

Hutchinson's ecological niche for individuals

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1 Abstract

2 We here develop a concept of an individualized niche in analogy to Hutchison's concept of the ecological niche
3 of a population. We consider the individualized (ecological) niche as the range of environmental conditions
4 under which a particular individual has a fitness expectation of ≥ 1 . We address four specific challenges that occur
5 when scaling the niche down from populations to individuals: (1) We discuss the consequences of uniqueness
6 of individuals in a population and the corresponding lack of statistical replication. (2) We discuss the dynamic
7 nature of individualized niches and how they can be studied either as time-slice niches, as prospective niches or
8 as trajectory-based niches. (3) We discuss the dimensionality of the individualized niche, that is greater than the
9 population niche due to the additional dimensions of intra-specific niche space. (4) We discuss how the
10 boundaries of individualized niche space can to be defined by expected fitness and how expected fitness can be
11 inferred by marginalizing fitness functions across phenotypes or environments. We frame our discussion in the
12 context of recent interest in the causes and consequences of individual differences in animal behavior.

13 Keywords: ecological niche theory, individual differences, individualized niche, Darwinian fitness

14

15 Introduction

16 Individuals differ consistently in their behavior and their relations to the environment. We here aim to explore
17 how individual differences can be integrated into the ecological niche concept to yield a utile concept of an
18 individualized niche. We first discuss recent progress in the study of consistent individual differences in animal
19 behavior. We next briefly review ecological niche concepts and its different definitions. We then discuss the
20 application of the Hutchinsonian ecological niche concept at the level of individuals. Our arguments are based
21 on the idea that since individuals differ phenotypically, they often also differentiate their positions in the
22 environment, eventually generating individualized niches. We structure our discussion of the individualized
23 niche along four key questions: How can we deal with the fact that individuals are not statistically replicated?
24 How can we incorporate time in the study of individualized niches? Which dimensions constitute individualized
25 niches? Where are the boundaries of individualized niches? These four questions, we think, reflect important
26 considerations, when implementing the concept of niche at the level of individuals.

27 We write this review from the perspective of empirically working behavioral ecologists. We therefore envision
28 populations of individually distinct animals such as vertebrates or arthropods. While we are interested in the
29 causes and consequences of individual differences, we do not see a particular individual as the object of study.
30 Instead, we strive to understand how individual differences contribute to population-level processes. It is
31 therefore the state and dynamic of population composition that interests us. We, therefore, like many other
32 researches in the field, use statistical summaries at the level of populations to study individual differences. This
33 perspective relies on the law of large numbers and aims to understand general patterns and processes, rather
34 than individual life-histories. We think that our individualized niche concept will be valuable to a large range of
35 population ecologists who are interested in the ecological consequences of individual differences.

36 Consistent individual differences

37 Consistent individual differences have been in the spotlight of behavioral ecology for the last two decades (Sih
38 et al. 2004). There are now hundreds of studies that report on individual differences in behavior across a large
39 array of species, including vertebrates and invertebrates (Bell et al. 2009). A particular interest has been on
40 behavioral traits that represent general attitudes to the environment when they are temporally consistent and
41 correlated across contexts (Dochtermann and Dingemans 2013; Kaiser and Müller 2021). Individually

42 consistent, context-general traits are often called animal personality traits, temperament traits, coping styles or
43 behavioral syndromes (Kaiser and Müller 2021; Réale et al. 2007). The pace-of-life syndrome, for example,
44 encompasses physiological, behavioral and life-history components and has been linked to personality and
45 survival (Réale et al. 2010; Ricklefs and Wikelski 2002). As a result, the focus has shifted towards studying the
46 implications of in animals behavioral variation in animals (Wolf and Weissing 2012).

47 From an evolutionary perspective, all individual differences that have a heritable basis can evolve by natural
48 selection. Indeed, individual differences in behavior often have a significant heritable basis (Dochtermann et al.
49 2015; Stirling et al. 2002). It has been shown that animal personalities differences can be systematically selected
50 for, thus maintaining inter-individual variation in behavior (Wolf et al. 2007). Furthermore, intraspecific variation
51 affects interspecific interactions and ultimately species' coevolution (Moran et al. 2020). Consequently, the
52 position of individuals in the environment can both be the cause and the consequence of behavioral differences,
53 owing to the individual x environment interaction being bidirectional.

54 Individual differences in behavior also have ecological consequences, because they have an impact on the way
55 in which individuals interact with their environment. Particularly, phenotypic variation can affect population
56 dynamics through resource polymorphism (Dall et al. 2012). In fact, intraspecific competition might be a
57 fundamental cause of behavioral variation (Bergmüller and Taborsky 2010). Reduced competition over
58 resources increases the carrying capacity of an area and promotes resilience of populations (Wolf and Weissing
59 2012). In analogy to community dynamics, resource partitioning among phenotypes reduces intraspecific
60 competition and facilitates population persistence and growth (Araújo et al. 2011; Layman et al. 2015).

