How to Balance Conceptual Unity and Plurality: The Case of the Individualized Niche Concept

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Abstract

Many philosophical discussions about biological concepts have focused on arguments for conceptual pluralism or monism, an approach that threatens to obscure the nuances of conceptual structure. We characterize the structure of the individualized niche concept based on the results of a qualitative empirical study we conducted within an interdisciplinary, biological research center. Our findings show that this biological concept balances the aims of conceptual unity and plurality through exhibiting a structure of a single core concept that permits several distinct conceptions. We conclude from our case study that some scientific concepts have complex structures that might be overlooked when only focusing on disputing about monism and pluralism. We also recommend that the plurality of conceptions of the individualized niche concept be retained because each of the conceptions has potential benefits, and because the conceptual structure is sufficiently unified to support the aims of the research center.

Keywords: Individualized Niche, Conceptual Pluralism, Unification, Concept Structure, Qualitative Empirical Study, Philosophy *in* Science

1. Introduction

Many philosophical discussions have focused on arguing about whether pluralism or monism about specific biological concepts is most convincing (e.g., the concepts of species, population, fitness, biodiversity, homology, lineage, biological individual, gene, etc.). Monists argue that such concepts are or should be subject to a single, unified definition that is applicable across contexts. To illustrate, Millstein proposes a single causal interactionist population concept for ecology and evolutionary biology (Millstein 2009, 2010) and defends it against pluralistic objections (Stegenga 2010). Another example is the debate about the concept of fitness, which is often understood as a search for "*the* fundamental concept that underwrites all explanations invoking natural selection" (Kellert et al. 2006, xxv; see also Reydon 2021). In contrast, pluralists about biological concepts argue that such concepts are disunified, fragmented or have distinct meanings in different applications or biological fields. Conceptual pluralism has been notably advocated in regard to the species category (e.g., Kitcher 1984; Dupré 1993; Stanford 1995; Brigandt 2003), but also in regard to other biological concepts, such as homology (Jamniczky 2005), lineage (Neto 2019), and biodiversity (Popa 2022). Some pluralists see conceptual fragmentation and polysemy as beneficial, for example because complex phenomena might be best captured by a plurality of models (e.g., Kellert et al. 2006, xxvi). Others have argued that scientific concepts that are not subject to a unified definition should be eliminated and for instance replaced by a plurality of more local concepts (e.g., Ereshefsky 1992; Taylor and Vickers 2017; Santana 2018).

We show that this focus on debating pluralism versus monism about biological concepts can miss epistemic insights because attention may be directed away from the complexities of conceptual structure. We show that biological concepts can have features of unity and plurality at the same time, for instance by exhibiting the structure of a core concept permitting multiple conceptions. We develop a detailed case study utilizing qualitative empirical research on the concept of an individualized niche. The concept of an individualized niche derives from the concept of a population's ecological niche and refers roughly to the set of (e.g., environmental) factors affecting the fitness¹ of an individual organism, supposing that organisms within a population are often heterogeneous or specialized (e.g., Robertson et al. 2015; Schirmer et al. 2020; Székely et al. 2020; Carlson et al. 2021; Takola and Schielzeth 2022)². We characterize the structure of this concept in detail to show that it exhibits both unity (it has a clearly defined, shared core meaning) and plurality (it permits multiple nonequivalent, partly inconsistent conceptions). Biologists often have good reasons to aim for both conceptual unity and plurality and must balance these desiderata in a way that is not well-captured by debates that focus on monism and pluralism as general alternatives.

Our paper has implications for biological research on individualized niches and related phenomena. The biologists of a large interdisciplinary research center "TRR-CRC 212 "A Novel Synthesis of Individualisation across Behaviour, Ecology and Evolution: Niche Choice, Niche Conformance, Niche Construction" (in the following referred to as 'CRC'), funded by the German Research Foundation, have raised concerns about whether the CRC has a sufficiently unified conceptual framework. As philosophers in residence at the CRC, we are able to make recommendations as to

¹ Here we follow closely the language used by CRC biologists. We have not taken a stance on how the notion of fitness used in the CRC should be interpreted, but many of the biologists seem to assume a notion of individual (organismal) fitness, measured via fitness proxies such as body condition, growth rate, or cortisol levels.

² Because this is a relatively new research area, many of the cited papers do not use the exact phrase "individualized niche," but they are clearly about the niches of (types of) individuals.

whether the observed conceptual plurality is an obstacle to the group's research agenda. We argue that the CRC is not working with three distinct concepts but rather with three conceptions of a core concept. We argue that each of the identified conceptions has potential benefits and therefore do not recommend revising the conceptual structure, but rather suggest further and explicit thought about which conception is beneficial for which research questions and aims.

In Section 2, we summarize the methodology of the qualitative empirical study we conducted. In Section 3, we present reasons favoring conceptual unity and plurality in biological practice. In Section 4, we present our findings about the unifying core features of the individualized niche concept. In Section 5, we present sources for a plurality of conceptions; Section 6 then introduces the three conceptions. In Section 7, we argue that the balance of unity and plurality is beneficial and should be main-tained.

