

Are stable isotope ratios suitable for describing niche partitioning and individual specialization?

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Abstract. As concerns about anthropogenic and natural disturbance grow, understanding animal resource use patterns has been increasingly prioritized to predict how changes in environmental conditions, food web structure, and population dynamics will affect biological resilience. Among the tools used to assess resource use, stable isotope analysis has proliferated in ecological studies, particularly in relation to describing intra- and interspecific variation in trophic interactions. Despite a growing need to disseminate scientific information, the inherent limitations of stable isotope ratios and inappropriate synonymizing of distinct evolutionary and ecological processes may mislead ecological inferences in natural systems. This situation necessitates a re-evaluation of the utility of stable isotope ratios to address certain ecological questions. Here, we assess the efficacy of stable isotope ratios to describe two fundamental ecological processes, niche partitioning and individual specialization. Investigation of these processes has increased substantially in accordance with increased access to stable isotope data. This article discusses the circumstances and approaches that are necessary to evaluate niche partitioning and individual specialization, and outlines key considerations for the associated application of stable isotope ratios.

Key words: competition; generalists; resource partitioning; specialists; trophic interactions.

INTRODUCTION

Since the seminal work of George E. Hutchinson, species have been defined in terms of their fundamental niche, that is, the potential resource space a population and/or species may occupy, and realized niche, that is, a more flexible proportion of niche space that is occupied in light of intra- and interspecies interactions (Table 1; Elton 1927, Hutchinson 1957, Junker et al. 2019). Although ecological niches are dynamically shaped by evolutionary processes, including adaptation, a growing realization is that many ecosystems are changing at rates faster than many populations can respond, adding to conservation concerns (Radchuk et al. 2019). However, empirical evidence suggests that some taxa and food webs may be more suited to environmental change based on niche widths and niche filling, particularly “generalists” and communities comprising populations that partition resources during periods of equilibrium (Table 1; Ricklefs 2010, Bartley et al. 2019). As such, understanding an organism’s niche is fundamental to its

conservation and management during this period of accelerated environmental change.

Generalist species occupy broad ecological niches and often include populations that display high phenotypic variability in resource use patterns among individuals, consequently reducing intraspecific competition (Table 1; Van Valen 1965, Maldonado et al. 2017). In the event of disturbance, generalist populations are typically more resilient than specialists, because of their ability to fill vacant niche space in response to the loss of maladjusted individuals, assuming heterogeneity within populations (Table 1; Jiguet et al. 2006, Bartley et al. 2019). Comparably, interspecific variability in resource exploitation increases resilience to perturbation when complementarity is high, because greater community-level resource consumption fosters the maintenance of stable states when a diversity of functionally similar species coexist through niche partitioning (Table 1; Hardin 1960, Finke and Snyder 2008, Adam et al. 2015). Consequently, understanding the spatial and temporal dynamics of animal resource use patterns complements the broader conservation objectives of promoting and maintaining biodiversity. However, investigations of this type must be conducted with care to ensure inferences are appropriate.

Stable isotope ratios are among the most common proxies to describe resource use patterns in the context

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TABLE 1. Definition of terms and supporting literature relating to niche partitioning and individual specialization referenced in this study.

