

## The dimensionality of individual niche variation

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**Abstract.** The inherently multidimensional nature of the niche has not yet been integrated into the investigation of individual niche specialization within populations. We propose a framework for modeling the between- and within-individual components of the population niche as a set of variance-covariance matrices, which can be visualized with ellipses or ellipsoids. These niche components can be inferred using multiple response mixed models, and can incorporate diverse types of data, including diet composition, stable isotopes, spatial location, and other continuous measures of niche dimensions. We outline how considering both individual and population niches in multiple dimensions may enhance our understanding of key concepts in ecology and evolution. Considering multiple dimensions as well as the within-individual component of variation can lead to more meaningful measures of niche overlap between species. The impact of a population on its food web or ecosystem can depend on the degree of individual variation (via Jensen’s inequality), and we suggest how the dimensionality of individual specialization could amplify this effect. Finally, we draw from concepts in quantitative genetics and the study of animal personalities to propose new hypotheses about the ecological and evolutionary basis of niche shifts in multiple dimensions. We illustrate key ideas using empirical data from sea otters, wetland frogs, and threespine stickleback, and discuss outstanding questions about the consequences of multidimensional niche variation. Setting variation among individuals in an explicitly multivariate framework has the potential to transform our understanding of a range of ecological and evolutionary processes.

**Key words:** *individual specialization; Jensen’s inequality; multidimensional niche; niche overlap; niche shift; quantitative genetics; stable isotope analysis.*

### INTRODUCTION

The ecological niche of an organism defines how it interacts with all aspects of its environment, and is thus an inherently multidimensional construct (Hutchinson 1957). Niches have traditionally been modeled as properties of populations or species, but it is increasingly apparent that many populations are collections of ecologically heterogeneous individuals that vary in how they interact with their environment (Bolnick et al. 2003, 2011, Araújo et al. 2011). Individual specialization is a form of intraspecific niche variation that occurs when individuals only use a subset of the population’s resource base for reasons not attributable to sex, age class or discrete morph. The realization that individual specialization is

widespread necessitates a re-think of niche concepts to ensure that intraspecific variation is adequately modeled. In particular, the study of individual specialization has not been fully integrated with the concept of the niche as a multidimensional ecological space.

A multidimensional view of individual specialization has the potential to transform our understanding of niche dynamics and to bring together disparate approaches including stable isotope analysis, spatial ecology, quantitative genetics, and trait-based community ecology. The development of new technologies and methods has enhanced our ability to measure the use of resources and space by individuals at increasingly fine scales. For example, refinements to the use of ecological tracers such as stable isotopes allow the estimation of trophic niche parameters at multiple time scales (Layman et al. 2012). At the same time, tracking technology and remote sensing techniques allow measurements of the behavior and space use of individuals with ever-greater precision and for longer periods (Pimm

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et al. 2015). Many recent studies using these and other methods have produced data for numerous species encompassing multiple dietary, habitat or behavioral dimensions (Fig. 1). With an appropriate and explicitly multivariate conceptual and analytic framework, these data sources can be used to ask fundamental questions about the dimensionality of individual variation.

In this article, we outline a conceptual framework for investigating individual specialization in multiple dimensions, and explain how this perspective adds to our understanding of ecological and evolutionary processes. We develop two related arguments: that robust measures of individual niche variation should consider multiple niche axes and their covariances rather than each axis in isolation, and that studies of multidimensional resource use should integrate both the between- and within-individual components of niche variation. We show how this framework can alter predictions about key outcomes including the extent of niche overlap between species (particularly in stable isotope studies), the effect of individual variation on population mean processes and interactions (e.g., via Jensen's inequality), and the expected trajectory of niche shifts under ecological change. Along the way, we illustrate these ideas using analyses of empirical and simulated niche data, and propose several novel and testable hypotheses about the consequences of multidimensional individual specialization.

## A FRAMEWORK FOR INVESTIGATING MULTIDIMENSIONAL INDIVIDUAL SPECIALIZATION

In what follows, we define the niche in terms of resource use: discrete resource types, or more often continuous measures such as prey size or water depth. This usage aligns with the "classical niche theory" that is the basis of numerous ideas pertaining to niche width, niche overlap, community assembly and speciation (MacArthur and Levins 1967, Pianka 1973, Whittaker et al. 1973, Dieckmann and Doebeli 1999, Ackerly and Cornwell 2007). We acknowledge the value of other conceptions of the niche such as species' requirements for and impacts on discrete 'niche factors' (Tilman 1982, Chase and Leibold 2003, Letten et al. 2016), and see value in the exploration of how multidimensional individual specialization affects other elements of niche theory.

Individual specialization in resource use can be measured by partitioning a population's total niche width (TNW) into two additive components: the within-individual component (WIC) and the between-individual component (BIC). The WIC is the average breadth of resources used by each individual in the population, while the BIC is the variation among individuals in average resource use (Fig. 2A). Either narrower (low WIC) or more segregated (high BIC) realized niches of individuals can therefore increase the degree of individual