2. Methodology

In 2023 we conducted a qualitative empirical study within the CRC, an interdisciplinary research group at the Universities of Bielefeld and Muenster with about 50 researchers (including postdoctoral researchers and PhD students) from ecology, evolutionary biology, behavioral biology, theoretical biology, statistics, and philosophy of biology who study niche-related phenomena at the individual level. Our study included a questionnaire, semi-structured interviews with 12 researchers from the CRC, and various collaborative activities with CRC biologists. One goal of this study was to characterize how the biologists think about individualized niches, including whether they endorse a unified definition or have a diversity of views.³

Since we are members of the CRC, we share central research goals and interests with CRC biologists, including that of developing a sufficiently integrated conceptual framework for the CRC. Methodologically we adopt a collaborative, philosophy *in* science approach (Pradeu et al. 2024) since our findings are communicated to CRC biologists with the aim of guiding their ongoing conceptual development. As part of our collaborative activities, we have attended and participated in research talks, retreats, workshops, and working groups. Most relevant for this paper, we hosted a workshop in December 2023 aimed at collaboratively clarifying the individualized niche concept. The workshop was attended in hybrid format by 23 CRC biologists, which is nearly half of the CRC's members. During this workshop, we collected examples supporting each of the three identified definitions of the individualized niche (environmental, strategy-based and inclusive; Section 6) as well as the biologists' ideas about their strengths and weaknesses.

³ A more detailed description of our methodology, our summarized data, and complete questionnaire and interview questions are published as an Open Science Framework project (Morrow et al. 2024).

The questionnaire was distributed to most researchers in the CRC (6 philosophers were excluded from all parts of the study) in the summer of 2023. There were 23 responses, of which 11 were from principal investigators, 2 were postdoctoral researchers and 10 were doctoral students, representing a 51% response rate from biologists in the CRC. The online questionnaire contained short-response questions about the individualized niche concept as well as other questions about their research methods.

The semi-structured interviews lasted between 30 and 55 minutes, usually in the interviewee's office. Each interview was conducted by two interviewers and one interviewee. Of the 12 interviewees (42% women), 1 was a postdoctoral researcher and 2 were doctoral students, while the remainder were principal investigators. In total we interviewed 27% of the biologists in the CRC. We selected interviewees studying a variety of model organisms, research questions and from varying disciplinary backgrounds to achieve breadth. During the interviews, one of the interviewers asked questions about individual-based research (findings not utilized in this paper), then the other interviewee asked questions about the individualized niche concept. We converted audio recordings of the interviews to text transcripts by first using the AI software noScribe, followed by proofreading of the transcriptions against the audio recordings by several people. AI software was used only to assist with converting audio to text and was not used in any of our analysis.

The questionnaire answers and the interview transcripts were analyzed by assigning codes, phrases that summarize important ideas expressed in passages. Our starting codebook (MacQueen et al. 1998) was generated using a theory-driven, topdown methodology in view of our research questions. For example, we developed a list of codes identifying different views about what counts as a niche dimension (Section 5). The draft codebook was then revised in a bottom-up manner in the process of analyzing the transcripts (for example, some codes were modified to better suit repeated ideas from the interviews). This blend of top-down and bottom-up methodology was selected to analyze the data in a manner that reflects the content of the interviews while also addressing our research questions. The following sections present a mixture of summary coding results and direct quotes from our interviews.

3. Conceptual Unity and Plurality in Biological Practice

Our case study reveals that in practice, biologists often face the need to balance conceptual unity and plurality, leading to concepts with complex and flexible structures. This section first analyzes the aims and reasons that CRC biologists have for favoring conceptual unity versus plurality. Second, we specify what consequences this has for the structure of the individualized niche concept.

3.1 Perspectives on Conceptual Unity and Plurality

Our findings show varying perspectives of CRC biologists about the presence and the advantages or disadvantages of conceptual plurality. Of the 12 biologists we interviewed, 7 interviewees endorsed (i.e., expressed positive attitudes towards) conceptual plurality. Eight interviewees recognized an (apparent) plurality of individualized niche concepts (5 overlapping with code "endorse plurality"), that is, they indicated that they think different biologists or research projects in the CRC may utilize different concepts of the individualized niche (we later sharpen this claim with our use of a concept-conception distinction). In sum, a total of 10 of 12 interviewees either recognized or endorsed conceptual plurality. In general, pluralism might be expected in the CRC because it consists of researchers from diverse disciplinary backgrounds working on different research questions and animal species.

On the other hand, 2 of the interviewees endorsed a single unified individualized niche concept, and a third interviewee recognized a single unified individualized niche concept (but co-occurrence with code "recognizes plurality")⁴. Hence, a total of 3 of 12 interviewees either recognized or endorsed conceptual unity. Moreover, 6 interviewees referred to the official definition of the individualized niche concept stated in the CRC's documents (including funding applications), signaling awareness of conceptual unity as an aim of the CRC.

The questionnaire results contrast with the interview results in that they reflect a more limited awareness of conceptual plurality. In response to the question, "Are you aware of alternative concepts/understandings of individualized niches?", only 6 respondents answered "yes" (26%). There are two plausible reasons for this. First, 5 of the 6 respondents who answered "yes" are principal investigators, i.e., relatively senior members of the CRC. Earlier career researchers, who are more represented in the questionnaire responses than in the interviews, are expected for various practical reasons to have less acquaintance with the conceptual-theoretical framework of the CRC. In addition, during the interviews the biologists were asked to discuss in detail examples of individualized niches. This may have prompted some to recognize conceptual differences that did not come to mind in the much briefer questionnaire answers. While our interviews show that many (especially senior) CRC members are positive towards plurality, the questionnaire results illustrate that many of the biologists have only become aware of the conceptual plurality after our study.

