Hutchinson's ecological niche for individuals

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Abstract

We here develop a concept of an individualized niche in analogy to Hutchison's population-level concept of the ecological niche. We consider the individualized (ecological) niche as the range of environmental conditions under which a particular individual has expected lifetime reproductive success of ≥1. Our concept is essentially ecological primarily in the sense of fit of individual phenotypes to the contemporary environment and we do include evolutionary fitness here as an evaluative parameter of niche fit. We address four specific challenges that occur when scaling the niche down from populations to individuals. In particular, we discuss (1) the consequences of uniqueness of individuals in a population and the corresponding lack of statistical replication, (2) the dynamic nature of individualized niches and how they can be studied either as time-slice niches, as prospective niches or as trajectory-based niches, (3) the dimensionality of the individualized niche, that is greater than the population niche due to the additional dimensions of intra-specific niche space, (4) how the boundaries of individualized niche space can be defined by expected lifetime reproductive success and how expected reproductive success can be inferred by marginalizing fitness functions across phenotypes or environments. We frame our discussion in the context of recent interest in the causes and consequences of individual differences in animal behavior.

Keywords: ecological niche theory, individual differences, individualized niche, intraspecific variation, phenotype-environment interactions, developmental plasticity

Introduction

Individuals differ consistently in their behavior and their relations to the environment. We here aim to explore how individual differences can be integrated into the ecological niche concept to yield a utile concept of an individualized niche. Many of the individualized niche aspects that we discuss have metaphorical value that may help in structuring research (or in modelling studies), but some aspects can also be quantified empirically in natural systems. We first discuss recent progress in the study of consistent individual differences in animal behavior. We next briefly review ecological niche concepts and their different definitions. We then discuss the application of the Hutchinsonian ecological niche concept at the level of individuals. Our arguments are based on the idea that since individuals differ phenotypically, they often also differentiate their positions in the environment, eventually generating individualized niches. We structure our discussion of the individualized niche along four key questions: How can we deal with the fact that individuals are not statistically replicated? How can we incorporate time in the study of individualized niches? Which dimensions constitute individualized niches? Where are the boundaries of individualized niches? These four questions, we think, reflect important considerations, when implementing the concept of the niche at the level of individuals.

We write this essay from the perspective of empirically working behavioral ecologists. We therefore envision populations of individually distinct animals such as vertebrates or arthropods. While we are interested in the causes and consequences of individual differences (including, but not limited to, animal behavior), we do not see a particular individual as the object of study. Instead, we strive to understand how individual differences contribute to population-level processes. It is therefore the state and dynamic of population composition that interests us. We, like many other researchers in the field, use statistical summaries at the level of populations to study individual differences. This perspective relies on the law of large numbers and aims to understand general patterns and processes rather than individual life histories.

Being interested in the consequences of individual niche specialization does not mean that we include long-term or evolutionary consequences in the individualized niche definition that we develop here. Whether a particular phenotype will spread in a population depends on how phenotypic variation is inherited and how particular phenotypes perform in comparison to other phenotypes in the population. We see both aspects, inheritance and relative performance, as very important topics, but not immediately relevant to the definition of the individualized niche as such. We think of the individualized niches as current performance of a particular phenotype in the momentary environment. The concept is thus foremost an ecological and functional concept.

Consistent individual differences

Consistent individual differences have been in the spotlight of behavioral ecology for the last two decades (Sih et al. 2004; Réale et al. 2007). There are now hundreds of studies that report on individual differences in behavior across a large array of species, including vertebrates and invertebrates (Bell et al. 2009). A particular interest has been on behavioral traits that represent general reactions towards the environment, especially when these traits are temporally consistent and correlated across contexts (Kaiser and Müller 2021; Dochtermann and Dingemanse 2013). Individually consistent, context-general traits are often called animal personality traits, temperament traits, coping styles or behavioral syndromes (Kaiser and Müller 2021; Réale et al. 2007). A common research framework, relating to consistent individual differences, is the pace-of-life syndrome, which encompasses behavioral, physiological and life-history components. The pace-of-life syndrome has been linked to personality and survival (Ricklefs and Wikelski 2002; Réale et al. 2010), while it has laid the foundations for the study of implications of behavioral variation (Wolf and Weissing 2012).

From an evolutionary perspective, all individual differences that are heritable can evolve by natural selection. Indeed, individual differences in behavior often have a significant heritable basis (Stirling et al. 2002). It has been shown that animal personality differences can be systematically selected for, thus maintaining inter-individual variation in behavior (Dochtermann et al. 2015; Wolf et al. 2007). Furthermore, intraspecific variation affects interspecific interactions and ultimately species' coevolution (Moran et al. 2021). Consequently, the position of individuals in the environment can both be the cause and the consequence of behavioral differences, owing to the individual *x* environment interaction being bidirectional (Dingemanse and Wolf 2013).

Individual differences in behavior have ecological consequences, because they have an impact on the way in which individuals interact with their environment. For example, phenotypic variation can affect population dynamics through polymorphism in resource use (Dall et al. 2012). Indeed, intraspecific competition might as well be a fundamental cause of individual differences in behavior (Bergmüller and Taborsky 2010). Reduced competition over resources – as a result of specialization at the level of individuals – can increase the carrying capacity of a habitat and promote resilience of populations (Wolf and Weissing 2012). Thus, in analogy to community dynamics, resource partitioning among phenotypes can reduce intraspecific competition and facilitate population growth and persistence (Araújo et al. 2011; Layman et al. 2015). Indeed, an extensive review of empirical evidence on consequences of intraspecific variation showed that inter-individual diversity increases establishment success, range size, population stability and resilience, while it decreases extinction risk and vulnerability to climate change (Bolnick et al. 2011; Forsman and Wennersten 2016). Intraspecific variation in population-related traits can thus alter population and community dynamics (Bolnick et al. 2011; Araújo et al. 2011). We think that an individualized ecological niche concept can provide a fruitful perspective on individual differences.

The ecological niche

The concept of the ecological niche is fundamental in Ecology. The term was initially vaguely defined and used to describe the ecological position, habitat and requirements of species (Packard 1894; Grinnell 1917; Allen 1882, see Gibson-Reinemer 2015). First composed definitions of the ecological niche were presented by Elton (1927) and Grinnell (1928). Elton (1927) defined the ecological niche in terms of the species' function within a community and its relations to other species. This view is focused on the functional role of species and is mostly used in community and functional ecology. Grinnell (1928) proposed the ecological niche as the physical place that species are adapted to. According to this definition, niche is a synonym of habitat or position of species in the environment.

The first reviews on the ecological niche emerged quite early (Hutchinson 1978). Since the introduction of the term, the definition of the ecological niche was a topic for debate. Hurlbert (1981) published a collection of more than 20 quotes defining the ecological niche. We expanded this collection of definition quotes to present, resulting in 36 definitions (Table S1). Some of these definitions are only subtly different. However, ecological niche concepts can be broadly categorized into environment-based concepts and function-based concepts. Environment-based concepts include the ecological niche as the habitat/environment (Grinnell 1917; Grinnell 1928; Gause 1934; Dice 1952; Odum 1959) or as abstract environmental space (Hutchinson 1957; Root 1967; Macfadyen 1957). Function-based concepts include the functional role of a species (Elton 1927; Clarke 1954) or its trophic position (Elton 1950; Weatherley 1963). Some definitions also include a combination of environmental requirements and effects on resource availability (Chase and Leibold 2003).

