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Individual Specialization

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Abstract

Natural populations are collections of ecologically diverse individuals, which are often specialized in small subsets of the population niche. Nearly two decades after the concept of individual specialization was formally coined, accumulated evidence confirms that this phenomenon is prevalent in nature across a myriad of taxa and has major ecological, evolutionary, and conservation implications. Ecologists now possess a diverse toolbox of methods to quantify niches at the scale of individuals with unprecedented accuracy. Despite recent advances on the relevance of individual specialization for higher levels of biological organization (e.g., populations, communities), key questions about its causes and consequences remain unanswered.

Key Points

- Explain how and why individuals within natural populations may diverge in their niches.
- Define individual specialization and how to quantify the magnitude of this phenomenon.
- Summarize evidence of individual specialization across taxa and functional groups of consumers.
- Present the proximate and ecological causes of individual specialization.
- Synthetize the implications of individual specialization for higher levels of biological organization, evolution and conservation.
- Suggest future research directions.

Introduction

Biological differences between species are often conspicuous when we look at nature. Not surprisingly, ecologists have traditionally focused on interspecific differences to describe, explain and predict biodiversity patterns (Rudolf *et al.*, 2014). For instance, classic predator-prey models rely on species-level parameters, and food webs usually represent how energy flows via trophic links between species (Miller and Rudolf, 2011; Guimarães, 2020). By designating species as the fundamental unit of interest, ecologists make models more tractable and data collection more feasible. Nevertheless, this approach relies on the assumption that speciesor population-level averages are good representations of species or populations, implying that variation within species is negligible or simply noise. This typological view of nature is pervasive in ecological theory.

A fast-growing number of empirical studies has challenged this commonplace assumption by demonstrating that intraspecific variation is widespread in nature. It is now evident that natural populations of various animal taxa are actually collections of



Fig. 1 (a) Hypothetical example of a unidimensional resource-utilization niche. Bars represent the frequency of use of different resource types along the niche axis (e.g. prey types, prey size categories). For visualization purposes, we adopted a smoothed, Gaussian version of this resource-utilization niche (right) in the following figures. Based on the classic example of the sea otter, *Enhydra lutris*, in which individuals are specialized in particular prey types (e.g., urchins, snails or sea stars), we present schematic figures to depict distinct scenarios of how individual niches (blue curves) can combine to shape the population niche (gray curve): (b) A specialist population niche width) composed of generalist individuals (although they consume only snails, their niches are identical to the population niche); (c) Individual specialization: A generalist population composed of specialist individuals (each individual consume only a subset of the population niche); (d) A generalist population composed of generalist individuals consume all prey types used by the population as a whole).

ecologically diverse individuals, which vary in how they interact with conspecifics, heterospecifics, and their environment (Dall *et al.*, 2012; Araújo *et al.*, 2011; Bolnick *et al.*, 2003b). More important, this variation has major ecological and evolutionary implications (Des Roches *et al.*, 2018; Bolnick *et al.*, 2011).

This article focuses on a particular type of intraspecific variation in which individuals in the same population consistently use different resource types (Figs. (1) and (2)). Ecological differences between sex and ontogenetic classes have long been considered as important sources of intraspecific niche variation (Schoener, 1986), but they alone do not fully explain the prevalence and magnitude of niche diversity within populations. Notably, individual specialization often occurs between individuals of the same sex and ontogenetic stages (Kernaléguen *et al.*, 2015). In contrast with the classic niche literature, individual specialization studies explicitly consider niches as properties of individuals rather than species or entire populations (see *Defining individual specialization* below). Herein, although we primarily focus on individual niche specialization, it is important to bear in mind that the concepts, methods, and hypotheses here presented have important parallels with other emerging sub-fields of individual variation, such as animal personalities (Sih *et al.*, 2012; Toscano *et al.*, 2016; Réale and Dingemanse, 2010) and intraspecific approaches in traitbased ecology (Violle *et al.*, 2012). The integrated advance of these different sub-areas will allow us to elucidate with unprecedented clarity the incidence, the causes and the implications of individual diversity in nature.

Defining Individual Specialization

The term *"individual niche specialization"* brings together three key concepts with an intricated history in ecology and evolutionary biology (individuals: Huneman, 2014; niche: Chase and Leibold, 2003; specialization: Devictor *et al.*, 2010). Therefore, it is important to define these concepts in the context of the literature on individual niche specialization and show how it relates to the classic literature. Individual specialization studies generally use the term *niche* in reference to the resource-utilization definition by MacArthur and Levins (1967),



Fig. 2 How can foraging decisions over time drive niche variation within populations? This schematic figure shows multiple and sequential foraging events by four individuals of the sea otter *Enhydra lutris* in the same population. The population as a whole is generalist, consuming different prey (urchins, sea stars, and snails), and individuals show different degrees of specialization by consistently consuming particular prey types. The scenario depicts that populations can be a mixture of individual generalists (e.g., individual j) and specialists (individuals i, k, j).

in which the niche of a given organism can be represented as the relative use of resources along a specific niche axis or even along multiple axes (Schoener, 2009) (**Fig. 1**(a)). Studies on individual specialization have applied this definition and have mostly, but not necessarily, explored niche axes associated with the use of trophic resources (e.g., prey size and taxon) (Araújo *et al.*, 2011; Bolnick *et al.*, 2003b; but see Carlson *et al.*, 2021). The term *specialization* in turn has classically referred to a narrower niche width in relation to a given referential (i.e., *generalism*), empirically meaning the use of fewer resources compared to another consumer (Pianka, 2017; Futuyma and Moreno, 1988) (i.e., a specialist individual has a narrower niche than a generalist individual).