CRC biologists also have good reasons to strive for conceptual unity, as expressed by these interviewees:

"I think it's important that we all have the same core concept, but it's okay to diversify them in the different fields also. So, to modify it depending on a specific question under study. [Interviewer:] Could you say a little more about the importance of having a shared core concept? [Interviewee:] It's easier to talk to each other, if you all have a different understanding of what a niche is, then you could not

⁴ This overlap shows that some biologists recognize conceptual unity and plurality at the same time.

really meaningfully discuss. And also to write papers, for example, you need to have at least a sufficiently similar concept of the niche to be able to communicate to the scientific community what you think." (Interviewee 4)

[Interviewer:] "Do you think it would be good or bad or neutral if people had different definitions of the individualized niche?" [Interviewee:] "I think they shouldn't be too different. So, I mean, we have to have some common ground in this CRC to, that it makes sense at all. And I think because it's so interdisciplinary, also within biology, so maybe different aspects of biology with behavior and ecology and evolution, at least this concept we should have of the same idea because the research we do is so different. And this should be the unifying part of it." (Interviewee 10)

While many of the biologists we interviewed are open-minded or positive about plurality, the quotes show that professional needs also pull in the direction of unity within the CRC. For instance, CRC researchers need to present a unified view of their research program for external communication and funding evaluation. In addition, a unified conceptual framework is important for setting a shared research agenda and for integrating knowledge in the CRC (Kaiser and Morrow 2025). When members of the CRC utilize different definitions of a shared research target, this creates complications for summarizing findings and obstacles for interdisciplinary collaboration. Moreover, miscommunications or misinterpretation can happen when biologists use polysemous terms, a frequent concern in the philosophical literature on pluralism (e.g., Gough 2022). In Section 7 we address some of these concerns and argue in favor of retaining the plurality.

3.2 The Structure of the Individualized Niche Concept

The fact that the biologists of the CRC have motivations for both conceptual unity and plurality affects their conceptual practices. The concept of the individualized niche combines unified features with pluralistic features, which we will analyze in terms of a one concept-multiple conceptions structure. The unifying features of the concept are the shared core assumptions that constitute its meaning and guide the research of the CRC (Section 4). We use the term 'conception' to refer to the variable, more specified definitions of the individualized niche arising from, for instance, diverging views about what are legitimate niche dimensions (Sections 5-6).

The concept-conception distinction is often traced back to Rawls and his theory of justice (1971). Rawls used the distinction to analyze contested concepts (e.g., the concept of justice) and to explain how defenders of alternative accounts can disagree without talking past each other: they have a shared concept, but conflicting conceptions (see also Brun 2022).⁵ This phenomenon also occurs in our case study. We argue that in the CRC there is a single concept of the individualized niche, whose meaning is constituted by certain core assumptions. However, these

⁵ We only adopt Rawls' general view of the concept-conception distinction, not his more specific, teleological approach (Lalumera 2014).

core assumptions raise questions that can be differently answered, giving rise to diverging individualized niche conceptions.

We suggest that the individualized niche concept is one of many biological concepts that balances conceptual pluralism and unity. For some concepts, the concept-conception distinction is suitable to specify their structure. However, there are other philosophical frameworks that might be suitable for characterizing the structure of other biological concepts. For instance, Neto (2020) argues that many biological concepts are *imprecise* in the sense of having a general, underspecified meaning that permits different specifications in different contexts. Neto's account does not fit our case exactly because the core individualized niche concept is precise and specific in many regards. A second example is from Brigandt (2003), who argues that there is a general species concept, which is an "investigative-kind concept" (2003, 1309) that sets the standard for what counts as a good concrete species concept. We again do not think the details of this framework capture the individualized niche case, but that this conceptual structure would also be an example of a way conceptual unity and plurality are balanced. To conclude, practicerelevant accounts of biological concepts ought to give detailed accounts of conceptual structure that move beyond debates about whether monism or pluralism is correct.

4. Unifying Features of the Individualized Niche Concept

There are five interrelated core assumptions that are central to characterizing individualized niches and strongly influence the research projects in the CRC. These core assumptions characterize the individualized niche concept as studied within the CRC, the target of our study; we assume that across biology there is a plurality of additional niche concepts, a situation not addressed by the present study. These five core assumptions are evident within internal CRC documents, our interpretation of publications by CRC members, and the results of our interview analysis.

First, individualized niches are characterized as *n*-dimensional hypervolumes, which is borrowed from the Hutchinsonian (population-level) niche concept (Hutchinson 1957), although in other respects the CRC's individualized niche concept differs from the Hutchinsonian concept. The individualized niche is represented as a region in a high-dimensional space, where the dimensions of that space represent factors such as prey density or water depth. Individualized niches are distinguished from habitats because they are not locations in physical space. However, space matters when studying individualized niches given that individuals occupy physical spaces in which different conditions can be present. For example, benthic divers of the Galápagos sea lion (*Zalophus wollebaeki*) forage in shallow and flat seabed areas and prey on solitary living benthic fish, whereas pelagic divers forage mainly at

depths between 100 and 200 m, where they utilize high-density prey patches (Schwarz et al. 2021). So, these sea lions realize different individualized niches.

In the interviews, this first assumption was common. Nine of 12 interviewees referred to the idea that individualized niches are *n*-dimensional volumes (code "ind. niche as n-dimensional hypervolume/ hyperspace/ set of parameters"); 2 interviewees explicitly mentioned that individualized niches are not concrete locations (code "ind. niche is NOT a location"). The following quote exemplifies this first assumption:

"So, I think my working definition is always like the individualized niche is an *n*-dimensional space that the individual inhabits. [...] It's like we have these *n*-dimensional space and each individual is sitting in a little bit different space than the other one." (Interviewee 11)