The most popular and widely cited definition of ecological niche was proposed by Hutchinson (1957, 1978). Hutchinson defined the ecological niche as a hypervolume in an n-dimensional (abstract) environmental space that allows a population to persist indefinitely. Hutchinson distinguished between fundamental and realized niches, which correspond to an ecological niche before and after accounting for interspecific competition, respectively. While the Hutchinsonian niche concept is primarily defined in terms of place in the environment, it does include some functional aspects, in particular owing to the distinction between the fundamental and the realized niche. Rosado et al. (2016) claim that Hutchinson built on Grinnell's idea, while others (Colwell and Rangel 2009; Swanson et al. 2015) argued that the concept of the hypervolume was introduced by Gause (1934). Independently of Hutchinson's source of inspiration, the *n*-dimensional hyperspace is until today a fundamental concept in ecology and evolution. We therefore explore how this concept can be usefully applied at the level of individuals.

The ecological niche for individuals

The recent interest in the study of individual differences highlights current focus on ecological differences between individuals within populations. Here we address the applicability of the Hutchinsonian niche concept at the level of individuals. Some early work on ecological niches already included discussions on the importance of individual differences within a population. vanValen (1965), for example, pointed out that individuals differ on how they use available resources and that population niche width is driven by the variation between individuals (Niche Variation Hypothesis). Roughgarden (1972) pioneered the idea to use individual differences in trait expression as proxies for resource use. Traits of individuals are here used as substitutes for the environmental dimensions, which are more difficult to measure. Roughgarden's ideas gave rise to a vibrant field of functional trait analyses (Violle et al. 2007). In the meantime, large databases of functional traits have been compiled, in particular for plants (Fraser 2020; Kattge et al. 2020), albeit only part of these data focus on individual differences.

Although the study of intraspecific variation has been neglected for some decades, it revived around the turn of the last century (Bolnick et al. 2003). Individual niche specialization has been studied empirically mostly with a focus on diet, while studies focusing on habitat selection, behavior, or labor division are less numerous (Ingram et al. 2018; Dall et al. 2012; Bolnick et al. 2003). Notably, individualized niches have been even more vaguely defined than concepts of the ecological niche as such (Bergmüller and Taborsky 2010; Müller et al. 2020; but see Trappes et al. 2021). This is partly because the concept is broad and encompasses aspects that can better be kept apart. The aim of our essay is to bring structure into the individualized niche concept and provide definitions of the individualized niches in the broad sense, but also facets that are best treated under different (sub-) labels. In our view, there are four main challenges when applying the concept of the ecological niche to individuals: 1) the question of uniqueness, 2) the questions of time, 3) the question of dimensions and 4) the question of boundaries. We first start with working definitions of the ecological niche of individuals before addressing the specific challenges.

Working definition of the individualized niche

Hutchinson (1957) defined the (fundamental) ecological niche of a population as the range of environmental conditions in which a population can persistent indefinitely. Infinite persistence implies non-negative population growth rates in the long term. Scaling down to individuals, we propose a working definition of the individualized (ecological) niche as the range of environmental conditions that provide an expected lifetime reproductive success of ≥1 to particular individuals.

Before going into more detailed aspects of our individualized niche concept, we want to highlight two important aspects: First, lifetime reproductive success (commonly used as a measure of absolute fitness) serves as the currency of the phenotype-environment match in our concept and not as the determinant of contemporary selection. This aligns with the Hutchinsonian niche being an ecological, rather than evolutionary, concept. Research on how the individualized niches evolves might have to consider the comparative performance (relative fitness) of alternative phenotypes, including an adjustment of the mode of reproduction. Second, we highlight that the individualized niche as used in this manuscript is defined by the environment that an individual lives in, not by its phenotype. The phenotype can act as a mediator that affects fit to the environment (Trappes et al. 2021), but does not represent a part of the niche itself.

The questions of individual uniqueness

One issue when defining niches at the level of individuals is that individuals are (by definition) not identical, impeding statistical replication. The ecological (Hutchinsonian) niche of a population can be estimated by quantification of where different members of the population can be found in environmental space. Here, individuals serve as replicates at the level of the population and can thus occupy the same niche. However, individuals themselves can only be found at a particular point of environmental space. (We leave the discussion of integration over time for the following section.) Hypervolumes at the level of populations become points in environmental space at the level of individuals. In loose analogy to Hutchinson's realized niche, we call each of these points the *realized individualized niche*. However, the point where an individual happens to live almost certainly does not cover the range of environmental conditions under which it could have occurred. The *potential individualized niche* thus includes all environments where a particular individual would (or could) have had an expected lifetime reproductive success of ≥1 (Fig. 1). This means the potential individualized niche is defined by a space of unobservable outcomes. How can we deal with the problem that realized individualized niches are incidental instantiations of points in environmental space and that potential individualized niches are unobservable outcomes?

There are at least partial solutions to both issues. A common approach in the study of realized individualized niches is to address the question on the level of populations and to integrate over time. If we collect replicate observations per individual over short but meaningful time intervals, we can use variance decomposition approaches to quantify population-level variability in realized niches. One approach is the estimation of individual-level repeatabilities that quantify the proportion of variation that is explained by individual differences (Nakagawa and Schielzeth 2010; Bell et al. 2009). The idea here is to treat individuals as ephemeral instantiations, but to view the population-level individual variation as a stable population-level feature of the magnitude of individual differences in realized individualized niches.

Even with replicates over short meaningful time intervals, it is *de facto* impossible to cover the full potential niche of an individual. At least in observational studies under natural conditions, environmental covariation in space and time will prevent individuals to be observed across the full range of potential environments in which it could have expected lifetime reproductive success of ≥1. Experimental approaches offer a partial solution if individuals can be translocated to a range of different environments (Wilson et al. 2019). Some measure of current performance can then be used as a proxy of reproductive success across a range of environments (sacrificing the value of a fixed boundary for defining the niches, see discussion below). However, experimental approaches are necessarily limited to few dimensions of environmental space. An ultimate limit to experimental exploration of the potential individualized niche is also set by the lifespan of an individual, since potential individualized niches are almost certainly substantially larger than realized niches.

An alternative approach is to marginalize across phenotypes (or genotypes) when mapping individualized niches (Fig. 2). This is rooted in Roughgarden's (1972) idea to use traits of individuals as proxies for resource use. Individuals are here used as replicates to establish a distribution of phenotype-specific environments. In principle, this can be done across many different traits. While individuals are used as tokens of types in particular phenotypic dimensions, individuals are typically unique in their trait combinations. In principle, it will be possible to predict an individual's niche from its unique combination of traits. Such predictions are also possible for non-linear relationships, provided that the form of the mapping function is none. A limit is set only if interactions between traits are strong and poorly replicated in a population. In such cases, trait combinations in some individuals might be so unique that prediction becomes impossible, a limit that is shared with phenotypic novelties.