61 The ecological niche

62 The concept of the ecological niche is fundamental in ecology. The term was initially vaguely defined and used
63 to describe the ecological position, habitat and requirements of species (Allen 1882; Grinnell 1917; Packard
64 1894, see Gibson-Reinemer 2015). First composed definitions of the ecological niche were presented by Elton
65 (1927) and Grinnell (1928). Elton (1927) defined the ecological niche in terms of the species' function within a
66 community and its relations to other species. This view is focused on the role of species and is mostly used in
67 community and functional ecology. Grinnell (1928) proposed the ecological niche as the physical place that

68 species is adapted to. According to this definition, niche is a synonym of habitat or position of species in the
69 environment.

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

80 The most popular and widely used definition of ecological niche was proposed by Hutchinson (1957; 1978).
81 Hutchinson defined the ecological niche as a hypervolume in an n-dimensional (abstract) environmental space
82 that allows a population to persist indefinitely. Hutchinson distinguished between fundamental and realized
83 niches, which are ecological niches before and after accounting for competition, respectively. Rosado et al.
84 (2016), claim that Hutchinson built on Grinnell's idea while others (Colwell and Rangel 2009; Swanson et al.
85 2015) argued that the concept of the hypervolume was introduced by Gause (1934). Independently of
86 Hutchinson's source of inspiration, the n-dimensional hyperspace is until today a fundamental concept in
87 ecology and evolution. We therefore explore how this concept can be usefully applied at the level of individuals.

88 The ecological niche for individuals

89 The recent interest in the study of individual differences highlights current interests in ecological differences
90 between individuals within populations. Here we address the applicability of the Hutchinsonian niche concept
91 at the level of individuals. Some early work on ecological niches already included discussions on the importance
92 of individual differences within a population. van Valen (1965), for example, pointed out that individuals differ
93 on how they use available resources. Roughgarden (1972) pioneered the idea to use individual differences in
94 trait expression as proxies for resource use. Traits of individuals are here used as substitutes for the more difficult

95 to measure environmental dimensions. Roughgarden's ideas gave rise to a vibrant field of functional trait
96 analyses (Violle et al. 2007). In the meanwhile, large database of functional traits have been compiled, in
97 particular for plants (Fraser 2020; Kattge et al. 2020). However, we see two important limitations in how the
98 concept is currently applied. First, most of the analysis are based on easy-to-measure (soft) traits (e.g.
99 morphology) rather than ecologically relevant (hard) traits (e.g. physiology) (Nock et al. 2016). Second, most
100 functional trait analyses are focused on species differences rather than intra-specific variation.

101 The idea of individual differences in ecological niches has thus been entertained for several decades, but
102 concepts of individualized niches are even more vaguely defined than concepts of the ecological niche as such
103 (Müller et al. 2020; Trappes et al. 2021). In our view, there are four main challenges when applying the concept
104 of the ecological niche to individuals: 1) The question of uniqueness, 2) the questions of time, 3) the question of
105 dimensions and 4) the question of boundaries. We first start with working definitions of the ecological niche of
106 individuals before addressing the specific challenges.

107 Working definition of the individualized niche

108 Hutchinson (1957) defined the (fundamental) ecological niche of a population as the range of environmental
109 conditions in which a population can persistent indefinitely. Infinite persistence implies non-negative population
110 growth rates in the long run. Scaling down to individuals, we propose a working definition of the individualized
111 (ecological) niche as the range of environmental conditions that provides a fitness expectation of ≥ 1 to particular
112 individuals. We develop and justify this working definition below.

113 The questions of individual uniqueness

114 One issue when defining niches at the level of individuals is that individuals are (by definition) not identical,
115 impeding statistical replication. The ecological (Hutchinsonian) niche of a population can be estimated by
116 quantification of where different members of the population can be found in environmental space. Here,
117 individuals serve as replicates at the level of the population. However, individuals themselves can only be found
118 at a particular point of environmental space. (We leave the discussion of integration over time for the following
119 section.) Hypervolumes at the level of populations, become points in environmental space at the level of

120 individuals. In loose analogy to Hutchinson's realized niche, we call each of these points the *realized*
121 *individualized niche*. However, the point where an individual happens to live almost certainly does not cover the
122 range of environmental conditions under which it could have occurred. The *potential individualized niche* thus
123 includes all environments where a particular individual would (or could) have had a fitness expectation of ≥ 1
124 (Fig. 1). This means the potential individualized niche defines a space of counterfactuals. How can we deal with
125 the problem that realized individualized niches are incidental instantiations of points in environmental space
126 and that potential individualized niches are unobservable counterfactuals?

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

135 Even with replicates over short meaningful time intervals, it is *de facto* impossible to cover the full potential
136 niche of an individual. At least in observational studies under natural conditions, environmental covariation in
137 space and time will prevent individuals to be observed across the full range of potential environments in which
138 it would have a fitness expectation of ≥ 1 . Experimental approaches offer a partial solution if individuals can be
139 translocated to a range of different environments (Wilson et al. 2019). Some measure of current performance
140 can then be used as a proxy of fitness across a range of environments. However, experimental approaches are
141 necessarily limited to few dimensions of environmental space. An ultimate limit to experimental exploration of
142 the potential individualized niche is also set by the lifespan of an individual, since potential individualized niches
143 are almost certainly substantially larger than realized niches.