A second core assumption about individualized niches is that they result from applying the species- or population-level notion of an ecological niche to individuals. These can be token individuals or types of individuals, such as fire salamander larvae (*Salamandra salamandra terrestris*) or male adult Guinea pigs (*Cavia aperea f. porcellus*). Niches of individuals differ from each other in biologically significant ways, for instance, in how they socially interact with conspecifics or which environmental factors they utilize. This individual specialization can have ecological and evolutionary consequences. In the interviews, 3 of 12 interviewees claimed that the individuals (code "ind. niche as population/species niche concept applied to individuals"). In the following quotes the first biologist explains that when the population-level Hutchinsonian niche concept is transferred to the individual level, one needs to replace population persistence with individual fitness; the second biologist expresses the idea that individuals occupy different parts of a population's niche space during their development:

"So, conceptually, there's not much new to it, I would say. It's really transferring the Hutchinson's niche concept to the individual level, recognizing it's not, let's say, persistence indefinitely at the population level but a measure, a proxy for fitness to get pretty much at the same conceptual...[idea]" (Interviewee 8)

"I would say that individualized niche is the range in the niche space that an individual occupies during their lifetime." (Interviewee 12)

The third core assumption is that individualized niches are shaped by individual-environment interactions. CRC biologists study three major mechanisms describing how individualized niches change: niche choice, niche conformance and niche construction (Müller et al. 2021; Trappes et al. 2022; Kaiser and Trappes 2023; Kaiser et al. 2024). In cases of niche choice an individual selects a different environment, in niche conformance the individual adjusts its phenotype to its local environment, and in niche construction the individual makes changes to its environment. All three mechanisms change the individualized niche realized by an individual. Five of 12 interviewees prominently referred to individual-environment interactions when explaining the concept of an individualized niche (code "ind. niche as individual-environment interactions"). The following quotes illustrate this:

"The niche comes about through the interaction of the individual with the environment." (Interviewee 4) "For me, the easiest way to think about niche is the interactions that they have. So, how they interact with the environment, or abiotic, and with the biotic environment." (Interviewee 12)

Fourth, individualized niches are said to be realized⁶ by individuals (see, e.g., Müller et al. 2020) and do not exist in the environment apart from individuals. While this assumption is largely shared by CRC members (if sometimes implicitly), it may be interpreted in a weaker or stronger way. In a weaker sense, individualized niches can only be characterized with reference to particular (types of) individuals. In the stronger sense, some CRC members have viewed individuals as being parts of individualized niches (Kaiser et al. 2024). This fourth assumption is clearly visible in some of the interviewe, although a corresponding code was not included. For instance, one interviewee states that individualized niches are realized by individuals, contrary to niches "belonging to" individuals, like properties do:

"I wouldn't say a niche can belong to an individual. An individual can change the niche, individualize. But what is "belong"? Or what does it mean "belong to"? [Interviewer:] Is realized by? Is there a term you would prefer? [Interviewee:] Yeah, realized by is, I think, better. If you would say, "It belongs to an individual", it sounds a little bit like an extended phenotype, something like that. [...] But I wouldn't say a niche is an extended phenotype. The niche comes about through the interaction of the individual with the environment. It doesn't belong to it, I would say." (Interviewee 4)

Another interviewee emphasizes that individualized niches are not environmental spaces that individuals enter. This is expressed by saying that niches are realized by individuals:

"I was trained in biology, I always had a teacher who said an individual cannot go into a certain niche, but it realizes a niche. And that is really my kind of education I got, and I think that's a really big difference. If you say there's a niche and an insect enters it, then it's really the environmental space, but if an individual realizes a certain niche, that's something different." (Interviewee 7)

The fifth core assumption is that only those factors that affect an individual's fitness can be niche dimensions. CRC biologists represent individualized niches as fitness functions over multidimensional niche space. Hence, in a two-dimensional representation with just one niche dimension, on the *x*-axis we have a factor such as

⁶ This use of the term "realize" should not be confused with either the Hutchinsonian distinction between the fundamental and realized (i.e., actual) niche (see below) or with the technical sense of "realize" used in metaphysics.

water temperature; and on the *y*-axis we have the fitness of the individual (Fig. 1). The curve represented in Figure 1 is referred to as an individual fitness function.



Fig. 1: The individualized niche as a two-dimensional space

The fundamental individualized niche is the area in which the individual has positive fitness, while the realized individualized niche is the point on the curve actually realized by the individual, which is the individual-level correlate of the fundamental-realized population niche distinction attributed to Hutchinson (1957; Takola and Schielzeth 2022). In empirical studies, the fitness of a *focal* individual (i.e., the individual whose niche is studied) is usually measured in terms of fitness proxies, such as growth rate, body condition, short-term reproduction rate, parasite load, etc. In the interviews, 4 of 12 interviewees characterized individualized niches by referring to individual fitness functions (code "ind. niche as shaped by individual fitness functions"); 3 other interviewees made claims that suggested that individualized niches are individuated by referring to the individual's fitness (code "individuation by fitness (y-axis)").

These assumptions are shared within the CRC and form the core of the individualized niche concept as it is applied in the CRC's research.⁷ Thus, the individualized niche concept is not an example of a patchwork concept in which distinct uses of a concept lack shared core assumptions (although the three conceptions we characterize may otherwise be similar to "patches"; Haueis 2024). We interpret the CRC as utilizing a single concept that is partly unified in virtue of these shared assumptions. This degree of unification of the individualized niche concept contributes to aims within the CRC, including clear communication, setting a shared research agenda, and fostering interdisciplinary collaborations and epistemic integration (Section 3).

⁷ We leave it open whether distinct individualized niche concepts might be developed in other research programs. In general, we hold that there is a plurality of niche concepts in biology.

5. Sources of Conceptual Plurality

The core assumptions about individualized niches introduced in the previous section contribute to conceptual unity because they are broadly endorsed in the CRC, constitute the core meaning of the concept, and help to guide CRC research. However, some of these assumptions raise questions which can be answered differently. In this section we identify three sources that can *potentially* give rise to plurality, that is, they could result in distinct conceptions of the individualized niche.