Although evolutionary ecologists have long recognized the relevance of intraspecific niche variation in nature (Van Valen, 1965; Roughgarden, 1972), the concept of individual specialization was formally coined less than two decades ago. The seminal paper by Bolnick *et al.* (2003b) defines individual specialization as either (1) *"the degree to which individuals' diets are restricted relative to their population"* or (2) *"the overall predominance of individual specialists in a population"*. Note that definition (1) specifically mentions diets, but individual specialization can also be measured in other niche dimensions; and that definition (2) requires defining what an individual specialist is, which Bolnick *et al.* (2003b) described as *"an individual whose niche is substantially narrower than its population" niche for reasons not attributable to its sex, age, or discrete* (a priori) *morphological group"*. Importantly, contrary to the usage of *specialization* in the classic literature, individual specialization refers to the relative width of individual and population niches, not their absolute values. Consequently, individual specialization is not necessarily associated with individuals having narrow niches (Fig. 1(b)), but instead with individuals having narrower niches than their population (Fig. 1(c)), i.e., it is a relative concept.

In summary, individual specialization can be defined as a phenomenon in which generalist populations (i.e., that use a large diversity of resources) are collections of individuals relatively specialized in particular types of resources (Figs. 1(c) and (2)). Importantly, the degree to which individuals are specialist in relation to their populations varies substantially across populations, taxa, and ecological contexts: while some populations are composed of generalist individuals that consume the entire resource distribution of their population, others are composed of individuals highly specialized in small subsets of the population niche, and others by a mixture of individual generalists and specialists (Fig. 2). It is also important to note that, although individual specialization emerges from individual's foraging decisions, it is measured at the level of populations, not individuals. Finally, there is not a rule of thumb or threshold from which a certain degree of individual specialization is considered significant; it's a continuous measure and needs to be interpreted as such.

Empirical Evidence

Bolnick *et al.* (2003b) sparked a plethora of studies about individual specialization in natural populations in the last two decades (Fig. 3). The review by Araújo *et al.* (2011), combined with the instances presented in Bolnick *et al.*, 2003b, added up to 189 species exhibiting some degree of individual specialization. Since then, numerous studies have investigated individual niche specialization in



Fig. 3 Temporal trend in the cumulative number of studies (n = 394 studies) about individual specialization from 2000 to 2020. Data were obtained from Web of Science on April 10th, 2021 (search term: "*individual speciali**"; categories: ecology, marine freshwater biology, zoology, evolutionary biology, oceanography, behavioral sciences, fisheries, and ornithology).

populations of diverse vertebrate and invertebrate taxa. For instance, Ceia and Ramos (2015) identified 94 studies that examined individual specialization in 42 seabird species. Notably, studies in the last decade have reported new evidence of individual niche specialization across diverse functional groups of consumers: from top predators (Balme *et al.*, 2020; Kernaléguen *et al.*, 2016a) to strictly herbivorous species (Bison *et al.*, 2015; Jesmer *et al.*, 2020); from tropical to polar species (Camargo *et al.*, 2021; Thiemann *et al.*, 2011); from freshwater to marine consumers (Kuhlmann and McCabe, 2014; Bodey *et al.*, 2018; Neves *et al.*, 2021); from pollinator (Szigeti *et al.*, 2018) to parasitoid insects (Polidori *et al.*, 2013); from social (Sheppard *et al.*, 2018) to solitary consumers (Rosenblatt *et al.*, 2015); from common to rare, endangered species (Costa-Pereira *et al.*, 2017; Lunghi *et al.*, 2020), from native to invasive and urban species (Dickman and Newsome, 2015; Larson *et al.*, 2020). Importantly, while many of these studies show populations displaying elevated degrees of individual specialization, others show low or negligible amounts of interindividual niche variation (Zalewski *et al.*, 2021; Ceia and Ramos, 2015; Codron *et al.*, 2012). In sum, we now have extensive empirical evidence available to confirm that individual niche specialization occurs across diverse types of organisms and ecosystems, and many geographic areas.

Acquiring Individual-Level Niche Data

As in any ecological study, sample sizes (i.e. number of individuals) required to obtain a reliable estimate of the degree of individual specialization in a population are an important issue that needs careful consideration. We strongly recommend that researchers employ resampling procedures to assess the statistical power necessary to obtain reliable estimates of individual specialization (Araújo *et al.*, 2014). What makes the study of individual specialization different from other ecological studies is that in the latter individuals are normally treated as the level of replication, whereas in order to quantify individual specialization one needs multiple observations per individual, which poses an additional challenge.

The time scale of individual specialization and the biological question at hand are of utmost importance for sampling design. Depending on the species, individual specialization can occur at very short time scales (e.g., less than one day), such as in the cabbage butterfly, *Pieris rapae* (Lewis, 1986), or very long time scales (e.g., years), as in the sea otter, *Enhydra lutris* (Estes *et al.*, 2003). Additionally, researchers may be interested in measuring individual specialization during specific periods of time or events, such as seasons, migrations or during reproduction (McCall *et al.*, 2016; Cherel *et al.*, 2009; van Donk *et al.*, 2017).

Sampling individuals repeatedly over time (i.e., longitudinal sampling) is ideal to study individual specialization (Fig. 2), because not only it allows the determination of the time scale of individual specialization, but it can be tailored to the biological

question at hand. In this regard, recent advances in telemetry techniques have provided new types of longitudinal data, allowing the record of the use of space and migration patterns of individuals (Kerches-Rogeri *et al.*, 2020; Rezek *et al.*, 2020; Kernaléguen *et al.*, 2016b; Harrison *et al.*, 2019; Brodersen *et al.*, 2012). These represent poorly explored dimensions of individual niches, which will provide a better understanding of the mechanisms and implications of individual specialization.