Term	Definition	Relevant literature
Niche partitioning		
Scenopoetic variables	Relating to ecological variables that do not interact, and change very slowly over time, and may involuntarily affect fitness. Commonly used in relation to environmental and/or topographic variables	Hutchinson (1978); Soberón and Nakamura (2009); Soberón (2010)
Bionomic variables	Factors that affect a species fitness, which can be directly regulated. Often used in relation to interspecies interactions (e.g., predation, diet)	Hutchinson (1978); Soberón and Nakamura (2009); Soberón (2010)
Ecological niche	An <i>n</i> -dimensional hypervolume of scenopoetic and bionomic variables that describes a species role in its environment	Hutchinson (1957, 1978)
Fundamental niche	An ecological hypervolume of scenopoetic and bionomic axes in which a species can survive and reproduce, not considering interspecies interactions	Hutchinson (1978)
Realized niche	An ecological hypervolume of scenopoetic and bionomic axes in which a species can survive and reproduce considering interspecies interactions	Hutchinson (1978)
Eltonian niche	The functional role a species may have in its environment, considering intra- and interspecies interactions	Elton (1927); Soberón (2007); Dehling and Stouffer (2018); Junker et al. (2019)
Grinnellian niche	The environmental/abiotic conditions over which a species can survive and reproduce. Congener to the <i>habitat niche</i> and/or <i>spatial niche</i>	Grinnell (1917); Soberón (2007); Junker et al. (2019)
Trophic niche	Niche hypervolumes typically relating to diet and foraging behavior. Congener to the <i>Eltonian niche</i>	Olalla-Tárraga et al. (2017); Lunghi et al. (2018)
Isotopic niche	Variability in single or multiple isotopes measured in an individual, population, species, assemblage, or community that results from variability in use of specific niche axes combined with animal physiology	Bearhop et al. (2004); Newsome et al. (2007, 2012); Jackson et al. (2011); Shipley and Matich (2020)
Niche partitioning	Differentiation in one or more axes of the realized niches of co-occurring species generated by interspecific competition for limiting resources, which inhibits extinction of the lesser competitor	Gause (1934); Hutchinson (1959); Augustyn et al. (2016)
Niche complementarity	When hypervolume properties are shared such that species appear tightly packed	Roughgarden (1974a); Werner (1977)
Niche functional redundancy	When two or more species exhibit the same/similar functional role within a food web; if one species is removed impact is limited at the community/ecosystem level	Lawton and Brown (1993); Rosenfeld (2002)
Niche filling	The exploitation of available niche space that may be new or vacated by a previous species (e.g., due to localized extinction)	Price et al. (2014); Sjödin et al. (2018)
Individual specialization		
Generalist	Population or individual that utilizes a large component of available resource space and typically occupies a broad ecological niche	Elton (1927); Hutchinson (1957, 1978)
Specialist	Population or individual that utilizes a small component of available resource space and typically occupies a narrow ecological niche	Elton (1927); Hutchinson (1957, 1978)
WIC (within individual component)	Intra-individual variation in resource use within a population	Roughgarden (1972); Bolnick et al. (2003)
BIC (between individual component)	Inter-individual variation in resource use within a population	Roughgarden (1972); Bolnick et al. (2003)
TNW (total niche width)	Total variability in a population's realized niche attributed to WIC and BIC	Roughgarden (1972); Bolnick et al. (2003)
Individual specialization	Variability in a population's realized niche is largely driven by inter-individual variation in resource use (BIC) not attributable to inter-individual differences in sex, age, or morphology	Roughgarden (1972); Bolnick et al. (2003)

of ecological niches, defined as the “isotopic niche” (Table 1; Newsome et al. 2007). The current popularity of this analytical approach is largely based on ease of sample collection, low cost of laboratory analysis, and the suite of analytical packages available to quantify

niche geometries (e.g., Jackson et al. 2011, Zaccarelli et al. 2013, Blonder 2016). Stable isotope ratios have thus been increasingly used to describe resource use patterns of populations within the context of resilience to environmental change, particularly for identifying the

processes of (1) niche partitioning (e.g., Quevedo et al. 2009, Matich et al. 2017), and (2) individual specialization (e.g., Newsome et al. 2012, Maldonado et al. 2017).

Despite the widespread use of stable isotope ratios to quantify patterns of niche partitioning and individual specialization, the ecological conditions that promote these processes are not universally acknowledged, leading to potential miscategorization of ecological conditions. Furthermore, it must be noted that there are distinct differences between isotopic niches and more traditional niche proxies that describe resource use through measurements of stomach contents (“trophic niches”) or habitat use (“spatial niches”) (Table 1; Flaherty and Ben-David 2010, Newsome et al. 2012, Petta et al. 2020, Shipley and Matich 2020). The goal of this commentary is to provide a timely reminder of the ecological conditions and appropriate methodology under which to evaluate niche partitioning and individual specialization. Further, we aim to outline various considerations to be made when applying bulk stable isotope ratios in these contexts to help refine research questions and frameworks a priori.

NICHE PARTITIONING

Fundamental niche partitioning refers to evolutionary change in populations or species in response to selection pressure generated by interspecific competition for limiting resources (Table 1; Hutchinson 1959, Augustyn et al. 2016). Herein we will describe niche partitioning at the population level, because species often comprise many disparate populations that elicit potentially variable ecological dynamics. When resource space is limited, functionally synonymous populations cannot exist at equilibrium, driving differentiation in aspects of their realized ecological niche to avoid extinction of the lesser competitor (Gause 1934). Niches can be partitioned when populations (1) specialize on different abiotic or biotic resources (i.e., resource partitioning), (2) are limited by the same resources but differ in the timing of resource use (i.e., temporal partitioning), and/or (3) differ in terms of where they experience and respond to limiting resources (i.e., spatial partitioning). Niche partitioning mechanisms by which populations avoid, limit, or endure competition cause intraspecific competition to be stronger than interspecific competition for both species. These mechanisms result in coexistence and enhance biodiversity (Finke and Snyder 2008). By contrast, competitive exclusion occurs when intraspecific competition is stronger than interspecific competition for one population (Blight et al. 2014), or when intraspecific competition is weaker than interspecific competition for both, favoring the species that can tolerate lower levels of the limiting resource (Gause 1934, Chesson 2000, Godwin et al. 2020). As such, to describe resource use patterns in the context of an ecological niche, the extent of competitive interactions and how they have evolved over time must be evaluated (Pearman