The first source of a plurality of conceptions is connected to the first (and fifth) core assumption. According to these assumptions, individualized niches are characterized in terms of niche dimensions which are relevant to the individual's fitness. The niche dimensions are represented on the *x*-axis of the individual fitness function. This raises the question of what is a legitimate niche dimension, that is, which types of factors should be represented on the *x*-axis of Figure 1? Are these only environmental conditions, or can behaviors and internal states of the focal individual also be considered niche dimensions?

In Section 6 we will show that these questions give rise to three distinct conceptions of the individualized niche. The *environmental* conception holds that only environmental conditions can be niche dimensions. The *inclusive* conception allows environmental conditions, behaviors and internal states of the focal individual to be dimensions of the focal individual's niche. The *strategy-based* conception in contrast treats (behavioral) strategies and sets of phenotypic traits of the focal individual as dimensions but not environmental factors.

A second potential source of plurality is connected to the fifth core assumption. Individualized niches are often represented by individual fitness functions. There are, however, divergent views about what to put on the *y*-axis (see Figure 1) and about what is the best fitness cut-off that determines where to place the boundaries of the individualized fundamental niche in multidimensional space. There have been discussions about whether the (fundamental) individualized niche should be the region of niche space in which the individual has positive (greater than 0) or replacement-level fitness (greater than 1 expected offspring). The following quote illustrates the reasoning behind the latter view:

"I think there is some vagueness of then what is it, given this fitness function, what is the individualized niche. Should there be some cut-off? [...] I think usually, yeah, it should not just have any positive fitness, because if it has a super small fitness, that might not be enough to have a lineage of surviving offspring in the future. [...] 1 is more meaningful, I think. An individual should kind of have at least one surviving offspring. That's, I guess, often used in, would be used in population niche models as well, I guess, that the population can replace itself, or stay constant in size. But that's a little bit more challenging for individuals" (Interviewee 02)

A widespread strategy is to put fitness proxies on the *y*-axis or, at least, to estimate fitness by measuring fitness proxies. The following quote illustrates the reasoning behind this strategy:

"We always, and I think this is true for most biologists, at least for me, that we use fitness proxies. But for example, in the [vertebrate species], they can live up to 50 years. I really have no idea how the lifetime reproductive success of that individual is. I will never have that. At least not in the wild. So we only use fitness proxies." (Interviewee 11)

When measuring fitness proxies, some biologists target the growth, survival or wellbeing of individual animals, rather than their reproduction. When asked in the interviews how they understand the individualized niche concept, some biologists mentioned persistence (2 of 12 interviewees), growth (3 of 12 interviewees), or an individuals' preferences or needs, instead of fitness. The described questions are still a matter of active discussion in the CRC and have not yet given rise to clearly distinct conceptions of the individualized niche.

The third potential source for plurality is that biologists with different disciplinary backgrounds and research interests focus on different subtypes of individualized niches. Most prominently there is a contrast between some CRC biologists studying ecological (individualized) niches and others focusing on social (individualized) niches. When studying ecological niches, biologists are interested, for instance, in trophic interactions or in the temperature ranges that different individuals can tolerate. Investigating social niches draws attention, for example, to the social interactions of the focal individual with conspecifics and to the social roles that an individual has in a social network (Kaiser et al. 2024). When asked about different definitions of the individualized niche that other members of the CRC use, one interviewee referred to this difference:

"It depends a little bit on the field. Those who are more from the ecology side would more focus on ecological niche dimensions whereas the behavior people are more interested in biotic interactions and interspecies interactions like social niches. [...] For example, as an ecologist you would not see big differences between the niches of individuals that have different positions in a social network. Or that are, for example, in dominance hierarchy, more up or down. For an ecologist they would have the same niche. But for a behavioral biologist the niche of a dominant individual is completely different from the niche of a subordinate individual. [...] normally ecologists would ignore these things, I guess." (Interviewee 4)

Our empirical findings support that all three sources exist and are recognized as possible sources of conceptual plurality. For example, when asking in the interviews "Do you think different projects or biological fields in the CRC conceptualize the individual niche differently?", 3 of 12 interviewees explicitly referred to the first source (niche dimensions), and 3 other interviewees referred to the third source (subtypes of niches). When asking the biologists what their preferred definition of the concept of the individualized niche is, 2 of 12 interviewees explicitly mentioned the second source (fitness thresholds).

6. Three Individualized Niche Conceptions

In this section we detail three conceptions of the individualized niche – the environmental, inclusive and strategy-based conceptions.⁸ After coding the interviews, we read through them again and checked for clear statements indicating that an interviewee endorses one of the three conceptions. The result was that 5 of 12 interviewees clearly endorses the environmental niche conception, 2 interviewees are proponents of the inclusive niche conception, and 1 interviewee defends the strategybased niche conception. Four interviews were unclear cases, that is, the interviewees did not explicitly and consistently throughout the interview endorse only one of the conceptions.⁹

6.1 Environmental Individualized Niche Conception

According to the environmental (individualized) niche conception, only features of the environment of a focal individual are dimensions of that focal individual's niche. Environmental conditions that can be niche dimensions range from abiotic conditions to individuals of other species to conspecifics. Abiotic conditions include, for example, water depth, water flow speed, temperature, available materials for nest construction, habitat structure, access to plant metabolites, food availability and quality, availability and intensity of light, etc. Biotic allospecific conditions include, for instance, prey sources, prey trophic position, presence of parasites, competitors, etc. Biotic conspecific conditions include, for example, availability of mating partners, individuals with different or the same ranking position (e.g., dominant, subdominant), offspring, (social) density, etc.