Stable isotopes have been extensively used in the study of individual specialization in the last few years. Stable isotopes reflect individuals' diets over time scales ranging from days to years depending on the tissue analyzed (Dalerum and Angerbjörn, 2005), providing a powerful tool to infer the temporal consistency of individuals' diets. Measures of the population variation in isotope values, the combination of tissues with fast (e.g., blood plasma) and slow (e.g., muscle) turnover rates, and the sampling of inert tissues (e.g., feathers, hair) have allowed the quantification of individual specialization and provided new insights on its causes (Matich *et al.*, 2011; Araújo *et al.*, 2007; Costa-Pereira *et al.*, 2019b; Martínez del Rio *et al.*, 2009; Newsome *et al.*, 2015b).

Often researchers are unable to obtain longitudinal data and use cross-sectional samples to investigate individual specialization, among which gut-content analysis has been the most popular. Recently, DNA metabarcoding have also become an important source of individual-level diet data (Villsen *et al.*, 2022). The problem with this type of data is that they represent a snapshot of individuals' niches. As such, they are strongly influenced by stochasticity and tend to inflate estimates of individual specialization. Having said that, gut-content analysis provides unvaluable information on the taxonomic composition of diets, which coupled with other types of data (e.g., stable isotopes) can be a useful approach (Layman *et al.*, 2012). Not surprisingly, individual specialization estimates based on gut contents tend to be stronger than those based on stable isotopes, but both estimates can be relatively well correlated (Araújo *et al.*, 2007; Costa-Pereira *et al.*, 2017, 2018c).

How to Quantify the Degree of Individual Specialization

Measuring the degree of individual specialization requires quantitatively comparing individual vs. population niches (**Fig. 1**). There are many different numerical approaches available in the literature to quantify the magnitude of individual niche specialization, from variance ratio approaches (Roughgarden, 1972, 1979) to indices based on individual-to-population niche overlap (Bolnick *et al.*, 2002) and consumer-resource networks (Araújo *et al.*, 2008). Below we present the most commonly used metrics in the literature based on continuous and discrete niche dimensions, as well as some recent quantitative developments in the field.

The first quantitative framework to measure intrapopulational niche variation was proposed half a century ago (Fig. 4). Roughgarden (1972) proposed that the total niche width of a given population (TNW) can be partitioned into two additive components: the variance in resource use within individuals (within-individual component; WIC) and the variance between individuals (between-individual component; BIC). Therefore, TNW = WIC + BIC (Fig. 4). This simple but elegant formulation allows us to quantify the proportion of TNW accounted for by within-individual variation, i.e., WIC/TNW, which is a widely used



Fig. 4 Schematic representation of Roughgarden's niche components in two contrasting scenarios of variation in resource use by individuals in the same population. Individuals' niches are represented as dark blue curves, while population niche is represented by the light blue curve. The total niche width of a given population (TNW, sepia bar) can be partitioned into two additive components : the variation in resource use within individuals (within-individual component: WIC, yellow bar) and the variation between individuals (between-individual component: BIC, pink bar), so that TNW = WIC + BIC. The ratio WIC/TNW measures the relative amount of the total niche variation accounted for by niche variation within individuals. (a) The degree of individual specialization is high when WIC explains just a small amount of TNW (i.e., WIC/TNW approaches 0), meaning that individuals have narrow and divergent niches (BIC accounts for most of TNW). (b) Conversely, the degree of individual specialization is low when individuals have wide niches relative to the population, so that WIC explains most of TNW (WIC/TNW approaches 1).

6 Individual Specialization

metric of individual niche specialization. As WIC/TNW approaches 0, WIC explains just a small amount of TNW, meaning that the degree of individual specialization is high as individuals have narrow and divergent niches (BIC accounts for most of TNW, Fig. 1 (b)). When WIC/TNW tends to 1 (Fig. 1(a)), individuals have wide niches relative to the population, so that WIC explains most of TNW and the degree of individual specialization is low. In summary, as individuals become more specialized in small subsets of the population niche, the degree of individual specialization increases, and WIC/TNW decreases (Fig. 4).

Roughgarden's niche components (WIC, BIC, and TNW) can be calculated for either continuous (e.g., prey size, prey nutritional content) or categorical (e.g., prey taxonomic identity) niche axes (Roughgarden, 1972, 1979). TNW can be expressed as the variance of total resource use of all individuals; BIC as the variance in mean resource use between individuals; and WIC as the average variance of resources within individuals. Specifically, when a single continuous niche dimension *x* is considered (e.g., prey size or color), x_{ij} represents the niche value (e.g., prey size) of the j_{th} prey item in individual *i*'s diet; thus, Roughgarden's niche components can be calculated as follows:

$$TNW = Var(x_{ij})$$
$$WIC = E[Var(x_j|i)]$$
$$BIC = Var[E(x_j|i)]$$

For discrete niche data (e.g., frequency of different resource taxa per individual), calculating these metrics requires a different numerical approach. We use the subscript "d" (i.e., WIC_d, BIC_d, and TNW_d) to denote the discrete formulation of Roughgarden's niche components. Roughgarden (1979) proposed using the Shannon-Weaver diversity index as a proxy for TNW. First, from the matrix of resource use (individuals x resource types), we can use the count (or mass or volume) of resources consumed by an individual *i* from a given resource type *j* (n_{ij}) to calculate the proportion of the *j*th resource type in the population *q*'s niche (q_i) as follows:

$$q_j = \frac{\sum_i n_{ij}}{\sum_i \sum_j n_{ij}}$$

In other words, the vector of q_i values represent the population resource use distribution, from which we can calculate TNW_d:

$$TNW_d = -\sum_j \ln q_j(q_j)$$

To break down TNW_d into WIC_d and BIC_d, we need three additional parameters: (1) $p_i =$ the proportion of all resources consumed by the population that are consumed by individual *i*; (2) $p_{ij} =$ the proportion of resources in individual *i*'s niche that belongs to the resource category *j*; and (3) $\gamma_{ij} =$ the proportion of the population's total use of resource *j* that was used by individual *i*. Then,

$$p_{ij} = \frac{n_{ij}}{\sum_j n_{ij}}$$

$$p_i = \frac{\sum_j n_{ij}}{\sum_i \sum_j n_{ij}}$$

$$\gamma_{ij} = \frac{n_{ij}}{\sum_i n_{ij}}$$

Finally, WIC_d and BIC_d can be obtained as follows:

$$WIC_{d} = \sum_{i} p_{i} \left(-\sum_{j} p_{ij} \ln(p_{ij}) \right)$$
$$BIC_{d} = \sum_{i} p_{i} \ln(p_{i}) - \left\{ \sum_{j} q_{j} \left[-\sum_{i} \gamma_{ij} \ln(\gamma_{ij}) \right] \right\}$$

Note that despite the different formulae to obtain Roughgarden's niche components from continuous versus categorical data, the fundamental property TNW = BIC + WIC remains true for both formulations.

As the original concept of individual specialization deals with "the degree to which individuals' diets are restricted relative to their population" (Bolnick et al., 2003b), an alternative approach to measure the magnitude of this phenomenon is computing the overlap between individuals' and population niches. Community ecologists have developed a variety of indices to calculate niche overlap between species from discrete resource use data, so Bolnick et al. (2002) adapted Schoener (1968) proportional similarity index (PS) to calculate the niche overlap between an individual *i* and its population using the PS_i index:

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j| = \sum_j \min(p_{ij}, q_j)$$

where p_{ij} remains the proportion of the *j*th resource type in individual *i*'s niche, and q_j the proportion of the *j*th resource type in the population niche. Therefore, PS_i equals 1 when individual *i*'s niche is identical to the population niche. Note that PS_i is an individual-level metric; thus, the degree of individual niche specialization in a given population can be obtained as the average of individuals' *PSi* values, i.e., the individual specialization index IS (Bolnick *et al.*, 2002). IS equals 1 when all *PS_i* values equal 1

(i.e., individuals' niches overlap completely with the population niche), assuming lower decimal values as the magnitude of individual niche specialization increases. Because IS values decrease as individuals become more specialist (i.e., lower *PSi* values), Bolnick *et al.* (2007) proposed the use of V = 1 - IS as a more intuitive metric of individual specialization.

Roughgarden's WIC/TNW and the IS index are the most commonly used metrics for quantifying the degree of individual specialization from resource use data. These two metrics are overall well correlated but have slightly different interpretations (Bolnick *et al.*, 2002). Importantly, both WIC/TNW and IS index can be easily calculated in the R package *RInSp* (Zaccarelli *et al.*, 2013), which also allows computing ad-hoc Monte Carlo and Jackknife resampling procedures to test if individuals use resources with similar probabilities from a shared set of available resources (Bolnick *et al.*, 2002; Araújo *et al.*, 2008).

Besides these classic metrics, some interesting additional quantitative approaches to quantify individual specialization have been proposed in the recent literature. These include approaches based on the analysis of individual-based ecological networks, which have revealed novel patterns and mechanisms of intraspecific variation in both antagonistic and mutualistic networks (Codron *et al.*, 2012; Araújo *et al.*, 2008, 2010; Dáttilo *et al.*, 2014; Lemos-Costa *et al.*, 2016; Tinker *et al.*, 2012). Additionally, the quantification of movement data has revealed how individuals differ in their interaction with the landscape (Kerches-Rogeri *et al.*, 2020; Bonnet-Lebrun *et al.*, 2018), offering a new perspective in the study of individual specialization (Costa-Pereira *et al.*, 2022). Finally, as niches by definition are multidimensional constructs, recent methods allow quantifying individual specialization in multiple niche dimensions (Costa-Pereira *et al.*, 2019a; Ingram *et al.*, 2018).

Most of these methods rely on frequentist maximum likelihood approaches to estimate resource use proportions, which can be problematic for small sample sizes and overestimate the degree of individual specialization. An exciting development in this direction is the use of Bayesian hierarchical approaches to quantify the uncertainty associated with individual and population niches (Coblentz *et al.*, 2017).

As we describe in *Acquiring individual-level data*, stable isotopes (δ^{13} C and δ^{15} N) are a prevalent source of data to modern studies in individual specialization (Bearhop *et al.*, 2004). Interestingly, the same underlying logic of Roughgarden's WIC/TNW and the IS index can be applied to estimate the degree of individual specialization from stable isotope data. For instance, many recently proposed methods allow estimating the magnitude of Roughgarden's niche components based on the relative variance in isotopic values between- and within-individuals (Matich *et al.*, 2011; Bond *et al.*, 2016; Newsome *et al.*, 2009; Costa-Pereira *et al.*, 2019b; Naya and Franco-Trecu, 2019). In this context, it is important to bear in mind that taking a single stable isotope sample per individual does not allow the quantification of the within-individual component of niche variation (i.e., WIC) (Ingram *et al.*, 2018). Analogous to the calculation of the IS index, Sheppard *et al.* (2018) presented the individual niche index (RINI), which uses multiple stable isotope samples per individual to quantify the overlap between individual and populational isotopic niches.