et al. 2008, Rosado et al. 2016). These ecological interactions are fundamental to the establishment and maintenance of community structure, biodiversity, and the realized niche of organisms (Krebs 2009).

The relationship of resource partitioning to niche partitioning is hierarchical—partitioning of abiotic or biotic resources can lead to behavioral, morphological, or physiological adaptations that result in niche differentiation (Table 1). Resource partitioning therefore signifies a divergence in resource use over evolutionary time between populations that once had greater overlap in their requirements (Walter 1991). This represents a compromise between pressures for character displacement and the disadvantages inherent to a shift in resource use (Table 1; Roughgarden 1976). Furthermore, resource partitioning, as a driver of niche partitioning, may be both a factor that encourages greater biodiversity and an underlying cause of efficient resource extraction by speciose communities, once assembled (Finke and Snyder 2008). MacArthur (1958) and Hutchinson (1959) originally described resource and niche partitioning, respectively, as the basis and outcome of evolutionary change among competing populations, and Schoener (1968, 1974) and Roughgarden (1976) maintained the original concepts. However, the terms niche partitioning and resource partitioning have frequently been synonymized in more recent literature. Although resource partitioning often receives greater attention, it is but one of three potential drivers of niche partitioning and should not be treated as a synonym.

A lack of adherence to the evolutionary context of niche partitioning and the misuse of related ecological terminology could have detrimental impacts on ecological inferences from the individual to the community level. To support the concept of niche partitioning, experimentation, often combined with theoretical or mechanistic models, is needed to determine if competition is driving the differential use of space and/or resources, or the timing of their use (Colwell and Fuentes 1975). Simply documenting differences in resource use between populations is not indicative of resource partitioning (Schoener 1974, Walter 1991). Biological literature of the 1960s to early 1980s largely adhered to the concept of resource partitioning as an evolutionary process that required rigorous testing of competitive interactions between populations (Walter 1991), and niche partitioning studies, probably owing to their complexity, rarely were published (Table 2). However, the synonymous use of differential resource use and resource partitioning beginning in the 1980s has led to a false equivalency between these processes, leading to scientists explaining ecological niches by referencing the by-products of their adaptive evolution (Walter 1991). Ecological characteristics, regardless of why they evolved, are now routinely upheld with little or no justification as features that lessen the impact of competition. Differences in resource use are relatively easy to document, whereas experimental support for resource

TABLE 2. Number of peer-reviewed journal articles per year that included resource partitioning or niche partitioning in the title using a combination of popular search engines (Web of Science, BIOSIS, Zoological Record).

Term	Source	1958–1985	1986–2000	2001–2020
Resource partitioning	Environmental Sciences/Ecology	6.0	16.4	23.0
Resource partitioning	Zoology	5.5	14.8	19.9
Resource partitioning	Marine/Freshwater Biology	2.0	6.2	9.2
Niche partitioning	Environmental Sciences/Ecology	0.9	3.6	20.6
Niche partitioning	Zoology	0.6	2.8	15.7
Niche partitioning	Marine/Freshwater Biology	0.1	1.1	7.5
Niche partitioning	Evolutionary Biology	0.2	0.9	5.0

Notes: Time periods include: 1958–1985, the introduction of the terminology (resource partitioning [MacArthur 1958]; niche partitioning [Hutchinson 1959]) to the review article by Toft (1985); 1986–2000 the late 20th century; and 2001–2020, the last 20 yr.

partitioning requires elegant designs and rigorous testing. The shift in terminology to a less precise concept has contributed to a steady increase in the number of resource partitioning publications, particularly in the last 20 yr, which is in accordance with a proliferation of studies that utilize stable isotope analysis (Table 2; Shipley and Matich 2020). Although they are increasingly useful tools, stable isotope ratios (e.g., $\delta^2\text{H}/\delta\text{D}$, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{18}\text{O}$, $\delta^{34}\text{S}$) are best when employed in complement to tracking, diet, and other methods used to collect behavioral information, and alone, may not provide enough information to yield accurate measures of niche partitioning (Shipley and Matich 2020).