144 An alternative approach is to marginalize across phenotypes (or genotypes) when mapping individualized niches
145 (Fig. 2). This is rooted in Roughgarden's (1972) idea to use traits of individuals as proxies for resource use.
146 Individuals are here used as replicates to establish a distribution of phenotype-specific environments. In
147 principle, this can be done across many different traits. While individuals are in practice used as tokens of types

148 in particular phenotypic dimensions, individuals are typically unique in their trait combinations. In principle, it
149 will thus be possible to predict an individual's niche from its unique combination of traits. A limit is set only if
150 interactions between traits are strong and poorly replicated in a population. In such cases, trait combinations in
151 some individuals might be so unique that prediction becomes impossible. This also applies to phenotypic
152 novelties.

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

163 Definition A: The *realized individualized niche* is the place in environmental space in which a particular individual
164 is found and has a fitness expectation of ≥ 1 . The realized individualized niche can be quantified empirically.

165 Definition B: The *potential individualized niche* is the volume in environmental space in which a particular
166 individual has a fitness expectation of ≥ 1 . The potential individualized niche cannot directly be quantified, but
167 significant parts of the niche space can usually be inferred.

168 The question of time

169 We have alluded to the integration across intervals of time above. This raises the more general questions about
170 whether the individualized niche refers to slices of time or to entire lifespans. The ecological niche of a
171 population is focused on entire lifespans. The ecological niche of a forest-dwelling frog, for example, includes a
172 network of forests and ponds, since adults require shelter in woodlands while in its juvenile stage, as a tadpole,
173 the frog requires ponds for survival and growth. Population persistence can only be achieved if both habitats

174 are available. One might argue that the equivalent is also true for individuals: that the individualized niche is a
175 lifetime niche. However, there are arguments why this simple application of lifetime niches loses important
176 intricacies of the individualized niche.

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

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

200 The prospective individualized niche does not give a life-time perspective except for the special case of a zygote.
201 Potential individualized niches are affected by previous development (and by accidents). Certain areas of

202 environmental space might not be available if irreversible developmental plasticity in early life-stages prevents
203 an individual from developing a matching phenotype (Nyman et al. 2018). Development has manifest
204 consequences for the individualized niche. The potential niche from a prospective perspective therefore changes
205 as individual's age. In fact, it always shrinks, as potentials must be available at early stages and can only be
206 reduced by individual decisions during development. The potential time-slice individualized niche, in contrast,
207 might vary across lifetime and might shrink or expand as an individual keeps adjusting its phenotype.

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

216 Definition C: The *time-slice individualized niche* is the environmental space in which a particular individual occurs
217 during a particular part of its development has a lifetime fitness expectation of ≥ 1 . The time-slice individualized
218 niche can be quantified empirically by taking repeated measurements.

219 Definition D: The *prospective individualized niche* is a volume in environmental space in which a particular
220 individual has a fitness expectation of ≥ 1 that includes the current and future potential niches. The prospective
221 individualized niche provides a focus on particular developmental decisions that affect future niche space.

222 Definition E: The *trajectory-based individualized niche* is a time-structured volume in environmental space that
223 allows for fitness expectation of ≥ 1 and that it different from alternative developmental trajectories. The
224 trajectory-based individualized niche provides a focus on alternative developmental trajectories that affect
225 potential niche space.

226 The question of dimensions

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

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

249 When scaling down from populations to individuals, the intraspecific context becomes external to the individual.
250 The presence or absence of conspecifics or conspecifics with particular traits values becomes an explicit part of
251 the individualized niche. The social context, for example, is part of the individualized niche, like the interspecific
252 community context in the ecological niche of populations. The social conditions that allow an individual to realize
253 a non-zero inclusive fitness are also known as the social niche (Saltz et al. 2016). The fact that the intraspecific
254 (including social) context is part of individualized niche dimensions represents one of the most important

255 differences to the population niche. The individualized niche, thus, consists of $n + s$ dimensions, where n
256 represents non-intraspecific dimensions, while s represents the dimensionality of the intra-specific niche space
257 (Fig. 6).

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

267 We suggest that the difference between the presence and absence of interspecific niche dimensions represents
268 a particularly interesting aspect of the individualized niche: How does the niche of an individual change
269 depending on the state of the population as a whole (including density and frequency of other phenotypes)? We
270 could call the niche space in all n (non-intraspecific) dimensions the fundamental individualized niche and the n
271 + s dimensions the realized individualized niche. Hutchinson used the presence or absence of competitors to
272 distinguish between fundamental and realized niche. Similarly, we may use the presence or absence of
273 conspecifics to differentiate between fundamental and realized individualized niche. This offers an interesting
274 perspective on the concept of soft vs. hard selection in evolutionary biology (Wallace 1975). Hard selection refers
275 to selection that is determined by the phenotype of the focal individual and its environment, while soft selection
276 occurs when selection is density- and frequency-dependent. Population density, phenotype frequencies and
277 social interactions are thus important components to the individualized niche.