Diet and habitat	Multiple habitat dimensions	Resource use-related behavior
<p><b>DIET AND MICROHABITAT</b></p> <ul style="list-style-type: none"> <li>-European eel (Cucherousset <i>et al.</i> 2011)</li> <li>-<b>Threespine stickleback</b> (Snowberg <i>et al.</i> 2015)</li> </ul> <p><b>DIET AND INSHORE VS. OFFSHORE HABITAT</b></p> <ul style="list-style-type: none"> <li>-Arctic charr (Knudsen <i>et al.</i> 2010; Hawley <i>et al.</i> 2016)</li> <li>-Australian sea lion (Lowther &amp; Goldsworthy 2011)</li> <li>-Brown trout (Brodersen <i>et al.</i> 2012)</li> <li>-Eurasian perch (Quevedo <i>et al.</i> 2009; Svanbäck <i>et al.</i> 2015)</li> <li>-Southern sea lion (Baylis <i>et al.</i> 2015)</li> </ul> <p><b>DIET AND FORAGING ROUTE/AREA</b></p> <ul style="list-style-type: none"> <li>-Antarctic fur seal (Kernaléguen <i>et al.</i> 2012)</li> <li>-Australian fur seal (Kernaléguen <i>et al.</i> 2015)</li> <li>-Desertas petrel (Ramirez <i>et al.</i> 2016)</li> <li>-Loggerhead sea turtle (Hatase <i>et al.</i> 2010; Peckham <i>et al.</i> 2011)</li> <li>-Northern gannets (Wakefield <i>et al.</i> 2015)</li> <li>-Southern elephant seal (McIntyre <i>et al.</i> 2010; Martin <i>et al.</i> 2011)</li> <li>-Subantarctic fur seal (Kernaléguen <i>et al.</i> 2012)</li> <li>-Wandering albatross (Ceia <i>et al.</i> 2012)</li> </ul> <p><b>DIET AND MACROHABITAT/ECOSYSTEM TYPE</b></p> <ul style="list-style-type: none"> <li>-American alligator (Rosenblatt &amp; Heithaus 2011)</li> <li>-Antarctic fur seal (Casper <i>et al.</i> 2010)</li> <li>-Bottlenose dolphin (Rossman <i>et al.</i> 2015)</li> <li>-Dolphin gull (Masello <i>et al.</i> 2013)</li> <li>-Gray snapper (Hammerschlag-Peyer &amp; Layman 2010)</li> <li>-Great egret (Voslamber <i>et al.</i> 2010)</li> <li>-Schoolmaster (Hammerschlag-Peyer &amp; Layman 2010)</li> <li>-<b>Sea otter</b> (Newsome <i>et al.</i> 2015)</li> <li>-White fish (Harrod <i>et al.</i> 2010)</li> </ul>	<p><b>Multiple habitat dimensions</b></p> <ul style="list-style-type: none"> <li>-Australian fur seal (Kernaléguen <i>et al.</i> 2015)</li> <li>-Australian sea lion (Lowther &amp; Goldsworthy 2011)</li> <li>-<b>Loggerhead sea turtle</b> (Hatase <i>et al.</i> 2007)</li> </ul> <p><b>Multiple diet dimensions</b></p> <p><b>MULTIPLE STABLE ISOTOPE DIMENSIONS AND PREY SIZE</b></p> <ul style="list-style-type: none"> <li>-Sea otter (Newsome <i>et al.</i> 2009)</li> <li>-<b>Thin-toed frogs</b> (this study)</li> </ul> <p><b>TROPIC POSITION AND BENTHIC VS. PELAGIC ENERGY CHANNEL</b></p> <ul style="list-style-type: none"> <li>-<b>Eurasian perch</b> (Quevedo <i>et al.</i> 2009; Svanbäck <i>et al.</i> 2015)</li> </ul>	<p><b>FORAGING BEHAVIOR AND PREY TYPE</b></p> <ul style="list-style-type: none"> <li>-Antarctic fur seal (Casper <i>et al.</i> 2010)</li> <li>-Australian fur seal (Kernaléguen <i>et al.</i> 2015)</li> <li>-Australian sea lion (Lowther &amp; Goldsworthy 2011)</li> <li>-Desertas petrel (Ramirez <i>et al.</i> 2016)</li> <li>-Great cormorant (Potier <i>et al.</i> 2015)</li> <li>-Guillemots (Woo <i>et al.</i> 2008)</li> <li>-Loggerhead sea turtle (Hatase <i>et al.</i> 2007)</li> <li>-New Zealand sea lion (Chilvers 2008; Chilvers &amp; Wilkinson 2009)</li> <li>-Northern gannets (Wakefield <i>et al.</i> 2015)</li> <li>-Southern elephant seal (McIntyre <i>et al.</i> 2010; Martin <i>et al.</i> 2011)</li> <li>-Southern sea lion (Baylis <i>et al.</i> 2015)</li> <li>-<b>Wandering albatross</b> (Ceia <i>et al.</i> 2012)</li> </ul> <p><b>BEHAVIORAL TRAITS AND MICROHABITAT USE</b></p> <ul style="list-style-type: none"> <li>-Bullhead (Kobler <i>et al.</i> 2011)</li> <li>-German blackcaps (Rolschausen <i>et al.</i> 2013)</li> </ul>

FIG. 1. Examples of vertebrate populations in which niche variation is known or likely to occur in multiple ecological dimensions, and which could be studied in an explicitly multidimensional framework. This figure presents a non-exhaustive list of taxa as well as key references. Taxa in bold correspond to the images shown. Image credits (clockwise from top left): (threespine stickleback, *Gasterosteus aculeatus*) Travis Ingram; (thin-toed frog, *Leptodactylus chaquensis*) Raul Costa-Pereira; (wandering albatross, *Diomedea exulans*) Mark Jobling, licensed under public domain via Wikimedia Commons ([https://commons.wikimedia.org/wiki/File:070226\\_wandering\\_albatross\\_off\\_Kaikoura\\_3.jpg](https://commons.wikimedia.org/wiki/File:070226_wandering_albatross_off_Kaikoura_3.jpg)); (Eurasian perch, *Perca fluviatilis*) Richard Svanbäck; (sea otter, *Enhydra lutris*) "Mike" Michael L. Baird, licensed under CC BY 2.0 via Wikimedia Commons ([https://commons.wikimedia.org/wiki/File:Sea-otter-morro-bay\\_13.jpg](https://commons.wikimedia.org/wiki/File:Sea-otter-morro-bay_13.jpg)); (loggerhead sea turtle, *Caretta caretta*) U.S. National Oceanic and Atmospheric Administration (NOAA), licensed under public domain via Wikimedia Commons ([https://commons.wikimedia.org/wiki/File:Loggerhead\\_Sea\\_turtle.jpg](https://commons.wikimedia.org/wiki/File:Loggerhead_Sea_turtle.jpg)).