The utility of stable isotope ratios as a basis for quantifying niche partitioning can only be properly evaluated if the theoretical underpinnings of the term are well understood and applied. The overlap of stable isotope ratios between populations is often used as a proxy measurement for competition in resource space; thus, it is often assumed that a lack of isotopic overlap is indicative of partitioning along specific resource axes. For example, a lack of overlap in carbon vs. nitrogen isotope space is often inferred as partitioning of Elton's (Elton 1927) trophic niche (e.g., diet; Table 1). Similarly, a lack of isotopic overlap in hydrogen ($\delta^2\text{H}$) or oxygen ($\delta^{18}\text{O}$) isotope space is used to support partitioning of Grinnellian niche components (e.g., altitude or geographic region; Table 1). Although we do not discount that resource partitioning may be the appropriate interpretation in some cases, it is certainly possible that other ecological (e.g., intraspecific variability in isotope ratios of prey populations) or physiological processes (e.g., interspecific variability in isotopic turnover rates of potential competitors) may be responsible for driving different isotopic compositions between populations (Shipley and Matich 2020). Local and/or regional biogeochemical processes (e.g., nutrient availability, temperature, and salinity) may promote additional isotopic variability in consumers by influencing isotopic baselines (McMahon et al. 2013) and the nutritional status and physiological condition of the consumer (Karlson et al. 2018). In isolation, a stable isotope approach is too coarse to quantify niche partitioning effectively, given the inherent detail and difficulty required of such an investigation.

Elemental signatures cannot directly track specific prey compositions or how prey size preferences may vary, which are necessary to assess trophic overlap among sympatric populations or entire species properly (Hammerschlag 2019). Stable isotope ratios are also unable to pinpoint occupancy patterns and the timing of resource acquisition in isotopically homogeneous environments when used alone (Hette-Tronquart 2019). Because dietary and habitat information inferred from stable isotope ratios are highly generalized, data are unable to discern if either was the result of competition for limiting resources.

The use of mixing models provides a framework to test relative levels of resource competition between co-occurring populations after data are normalized and converted to estimates of prey mixing space (Newsome et al. 2012, Manlick et al. 2019). Yet, challenges still emerge based on the granular scale of stable isotope ratios and the integration time over which tissues assimilate ecological information (Hette-Tronquart 2019), and recent quantitative assessments of niche partitioning using stable isotopes have recommend against its use (Flaherty and Ben-David 2010, Cummings et al. 2012, Hette-Tronquart 2019). Incorrect or variable use of terminology is largely responsible for the miscategorization of isotopic differentiation for niche partitioning, which is problematic in the field of ecology (Hodges 2008, Herrando-Perez et al. 2014). Determining what constitutes occupiable niche space and the thresholds that define niche partitioning has also been largely overlooked, as well as the complexity and number of niche dimensions evaluated (Blonder 2016). As such, we recommend the use of clear terminology for isotopic niches and differentiation, and distinctions from ecological niches and partitioning as originally developed (Table 1). More nuanced quantitative assessment of isotopic niches is also needed to reflect resource use overlap more accurately (Blonder 2016). Additionally, continued advances in tracking technology and genetic barcoding improve opportunities to assess spatiotemporal overlap in population occupancy, and offer high-resolution diet data from stomach contents and fecal swabs. Incorporation of these methods in collaboration with prey population monitoring by resource management agencies provides a

path forward for the study of niche partitioning using stable isotope ratios.

INDIVIDUAL SPECIALIZATION

Empirical observations have suggested that generalist populations (Table 1) are well suited to handle disturbance based on their exploitation of wide resource suites (Jiguet et al. 2006, Bartley et al. 2019). However, the individuals that constitute generalist populations are often heterogeneous in their ecological niches, necessitating an understanding of individual responses to changes in resource availability (Bolnick et al. 2007). Although some generalist populations include individuals that have niche widths comparable to that of the overall population, many are comprised of individuals with much narrower niche widths relative to population resource use across space and time (Bolnick et al. 2003, Vander Zanden et al. 2010). Such patterns are exemplified in populations of individual specialists, where variation in resource use between individuals is considerably greater than the variation in resource use within individuals, which may confer greater resilience based on such plasticity (Table 1; Roughgarden 1972, 1974*b*, Bolnick et al. 2002). Because ecological theory indicates that specialists are less resilient to environmental change than generalists in many contexts (Jiguet et al. 2006), considering the interplay between individual- and population-level patterns of resource use is increasingly relevant in the Anthropocene (Bolnick et al. 2011).