278 The question of boundaries

279 Hutchinson (1957) defined the boundaries of a population's niche by indefinite population persistence and thus
280 non-negative average growth rates in the long run. Population growth rates are determined by the ratio of births

281 to deaths in a population. The equivalent quantities at the level of individuals are reproduction and survival and
282 those can be used for determining the boundaries of individualized niches. However, there are three important
283 considerations, a rather easy and two harder ones, when translating this to the level of individuals.

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

293 The harder problem is which concept of individual fitness should be considered. It might be tempting to use
294 realized fitness, for example, quantified in terms of number of offspring produced. However, realized fitness has
295 a large stochastic component and is often a poor indicator of a particular individual's niche fit. We therefore
296 define the boundaries of individual niche space in terms of fitness expectations, which are functions of the
297 phenotype-environment combination (Fig. 7). Fitness expectations do not necessarily invoke propensities in the
298 sense of stochastic dispositions, but are rather build on statistical summaries that follow the law of large
299 numbers (Drouet and Merlin 2015). Individualized niches are thus identified by mapping fitness on phenotype-
300 environment combinations in the form of multidimensional fitness functions. Since there are no replicates of an
301 individual, there is no empirical solution, neither to decompose individual fitness into a stochastic and a
302 deterministic component, nor to quantify individual fitness across different environments. Resorting on fitness
303 components or replicated fitness proxies might be a viable solution (Patrick and Weimerskirch 2014).
304 Alternatively, we can marginalize across phenotypes (or, genotypes) and environments to estimate fitness
305 expectations in the form of fitness functions using different individuals as replicates (Figure 2).

306 One might wonder whether the boundaries of the individualized niche are defined by zero fitness expectations
307 or fitness expectations of one (Figure 7). One problem with fitness expectations is that they might get infinitely
308 small and it might be difficult to tell where they become zero. The condition of positive fitness expectations thus

309 forms a theoretical boundary that is difficult to determine empirically. We argue that while individuals cannot
310 persist indefinitely, they need to leave at least one offspring to perpetuate into future generations. A useful
311 threshold for the boundary of the individualized niches is thus an expected fitness of 1. We think that this makes
312 a useful benchmark in a gradual view of the individualized niche.

313 Conclusions

314 We have started with a discussion of individual differences in behavior. We now want to come back to this and
315 ask whether individualized niches are a mere rebranding of the study of individual differences. In brief, we think
316 there are subtle, but important differences. The aspect of individual differences that has ecological and
317 evolutionary consequences on the interactions between individuals and their environments is what we here
318 consider relevant to individualized niches. Not all individual differences in phenotype and behavior should
319 therefore be considered relevant to individualized niches (Trappes et al. 2021). While the literature on individual
320 differences focuses mainly on survival and fitness consequences, individualized niches focus on the
321 environment. In particular, individualized niches relate the phenotype-environment match with individual
322 differences (in line with Roughgarden 1972). Furthermore, in order to estimate individualized niches, the full
323 range of an individuals' ecology needs to be studied. This highlights the urge for longitudinal studies, because
324 usually repeatedly measured individual traits are necessary to verify that some aspect of the environment is
325 truly individualized.

326 We have introduced the fields of animal personality studies and the ecological niche concept and have discussed
327 how they blend in the concept of an individualized niche. We provide a working definition of individualized
328 niches that builds on Hutchinson's population-level ecological niche. However, there are important intricacies
329 when developing an individualized niche concept. Particularly important are (i) the differentiation between
330 realized and potential niches where the latter is defined by counterfactual arguments, (ii) the dynamic nature of
331 individualize niches with a time-slice, a prospective and a trajectory-based perspective, (iii) the inclusion of intra-
332 specific dimensions in the dimensionality of individualize niches and (iv) the need to define the boundaries of
333 individualized niche space by fitness expectations (not simply fitness realization). We hope that these
334 considerations help other scientists to further develop the concept of the individualized niche into a practicable
335 tool for empirical studies and conceptual progress.