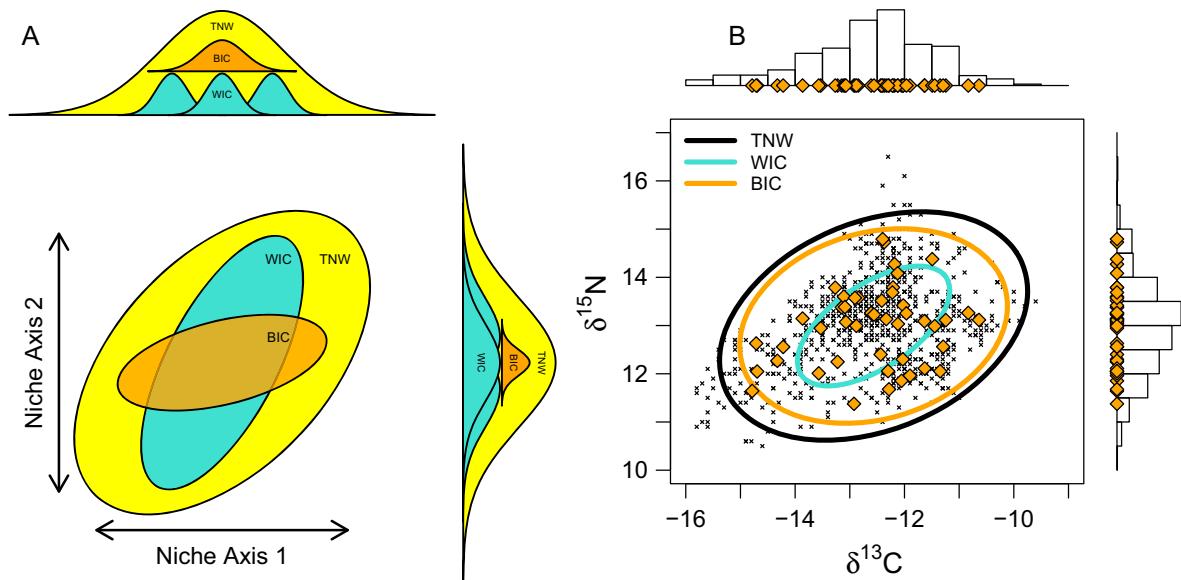


FIG. 2. (A) Translating the univariate representation of the BIC, WIC and TNW into multivariate ellipses. In this example, there is higher individual niche specialization (lower WIC/TNW) on niche axis 1 than niche axis 2, and consideration of both axes together reveals covariances in each component (with slightly different orientations). (B) Multivariate niche data for a sea otter (*Enhydra lutris*) population from Big Sur, California. 95% confidence ellipses represent the niche components in two dimensions (stable isotopes  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , serially sampled from vibrissae), while black symbols represent individual vibrissa segment isotope values and orange diamonds represent the individual means on the scatterplot and the histograms.

specialization in the population. These quantities are straightforward to define as variances in the case of a continuous niche axis such as prey size (Roughgarden 1972, 1974, Bolnick et al. 2002), or can be calculated using Shannon diversity indices as a proxy for variance when resource use is measured as frequencies of utilization of discrete food or habitat types (Roughgarden 1979, Bolnick et al. 2002). Alternative overlap-based measures of individual specialization are available for categorical data (Bolnick et al. 2002, Araújo et al. 2008), though these do not concurrently estimate population niche width. Measures of individual specialization based on resource categories typically do not consider quantitative differences between categories (e.g., prey size, nutritional value or trophic level), and can be influenced by the degree of taxonomic resolution (Newsome et al. 2015). To consider multiple, potentially covarying dimensions of resources use, we propose extending the analysis of the continuous niche components TNW, WIC and BIC into multiple ecological dimensions.

Much as the niche width of an individual or population can be measured as the variance of its resource use on a single continuous niche axis, so too can a multivariate niche width be defined based on variances and covariances of multiple niche axes. Given a suitable data set with repeated sampling of multiple niche dimensions for each individual (Box 1), we can extend the niche components TNW, WIC and BIC into matrix form. The BIC can be represented as an  $m \times m$  matrix **BIC** in which the diagonal contains the variance among individual

means for each of  $m$  dimensions, while the off-diagonals represent covariances between individual means for pairs of niche dimensions. The **BIC** matrix can be interpreted as a phenotypic variance-covariance matrix (**P**) in which the traits are niche axes, facilitating links to quantitative genetics (Box 2). A similar  $m \times m$  matrix can be constructed for **WIC**, with the elements representing the average within-individual variances and covariances. The population niche width is then represented as the matrix  $\text{TNW} = \text{WIC} + \text{BIC}$ . For example, given two niche axes  $x$  and  $y$  with multiple measurements  $j$  for each individual  $i$ , the covariance matrix between all measurements in the population (TNW) can be written as the sum of the covariance matrix for the residuals of each observation against individual means (**WIC**) and the covariance matrix for individual means  $\bar{x}$  and  $\bar{y}$  (**BIC**):

$$\text{Cov}[x_{ij}, y_{ij}] = \text{Cov}[x_{ij} - \bar{x}_i, y_{ij} - \bar{y}_i] + \text{Cov}[\bar{x}_i, \bar{y}_i]$$

The parameters of these matrices can be estimated using multiple response mixed models (Box 1). If data are approximately multivariate normal, each of these matrices can be visualized as a two-dimensional ellipse (Fig. 2) or a three-dimensional ellipsoid predicted to enclose a certain proportion of the multivariate distribution of resource use (e.g., 95%, or approximately 40% for a standard ellipse; Jackson et al. 2011).

These covariance matrices can be used to ask questions about the size and what we refer to as the ‘shape’ of the niche components. The size of a niche component

### Box 1: Data types and methodological considerations

Analyses of individual specialization in multiple dimensions can incorporate a variety of data types, so long as they represent biologically meaningful niche dimensions informed by natural history knowledge of a particular study system. Perhaps most straightforward will be longitudinal data sets where each individual receives a relatively precise measure for each niche dimension (e.g., microhabitat or prey size) at each sampling period. Normality of data is not necessary for the calculation of covariance matrices, although for some applications either a (multivariate) normal distribution or some other distribution will need to be assumed. Depending on the scale of different measurements, standardization via z-scores or log transformation may make the niche component matrices more readily interpretable, though it is important to note that the choice of transformation will influence the shape of the inferred niche components. Partially discretized data may still provide information about continuous underlying niche axes; for example, dietary niche dimensions may be measured using mean sizes or trophic positions for multiple prey categories (taxon or functional groups), rather than measuring each item separately. The effectiveness of this approach will likely depend on the number of prey categories and their distribution in niche space, and simulations may be useful in understanding the effects of this aggregation. Consideration should also be given to the timescale over which niche data are collected: single cross-sectional samples (e.g., from stomach contents) are biased unless each sample captures a sufficient number of independent resource use decisions, while samples collected over very long timescales might misrepresent the degree of individual specialization occurring at any given time (Araújo et al. 2011, Novak and Tinker 2015).

A general method that can be used to analyze multivariate niche data is multiple response generalized linear mixed models (MGLMM). This flexible modeling approach can incorporate fixed and random effects, as well as different response variable distributions. Software capable of fitting these models includes the commercial software ASReml, which fits models with restricted maximum likelihood (Gilmour et al. 2009), and the MCMCglmm package in the R environment (Hadfield 2010, R Core Team 2014), which employs Bayesian Markov Chain Monte Carlo analysis. Individual identity can be modeled as a random effect to obtain either the restricted maximum likelihood or the posterior mean of the variances and covariances between individuals in each dimension (**G**-structure, **BIC**). The residual variances and covariances (**R**-structure) then quantify all variation left over after individual effects and any other terms are accounted for, and correspond to the average within-individual variation (**WIC**). The two matrices **BIC** and **WIC** can be added to estimate the total niche width (**TNW**). MGLMMs can incorporate other levels in hierarchical sampling designs – for example, if multiple diet items are measured for each measurement of habitat – though to estimate the covariances in **WIC** it is important that at least some measurements of each niche axis are matched. A similar approach can be used to estimate and account for other forms of intraspecific niche variation (e.g., due to age class, sex, or discrete morph) by including them as additional fixed effects in the model.