In the interviews, 8 of 12 interviewees state that individualized niches include (as niche dimensions) environmental factors or are microenvironments (code "ind. niche as environmental conditions/ factors/ microenvironment")¹⁰; 3 interviewees (one overlap with code before) think of individualized niches as habitats or microhabitats (code "ind. niche as habitat/ microhabitat"). More specifically, 5 of 12 interviewees state that niche dimensions include environmental factors (code "n.dim. is environment"), 6 that abiotic environmental factors can be niche dimensions (4 overlap with code before), and 4 that social environmental factors can be niche dimensions (1 overlap with both codes before). Four of 12 interviewees argue that

⁸ For brevity, we often omit the term 'individualized' when speaking about the conceptions.

⁹ The unclarity was due to different factors: some interviewees focusing on NC³ processes or genetics rather than on niches per se in their research, some interviewees being at an earlier career stage and not having developed a clear niche conception yet, and other interviewees not clearly distinguishing proxies from niche dimensions (more in Section 6.1).

¹⁰ This is compatible with the inclusive niche conception.

internal factors cannot be niche dimensions (no overlap with three codes before). The environmental niche conception also is clearly recognizable in quotes from the interviews:

"So, normally I would say that niche dimensions are rather something that is coming from the environment, both biotic and abiotic. [...] So, immune states are of course also resulting from the interaction with the environment [...]" [Interviewer:] "Could those ever be niche dimensions?" [Interviewee:] "Immune state as such, I would say not, but the environmental aspects that lead to certain immune states, like how many parasites there are in the environment, that would be the niche dimension, whereas the immune state is a dimension of the organism itself." (Interviewee 4)

"I think anything that is inside the animal I would not consider as part of the niche. [...] So, it's not, you know, if you make everything the niche, what is the individual? [...] And then, I think if something internal can become external and then also affect other individuals, then it's immediately part of the niche again." (Interviewee 10)

"Traits are ubiquitous in biology. We refer to pretty much everything is a trait, but a niche dimension is always part of the biotic or abiotic environment. A niche dimension, for example, I would think never concerns an individual physiological, morphological, whatever trait. A behavior of an individual is the property of the individual, it's not a niche dimension. So, I would say a niche dimension is always, as I said, a biotic or abiotic component external to the individual." (Interviewee 8)

While the environmental niche conception is most popular among CRC members, it also faces some special difficulties in the context of behavioral research, which we however propose can be resolved using the notion of *niche proxies*. Proponents of the environmental niche conception encounter two difficulties: First, in the case of social niches (a focus of many behavior researchers) the environment of the focal individual is social and includes behaviors of conspecific individuals. According to this conception, behaviors of conspecifics are niche dimensions, whereas behaviors of the focal individual cannot be niche dimensions (because they are not part of its environment). The challenge is to empirically distinguish behaviors of focal individuals from behaviors of non-focal individuals, given that social niches are often studied in terms of social interactions involving the behaviors of focal and non-focal individuals (Kaiser et al. 2024). Without a clear distinction, it is difficult to conceptualize the social niche as environmental.

A second challenge arises from the fact that many studies of individualized niches focus on measuring phenotypic traits and internal states of animals. Often, differences in environmental parameters are more difficult to measure. For example, when studying individual differences in movement patterns of Antarctic fur seal pups (*Arctocephalus gazelle*), differences in the social environments of the pups can be studied only at the general level of distinguishing two different breeding colonies (low-density vs. high-density breeding site; Nagel et al. 2021). Studying behaviors and traits of individuals to gain information about environmental conditions has created conceptual confusion, as exemplified by the following quote:

"[I]n the [vertebrate species] studies we take as one measurement also stable isotopes to learn something about what they eat. So, then we get a lot of information about their niche, because we see what they eat. On the other hand, the stable isotopes become a trait of the individual itself. So, then it's hard to say whether this is now a niche dimension or a trait of the individual." [...] [Interviewer:] "Should that be considered a trait or a niche dimension? Or do you think it's sort of just fundamentally unclear?" [Interviewee:] I think it's fundamentally unclear, because it's a trait that is created by the interaction of the individual with its niche, but it becomes a trait in the end that you can measure in the individual. [...] So, I think stable isotopes are a nice example where it's completely unclear what it actually is." (Interviewee 4)

A few biologists of the CRC use the notion of a proxy to resolve this ambiguity. In their view, niche proxies are parameters that you measure to draw inferences about niches, just as you use fitness proxies to gain information about fitness. The biologists are operationalizing (or making measurable) certain environmental niche dimensions in terms of certain behaviors and traits of individuals. The following quote shows how the concept of a niche proxy is understood:

"I'm also studying the effects of these parasites on the sleep of [vertebrate species], how active they are during the day. This could also be a niche dimension. And the behavior, how active they are, some are a proxy. I think it's very difficult to measure the niche, but at the individual level we can measure proxies of the niche. The behavior, the adaptations, the physiological changes, immune changes. I don't see them as niche, but proxies of the niche. [...] If I can measure the individual, it's a proxy. If I can measure it outside the individual, it's a niche dimension." (Interviewee 12)

Appealing to the concept of niche proxies explains why some researchers measure individual behaviors and traits to characterize individualized niches, although they endorse the environmental niche conception. However, we should emphasize that this is not the view of all CRC members since some include individual traits as niche dimensions.