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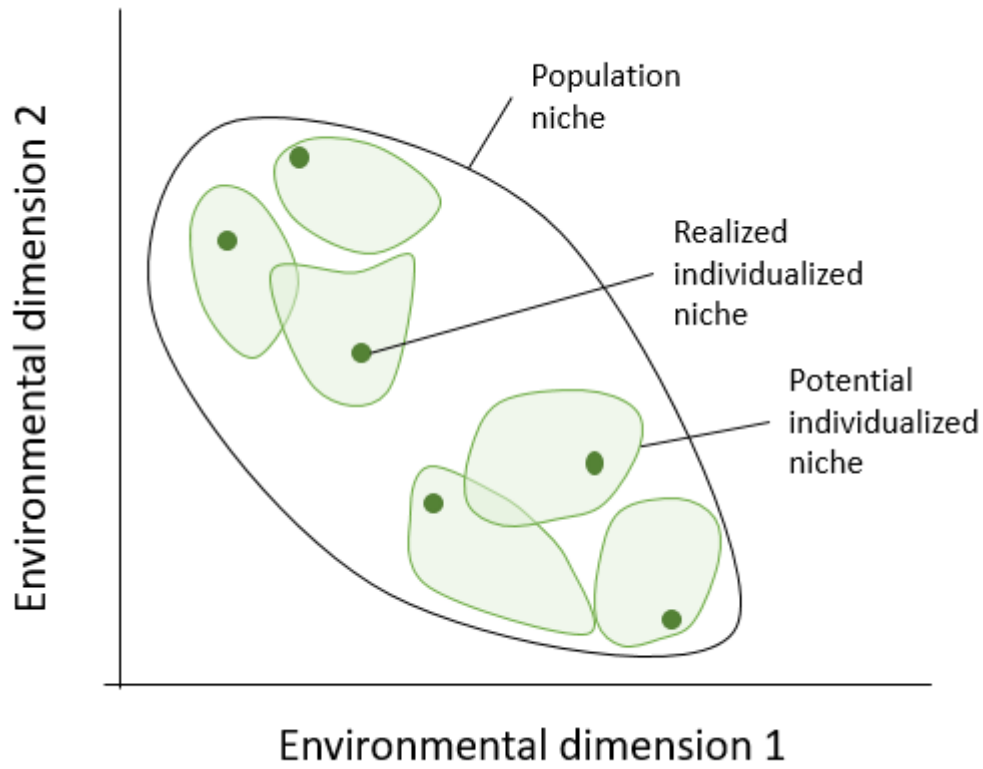
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471 Figures

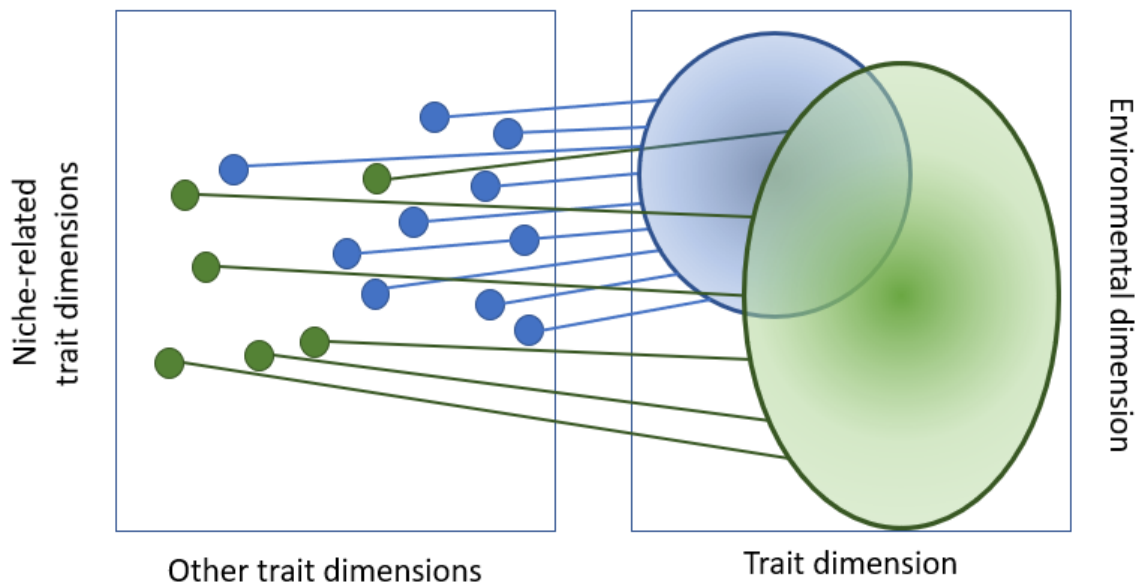
472 Figure 1: Schematic view of realized and potential individual niches occupy subspaces of the population niche.
473 Realized niches are points (or small volumes) in environmental space that occupy only part of the volume that
474 can potentially be occupied by an individual.