Visualization and interpretation of multivariate model fits will be simplest if the data are approximately multivariate normally distributed, and niche components can be displayed as ellipses or ellipsoids (Jackson et al. 2011, Swanson et al. 2015). However, MGLMMs can incorporate other data distributions, such as binomial or threshold models for binary data, and individual traits may be inferred on a latent scale. The development of methods for measuring standard statistical properties such as repeatability (Nakagawa and Schielzeth 2010) and power (Johnson et al. 2015) are ongoing for GLMs, so some validation is likely to be needed for analyses of individual specialization combining data distributions into multivariate measures of niche components.

A variety of hypotheses related to multivariate niche variation can be tested using MGLMMs. The fit of competing models can be compared using likelihood ratios or information criteria to assess support for a niche component – for example, to test for non-zero individual variance or covariance terms. A similar approach can test whether groups including age classes, sexes, or different species have the same or different **WIC**s or **BIC**s. Related hypotheses about the proportionality of matrices (e.g., is the **BIC** of a population following competitive release a scaled-up version of initial **BIC**) do not appear to be implemented in currently available MGLMM software, but should be straightforward extensions. As many of these methods are still in development, we recommend analyzing simulated or resampled data where possible to confirm the expected properties of the niche components in the absence of some process of interest.

can be measured as the sum of the eigenvalues of the corresponding matrix; this may be more interpretable if variables measured on different scales are first scaled to

produce z-scores. Analogous to the univariate metric **WIC/TNW**, the size of the **WIC** divided by the size of the **TNW** provides a multivariate measure where lower

### Box 2: Multivariate niche variation and quantitative genetics

Studies of multidimensional individual specialization can draw from the sizeable literature dealing with quantitative genetic variation and evolution of traits controlled by the combined action of many genes of small effect. Generalization of the breeder's equation permitted the use of matrix algebra to study genetic variation and response to selection in multiple correlated traits (Lande and Arnold 1983), and quantitative genetics has subsequently developed a rich set of methods for considering both genetic and environmental factors that influence evolutionary outcomes (Schluter 1996, Phillips and Arnold 1999, Steppan et al. 2002, Arnold et al. 2008). Several aspects of this work, particularly the study of **G**-matrices of additive genetic variation and covariation underlying traits, are applicable to our framework for studying multivariate niche variation.

The most straightforward such link is the fact that the **BIC** is in fact a specific type of phenotypic variance-covariance matrix (**P**-matrix) in which the traits are ecological dimensions such as diet or habitat use. This implies that  $\mathbf{BIC} = \mathbf{G} + \mathbf{E}$ : between-individual variation is determined by some combination of additive genetic (co)variation and environmental (co)variation. Therefore, the population niche  $\mathbf{TNW} = \mathbf{G} + \mathbf{E} + \mathbf{WIC}$ , adding within-individual variation to the conventional partitioning of phenotypic variation. We might anticipate that the genetic component will be low for traits often defined by flexible behavior and ecological interactions, but this is a hypothesis that should be tested when possible, as traits related to behavior (Box 3), environmental tolerance and resource use can have a substantial genetic basis (Mousseau and Roff 1987, Robinson and Page 1989).

It is therefore possible in principle to estimate quantitative genetic parameters for **BIC**, so long as a suitable combination of genetic and ecological data can be obtained. Either wild populations with pedigrees, or laboratory crosses released into a natural or semi-natural environment, could be used to infer the size and shape of the **G**-matrix relative to **BIC** and **TNW**. Quantitative trait locus mapping or genome-wide associations studies could be used to identify regions of the genome associated with different niche dimensions, and knowledge of the genetic architecture underlying niche variation may be valuable in predicting population responses to selection imposed by ecological change.

values represent stronger overall individual specialization. The relative size of each component can be visualized by comparing the ellipses (or ellipsoids) described above, though unlike the matrices themselves, the areas (or volumes) are not precisely additive. The shape of a niche component encompasses the variances of each niche axis along the diagonal of the matrix, as well as the covariances in the off-diagonal. Ecologically interesting properties of the shape of these matrices include their eccentricity (relative dominance of the first eigenvalue) and orientation (rotation of the matrix as defined by its eigenvectors). Measurement of the size and shape of the covariance matrices representing niche components can be used to test hypotheses about the causes and consequences of multidimensional individual specialization.

#### IMPLICATIONS OF MULTIDIMENSIONAL INDIVIDUAL SPECIALIZATION

In the following section we outline how individual specialization in multiple ecological dimensions has the potential to alter our understanding of a range of ecological and evolutionary processes. We build on a recent review of the consequences of intraspecific variation (Bolnick et al. 2011), and focus on the specific impacts that individual specialization in a multidimensional ecological niche space can have on processes in ecology and evolutionary biology.

#### *Coexistence and community structure*

Community ecology has been transformed by a modern understanding of the conditions for species coexistence over the past two decades (Chesson 2000), and recent studies have begun to consider the impact of intraspecific variation on coexistence and community assembly (Clark 2010, Violle et al. 2012, Barabás and D'Andrea 2016, Hart et al. 2016). However, these approaches have so far either considered only one niche axis at a time, or have considered multiple niche axes but not partitioned variation into between- and within-individual components. In this section we discuss how considering the dimensionality of between-individual and within-individual niche variation can yield new insights into the mechanisms responsible for coexistence and community assembly.

Recent theory states that the possibility for stable coexistence between species depends on the magnitude of both niche differences and fitness inequalities between them (Chesson 2000, Adler et al. 2013). Niche differentiation between species can be a stabilizing process by causing the average magnitude of intraspecific competition to exceed that of interspecific competition. The extent of niche overlap should thus be correlated with the strength of stabilizing processes favoring coexistence. As species compete simultaneously and interactively for different types of resources (e.g., microhabitats and prey

types), the true multivariate niche overlap can depend on both the dimensionality of the niche and the shape of niche components. In this context, the possibility of quantifying variation both between and within individuals of competing species in multiple dimensions (Fig. 3) is a powerful advantage of our framework, allowing more meaningful measurement of niche overlap.