6.2 Inclusive Individualized Niche Conception

According to the inclusive conception, niche dimensions encompass environmental factors (abiotic and biotic) as well as the focal individual's behaviors, phenotypic traits, and internal states (e.g., hormonal, immunological, potentially even genetic). The inclusive niche conception allows for as many environmental niche dimensions as the environmental niche conception (Section 6.1). Behaviors and other phenotypic traits as niche dimensions include, for example, stress response, behavioral responses (such as activity, exploration, boldness, aggression), surface compounds (on cuticle), greenery uptake (for nest construction), date of laying eggs, etc. Internal states of the focal individual include, for instance, its immune state, its metabolism (e.g., sugar level), its cortisol release, its gut microbiota, etc.¹¹

Our interview analysis provides empirical support for the claim that the inclusive niche conception is advocated by some CRC members. Six of 12 interviewees

¹¹ Genes are typically not included into the category of internal states. However, a few biologists included genes into that category or controversially discussed the possibility to do so.

state that internal factors can be niche dimensions (however, two with low certainty; code "n.dim. are internal factors (hormones, immune)"); 2 interviewees referred to the behavior of a focal individual as a niche dimension (one overlap with code before; code "n.dim. is behavior of focal individual").

Quotes from the interviews reveal some reasons for adopting a niche conception that is more inclusive than the environmental conception. These biologists emphasize that a niche is not just an environment, but comprises all factors that are around and within individuals:

"So, for me, the niche consists of many different aspects. The environment, of course, really the very narrow environment and what the individual faces and also what belongs to its physiology maybe and metabolism. [...] [Interviewer:] Do you have a general view about how to distinguish between niche dimensions and things that are just traits of the individual? [Interviewee:] Yeah, I think that's a good discussion, what we count as niche dimensions. So, some I think would only look at the external [...] factors [...] but for me also the metabolism and the size and aspects within the individual can be a part of the niche, and that makes it more broader because I do not see the niche only as the environment, but also as the [invertebrate individual] itself. [...] I think it's really all dimensions that are around and part of the individual, which can be the environment, the abiotic, biotic environment, and then the internal factors of the individual." (Interviewee 7)

"The way that I understand niche dimensions or the individualized niche, I really would say it can be anything [...] [Interviewer:] Do you think that there are some kinds of traits of individual organisms, say, that would not count as niche dimensions? [Interviewee:] Not that I can think of. [...] I think the assumption in [the CRC] is that any niche dimension that is potentially affecting fitness. [...] Yeah, I mean, cort-release is like stress response. And I think, absolutely, [...] that different individuals have a very different individual specific stress response. [...] I cannot think of any internal state that is not individual specific--not an individualized niche trait." (Interviewee 11)

In sum, the inclusive conception allows for environmental niche dimensions as well as for behaviors, traits and internal states to be dimensions of the niche.

6.3 Strategy-based Individualized Niche Conception

According to the strategy-based conception, individualized niches are spaces of alternative strategies that individuals employ, such as the different foraging strategies of the Galápagos sea lion (*Zalophus wollebaeki*) (Schwarz et al. 2021). Relatedly, individualized niches are characterized as (representations of) combinations of phenotypic traits of individuals, such as combinations of anti-predator traits. Other examples of strategy-based niche dimensions include, for example, activity budgets, habitat use preferences, immune responses, aggressive or cooperative behaviors, fast or slow pace of life, foraging strategy, flowering time, etc.

The strategy-based niche conception does not allow for environmental conditions as niche dimensions. Rather, environmental factors are conceived of as being separate from the niche, constraining or shaping the alternative strategies and

combinations of traits of the individual. The following quote exemplifies this conception:

"I think the most, the best definition for the niche is the space of alternative strategies. [...] And then talk about like spaces in the environment as a consequence of this. [...] My alternative is to see not the [environmental] space as the niche dimension but the individual decisions that individuals take, so their, both their behavior and also their morphology, whatever feature they have to see the traits as the niche essentially, that [is,] a particular trait space that makes for a living in a particular environment. And to look then at individual differences in trait combinations and ask, why do alternative trait combinations work equally well? Or work well conditional on being in one or the other environment or something like this, yeah? So, the trait space, I mean essentially the environment is providing a hole, or something, that allows for particular combinations of phenotypes, and the niche is the combination of phenotypes that works in a particular environment."

When explaining the strategy-based niche conception, this biologist emphasizes that even though the environment is crucial to individuating an individualized niche, environmental conditions are not niche dimensions. When asked about internal states (e.g., hormones, immune factors), the biologist responds that they could be niche dimensions, just as behaviors and traits of the focal individual also are niche dimensions.

In addition, the results of the interview analysis support that the strategy-based niche conception is endorsed by members of the CRC. Three of 12 interviewees (explicitly or implicitly) conceptualize the individualized niche as a behavioral strategy (code "ind. niche as behavioral strategy"); 2 interviewees conceive of the niche as a combination of traits (all overlap with code before; code "ind. niche as trait combinations").

To summarize, the strategy-based niche conception views niches as spaces of trait combinations or spaces of alternative (behavioral) strategies. In contrast, the environmental niche conception views niches as spaces of environmental factors, while the inclusive niche conception includes environmental factors, traits and behaviors among possible niche dimensions. While the niche itself is conceptualized differently, each of these views acknowledges that environmental factors, traits and behavioral strategies are all relevant to shaping the individualized niche.

7. Evaluating the Plurality of Individualized Niche Conceptions

In the preceding sections we detailed the structure of the individualized niche concept in the CRC, showing that it has core unifying features while also exhibiting a plurality of distinct conceptions. This raises the question of whether the degree of plurality is in tension with the aims of the CRC and whether it would be better to, for instance, eliminate the plurality by selecting just one conception. Important reasons for striving for a unified conceptual framework include facilitating collaboration and integration of knowledge from multiple disciplines, the need for clear internal and external communication, and the need to present a consistent research agenda in funding application materials (Section 3.1; Kaiser and Morrow 2025). Some biologists have been concerned that a plurality of concepts might threaten these aims. Our first step towards addressing this concern is our argument that there is a single core concept within the CRC and the divergent definitions should be considered conceptions of this same concept.