Quantitative tools used to measure individual specialization (IS), predominantly with regards to dietary behavior, often follow the framework of Roughgarden (1972) by assigning variance in resource use within individuals (within individual component of variation [WIC]) and between conspecifics (between individual component of variation [BIC]). When combined, WIC and BIC sum to the total variability in a population's realized niche (total niche width [TNW]; Roughgarden [1972, 1974*b*]). The degree of IS is typically expressed as WIC:TNW, where values approaching 1 suggest individuals utilize much of an available resource axis and exhibit low IS (Bolnick et al. 2002). Ultimately, these patterns indicate how individual realized niche widths compare to the realized niche of the population, which are often compared across populations and/or species and contexts (e.g., food web structure, environmental conditions, human disturbance). Bulk stable isotope ratios have become widely used to describe patterns of dietary IS in many terrestrial (e.g., Araújo et al. 2009, Maldonado et al. 2017), freshwater (e.g., Harrison et al. 2017), and marine taxa (e.g., Matich et al. 2011, Wiley et al. 2019), because they can be applied to quantify individual- and population-level parameters of variability along resource axes. For example, $\delta^{13}\text{C}$ may be used to investigate IS of habitat use/primary production sources, whereas $\delta^{15}\text{N}$ may reflect IS in dietary preference (e.g., exploiting prey of different trophic/functional roles).

In light of the limited ecological context needed to generate IS parameters, the isotopic composition of tissues with different isotopic turnover rates (i.e., those reflecting different temporal windows) may be used to quantify conservative estimates of variability for individual isotopic niche parameters within populations, without the need for data on food web end members. However, a broader ecological context increases the scope from which inferences can be drawn regarding IS dynamics, because the length of resource axes and factors that can limit access to resources generally control behavior (e.g., predation, competition, productivity [Elton 1927, Hutchinson 1957]). This relationship provides an opportunity for studies to test hypotheses concerning causative factors that may shape realized niches. Unlike niche partitioning, IS indices solely generated from stable isotope ratios are based on individual resource use patterns within the scope of the population rather than resource availability and interspecific competition, and are thus independent of food web structure. Consequently, we encourage the exploration of stable isotope ratios as a tool to improve our understanding of individual specialization across contexts, but several considerations are needed to ensure IS values are appropriately quantified and interpreted, and can be compared across studies.

First, IS cannot be inferred from bulk stable isotope ratios of a single tissue that does not allow for serial sampling or combination with additional prey data (e.g., to generate mixing models [Newsome et al. 2012, Reum et al. 2020]), and/or other dietary measures, such as stomach content analysis (Araújo et al. 2009). Despite interindividual differences in isotopic composition across a population, some of the factors that confound the use of stable isotopes to measure niche partitioning directly (see Niche Partitioning) also inhibit the ability to quantify IS from a single tissue. A minimum of two tissues with considerably different isotopic turnover rates (we recommend a twofold difference in half-lives or more) must be analyzed to quantify IS, or a metabolically inert tissue (e.g., vibrissae, vertebrae, teeth) must be serially sampled to determine if isotopic variability is predominantly attributed to within individual (WIC) or between individual components (BIC) of total resource space.

Second, because of inherent differences in trophic discrimination factors (TDFs), isotope values from different tissues should be normalized to ensure accurate WIC and BIC calculations (Hussey et al. 2012). Tissue-specific TDFs must be subtracted from each tissue used for analysis to standardize the tissues against each other. Without TDF standardization, WIC values may be more influenced by physiological differences/similarities, such as amino acid composition, that drive tissue-specific isotope fractionation rather than temporal variability/stability in dietary interactions (McMahon and McCarthy 2016, Lübcker et al. 2020).