Both the between- and within-individual components of the population's niche will determine the true niche overlap between species, but in practice niche overlap is often calculated without considering within-individual variation. For example, a popular use of stable isotope data (e.g.,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) is to infer niche overlap of multiple species in a community. However, most isotope studies rely on a single sample per individual, and if the tissue analyzed has a relatively slow turnover rate (such as muscle), it will largely indicate only the **BIC** of the population's total niche width (as well as various sources of error) and neglect the **WIC**. It may be possible to estimate the **WIC** if multiple isotope samples can be obtained per individual, either by serially sampling inert tissues such as vibrissae or by sampling multiple tissues that vary in turnover time and integrate diet over different time scales (Fig. 2B; Newsome et al. 2009, Matich et al. 2011). However, even in these cases we note that a substantial part of the within-individual variation is likely to be missed, as each tissue sample will still represent an average over multiple diet items consumed over the relevant time scale. In the more common scenario of a single sample per individual, niche estimates incorporating primarily the **BIC** can be expected to underestimate niche overlap, especially in

species in which **WIC** is large relative to **TNW**, or **WIC** and **BIC** have very different shapes. As an example, we show how adding repeated measures of multiple niche dimensions for each individual (i.e., incorporating **WIC**) can increase the perceived niche overlap between congeneric thin-toed frog species (*Leptodactylus* spp.) in the Pantanal wetlands of Brazil (details in Appendix S1). In this system, we can obtain a more meaningful measure of niche overlap when multiple niche dimensions (prey  $\delta^{13}\text{C}$  and prey size) are measured together, and when the **WIC** (based on multiple samples in each frog's gut contents) is considered along with the **BIC** (Fig. 3).

While improved measurement of niche overlap is important, the degree and shape of individual niche variation also have the potential to impact species coexistence. Recent theory predicts that individual variation in a single dimension should impede coexistence by causing individuals to compete more strongly with ecologically similar heterospecifics than with dissimilar conspecifics (Barabás and D'Andrea 2016, Hart et al. 2016). Other theoretical work emphasizes the role of individual differences in responses to environmental variation (Clark et al. 2007, 2010, 2011), or species differences in the shape of nonlinear functional responses (Armstrong and McGehee 1980). In general, we can predict that species coexistence is more likely if species differ not only in niche position but also in the shape of niche variation, meaning they will respond differently to multiple environmental variables. Species' niche components can be compared in our framework: multiple response GLMMs can model shared or different niche components for each

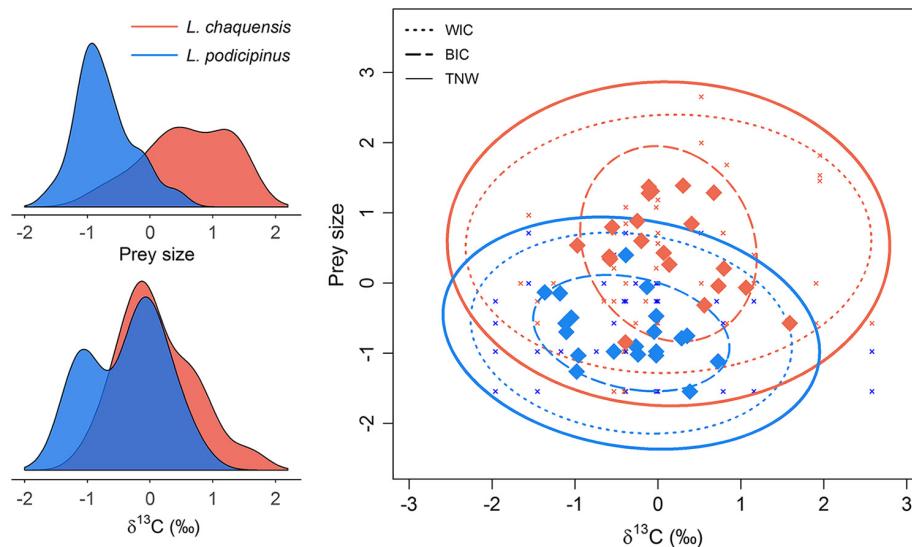


FIG. 3. Illustration of how the dimensionality of niche variation may relate to perceived measures of niche overlap between two congeneric frog species (*Leptodactylus* spp.) from the Pantanal wetlands, Brazil. When examined one niche axis at a time, the two species appear to have relatively high overlap in relation to  $\delta^{13}\text{C}$ , but not to prey size (left panels). Considering both niche axes simultaneously, niches can be represented as 95% confidence standard ellipses for the **BIC**, **WIC** and **TNW**. Species show low overlap when only the **BIC** is examined (dotted lines, as is usually the case for stable isotope niche data), but in fact the overlap is considerably high when **WIC** is considered (solid lines). Crosses represent the position of each prey found in gut contents and diamonds represent the individual frogs' means of prey size and  $\delta^{13}\text{C}$ .

species, and methods for matrix comparison (Phillips and Arnold 1999, Stepan et al. 2002) could be adapted to test for similarity in the shape of the **WIC** or **BIC**. We could therefore extend hierarchical approaches to trait-based ecology (Violle et al. 2012) by partitioning the community niche structure into variation between species, between individuals and within individuals.

*Food web and ecosystem processes*

Intraspecific variation in one or more niche dimensions has the potential to modify a species' impact on other trophic levels, and on broader food web and ecosystem functions. The diversity of discrete genotypes in clonal species can have ecosystem-scale consequences analogous to the effects of species diversity on ecosystem function (Whitham et al. 2006, Hughes et al. 2008), and continuous variation among individuals can be expected to have many of the same effects (Bolnick et al. 2011, Moran et al. 2016). One significant mechanism by which intraspecific variation can alter a species' contribution to ecological processes can be explained by a mathematical expression known as Jensen's inequality (Jensen 1906, Ruel and Ayres 1999, Moran et al. 2016). For a process that is a concave function of a trait or niche

measure that varies among individuals, the mean function value of all individuals will be lower than the function expressed at the population mean trait value (while the reverse is true for convex functions). Thus, individual niche variation should decrease the population-level outcome for concave functions such as saturating functional responses, thermal performance curves or unimodal relationships between a resource axis and resource productivity (Martin and Huey 2008, Denno and Lewis 2009, Bolnick et al. 2011). These effects should translate into multiple dimensions when the process of interest varies as a concave (or convex) function of multiple trait or niche dimensions (Madansky 1959), but detailed theoretical explorations of the consequences of Jensen's inequality in multiple dimensions are rare (see, however, Evans et al. 2013). To illustrate the potential effects, we used a set of simulations where performance is a strictly concave function of multiple ecological traits. We show that the magnitude by which intraspecific variation reduces population mean performance can increase with niche dimensionality, total niche width, and the extent of individual specialization (Fig. 4, details in Appendix S1). A full theoretical treatment will be needed to clarify these predictions and to evaluate how the effect is influenced by the covariance between niche axes or by