Both realized and potential niches might be of interest to ecologists. In some cases, the environmental space that is occupied by an individual might be incidental. In other cases, however, features of an organism might influence the realized niche space that can be occupied. Many insect species, for example, show developmentally plastic wing length polymorphisms (Harrison 1980; Zera and Denno 1997). Wing length affects dispersal abilities and thus the range of environments an individual can reach. Short-winged individuals might, in principle, be able to survive and reproduce in very diverse environments (thus they might have a wide potential niche), but in reality, they are limited to the realized niche at their local patch. The developmental pathway to develop long-winged, dispersive phenotypes might not affect the potential niche as defined above, but might result in a much wider array of realized individual niches. Sampling of environments is only possible for an individual with sufficient mobility.

We may distinguish a third form of the individualized niche, the *fundamental individualized niche*. The difference to the potential individualized niche is very subtle and probably not too relevant in practical applications, so the two might often be used interchangeably (see Trappes et al. 2021). Huntchinson's fundamental ecological niche is the environmental space that is occupied by a population in the absence of specific environmental factors (competitors, predictors, dispersal barriers). This is appropriate for populations, because if a species is absent from a potentially suitable habitat, it is so for a reason. Individuals, however, exist only as a single copy and can be absent from many suitable environments, not for specific, but for arbitrary or random reasons (e.g. being born in a specific place). The term fundamental individualized niche might thus be used for the individualized niche in the absence of particular external (usually intraspecific or interspecific) factors, while the term potential niche does imply coincidental absence from some environments – simply because individuals cannot be at multiple places at a time. The reference space of the potential individualized niche is usually the realized niche of the population, while the reference space for the fundamental environmental niche are all possible environments. The distinction is specific to the individualized niche, since replication is less of an issue for the niche of the population.

Definition A: The *realized individualized niche* is the place in environmental space in which a particular individual is found and has an expected lifetime reproductive success of ≥1. The realized individualized niche can be quantified empirically.

Definition B: The *potential individualized niche* is the volume in environmental space in which a particular individual could be found with an expected lifetime reproductive success of ≥1. The potential individualized niche cannot directly be quantified, but significant parts of the niche space can usually be statistically inferred.

The question of time

We have alluded to the integration across intervals of time above. This raises the more general questions about whether the individualized niche refers to slices of time or to entire lifespans. The ecological niche of a population is focused on entire lifespans. The ecological niche of a forest-dwelling frog, for example, includes a network of forests and ponds, since adults require shelter in woodlands while in its juvenile stage, as a tadpole, the frog requires ponds for survival and growth. Population persistence can only be achieved if both habitats are available. One might argue that the equivalent is also true for individuals: that the individualized niche is a lifetime niche. However, there are arguments why this simple application of lifetime niches loses important intricacies of the individualized niche.

Throughout an individual's life, developmental decisions impact niche space later in life (West-Eberhard 2003). The development of long wings in grasshoppers, for example, is triggered by increased population density (Poniatowski and Fartmann 2009). All (or at least most) individuals seem to have the potential to develop the long-wing phenotype under high population density, but remain short-winged under low population density. Potential niches of long- and short-winged individuals are therefore no different at birth, since all (or at least most) individuals have the potential to develop into either phenotype. It is a specific time during development when niches of short- and long-winged phenotypes split. Another example is given by match-based phenotypic adjustments. Some species of grasshoppers, for example, are able to change their body coloration during development (Rowell 1972; Dearn 1990). Since body color affects background-dependent crypsis, individuals of different color morphs have different individualized niches in the sense of environmental conditions under which they can survive and reproduce. At birth, individuals have the same potential for alternative body colors, therefore they have the same potential individualized niches. However, after phenotypic adjustment, their niches become different. A focus on lifetime niches misses the importance of such critical developmental decisions.

We therefore think that the individualized niche (whether realized or potential) is most fruitfully viewed from two perspectives. A time-slice perspective looks for individual niches within certain life stages or other relevant periods of time (such as different seasons). The study of such *time-slice individualized niches* (Fig. 3) allows insights into individual differences in niche use and short-term phenotypic adjustments. A now-and-in-the-future perspective looks at individual niches with a focus on sensitive phases or developmental switch-points and their lifelong consequences (Sachser et al. 2020). We call this now-and-in-the-future perspective, the *prospective individualized niche* (Fig. 4), as the space of environments in which an individual can survive and reproduce given its current phenotype and its developmental opportunities. The prospective individualized niche is the time-structured space of potential niches.

The prospective individualized niche does not give a lifetime perspective except for the special case of a zygote. Potential individualized niches are affected by previous development (and by accidents). Certain areas of environmental space might not be available if irreversible developmental plasticity in early life-stages prevents an individual from developing a matching phenotype (Nyman et al. 2018). Development has manifest consequences for the individualized niche. The potential niche from a prospective perspective therefore changes as individuals age. In fact, with the possible exception of accidents, it always shrinks, as potentials must be available at early stages and can only be reduced by individual decisions during development. The potential time-slice individualized niche, in contrast, might vary across lifetime and might shrink or expand as an individual keeps adjusting its phenotype.

Accidents and 'bad luck' represent a special case to be considered. Purely coincidental events that might affect any individual with equal probability should not be considered in affecting expectations of lifetime reproductive success. However, not all risks are equally distributed across environments. If individualized niches are unequally risking, then (some) accidents are in fact non-random and genuinely affect fitness expectations. Some individuals may select risky environments with high variance in reproductive success while others select safer environments (Moran et al. 2021) . For example, all individuals may have the same probability of being killed by a storm, while choosing to nest in areas with high predator density (or not) affects the reproductive success non-randomly.

However, there is room for a lifelong perspective. We think it is usually meaningless to reconstruct realized individual niches post-mortem for its own sake, since in biology we are rarely interested in unique individuals that represent an ephemeral phenomenon. Rather we aim to understand general patterns and mechanisms. A compilation of individual lifetime niche trajectories (with dynamic changes throughout life) can expose alternative developmental trajectories as bundles of alternative realized niches that change across age (Fig. 5). Such a trajectory-based lifetime perspective helps to answer the question how individualized niches arise during development. We therefore call specific life-history trajectories in environmental space the *trajectory-based individualized niche*.

<u>Definition C:</u> The *time-slice individualized niche* is the environmental space in which a particular individual occurs during a particular part of its development and has an expected lifetime reproductive success of ≥1. Aspects of the time-slice individualized niche can be quantified empirically by taking repeated measurements.

<u>Definition D:</u> The *prospective individualized niche* is a volume in environmental space in which a particular individual has an expected lifetime reproductive success of ≥1 that includes the current and future potential niches. The prospective individualized niche provides a focus on particular developmental decisions, which affect future niche space and can be quantified empirically.

Definition E: The *trajectory-based individualized niche* is a time-structured volume in environmental space that allows for expected lifetime reproductive success of ≥1 and that is different from alternative developmental trajectories. The trajectory-based individualized niche provides a focus on alternative developmental trajectories that affect potential niche space and can be quantified empirically.

The question of dimensions

Hutchinson (1957) defined the ecological niche as an *n*-dimensional space of environmental dimensions: abiotic (scenopoetic) and biotic (bionomic) factors. Attributes of the focal species, such as specific phenotypes, are not dimensions of the environmental niche. Instead, traits are features that allow a species to occupy a specific environment, for example by providing the ability to exploit particular resource (and traits can be used as proxies for resource use, Roughgarden 1972). Hutchinson distinguished the fundamental niche, the space that can be occupied by a particular species in principle, from the realized niche, the space occupied by a particular population in face of competition. Since the presence of the other species is just a particular dimension of environmental space, the main function of the realized vs. fundamental niche distinction is highlighting how a particular inter-species interaction can affect niche use (a clearly functional perspective). The realized niche is thus the niche of a species in $n - 1$ environmental dimensions.