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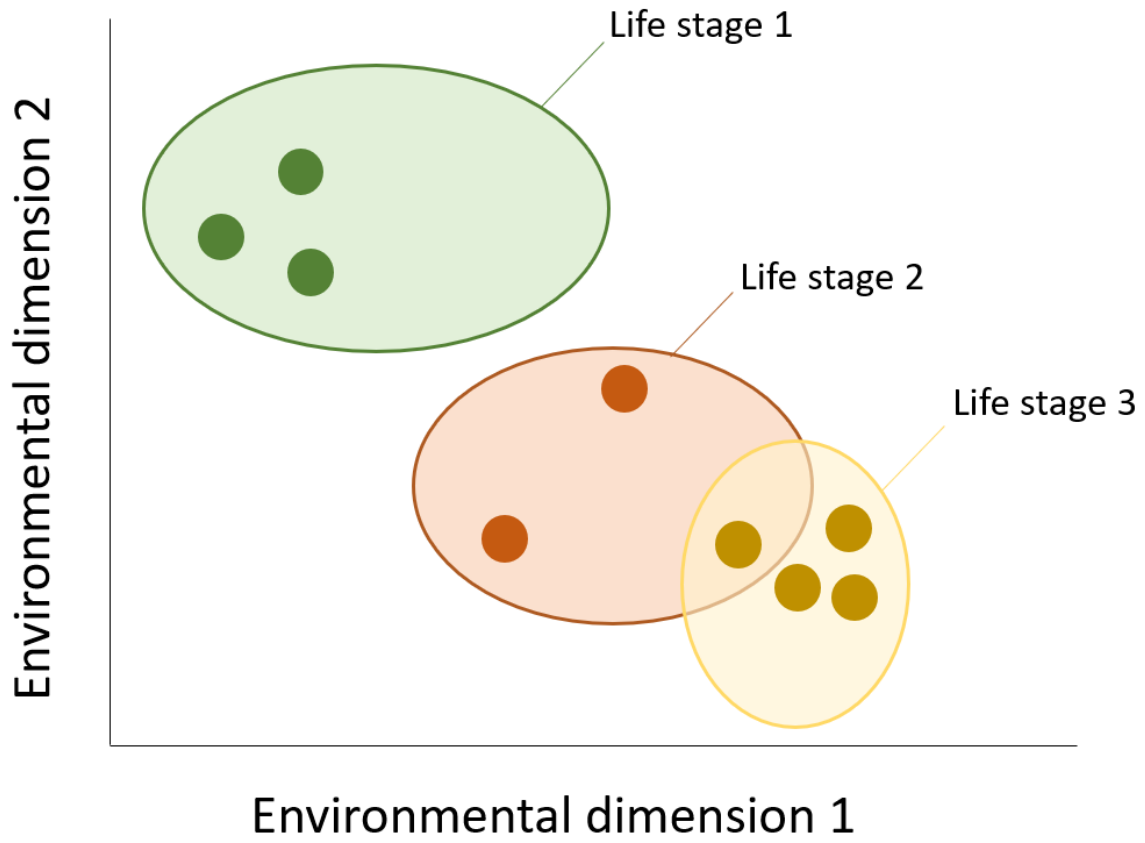
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477 Figure 2: Schematic view of the idea of using population-level patterns to predict individualized niches and
478 fitness consequences. Colors show different types of individuals (e.g. females and males). The left plot shows
479 two trait dimensions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



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

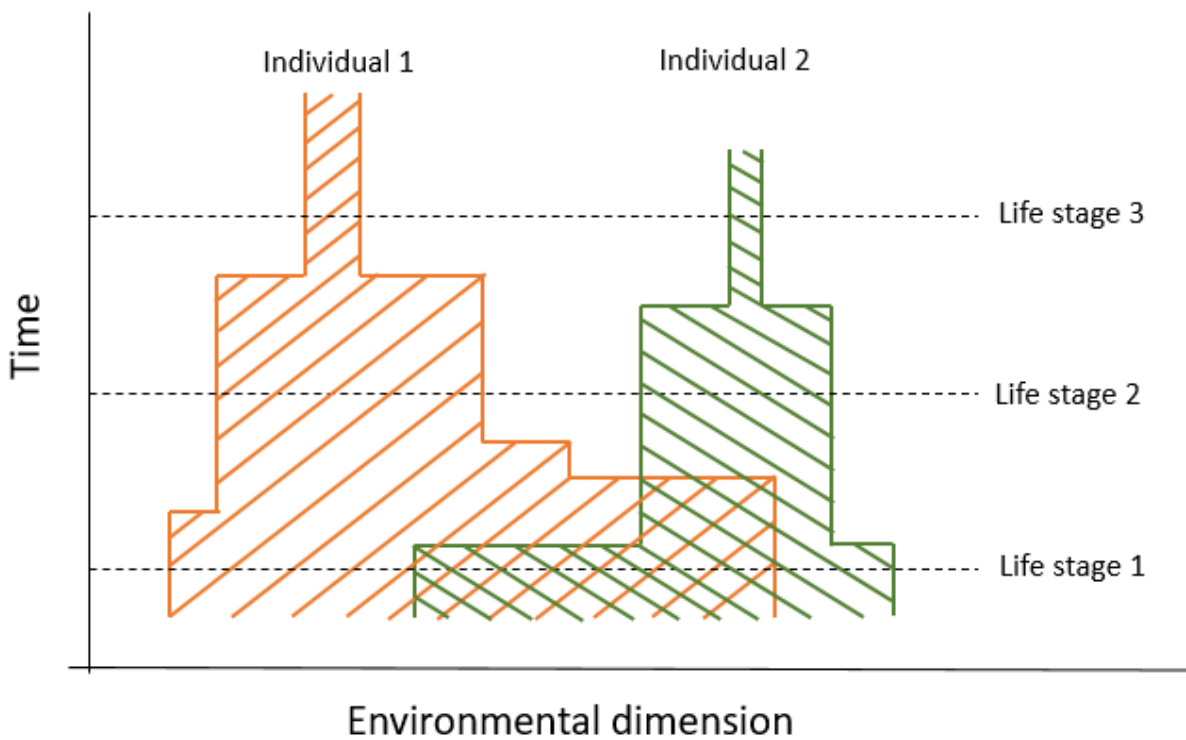


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489 Figure 4: Schematic view of prospective individualized niches of two individuals. Shaded areas show the potential
490 niche, dashed horizontal lines mark snapshots at three life stages. Steps in individual potential niches mark
491 developmental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