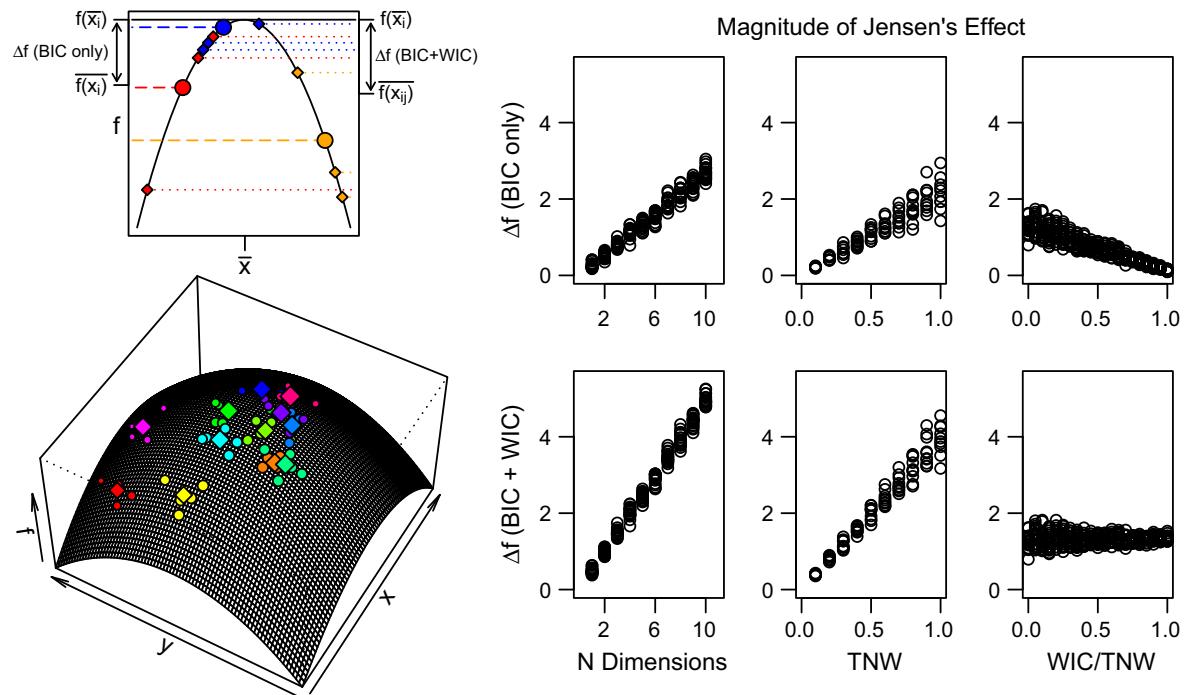


FIG. 4. Jensen's inequality in multiple dimensions. Top left: for a concave function  $f$  of a trait  $x$ , the mean individual function will be less than the function evaluated at the mean trait value if individuals vary in  $x$  (left axis), and the mean function will be further depressed if within-individual variation in  $x$  is accounted for (right axis). Individual means are represented by colored circles and within-individual variation is represented by diamonds of the same color. Bottom left: illustration of a function (quadratic) that is concave in two dimensions, with symbols as in the one-dimensional panel. Panels on right: the magnitude of the decrease in the value of a strictly concave function due to Jensen's inequality depends on the number of dimensions, the total niche width (TNW, given two dimensions), and the degree of individual specialization (given two dimensions and constant TNW).

mixtures of convex and concave functions. Experimental manipulations of the degree of individual variation in multiple traits may then reveal whether the expected effects of multidimensional niche variation are evident in empirical systems.

Another scenario in which the dimensionality of niche variation may have particular importance is when diet diversity encompasses both “horizontal” and “vertical” dimensions of food webs. The horizontal diversity refers to the variety of species within a trophic level, potentially encompassing energy pathways supported by multiple primary producers, while vertical diversity refers to variation across trophic levels or in trophic position (Matthews et al. 2010). Empirical evidence indicates that intraspecific competition in a consumer can drive population niche expansion via increased between-individual variation (Svanbäck and Bolnick 2007, Araújo et al. 2011, Tinker et al. 2012, Jones and Post 2016), but the degree to which this process impacts lower trophic levels could depend on the dimension in which niche expansion is most pronounced. One possibility is that niche expansion will occur via increased horizontal diet variation such that all individuals specialize on prey at the same trophic level. In this case, the total strength of top-down control may be enhanced due to the increased consumer population size, even if the per-capita impact is lower because the impact is spread across more trophic links (Bolnick et al. 2011). In contrast, if niche expansion involves increased vertical diet variation (omnivory) and individuals specialize on prey at different trophic levels, top-down control may be dampened (Bruno and O’Connor 2005) despite the increase in consumer density. A related phenomenon is the coupling of distinct food webs via horizontal diet diversity of top predators, which under some conditions is predicted to stabilize the larger system (McCann et al. 2005, Rooney et al. 2006). Horizontal niche variation will alter the degree of coupling if individuals specialize on distinct energy sources (e.g., pelagic vs. littoral; Quevedo et al. 2009), whereas vertical niche variation may not affect the degree of coupling. Knowledge of the extent and shape of individual specialization in multiple dimensions may therefore allow us to predict qualitatively different trophic dynamics and ecosystem processes.

#### *Niche shifts and ecological speciation*

Thus far we have focused on potential effects of multidimensional individual niche variation that do not necessarily involve a change in the niche position of the focal species. Of course, many important questions in ecology and evolution concern shifts in the population mean niche position: single populations may undergo niche shifts in response to biotic or abiotic environmental changes, while speciation often involves the evolution of distinct niches in newly formed species. We argue that given the natural links between quantitative genetic theory and multidimensional individual specialization

(Box 2), consideration of the dimensionality of niche variation will enrich our understanding of the ecological and evolutionary dynamics of niches.