In analogy to Hutchinson's ecological niche of the population, we define the individualized niche in terms of environmental dimensions, explicitly including all biotic and abiotic factors that are external to an individual. There is no need to restrict the factors to those that are causally relevant to an individual's reproductive success. Some environmental dimensions might have little influences on reproductive success, however this is an empirical finding and should not condition the use of particular environmental dimensions. It is sometimes argued that niche dimensions should be independent, i.e. orthogonal (Blonder et al. 2018). Often they will not be orthogonal and some subspaces will not be realized in any real physical location. It is thus impossible to infer whether some environmental combinations represent part of the niche of an individual (or population). However, it is most useful to define niche space by evidence for presence of an individual rather than lack of evidence for an absence. Combinations of environmental dimensions that are not realized in the real world should thus not be regarded as part of the ecological niche of individuals (or populations). While niche dimensions might not be orthogonal in the real world, it is fair to treat them as orthogonal in hypothetical environmental space.

When scaling down from populations to individuals, the intraspecific context becomes external to the individual. The presence or absence of conspecifics (including potential mates) or conspecifics with particular trait values become an explicit part of the individualized niche. The social context, for example, is part of the individualized niche, like the interspecific community context in the ecological niche of populations. The social conditions that allow an individual to realize a non-zero inclusive fitness are also known as the social niche (Blonder et al. 2018; Saltz et al. 2016, see below for a discussion of setting the boundaries). The fact that the intraspecific (including social) context is part of individualized niche dimensions represents one of the most important differences to the population niche. The individualized niche, thus, consists of $n + s$ dimensions, where n represents non-intraspecific dimensions, while s represents the dimensionality of the intra-specific niche space (Fig. 6).

The intraspecific context is broader than the social settings. Population density and the frequency of other phenotypes of the same species may impact the individualized niche even without social interactions (van Benthem and Wittmann 2020). Some prey species such as grasshoppers are color polymorphic (Rowell 1972) and some of their predators develop search images to specialize on the most frequent morph in a population (Bond 2007). The expected lifetime reproductive success of an individual with a particular body color may thus depend on the frequency of that color morph in a population – even if all other environmental dimensions are identical. Rareness of a particular phenotype can be an advantage even when the phenotype in itself coveys no general benefit (Violle et al. 2017). Such processes give rise to frequency-dependent selection, affecting the niche space of individuals, since some phenotypes might be advantageous under some states of the population but not under others.

We suggest that the difference between the presence and absence of intraspecific niche dimensions represents a particularly interesting aspect of the individualized niche, especially since the social environment can have profound influences on later individual phenotypes (Jäger et al. 2019): How does the niche of an individual change depending on the state of the population as a whole (including density and frequency of other phenotypes)? This offers an interesting perspective on the concept of soft vs. hard selection in evolutionary biology (Wallace 1975; Bell et al. 2021). Hard selection refers to selection that is determined by the phenotype of the focal individual and its environment, while soft selection occurs when selection is density- and frequency-dependent. Population density, phenotype frequencies and social interactions are thus important components of the individualized niche.

The question of boundaries

Hutchinson (1957) defined the boundaries of a population's niche by indefinite population persistence and thus non-negative average growth rates in the long term. Population growth rates are determined by the ratio of births to deaths in a population. The equivalent quantities at the level of individuals are survival and reproduction and those can be used for determining the boundaries of individualized niches. However, there are three important considerations, a rather easy and two harder ones, when translating this to the level of individuals.

The easy complication is the question of whether niche boundaries are sharp borders or gradual zones of niche fit. In fact, this consideration applies to both individualized and population niches and can be solved by working with continuous values of population growth rates (in the case of populations) or lifetime reproductive success (in the case of individuals). This results in a nuanced view of core and marginal niches space. A minor complication is that population growth rates and individual lifetime reproductive success are often low under most suitable environmental conditions if population growth rate (and individual lifetime reproductive success) are density-dependent and a population is near its local carrying capacity (Engen and Sæther 2017). This is less of a problem for the individualized niche if population density is considered as one of the niche dimensions. Nevertheless, even in case of the ecological niche of a population, population size (or population density) can be used to estimate the soft borders of niche boundaries.

The harder problem is which concept of individual lifetime reproductive success should be considered. It might be tempting to use realized lifetime reproductive success, quantified in terms of number of offspring produced. However, realized lifetime reproductive success has a large stochastic component and is often a poor indicator of a particular individual's niche fit. If we use realized lifetime reproductive success (as e.g. Saltz et al. 2016 seem to do), then we do have a problem with individuals that have thrived throughout live, but have bad luck and do not reproduce by some coincidence (see above for a discussion of risk factors). They would be said to be out of their niche, because their realized lifetime reproductive success (even inclusive realized fitness) is zero. We therefore define the boundaries of individual niche space in terms of expected lifetime reproductive success, which are functions of the phenotype-environment combination (Fig. 7). Expectations of reproductive success do not necessarily invoke propensities in the sense of stochastic dispositions, but are rather build on statistical summaries that follow the law of large numbers (Drouet and Merlin 2015). Individualized niches are thus identified by mapping lifetime reproductive success on phenotype-environment combinations in the form of multidimensional fitness functions. Since there are no replicates of an individual, there is no empirical solution, neither to decompose individual lifetime reproductive success into a stochastic and a deterministic component, nor to quantify individual lifetime reproductive success across different environments. Resorting on fitness components or fitness proxies might be a viable solution (Patrick and Weimerskirch 2014). However, with fitness components we have to abandon (or at least adjust) the absolute threshold of expected lifetime reproductive success of ≥1. Work with fitness components will thus discover mostly gradual (soft) rather than sharp boundaries and this could be done even with relative fitness. Alternatively, we can marginalize across phenotypes (or genotypes) and environments to estimate expected lifetime reproductive success in the form of fitness functions using different individuals as replicates (Figure 2).

One might wonder whether the boundaries of the individualized niche are defined by zero lifetime reproductive success or lifetime reproductive success of one (Figure 7). One problem with reproductive success expectations is that they might get infinitely small and it might be difficult to tell where they become zero. The condition of (simply) positive reproductive success expectations thus forms a theoretical boundary that is difficult to determine empirically. We argue that while individuals cannot persist indefinitely, they need to leave at least one offspring to perpetuate into future generations. A useful threshold for the boundary of the individualized niches is thus the (long-run) expectation to produce one descendant. We think that this makes a useful benchmark in a gradual view of the individualized niche.

A further consideration is whether the benchmark value of lifetime reproductive success should better be set to two offspring in outcrossing sexually reproducing organisms. As stated above, evolutionary applications need consider the mode of reproduction of the focal organism and aspects of relative performance. In outcrossing organisms each offspring has two parents and the average contribution to future generations thus needs to be 2 (among all parental) in stable populations. However, the situation is already more complicated for facultatively outcrossing individuals. While we do see value in applying a threshold of expected lifetime reproductive success of at least two in some cases, we believe that a threshold of one offspring can served as a universal benchmark in ecological applications: It allows one individual to be replaced by one offspring. Species-specific peculiarities about inheritance (including common aspects such as outcrossing) need to be included when studying the long-term fate and evolution.