Moreover, there are also reasons why the plurality of conceptions is expected to be beneficial. In Section 3.1 we mentioned that CRC biologists have different disciplinary backgrounds (e.g., ecology, evolutionary biology, behavioral biology) and different additional expertise (e.g., genetics, epigenetics, infochemicals, immunology), and this diversity of research areas may benefit from conceptual plurality. In line with this, one interviewee traces the environmental niche conception to ecology and the strategy-based niche conception to evolutionary biology:

"I mean, the niche, the environmental niche, this comes from ecology. And it's about I think largely the view of having those many individuals as replicates for a species. There's a species-specific preference. And you collect data on where the species occurs. Individuals are considered exchangeably. And this allows some inference. For example, you can predict like which communities of species assemble. This is largely what ecology is concerned with. [...] I think the strategy-based niche comes more from evolutionary biology. Because here the question is what alternative phenotypes are good to make a living? [...] So, for the [invertebrate individuals], I do think they are probably born like alternative colors. And they have some behavioral responses to this in that they search out different places because this is where they are best at hiding. That's the idea. So, I think it's one concept coming more from ecology, one more from evolutionary biology. But I think they are both interesting. It depends what you want to know. I think ideally, they go hand in hand. So, they are both analyzed. Just slightly different perspectives." (Interviewee 9)

The biologists in the CRC have different disciplinary backgrounds, address different research questions, study organisms of differing species and sizes, and use different methods in both the laboratory and field. This diversity contributes to creating conceptual plurality. At the same time, it is a good reason to retain plurality since some flexibility in what can be considered a niche dimension may be beneficial by allowing for many research questions, study designs and methodologies. For instance, thinking about individualized niches according to the strategy-based niche conception focuses attention on the plasticity of individuals and the potential of individuals to adopt alternative strategies to adjust to a particular environment. In contrast, the environmental conception focuses attention on the factors present in the environment and directs attention to environmental variability and how individuals are influenced by encountering differing factors in the environment.

Each of the conceptions of the individualized niche has some advantages at a general conceptual level. A key advantage of the environmental conception is that it maintains a clear distinction between the niche and the individual organism, unlike the inclusive conception. Because the inclusive conception includes both individuals'

traits and environmental factors as niche dimensions, this conception is clearly distinct from that of the habitat and of the environment, whereas the environmental niche conception sometimes invites conflation of the niche concept with the concept of habitat or concrete environment. This benefit of the inclusive conception is emphasized by its proponents:

"Yeah, so I want to make a clear distinction between it [the individualized niche] and just simple environment, because why would we call it a niche? You could also just say it's the environment that differs, and I think then the environment is the ecological environment. But if you want to make a case that the niche is something special or something different, then we need to consider also other aspects, and that would be the direct interaction between the individual and the environment, and that is influenced in both directions, with also size and metabolism and so on, factors, aspects, dimensions of the individual itself." (Interviewee 7)

The strategy-based conception focuses the most attention on the importance of individual plasticity while also maintaining a clear distinction among the niche, the concrete individual and the concrete habitat. On the other hand, some biologists find it problematic that environmental factors are entirely excluded from being niche dimensions and merely influence the niche.

Given that each of the conceptions has identifiable strengths and weaknesses for thinking about individual-environment interactions and given that there are members of the CRC who already endorse each of the conceptions, we recommend that the plurality of conceptions within the CRC be retained. We agree that the aims of unity in the CRC are important but have shown that the CRC's individualized niche concept already exhibits a moderate degree of unity (Section 4). Additionally, the plurality of conceptions is likely to be beneficial because it contributes to facilitating the very diverse array of research projects present in the CRC. The conceptual structure that has emerged in the CRC balances the objectives of the biologists by maintaining sufficient unity for communication and a shared research agenda, while also being flexible enough to support a variety of research projects and disciplinary backgrounds.

8. Conclusions

The literature on scientific concepts includes many debates about whether specific scientific concepts, such as that of species, lineage, gene, or biodiversity, support either conceptual monism or pluralism (or eliminativism). We have analyzed the structure of the CRC's individualized niche concept and shown that it is a single concept with a core meaning, yet it permits a plurality of distinct conceptions. This type of conceptual structure balances the aims of unification and plurality. The way these aims are balanced might be overlooked in philosophical debates that focus on disputing monism versus pluralism. We are not claiming that arguments for conceptual monism

or pluralism are ill-founded but rather that they represent a limited philosophical research focus.

Moreover, we conclude that the existing structure of the individualized niche concept is well-suited to the aims of the CRC. The concept has enough of a unified core that it can permit a clear shared research agenda, while allowing enough flexibility for conceptions to be specified in different ways, for example with respect to the question of what can be niche dimensions. The balance of these desiderata (unity and plurality/flexibility) would be lost if we were to recommend either adopting only a single conception or dissolving the shared concept in favor of a plurality of disunified concepts.

Our contributions as philosophers to the CRC have included developing this concept-conception account of the implicit conceptual structure within the CRC and raising awareness among the biologists of the diversity of conceptions. With increasing awareness, researchers should be more explicit about when and why a certain conception is in use, and in turn this will reduce the threat of confusion or miscommunication arising from the plurality. This paper illustrates how philosophy *in* science can contribute to scientific research programs by undertaking detailed characterization and evaluation of conceptual structures that are implicit in developing empirical research, communicating findings to working scientists, and making recommendations about whether existing conceptual structures are suited to the scientists' aims.

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