A shift in the average niche position of a population will involve some combination of evolutionary change and phenotypic plasticity. When niche variation among individuals is partially heritable, selective pressures such as biotic interactions may drive an evolutionary shift in the niche position. For example, competition and predation by an intraguild predator, prickly sculpin (*Cottus asper*), have led threespine stickleback (*Gasterosteus aculeatus*) to undergo an evolutionary shift toward increased use of zooplankton and open water habitats (Ingram et al. 2012, Miller et al. 2015). A byproduct of predator-induced life history evolution in Trinidadian guppies (*Poecilia reticulata*) is a shift by guppies in high-predation environments to feed at a higher trophic level (greater reliance on invertebrates than algae) than populations in low-predation environments (Zandonata et al. 2011). Finally, the native lizard *Anolis carolinensis* has undergone an evolutionary shift to use more arboreal microhabitats following the invasion of Florida by its congener *A. sagrei* (Stuart et al. 2014). Other niche shifts can occur without evolutionary change, where species with flexible foraging and habitat selection behaviors alter their resource use within a generation. Short term (e.g., within-generation) responses to the presence of predators or competitors have been shown for both the niche position of a focal species (Vander Zanden et al. 1999, Eklöv and Svanbäck 2006) and for the degree of niche variation among individuals (Bolnick et al. 2010).

We propose that the dimensionality of individual variation may bias the direction of niche shifts in response to biotic or abiotic changes. When a species undergoes an evolutionary response to selection on a heritable trait, a well-established body of theory and empirical study shows that the dimensionality and orientation of the G-matrix can bias the direction of phenotypic evolution along ‘genetic lines of least resistance’ (Schluter 1996, McGuigan et al. 2005, Hansen and Houle 2008, Dochtermann and Dingemans 2013). If genetic variation underlies between-individual niche variation (Box 2), we can therefore predict that ecological niche shifts will be biased in the direction of greatest genetic variation. It is also conceivable that the shape of niche variation can bias the direction of niche shifts that occur via behavioral flexibility or other forms of phenotypic plasticity, even in the absence of evolutionary change (Box 3). If individuals exhibit flexibility that allows shifts toward novel or underutilized resources, this flexibility may manifest as the WIC within a population prior to the niche shift. The shape of the WIC might influence the direction of the niche shift if it reflects constraints on the extent of plasticity, where only particular regions of niche space can be readily explored by an individual. In contrast, if niche shifts occur as individuals learn from the resource acquisition behavior of more successful individuals, the type of individuals available to imitate should be determined by

### Box 3: Multivariate niche variation and behavior

Appreciation for the importance of between-individual variation has also increased in behavioral ecology. Our framework shares similarities with methods used in the study of repeatable individual differences in behavior (Dall et al. 2012). These differences, sometimes called animal personalities, manifest as behavioral syndromes when individuals vary in multiple correlated behaviors. For example, a proactive behavioral syndrome is associated with positive covariance between boldness, activity, and aggression. Behavioral ecologists have applied statistical methods including (generalized) linear mixed models to partition behavioral variation within vs. among individuals (Dingemans and Dochtermann 2013).

In addition to methodological similarities, multidimensional behavior and multidimensional niche variation may be linked directly when behavioral variation underlies resource selection. For example, bolder individuals are predicted to use habitats farther from shelter and to forage on prey that expose the individual to greater predation risk. Early work on behavioral variation in fishes examined the use of sheltered nearshore habitats vs. exposed open water habitats, aligning the position of an individual on the bold-shy personality axis with its use of specific habitats and prey types (Wilson et al. 1993). In fact, variables such as time spent in exposed vs. sheltered habitats are measures of resource (microhabitat) use that also serve as proxies for personality traits. Despite these links, the same individuals are rarely measured for both behavioral and niche data, particularly in field conditions. Paired measures of behavior and resource use for the same individuals could be incorporated into a larger multivariate analysis to examine linkages between personality and individual specialization.

Examination of behavioral variation may also help us to interpret the within-individual component of niche variation. As outlined in our discussion of niche shifts, the orientation of the **WIC** might bias the direction of a niche shift if this variation reflects the extent of behavioral flexibility of each individual. In the framework we have presented, the **WIC** is treated as a population-level covariance matrix estimated using the average of each individual's variation and covariation in resource use. However, individuals with greater exploratory behavior or activity levels may be more likely to sample novel prey items, potentially leading to between-individual variation in the degree of within-individual variation (Cleasby et al. 2015). While this form of heterogeneity among individuals is missed when **WIC** is calculated as an average, it can be incorporated into hierarchical models if variation in individual niche width is of interest.

the size and shape of the **BIC**. These scenarios should lead to rather different predictions if the **WIC** and **BIC** have very different orientations. We therefore propose the novel hypothesis that the trajectory of a niche shift may

be influenced by the shape of multidimensional niche variation, and be biased toward the 'ecological lines of least resistance' represented in the multivariate niche components **WIC** and/or **BIC** (Fig. 5).

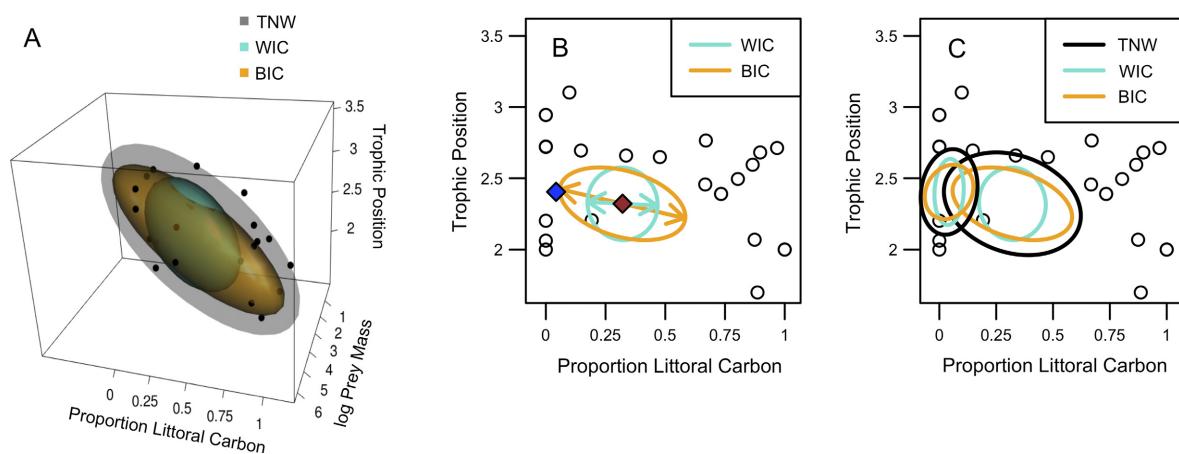


FIG. 5. Multidimensional diet variation in threespine stickleback. (A) three-dimensional niche variation in the proportion of littoral carbon, trophic position, and prey size, represented by standard ellipsoids for a population with both littoral and pelagic prey bases. (B) Niche components **BIC** and **WIC** represented as standard ellipses for the first two dimensions for the same population, with the direction of greatest variation indicated by arrows and the direction of the niche shift (to the "pelagic" enclosed population type) indicated by the blue symbol. (C) Niche components **TNW**, **BIC** and **WIC** for both population types.