Conclusions

We have started with a discussion of individual differences in behavior. We now want to come back to this and ask whether individualized niches are a mere rebranding of the study of individual differences. In brief, we think there are important differences. First, in our concept it is not the phenotype itself that represents the individualized niche, but the environment that an individual lives in. Not all individual differences in phenotype and behavior are thus relevant to the individualized niche (Trappes et al. 2021). It is the subset of individual differences which mediate phenotype-environment matches (Edelaar and Bolnick 2019) are relevant to the individualized niche. While the literature on individual differences focuses mainly on survival and fitness consequences of individuals, the individualized niche focuses on the environment and, in particular, relate the phenotype-environment match to individual differences (in line with Roughgarden 1972). Furthermore, in order to estimate individualized niches, the full range of an individuals' ecology and life history needs to be studied. This highlights the urge for studies, which incorporate lifetime-long observations of individuals.

We have introduced the fields of animal personality studies and the ecological niche concept and have discussed how they blend in the concept of an individualized niche. We provide a working definition of individualized niches that builds on Hutchinson's population-level ecological niche. However, there are important intricacies when developing an individualized niche concept. Particularly important are (i) the differentiation between realized and potential niches where the latter is defined by unobservable outcomes, (ii) the dynamic nature of individualized niches with a time-slice, a prospective and a trajectory-based perspective, (iii) the inclusion of intra-specific dimensions in the dimensionality of individualized niches and (iv) the need to define the boundaries of individualized niche space by expected lifetime reproductive success (not realized lifetime reproductive success). We hope that these considerations will help other scientists to further develop the concept of the individualized niche into a practicable tool for empirical studies and conceptual progress.

There are important challenges in applications of the individualized niche concept. One of them is the efficient identification of relevant niche axis. While the niche in itself is highly multidimensional, there are likely a few important niche dimensions that matter the most, in order to explain individual differences within populations. Therefore, the challenge for practitioners will be to find ways to reduce the dimensions of individualized niches to those variables, which are important for individuals. The second is the efficient use of statistical models to predict fitness expectations. Nonlinearities and interactions complicate the prediction of fitness expectation (and any marginalization across individuals), so that the functional relationships need to be sufficiently well known. Linear prediction and simple (additive or multiplicative) interactions might be the first approximations in practice, but are likely overly simplified. The third challenge is the efficient use of good proxies of lifetime reproductive success in all case where it cannot be determined directly.

While we see our concept mostly of metaphorical value, we also think it has practical implications. As a metaphorical concept, it can provide thinking aids for new scientific avenues. Importantly, we provide subcategories of the concept that, we think, may help to distinguish unequal aspects that are sometimes treated under the term 'individualized niche'. We thus bring structure to the concept. We also provide practical advice on empirical quantification of the individualized niche. The realized and the trajectory-based individualized niches can be quantified quite directly, via repeated observations of the same individuals. The time-slice niche is already often quantified, in many animal personality studies, though a stronger focus on individualized phenotype-environment matches is desirable. The prospective niche can be quantified empirically by focusing on the consequences of developmental switch-points and might even provide fresh views on animal behavior. The potential individualized niche is the most complicated to be measured empirically and requires some grouping of individuals with similar phenotypes, but still provides more detailed perspective of the ecological niches than Hutchinson's population niche. We hope that the individualized niche, in its different flavors, allows a more informative view of what is often treated as the niches of the population. Individuals differ and this often has ecological and evolutionary consequences. The main challenge will be the identification (and quantification) of relevant niche dimensions within the full niche space, which is characterized by high dimensionality.

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Figures

Figure 1: Schematic view of realized and potential individual niches occupy subspaces of the population niche. Realized niches are points (or small volumes) in environmental space that occupy only part of the volume that could potentially be occupied by an individual.

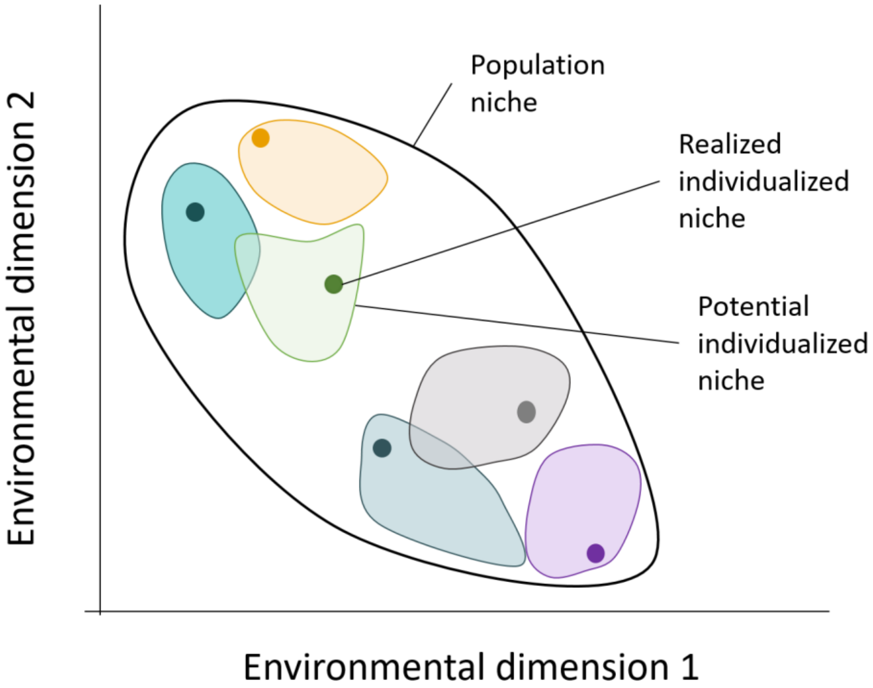

Figure 2: Schematic view of the idea of using population-level patterns to predict individualized niches and fitness consequences. Colors show different types of individuals (e.g. females and males). The left plot shows two trait dimensions of which one is informative for occupancy of specific environments. The right plot shows a multivariate fitness distribution that depends on phenotype (here shown by different colors and on the abscissa) and environments. Fitness arises from the combination of phenotypes and environments. Darker colors show higher fitness expectations.

