen in the CRC? Check as many boxes as you like.

- using a concept from another discipline in your research
- developing common concepts
- incorporating theories from other disciplines in your research
- developing a common theory
- using a method from another discipline in your research
- exchanging methods across disciplines
- developing new methods together with researchers from other disciplines
- developing explanations that use knowledge from different disciplines
- using the data from another discipline in your research
- showing the relevance of your data to multiple disciplines
- other: ...

23. What are the merits of synthesizing or integrating knowledge from different biological fields?

24. In the CRC we are studying individualized niches and the mechanisms of niche choice, conformance and construction (NC<sup>3</sup>). In your opinion, how do these shared concepts contribute to integrating the different biological fields? Please provide an example from your research.

## **Appendix 2: Interview Guide Questions**

### **Part I: Basics**

1. The CRC studies individuals and their interactions with the environment. What sorts of phenomena do you study in your research?

## **Part II: Epistemology**

2. What is your unit of research? E.g., individual, family, colony, population, species
3. Do you consider your research to be group or individual based?
4. How does individual based research differ from research on groups?
5. If you were to explain research that focuses on individuals, say individual based research, how would you do that?
6. Do you think we can learn about individuals from studying groups?
  - a. What kinds of assumptions need to be made to apply knowledge from groups to individuals?
  - b. Are there any difficulties that could come up when doing this?
    - i. Do you think these difficulties can be overcome?
    - ii. Do you have any examples of how they could be overcome? Either from empirical or from theoretical research?

## **Part III: Niche Concept**

7. What examples of individualized niches do you study in your research?
8. Please pick one example of an individualized niche.
  - a. What is the focal individual in this example?
  - b. Which niche dimensions do you study?
  - c. Which traits of the focal individual do you study?
9. In general, how do you distinguish between niche dimensions and traits of the individual?
10. An individualized niche contains many different dimensions. How do you decide to study certain niche dimensions, but not others?
11. Do you think that internal conditions of the focal individual, such as genes, immunological factors, hormonal states, can be part of individualized niches?
  - a. [If not already done:] Please explain why.
12. What do you think are the main challenges for empirically studying individualized niches?
  - a. How do you meet these challenges?
13. How do you understand the individualized niche; how would you define it?
14. Do you think different projects or biological fields in the CRC conceptualize the individualized niche differently?
  - a. If yes: Please explain the differences. Please provide an example.
15. What role does the individualized niche concept play in your research?
  - a. Please give an example.

- b. Is the niche concept primarily important for framing or selling your research or does it also influence your measurements or experiments?

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