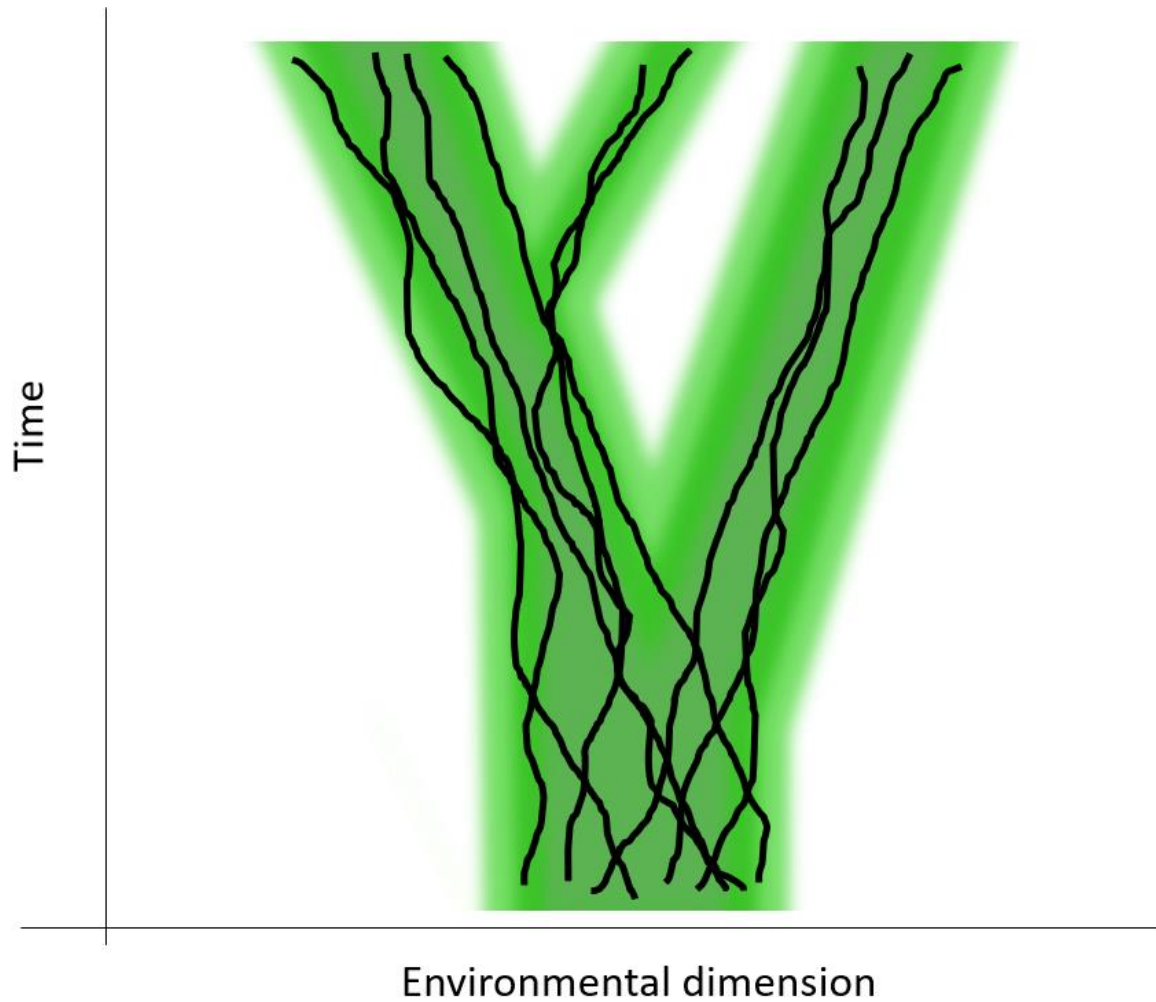
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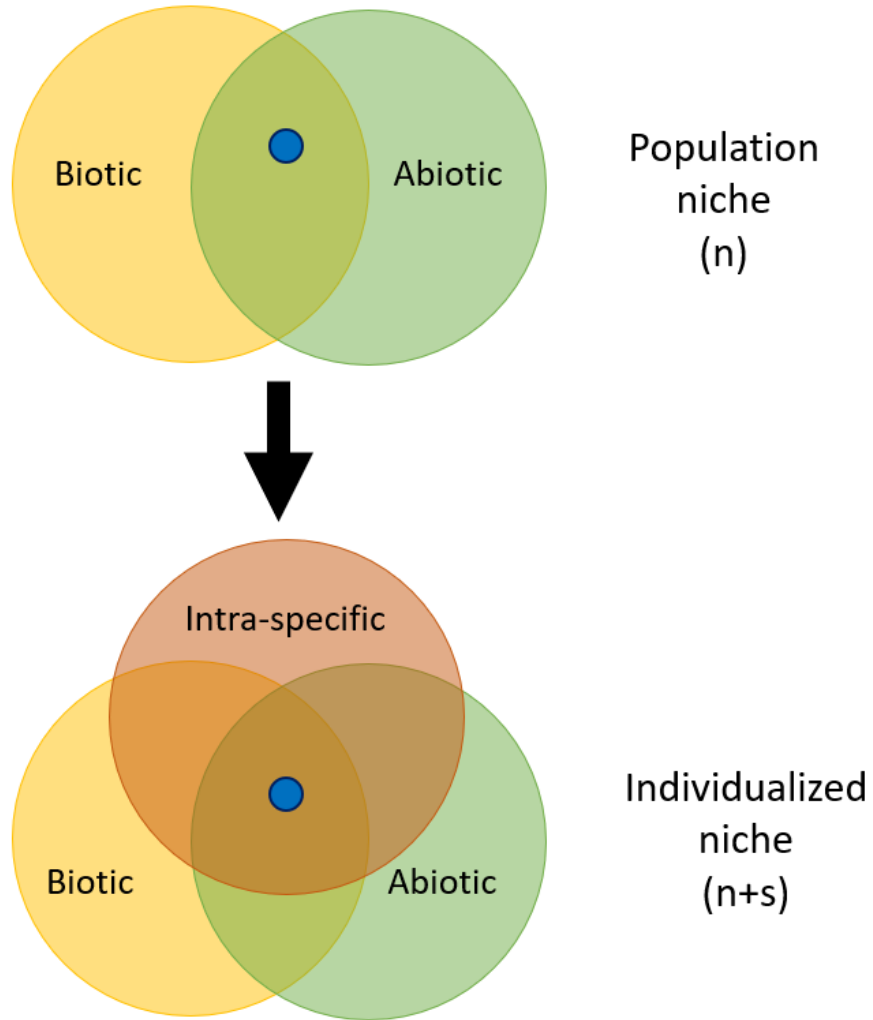
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498 Figure 5: Schematic view of lift-time trajectory-based niches that emphasize alternative developmental
499 pathways. Black lines show individual developmental trajectories in niches space. The green background
500 schematically highlights alternative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