Third, because IS indices are unitless, they have limited meaning without comparison to IS values from

other populations, regions, and time periods. However, as for assessments of niche partitioning, comparison of IS among populations requires full appreciation for the biogeochemical processes that may influence local/region isotopic consumer regimes. Furthermore, dissimilar or limited sample sizes can heavily influence comparative inferences. Like other methods that exploit isotopic variance to quantify niche dynamics (e.g., minimum convex polygons [Layman et al. 2007]; ellipses [Jackson et al. 2011], fixed kernel density [Blonder 2016]), outliers can impact specialization calculations, especially in data sets with small sample sizes. Sample size also impacts the isotopic ranges that determine WIC, BIC, and TNW, and can confound estimates of IS if data sets do not approach saturation in variability. Investigations into how sample size may influence estimates of isotopic IS components are lacking, however, and should be conducted using simulation modeling approaches and tested with empirical data. Assessing and reporting sample sizes therefore is imperative for standardizing the use of stable isotopes to quantify IS in future studies, and sensitivity analysis is strongly encouraged to ensure most (if not all) population variability has been sampled. Normalizing data through proportional values (Newsome et al. 2007) could help alleviate these challenges, particularly for studies with limited understandings of isotopic baselines and food web end members that cannot confidently assess if increasing sample size would significantly impact TNW and BIC estimates. Additionally, the use of mixing models to estimate the trophic ecology of individuals based on predator and prey isotopic ratios provides a separate approach that may increase the robustness of IS calculations when data are available (Newsome et al. 2012, Reum et al. 2020).

Finally, the number of tissues selected for analysis may influence delineations between populations that do and do not exhibit statistically significant IS. Because IS values are unitless, comparison to a null model (that assumes a generalist population where all individuals sample equally across the diet distribution) is needed to discern if a population is composed of individual specialists (Maldonado et al. 2017). The R package RInSp (Zaccarelli et al. 2013) uses a nonparametric Monte Carlo procedure to generate a null IS value from a predefined number of replicates based on the diet or isotopic data of the population, which can then be statistically compared to the population's IS value. Expectantly, the null value approximates $1 - n/n^2$ based on $(a + b + c \dots k)^n$ for diet studies, where k = available prey items for the population, and n = maximum number of consumed prey items, in order to account for increased WIC when more prey items are available. Concomitantly, the null model for stable isotopes follows diet studies, with $k = n$, which equal the number of tissues used to calculate IS. As the number of tissues increases, variability within individuals predictably increases for individual specialists in line with potential prey items assessed in diet studies. As such, directly comparing IS values for studies that employ

different numbers of tissues could lead to inaccurate inferences if null values are not considered. For example, an IS (WIC:TNW) value of 0.40 resultant from stable isotope ratios of two tissues would not indicate statistically significant individual specialization based on the null IS value, whereas a study using three tissues with the same IS value (0.40) would conclude the population exhibits significant individual specialization. These types of comparisons may also have consequences for diet studies if the number of available diet items and/or the maximum number of consumed diet items vary across populations. To address these issues, tissue types and the number of tissues used to quantify IS within taxonomic groups should be reported, and potentially standardized, to ensure values are interpreted accurately and are comparable across studies.

CONCLUSIONS

As growing global databases provide increased accessibility to information, and the scientific questions we address grow in scale and consequence, ensuring appropriate data usage is increasingly important. Intensifying concerns over climate change, habitat deterioration, and animal behavior have in part led to increased applications of stable isotope ratios to evaluate various niche components of individuals, populations, and ecological communities (Shipley and Matich 2020). Yet the application of stable isotope ratios should be considered carefully, particularly for broad-scale questions directed toward testing ecological theory, which often require a suite of carefully collected data from various sources. A lack of recognition of the ecological processes that promote resource partitioning has led to the miscategorization of ecological conditions in some studies, providing unsuitable foundations for the interpretation of results. Similarly, synonymous misuse of distinct terminology, like equating interspecific variability in resource use with niche partitioning, and isotopic niche with trophic niche has led to unfounded conclusions about populations and food webs (Petta et al. 2020), affecting our perception of resilience in some circumstances. Although stable isotope ratios are valuable for investigating resource use patterns, their coarse scale limits their application to studying niche partitioning in isolation, particularly without an understanding of resource availability and competition among sympatric populations.

Yet stable isotope are a valuable tool across other ecological conditions, and their use to study individual specialization holds promise. Dietary specialization using stomach contents has expanded our understanding of resource use patterns across ecosystems, and broadened our understanding of food web diversity (Bolnick et al. 2011). Stable isotopes may provide a complementary path by assessing variability in broad-scale individual resource use patterns over extended time periods, but appropriate data and thresholds are required. Similar to other methods, stable isotope analysis is not universally

appropriate or inappropriate. The efficacy of its application is contingent on the hypotheses or questions being addressed by the researcher and the overall methodological approach of the study. Thus, reassessing the questions of interest and the conditions in which these questions can be answered using stable isotopes is needed to determine their utility at this time of data-driven ecology.

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