In sum, the decision on which quantitative approach will be used to measure the degree of individual variation, therefore, depends on the specific aims of the study and the type of niche data collected. A general and potentially unifying approach to quantify individual specialization from various niche data types is mixed-effect models (Ingram *et al.*, 2018). This approach has been widely used in animal personality studies to test the repeatability of behavioral traits when assayed multiple times per individual (Dingemanse and Dochtermann, 2013). Analogously, the "repeatability" in resource use can be assessed in mixed-effect models by considering individual identity as the random effect of interest, which allows partitioning niche variation into within-and between-individual variance components (Kerr and Ingram, 2021; Costa-Pereira *et al.*, 2019a). Importantly, this approach can be implemented in both Frequentist and Bayesian frameworks, can accommodate different error-distributions, and allows quantifying multidimensional individual specialization (Ingram *et al.*, 2018).

Proximate Causes

Individuals' intrinsic traits may affect their trophic preferences and performance. Therefore, in order to understand how individual specialization emerges and is maintained in natural populations, we first need to elucidate why conspecific individuals that share a common environment may diverge in their realized niches. Optimal Foraging Theory provides a solid body of predictions regarding what is the best trophic strategy consumers should adopt to maximize their net energy income (Stephens and Krebs, 1986; Schoener, 1971); i.e., should I consume or ignore this resource? The optimal decision involves considering environmental factors (e.g., prey density, energy content, and spatial distribution), as well as intrinsic traits linked to consumers' phenotypes. Conspecifics often differ considerably in morphology, behavior, and physiology, which affects their abilities to find, capture, subdue, handle and digest distinct resource types (Bolnick *et al.*, 2003b). The combination of these extrinsic and intrinsic factors results in intraspecific variation in rank preferences and, consequently, different optimal diets (Svanbäck and Bolnick, 2005). Therefore, continuous phenotypic heterogeneity within populations has the potential to generate variation in the efficiency to explore different resources, causing niche variation within populations (Maldonado *et al.*, 2019; Toscano *et al.*, 2020, but see Kerr and Ingram, 2021; Toscano *et al.*, 2022).

Functional trade-offs are a powerful underlying mechanism driving variation in resource use between individuals. The existence of trade-offs implies that individuals adopting a specific foraging strategy necessarily underperform when adopting an alternative strategy. For instance, variation in functional morphology can impose biomechanical trade-offs in handling or capturing prey with contrasting locomotion modes or defense strategies (Svanbäck and Eklöv, 2003). Also, cognitive trade-offs can limit individuals' ability to keep various search images while foraging or to handle prey (Werner *et al.*, 1981; Lewis, 1986). After resources are consumed, physiological trade-offs linked to the production of digestive enzymes or detoxification processes can limit efficient exploration of alternative prey types (Maldonado *et al.*, 2019; Afik and Karasov, 1995; Burrows and Hughes, 1991). By limiting individuals' ability to explore a variety of resources, trade-offs will contribute to interindividual diet variation.



Fig. 5 Main paths predicted by theory on how individual and population niches can interactively change. Considering a given population exhibiting a moderate degree of individual specialization (a), the population niche (TNW) can expand because individuals become more generalist (i.e., greater within-individual niche variation, WIC) (b), or because individuals diverge in their resource use (i.e., greater between-individual niche variation, BIC) (c). Also, the population niche can contract as a consequence of the contraction of individuals' niches (d). Finally, the population niche width can remain constant when individuals' niches expand and converge (i.e., greater WIC and lower BIC) (e). Plot (g) depicts these trajectories of niche variation relating the magnitudes of WIC and TNW in each scenario (vertical and horizontal bars, respectively). In trajectories leading from (a) to either (b) or (d) there is no change in the degree of individual specialization in the population; in the trajectory leading from (a) to (c) the degree of individual specialization increases; in the trajectory leading from (a) to (e) the degree of individual specialization decreases. We describe when each of these trajectories is expected to emerge across different ecological contexts in the section *Ecological causes*.

Two additional proximate mechanisms can lead to variation in realized niche within populations even when individuals actually have the same rank preferences for resources. First, differences in individuals' social status might facilitate or prevent access to optimal resources, driving niche variation between dominant and subordinate individuals within social groups (Forrester, 1991; Toscano *et al.*, 2016; van Overveld *et al.*, 2018; Sol *et al.*, 2005). Second, conspecific individuals might have contrasting nutritional requirements due to different reproductive (e.g., lactating females) or health status (e.g., parasitized individuals) (Lozano, 1991; Votier *et al.*, 2017).

Ecological Causes

The magnitude of individual specialization is not a fixed property of species, neither in space nor in time. Many studies have documented this labile nature of the magnitude of individual specialization across ecological contexts in space and time. Based on predictions from Optimal Foraging Theory, Araújo *et al.* (2011) propose that four ecological factors – namely intraspecific competition, interspecific competition, ecological opportunity, and predation – are expected to drive differences in individual specialization across populations. Importantly, the role of these extrinsic mechanisms in determining the incidence of individual specialization will also depend on intrinsic phenotypic traits (see *Proximate causes*) (Bolnick *et al.*, 2003b). Also, it is important to bear in mind that individual specialization depends not only on individual niche widths but also on population niche width (Fig. 1). Therefore, a complete understanding of how different ecological factors shape the degree of individual specialization requires elucidating how both population and individual-level niches change across populations in space and time (Fig. 5).