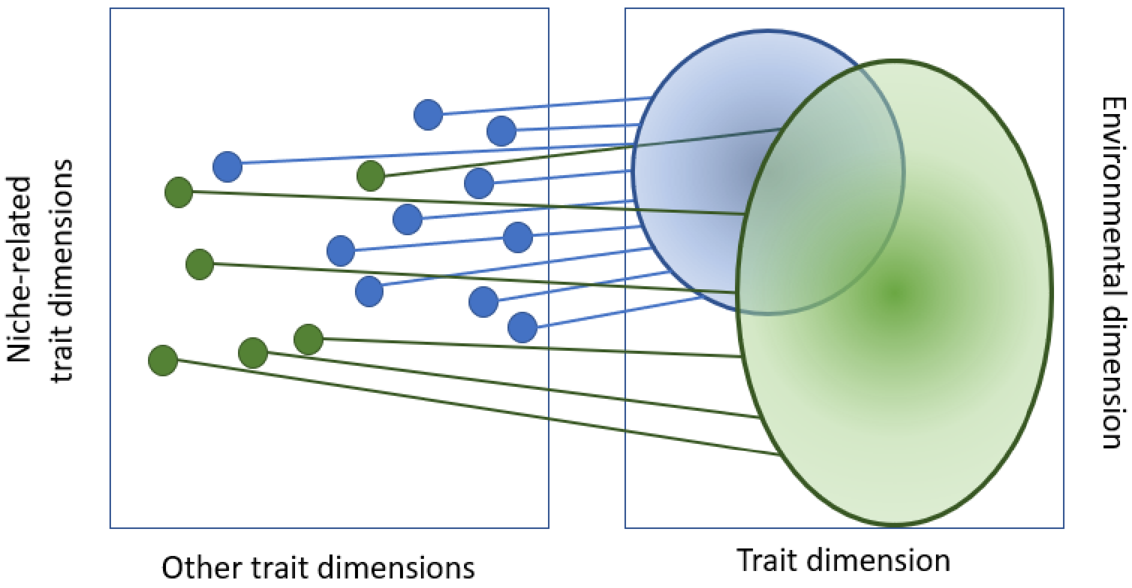

Figure 3: Schematic view of time-slice niches of an individual. Different colors refer to different meaningful life stages of on individuals. Filled dots show realized individual niches, while shaded areas show the potential individualized niches.

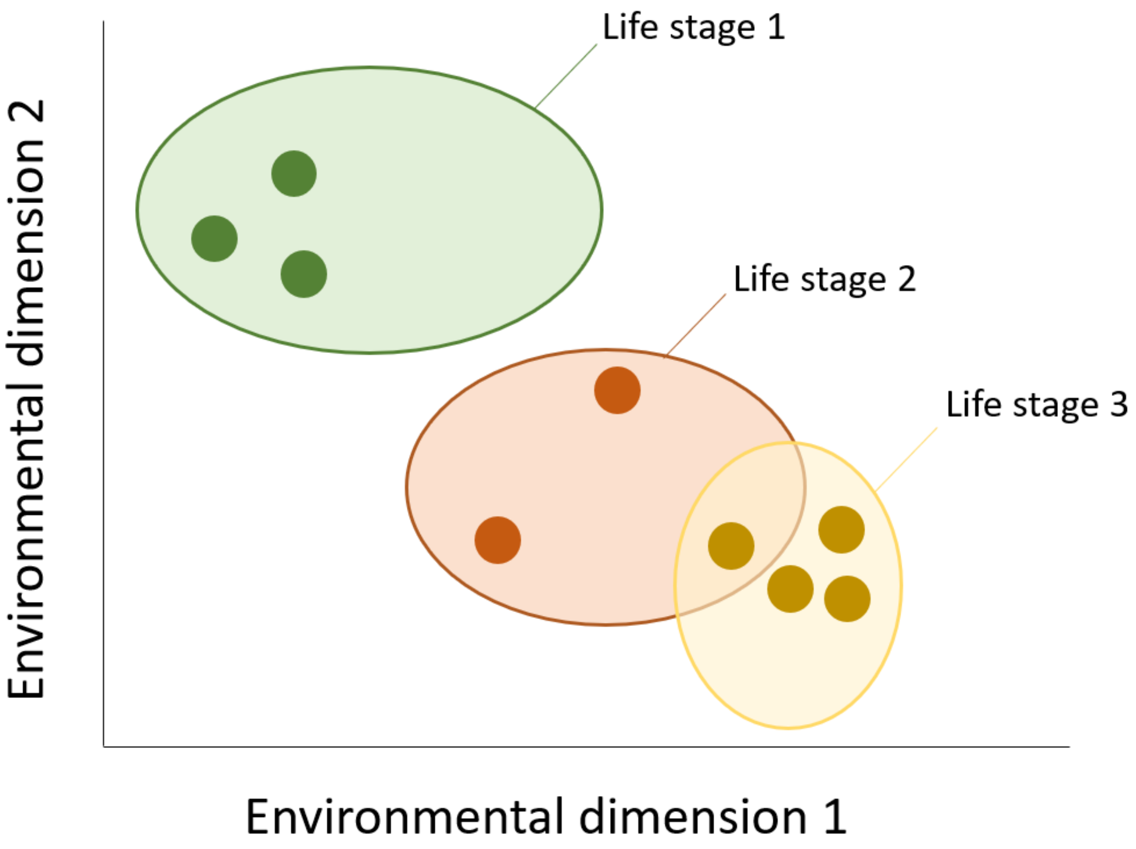

Figure 4: Schematic view of prospective individualized niches of two individuals. Shaded areas show the potential niche, dashed horizontal lines mark snapshots at three life stages. Steps in individual potential niches mark developmental decisions of (or accidental external influences on) an individual. The horizontal axis compresses lifetime niche dimensions onto a single axis. Potential niches can only shrink as an individual commits developmental decision. The width of the prospective niche at any time point illustrate the potential range of environments (now and in the future) in which an individual has an expected lifetime reproductive success of ≥1.

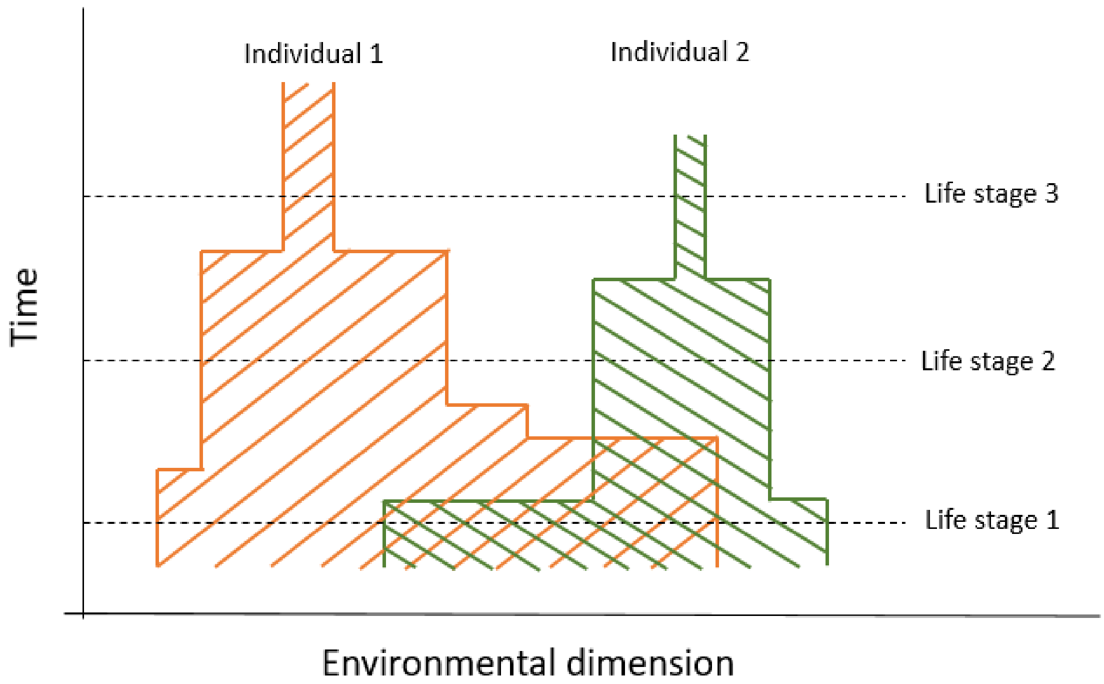

Figure 5: Schematic view of lifetime trajectory-based niches that emphasize alternative developmental pathways. Black lines show individual developmental trajectories in niches space. The green background schematically highlights alternative trajectories and switch points that can be identified from bundles of individual developmental trajectories.