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

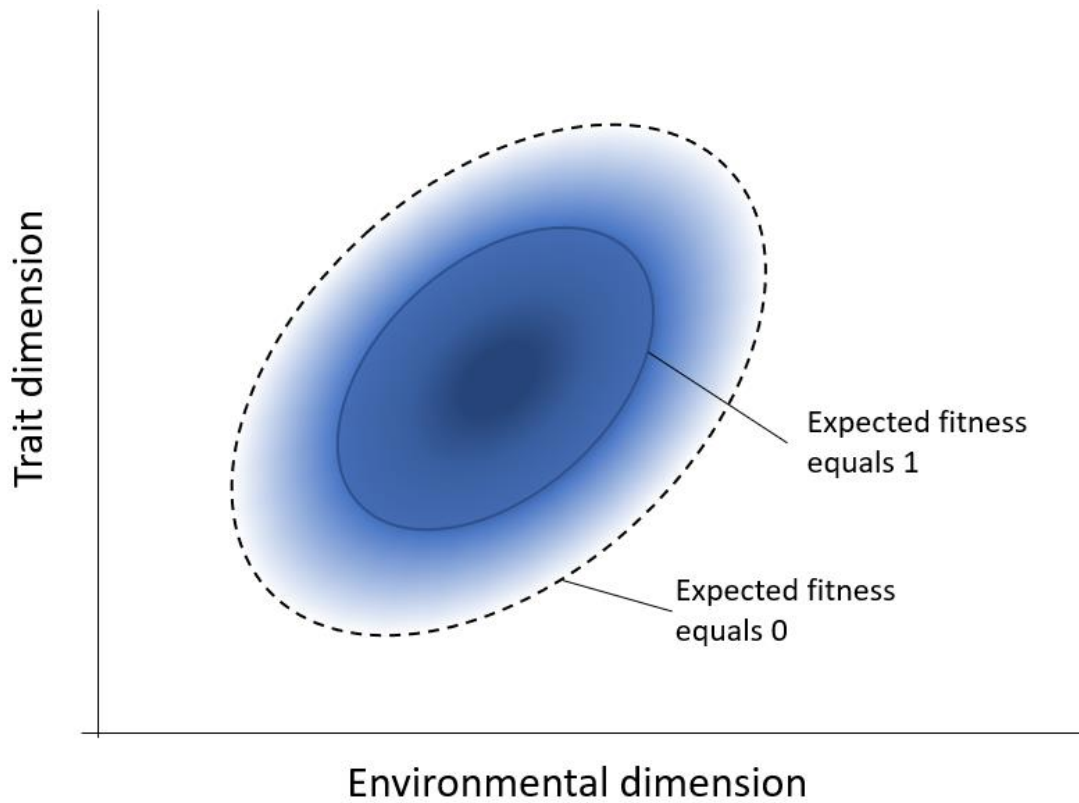


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509 Figure 7: Multidimensional fitness function and boundaries for the individualized niche. The graded blue area
510 shows the expected fitness kernel. The solid blue line marks what we consider the boundary of the individualized
511 niche at an expected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

513



514

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. <i>Toxostoma redivivum</i>). (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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