Intraspecific Competition

Competition between conspecifics is considered a major driver of intraspecific niche variation (Roughgarden, 1972; Costa-Pereira *et al.*, 2018c). In classic Optimal Foraging Theory, individuals should include alternative, less-profitable resources in their diets as preferred resources become scarce due to intraspecific competition, increasing both individual and population niche widths (Schoener, 1971). Therefore, population and individual niches are expected to expand at the same rate, which results in no chance in the degree of individual specialization in response to intraspecific competition (**Fig. 5**(a) and (b)). This prediction relies on the assumption that all individuals have identical rank preferences for resources (i.e., they have the same search and handling efficiencies) (Stephens and Krebs, 1986). However,

when individuals differ in their rank preferences, alternative scenarios can emerge (Svanbäck and Bolnick, 2005). In particular, under strong competition, different phenotypes may diverge in resource use by consuming different alternative resources (Svanbäck and Bolnick, 2005). In this scenario, intraspecific competition has a diversifying effect, promoting individual specialization via an expansion of the between-individual component of niche variation (Fig. 5(a) and (c)).

Most empirical research confirms this diversifying effect of intraspecific competition in different experimental and observational study systems (Svanbäck and Bolnick, 2007; Svanbäck and Persson, 2004; Tinker *et al.*, 2008; Agashe and Bolnick, 2010). Nevertheless, this response of individual specialization to intraspecific competition does not seem to be universal across taxa and ecological systems (Costa-Pereira *et al.*, 2018c; Sjödin *et al.*, 2018). In consumers with strong interaction strengths with their resources, Jones and Post (2013) argue that, after a given threshold of the strength of intraspecific competition, individuals have very limited resource options to choose from (e.g., when profitable prey types are totally depleted), which precipitates a reduction in population niches and consequent reduction in the degree of individual specialization (**Fig. 5**(a) and (d)). Therefore, although intraspecific competition has been historically pointed as a central factor shaping resource use in nature, its role in determining the dynamics of individual versus population niches is still not completely resolved.

Interspecific Competition

The theory on how interspecific competition shapes niches have a long history in ecology, mostly related to how populations respond to relaxed interspecific competition, i.e., ecological release (Pianka, 1976; MacArthur and Levins, 1967). Leigh Van Valen was the first to consider the interplay between intrapopulational niche variation and population niche width when interspecific competition is reduced. By studying bird populations in the continent (competitive environment) versus islands (relaxed competition environment), Van Valen (1965) proposed the Niche Variation Hypotheses (NVH), which states that populations released from interspecific competition have wider niches (greater TNW) because niche variation between individuals rises (greater BIC) (**Fig. 5**(a) and (c)). In other words, NVH suggests that competition release makes populations more generalized because individuals become more specialized (sensu Bolnick *et al.*, 2003b). This hypothesis has been tested in a variety of aquatic and terrestrial system, receiving mixed support from empirical studies (Araújo and Costa-Pereira, 2013; Bolnick *et al.*, 2007; Costa-Pereira *et al.*, 2019a; Maldonado *et al.*, 2017; Bison *et al.*, 2015; Pansu *et al.*, 2019; Maldonado *et al.*, 2019).

Van Valen's NVH is only one of the potential paths by which the population niche can expand as a result of ecological release from interspecific competitors. Bolnick *et al.* (2010) proposed the alternative scenario of "parallel release", in which individuals expand their own niches (greater WIC) towards new resources, so that population and individual niche widths expand similarly (**Fig. 5**(a) and (b)). As a result, the degree of individual specialization remains unchanged, a pattern which has received some empirical support (Costa-Pereira *et al.*, 2019a, 2018c). Although classic theory predicts that release from interspecific competition should result in population niche expansion, population niche may actually remain unchanged while all individuals become more generalized (i.e., individuals begin to use new resources, but these resources were already consumed by other conspecifics, thus the population niche does not expand). Therefore, individual niches expand (greater WIC) but variation between individuals collapses (reduced BIC) (**Fig. 5**(a) and (e)). In this "individual release" scenario (Bolnick *et al.*, 2010), reduced interspecific competition leads to a weaker individual niche specialization. In summary, theory predicts different paths by which population and individual niches may respond to interspecific competitors, and empirical studies have confirmed the complex nature of these effects. Thus, despite the long-standing interest of ecologists in how interspecific competition shapes niches (Van Valen, 1965), further studies are still needed to fully contemplate its effects on individual specialization.

Ecological Opportunity

The term ecological opportunity has multiple meanings in the ecological and evolutionary literature, but in the context of individual specialization studies, it denotes the diversity of available resources (Araújo *et al.*, 2011). Before explaining how ecological opportunity is predicted to influence individual specialization, it is key to clarify two points regarding this concept. First, ecological opportunity deals with the availability of different types of resources (e.g., prey richness), not their abundance and biomass. The effects of local resource quantity on the niches of individuals and populations relate to the patterns predicted by intraspecific competition (i.e., increased competition decreases the local abundance of resources). Second, competition and predation can reduce the diversity of available resources to consumers (Van Valen, 1965), but ecological opportunity also varies regardless of the intensity of competition or predation across ecological contexts, for instance, along gradients of productivity, habitat size or anthropogenic impacts (Costa-Pereira *et al.*, 2017, 2019a; Araújo *et al.*, 2014; Bolnick and Ballare, 2020; Costa-Pereira *et al.*, 2018a).