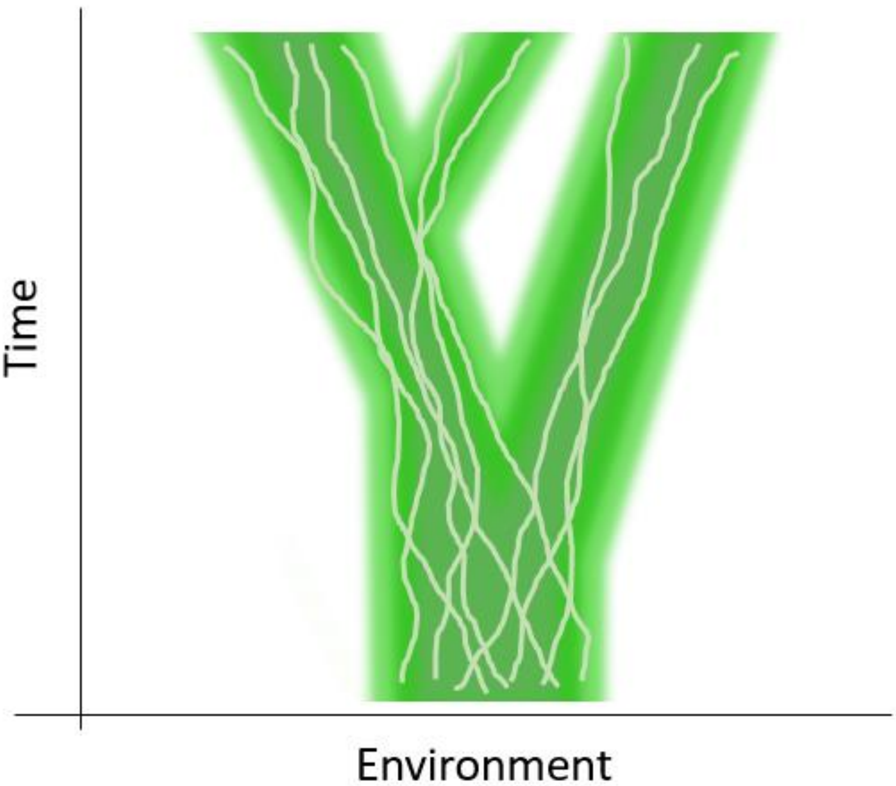

Figure 6: Dimensionality of the individualized niches. The population niche consists of n dimensions that encompass all environmental conditions under which a population persists. The individualized niche explicitly includes all intra-specific dimensions (such as population density and the frequency of alternative phenotypes).

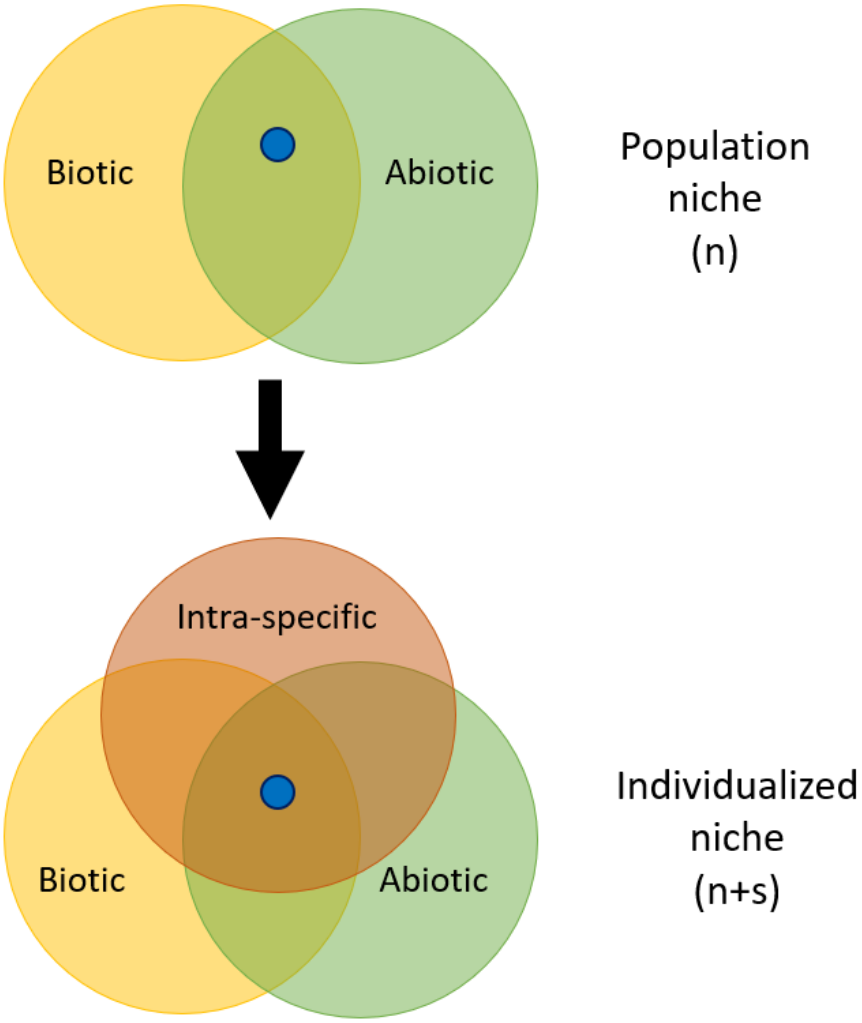

Figure 7: Multidimensional fitness function and boundaries for the individualized niche. The graded blue area shows the expected (absolute) lifetime reproductive success kernel. The solid blue line marks what we consider the boundary of the individualized niche at an expected isocline of 1. The dashed blue line marks the absolute boundary of where expected fitness drops to zero.