To illustrate how niche shifts may align with the shape of niche variation, we analyze data from a field experiment using enclosed populations of threespine stickleback (details in Appendix S1). Stickleback individuals vary in at least two dietary niche dimensions, trophic position and use of pelagic vs. littoral-derived carbon (Matthews et al. 2010, Arnegard et al. 2014). We manipulated habitat availability by building enclosures in habitats with access to littoral and pelagic prey typical of small lakes, as well as enclosures with restricted access to the benthic substrate. This manipulation effectively imposed a niche shift, and the direction of this shift aligned with the direction of greatest between-individual variation in the initial population. The niche shift also resulted in differences in the size and shape of the niche components between populations (Fig. 5, Appendix S1).

These predictions are also relevant for the study of ecological speciation, which occurs when reproductive isolation results in some way from divergent natural selection acting on the ecological niche (Schluter 2009, Nosil 2012). Ecological speciation involves a niche shift by one or both incipient species, and when the niche shift is multidimensional our hypotheses about the influence of the shape of niche components come into play. For example, differences between sympatric stickleback species also tend to align with the direction of greatest between-individual variation in single-species lakes (Matthews et al. 2010). There is theoretical and empirical support for the idea that when multifarious divergent selection acts simultaneously on multiple traits or niche dimensions, speciation is more likely to proceed to completion than when only a single trait is under selection (Rice and Hostert 1993, Nosil et al. 2009, Nosil 2012). This effect can result from increased total strength of divergent selection, or by dimensionality *per se* if selection affects a greater proportion of the genome (Rice and Hostert 1993, Nosil and Sandoval 2008). The number of dimensions in which individuals vary is also predicted to increase the likelihood that some aspect of this variation will be under disruptive selection (Doebeli and Ispolatov 2010), so the shape and size of the multivariate niche components might influence the probability of speciation. Given the central role of individual variation in models of ecological speciation and the likely multifarious selection imposed by divergence on environmental gradients such as water depth or elevation (Doebeli and Dieckmann 2003), understanding the dimensionality of individual specialization should improve our ability to predict when speciation will or will not occur.

#### CONCLUSIONS AND FUTURE DIRECTIONS

The concept of the niche is central to many ideas in ecology and evolutionary biology, and it is now apparent that measurement of niches at the population level often neglects important resource use variation at the individual level. While many niche concepts incorporate multiple ecological dimensions, little consideration has been

given to the dimensionality of individual ecological variation. We have shown how a framework for thinking about individual niches in multiple dimensions can enhance our understanding of a range of ecological and evolutionary concepts, and presented testable hypotheses based on this framework. We conclude by outlining some areas of further research that will help to place the idea of multidimensional individual specialization within a broader understanding of ecology and evolution.

As the niche components **TNW**, **BIC** and **WIC** have not been measured for most species, more data must be collected before we can identify generalities in the structure of multidimensional niche variation. Given more such measures, we can test whether the size and shape of niche components vary among taxa or ecosystems. Methods for comparing sets of variance-covariance matrices, such as eigentensor analysis (Aguirre et al. 2014) could be used to identify regularities in the structure of niche components. We could also analyze niche variation in an explicitly phylogenetic context (Maldonado et al. 2017), extending our hypotheses about niche shifts to multiple related species. If evolutionary divergence between species is constrained or guided by the available intraspecific variation, the matrix of divergence between species is predicted to align with intraspecific phenotypic (**P** or **BIC**; see Box 2) or genetic (**G**) variance-covariance matrices (Felsenstein 1988). We could use a similar approach to test whether among-species divergence can be predicted by the shape of either between- or within-individual ecological variation. In systems with substantial ecological variation among related species, it should be possible to assess the evolutionary history and the current diversity of multivariate niche components, which may then have implications for ecosystem function and coexistence.

For individual specialization to have a significant influence on either evolutionary or population dynamics, it should bear a relationship with some component of organismal fitness. Directional, stabilizing and disruptive natural selection has been measured on a wide range of morphological traits (Kingsolver et al. 2001) and numerous studies have evaluated the fitness consequences of behavioral variation among individuals (Dingemanse and Réale 2005, Smith and Blumstein 2008, Ballew et al. 2017), but attempts to link fitness to more direct measures of the ecological niche are much rarer (Bolnick and Araújo 2011). While the often messy nature of ecological data presents challenges in precisely measuring multivariate selection surfaces, the direct link between resource use and many ecosystem processes makes this a worthwhile goal. Similarly, understanding how multidimensional niche variation relates to the absolute fitness of a species (its population growth) and its relative competitive ability should enhance our understanding of population and community dynamics.

A key issue going forward will be integrating this perspective on multidimensional individual specialization with modern coexistence theory, perhaps by linking

measures of multivariate niche overlap to the strength of stabilizing mechanisms (Letten et al. 2016). Further, a reconciliation of the classical niche theory extended in our multidimensional framework with the treatment of ‘niche factors’ in many modern works (Chase and Leibold 2003) will need to be attempted. Individual variation in the use of different food sources and habitats is unlikely to be independent of measures such as the  $R^*$  that predict population-level resource consumption, though recent theory suggests that individual variation in either univariate resource use or demographic parameters should make coexistence of competitors less likely (Barabás and D’Andrea 2016, Hart et al. 2016). We acknowledge that our framework does not incorporate all current conceptions of the ecological niche, and stress the importance of a broader consideration of the dimensionality of individual niche variation.

Finally, in addition to cataloguing the incidence of individual specialization that encompasses multiple ecological dimensions, both the causes and consequences of multidimensional niche variation will need to be explored in more detail. Experimental studies of the potential drivers of shifts in the extent or shape of niche variation are likely to prove fruitful in identifying the causal factors and assessing how rapidly niche components change. It is not yet certain to what extent aspects of the shape of niche variation such as orientation or eccentricity may impact ecological or evolutionary processes, relative to the niche position or the overall degree of niche variation. Theoretical work in this direction, coupled with direct manipulation of the dimensionality of variation among individuals in suitable systems, should help us to understand the importance of the dimensionality of individual niche variation.

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TI proposed the manuscript topic; TI and RCP carried out the analyses for the case studies; TI and MSA wrote the first draft of the manuscript collaboratively, and TI, RCP and MSA contributed to revisions.

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