Ecological opportunity is predicted to favor individual niche specialization because a higher diversity of potential resources expands individuals' foraging options, providing scope for their niches to diverge (BIC) and the population niche to expand (TNW) as a consequence (Araújo *et al.*, 2011; Roughgarden, 1974) (Fig. 5(a) and (c)). The intuitive positive relationship between ecological opportunity (often measured as the diversity or richness of available prey) and the magnitude of individual specialization has been observed across different taxa in observational studies (Bolnick and Ballare, 2020; Costa-Pereira *et al.*, 2019a, 2017; Layman *et al.*, 2007).

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Predation

The direct and indirect effects of predation on individual specialization have been seldom explored in the empirical and theoretical literature (Eklöv and Svanbäck, 2006; Costa-Pereira *et al.*, 2018c). Araújo *et al.* (2011) proposed different mechanisms by which predators can either increase or decrease the degree of individual specialization in their prey populations. For instance, by controlling prey population sizes, predators might reduce the strength of intraspecific competition experienced by individuals, which tends to, but not necessarily, reduce individual specialization (**Fig. 5**(b) and (a)). In addition to this direct effect, predators often trigger changes in the foraging behavior of their prey. In some systems, predators can suppress individual specialization by forcing conspecifics to forage in a common, safe habitat type (e.g., forested areas or swallow, littoral waters) where ecological opportunity is limited to particular resource types (Eklöv and Svanbäck, 2006) (**Fig. 5**(b) and (a)). Alternatively, if some individuals within prey populations are more prone to forage in risky but more profitable habitats (i.e., variation in risk-aversion behavior), predators can actually promote individual niche specialization (Toscano *et al.*, 2016; Darimont *et al.*, 2007) (**Fig. 5**(a) and (b)).

Interactions Between Ecological Factors

Although theory predicts the specific, isolated effects of competition, ecological opportunity, and predation on individual specialization, populations are often experiencing all these factors simultaneously to varying degrees in nature. Importantly, the effects of these factors may not be independent (Costa-Pereira *et al.*, 2018c). A growing number of studies have found that gradients of competition, ecological opportunity, and predation can interact to shape population and individual niches (Costa-Pereira *et al.*, 2017; Newsome *et al.*, 2015b; Evangelista *et al.*, 2014; Costa-Pereira *et al.*, 2019a; Neves *et al.*, 2021). For instance, the diversifying effect of competition can be prevented by the lack of ecological opportunity (Newsome *et al.*, 2015b; Costa-Pereira *et al.*, 2017). Also, the relative importance and even the direction of the effect of these ecological factors can vary substantially across cooccurring species (Costa-Pereira *et al.*, 2018c; Bolnick *et al.*, 2010).

In addition to the four major mechanisms described above, Britton and Andreou (2016) suggest that parasites can alter phenotypic traits from their hosts and therefore also drive variation in resource use across conspecifics (e.g., niche differences between infected vs. uninfected hosts). Some studies have also begun to explore the potential of abiotic environmental variables (e.g., temperature, water transparency) (Lunghi *et al.*, 2020; Bartels *et al.*, 2012) and their stability over time (Dermond *et al.*, 2018) in driving variation in the degree of individual specialization across and within populations.

Consequences for Higher Levels of Biological Organization

Individual specialization emerges from individual-level decisions (e.g., foraging events), but this phenomenon can scale up to shape processes operating at higher levels of biological organization, from populations to ecosystems. For example, empirical and theoretical work has shown that individual niche variation may alter populations' stability, establishment success and extinction risk (Svanbäck and Persson, 2009; Agashe, 2009). Because intraspecific niche variation has the potential to change how organisms interact with heterospecifics and with their environment (Pollux, 2017), individual specialization may also influence processes at higher levels of biological organization, from communities to ecosystems. For example, individual niche specialization can shape patterns of metacommunities of trophically transmitted parasites (Cirtwill et al., 2016; Bolnick et al., 2020). Additionally, recent studies applying individual-based network analyses have provided new insights on how individual specialization can shape ecological interactions and the architecture of ecological networks (Guimarães, 2020). Bolnick et al. (2011) described six mechanisms by which intraspecific trait variation can affect the outcome of ecological interactions, laying the conceptual foundations for recent work on the magnitudes of individual specialization across co-occurring species (Franco-Trecu et al., 2014; Costa-Pereira et al., 2019a, 2018c; Cloyed and Eason, 2016), how they influence interspecific niche overlap (Costa-Pereira et al., 2019a) and ultimately species coexistence (Hart et al., 2016; Uriarte and Menge, 2018; Costa-Pereira et al., 2018c). Finally, a growing body of studies have investigated how trait or niche differences within populations can change ecosystem processes, such as decomposition rates and primary production, and ultimately impact the fluxes of matter and energy in both terrestrial and aquatic ecosystems (Evangelista et al., 2017; Fontana et al., 2019; Raffard et al., 2019; Allgeier et al., 2020). Despite these recent advances in our understanding of the importance of individual specialization to higher levels of biological organization and ecological interactions, we still need more theoretical work incorporating individual niche variation in classic community and ecosystem models, as well as empirical studies to test the predictions from these models and the generality of these scaling up effects from individuals to ecosystems.

Evolutionary Relevance

As a consequence of functional trade-offs, dietary specialization is often associated with individuals' phenotypes, which are shaped by genetic and environmental factors. In the latter case, individuals with the same genetic makeup can give rise to phenotypes specialized in different resources via phenotypic plasticity in response to environmental cues (Pfennig, 1992). Alternatively, individual specialists could arise via bet-hedging in unpredictable environments (Haaland *et al.*, 2020), but this possibility has never been empirically demonstrated.