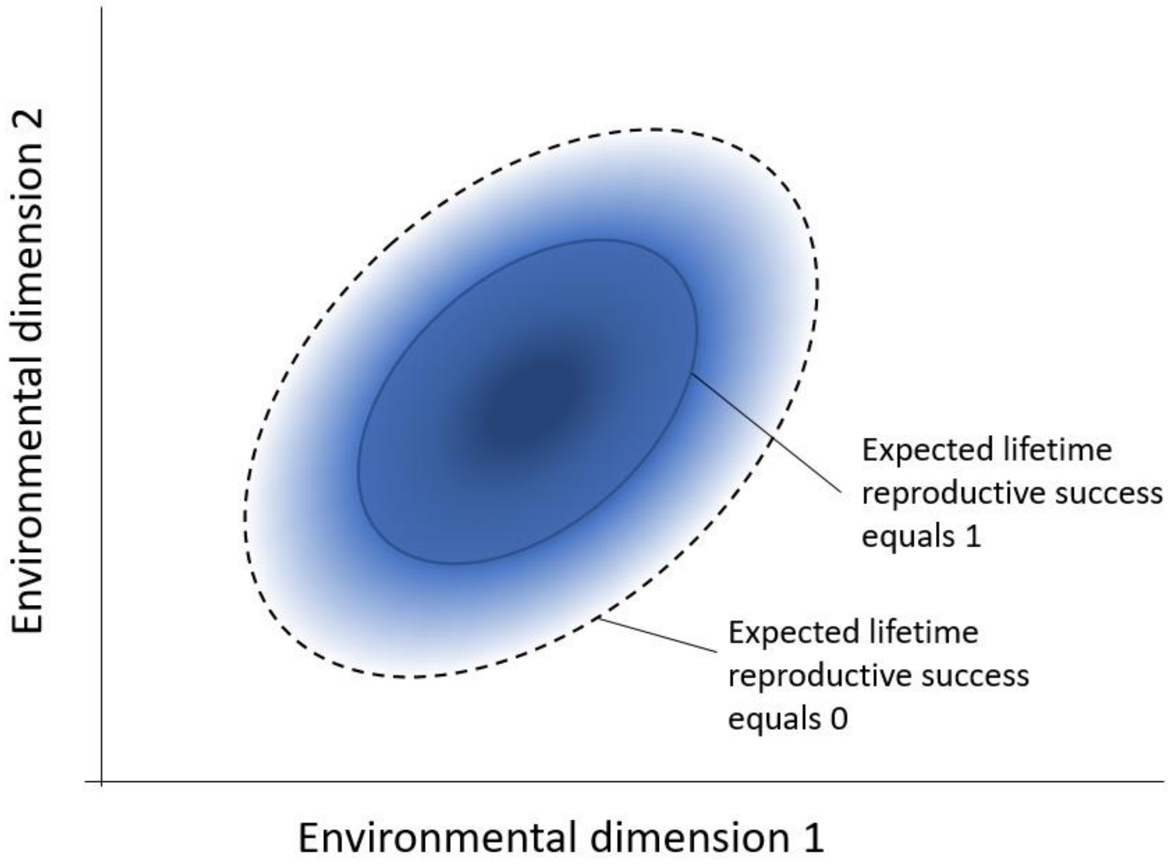

Table S1. List of definitions of the ecological niche (in chronological order) and their thematic category.

Reference	Definition(quote)	Category
Grinnell (1917)	Variables associated with the presence of a species (e.g. *Toxostoma redivivum*). (not quote)	Habitat
Elton (1927)	The status of an animal in its community, its place in the biotic environment, its relations to food and enemies.	Role
Grinnell (1928)	The ultimate distributional unit within which each species is held by its structural and instinctive limitations.	Habitat
Gause (1934)	Place a given species occupies in a community.	Environment
Elton (1950)	The mode of life and especially the mode of feeding of an animal.	Trophic
Dice (1952)	The ecologic position that a species occupies in a particular ecosystem, a consideration of the habitat that the species concerned occupied for shelter, for breeding sites and for other activities, the food that it eats and all the other features of the ecosystem that it utilizes. The term does not include, except indirectly, any consideration of the functions that the species serves in the community.	Environment
Clarke (1954)	The function of the species in the community, rather than its physical place in the habitat.	Habitat
Macfadyen (1957)	Niche as a multidimensional entity.[not well developed]	n-dimensional
Hutchinson (1957)	An n-dimensional hypervolume defined on axes representing all of the ecological factors relative to the species and every point in which corresponds to a state of the environment which permits the species to exist indefinitely.	n-dimensional
Odum (1959)	The position or status of an organism within its community and ecosystem resulting from the organism's structural adaptations, physiological responses, and specific behavior (inherited and/or learned).	Role
Weatherley (1963)	The nutritional role of the animal in its ecosystem, that is, its relations to all the foods available to it.	Trophic
Root (1967)	The niche is composed of several dimensions, each corresponding to some requisite for a species.	n-dimensional
MacArthur (1968)	Niche breadth is the "distance through" a niche along some particular line in niche space. (not quote)	n-dimensional
Odum and Barrett (1971)	The physical space and the functional role of a species in the community and its position in environmental gradients of temperature, moisture, pH, soil and other conditions of existence.	Habitat & Role
Van Valen (1971)	An adaptive zone in the niche of any taxon, especially a supra-specific one, and has two more or less independent components. One involves use of resources and the other involves resistance to predation and parasitism.	Resources

Vandermeer (1972)	A set of habitats.	Habitat
Clapham Jr (1973)	All the bonds between the population and the community and ecosystem in which it is found.	Habitat & Role
Maguire Jr (1973)	The genetically (evolutionarily) determined capacity (range of tolerance) and pattern of biological response of an individual, a species population or the whole species to environmental conditions.	Environment
Whittaker, Levin, and Root (1973)	Intracommunity role of the species.	Role
Wuenscher (1974)	The set of all environmental variables (habitat) and all organism responses and both the habitat and total response are subsets of the niche.	Habitat
Lack (1974)	The places where a species feeds within its habitat.	Trophic
Pianka (1974)	The sum total of the adaptations of an organismic unit. All the various ways in which a given organismic unit conforms to its environment. [periodic table of niches]	n-dimensional
Pielou (1975)	The set of conditions that a particular species experiences.	Environment
Colwell and Fuentes (1975)	A hypervolume in a space defined by axes representing the biotic and abiotic factors to which populations in the community respond differentially. The response of organisms to different environments is an essential component of the niche.	n-dimensional
Whittaker and Levin (1975)	The complete functional role a species within a given community.	Role
Pianka (1976)	Resource utilization spectra through both theoretical and empirical work of a growing school of population biologists.	Resources
Diamond (1978)	Resources a species uses, where it finds them and the strategy by which it harvests them.	Resources
Hurlbert (1981)	The realized niche should be defined as the set of resources used and it can apply to individual, population, species etc.	Resources
Pulliam (1988)	The set of environments where population growth rate is positive, in the absence of migration.	Environment
Leibold (1995)	I suggest the term requirement niche be used to describe requirements (Hutchinsonian) and impact niche for the per capita effects of species on their environments (Eltonian). Total niche is the combination of two.	Requirements
Jackson and Overpeck (2000)	Potential niche is the portion of environmental space that is capable of supporting populations of a species at time t, defined as the intersection of the fundamental niche for the species with the realized environmental space for time t. The potential niche will change shape, size and position within the environmental space as the realized environmental spaces changes through time and as the fundamental niche changes through evolution.	Environment

Pulliam (2000)	The landscape in the NICHE model (that we suggest) consists of a two-dimensional array of grid cells. The landscape represents the environmental conditions in 'ordinary physical space' and corresponds to what Hutchinson called 'biotope'.	Environment
Chase and Leibold (2003)	A joint specification of environmental conditions or variables that allow a species to have positive intrinsic growth rate along with the effects of that species on those environmental variables.	Environment
Kearney (2006)	A subset of those environmental conditions which affect a particular organism, where the average absolute fitness of individuals in a population is greater than or equal to one.	Environment
Cain, Bowman, and Hacker (2008)	The physical and biological conditions that the species needs to grow, survive and reproduce.	Environment
McInerny and Etienne (2012)	A term to describe abstractions of an organism's relationship to an 'ecosystem' as described by both effect and response interactions the organism has, both directly and indirectly, with and on other biotic/abiotic objects that are part of that ecosystem.	Environment

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