Since individuals with distinct foraging strategies can experience different rates of energy income or interact with different predators and parasites, individual specialization can generate fitness heterogeneity within populations (Bolnick *et al.*, 2003b). The relevance of this fitness heterogeneity to trait evolution will depend on the heritability of phenotypes associated with individual niche differences, which has received scarce attention so far (Gómez *et al.*, 2020). Studies in diverse taxa have investigated the fitness payoffs associated with generalist vs. specialist trophic strategies, and results do not point to a simple, universal optimal strategy (Bolnick and Araújo, 2011; Ceia and Ramos, 2015). While trophic generalist individuals display fitness advantages over specialists in some biological systems (Costa-Pereira *et al.*, 2019b; Navarro-López *et al.*, 2014; Manlick *et al.*, 2021), trophic specialists are favored in other instances (Pagani-Núñez *et al.*, 2015; Golet *et al.*, 2000; Terraube *et al.*, 2014). Still, intermediate trophic strategies (i.e., neither specialist nor extreme generalist) can be favored for some species (Zango *et al.*, 2019) but disfavored for others (Cucherousset *et al.*, 2011). In addition, some studies have found no clear relationship at all between foraging strategy and fitness outcomes (Kernaléguen *et al.*, 2016a; Woo *et al.*, 2008; Ceia and Ramos, 2015). Importantly, at least part of this evident variation in results can be related to the distinct temporal scales in which fitness and trophic strategies (i.e., temporal consistency) were quantified in these studies (Ceia and Ramos, 2015).

Under certain circumstances, niche variation between individuals can lead to disruptive selection, either because of functional trade-offs or because of frequency-dependent competition. As a consequence of trade-offs specialist phenotypes can be better foragers than generalist phenotypes (Svanbäck and Eklöv, 2003). When resources are diverse (e.g., bimodal) and trade-offs are strong enough, the fitness of generalist intermediate phenotypes averaged over both resources can be less than the fitness of specialist extreme phenotypes, leading to disruptive selection (Schluter, 1995; Robinson *et al.*, 1996). Moreover, when there is individual specialization intraspecific competition becomes frequency dependent. As a consequence, intermediate phenotypes, which are more common in the population, suffer disproportionately higher competition, leading to disruptive selection (Bolnick, 2004). It is worth noting that these two mechanisms are mutually non-exclusive and can operate at the same time (Martin and Pfennig, 2009). Importantly, theory indicates that ecologically-driven disruptive selection can not only maintain phenotypic variation within populations (Roughgarden, 1972), but also lead to evolutionary diversification, including ecological sexual dimorphism (Bolnick *et al.*, 2003a) and sympatric speciation (Dieckmann and Doebeli, 1999).

Conservation Relevance

Conservation biology has historically focused primarily on maintaining biological diversity between species. However, intraspecific diversity underpins key ecological functions and nature's contributions to people (Des Roches *et al.*, 2021); thus conservation biologists have begun to recognize the need to also conserve ecological diversity within species (Mimura *et al.*, 2017). Indeed, variation within and between populations can have similar or even greater impacts on ecosystems than taxonomic diversity itself (Des Roches *et al.*, 2018). In this sense, as anthropogenic impacts (e.g., selective harvesting and habitat fragmentation) often erode intraspecific diversity, fundamental ecosystem functions can be lost even if target species persist in impacted landscapes - i.e., cryptic function loss (McConkey and O'Farrill, 2015; Costa-Pereira *et al.*, 2018b). Individual niche specialization plays a particularly important role in this scenario because multiple ecosystem functions are associated with trophic interactions (e.g., pollination, seed dispersal, nutrient flow, top-down control in food webs). For instance, Manlick and Newsome (2021) suggest that individual specialization has the potential to compensate for functional losses associated with the pervasive process of biotic homogenization. Also, individual niche specialization may help to safeguard populations facing the loss of specific types of resources (Durell, 2000) and help species to persist in anthropogenic habitats (Newsome *et al.*, 2015a). Therefore, despite historically neglected in the conservation arena, it is increasingly evident that individual specialization plays an important role in the persistence of species and ecological interactions in a rapidly changing world.

Outlook and Future Directions

Nearly two decades after the seminal paper by Bolnick and colleagues (2003), our understanding of the incidence, causes, and implications of individual specialization has greatly increased. We now have accumulated evidence that individual specialization is a prevalent phenomenon in nature, with important implications to phenomena at higher levels of biological organization. We now also possess methods and quantitative tools to measure the niches of individuals and populations with unprecedented precision across space and time in a myriad of taxa. Still, there are many open questions about the causes and consequences of this phenomenon.

In addition to keep mapping the occurrence of individual specialization in the tree of life, we suggest that future theoretical and empirical studies should focus on some exciting emerging lines of research, as follows: (1) the multidimensional nature of individual specialization (Ingram et al., 2018), not only looking at Eltonian niche dimensions (i.e., resource use) but also Grinnellian niche axes (e.g., environmental associations) (Carlson et al., 2021); (2) the complex intersections between individual niche specialization and other facets of intraspecific ecological variation (e.g., animal personalities, trait-based models); (3) the interaction between proximate mechanisms (e.g., trade-offs) and ecological causes (e.g., competition, ecological opportunity) of individual specialization; (4) the consequences of individual specialization to species interactions, community patterns and ecosystem functioning; (5) the genetic basis and heritability of interindividual variation and its implications to eco-evolutionary dynamics. Resolving these fundamental but still open questions will certainly help us to better appreciate the importance of individual specialization as a central phenomenon shaping interactively ecological and evolutionary processes.

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