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A multivariate approach reveals diversity of ontogenetic niche shifts across taxonomic and functional groups

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Abstract

1. Shifts in the fundamental and realised niche of individuals during their ontogeny are ubiquitous in nature, but we know little about what aspects of the niche change and how these changes vary across species within communities. However, this knowledge is essential to predict the dynamics of populations and communities and how they respond to environmental change.
2. Here I introduce a range of metrics to describe different aspects of shifts in the realised trophic niche of individuals based on stable isotopes. Applying this multivariate approach to 2,272 individuals from 13 taxonomic and functional distinct species (Amphibia, Hemiptera, Coleoptera, Odonata) sampled in natural pond communities allowed me to: (1) describe and quantify the diversity of trophic niche shift patterns over ontogeny in multi-dimensional space, and (2) identify what aspects of ontogenetic shifts vary across taxa, and functional groups.
3. Results revealed that species can differ substantially in which aspects of the trophic niche change and how they change over ontogeny. Interestingly, patterns of ontogenetic niche shifts grouped in distinct taxonomic clusters in multi-variate space, including two distinct groups of predators (Hemiptera versus Odonata). Given the differences in traits (especially feeding mode) across groups, this suggests that differences in ontogenetic niche shifts across species could at least partially be explained by variation in traits and functional roles of species.
4. These results emphasise the importance of a multivariate approach to capture the large diversity of trophic niche shifts patterns possible in natural communities and suggest that differences in ontogenetic niche shifts follow general patterns.

KEYWORDS
body size, individual variation, intraspecific diversity, ontogeny, trophic niche

1 | INTRODUCTION

Identifying the patterns and processes that determine the trophic niche of individuals is essential to understand their ecological role in a community and how communities are structured (Duffy et al., 2007; Hutchinson, 1957). While the niche has traditionally been treated as a species trait, recent studies emphasise the importance of intraspecific niche variation within species (Bolnick et al., 2011; Miller & Rudolf, 2011; Violle et al., 2012). A large source of this intraspecific variation stems from differences in ontogenetic (developmental) stage: as individuals grow and develop, they typically also change their diet, habitat use, and morphology (Nakazawa, 2015; Polis, 1984; Sánchez-Hernández, Nunn, Adams, & Amundsen, 2019; Werner & Gilliam, 1984; Zhao, Villéger, Lek, & Cucherousset, 2014). As a consequence, ecological differences between stages within species can rival or even exceed differences between species (Polis,

1984; Rudolf & Rasmussen, 2013b; Rudolf, Rasmussen, Dibble, & Van Allen, 2014). Importantly, the type and strength of these ontogenetic niche shifts within species determine the functional role of a species in the ecosystem (Rudolf & Rasmussen, 2013a), the dynamics of populations and communities (De Roos & Persson, 2002; Miller & Rudolf, 2011; Persson et al., 2003; Schellekens, De Roos, & Persson, 2010; Takimoto, 2003; Toscano, Rombado, & Rudolf, 2016), and stability of ecological networks (Rudolf & Lafferty, 2011). To understand how ontogenetic niche shifts influence natural communities, we first need to understand how these shifts vary among species within communities. However, we know surprisingly little about the general patterns of ontogenetic niche shifts across species.

While ontogenetic niche shifts are clearly ubiquitous in nature, they also appear highly variable across species and environmental conditions (Costa-Pereira, Rudolf, Souza, & Araújo, 2018b; Hammerschlag-Peyer, Yeager, Araújo, & Layman, 2011; Kimirei et al., 2013; Rudolf & Lafferty, 2011; Sánchez-Hernández, Eloranta, Finstad, & Amundsen, 2017; Sánchez-Hernández et al., 2019). How much of this variation reflects differences in the life history, traits, or morphology of species versus differences in study system, environmental context, or methods used to measure niche shifts? To answer these questions, it is important to capture the full complexity and diversity of ontogenetic niche shifts patterns. For example, diets of earlier stages could be more variable and less restricted than those of later stages or vice versa (i.e. trophic niche contracts or expands over ontogeny) (Hammerschlag-Peyer et al., 2011; Zhao et al., 2014), and diets could shift (turnover) gradually over ontogeny or change abruptly (Werner & Gilliam, 1984).

Which aspects of the trophic niche change and how dramatic this change is (i.e. magnitude of change) probably depends on species' traits (Werner & Gilliam, 1984). For instance, because larger individuals can consume larger prey, the trophic position of individuals often increases over ontogeny (vertical niche shift) (Woodward et al., 2005). However, some predators are more gape limited than others (e.g. predators that pierce versus engulf prey). Such differences in morphology (feeding mode) could alter how body size scales with the ability to consume larger prey (Klecka & Boukal, 2013; Nakazawa, Ohba, & Ushio, 2013), and thus how the trophic niche changes over ontogeny. Similarly, in species where the diet is not strongly restricted by their size (e.g. large consumers specialised on small prey [filter feeders], herbivores, or detritivores) we would not necessarily expect a shift in trophic (vertical niche) position. However, they may still shift resources (e.g. due change in micro-habitat use) within a given trophic level (horizontal niche shift). In these species, *individual variation* (e.g. due to genetic differences) (Bolnick et al., 2003) may exceed variation among stages and potentially even decouple ecological differences from morphological variation (Ingram, Stutz, & Bolnick, 2011). If the latter scenario is common among species, ontogenetic differences are unlikely to explain much of the functional variation and niche differences within species. If traits indeed play a key role, then the nature and strength of ontogenetic niche shifts should differ predictably across functional and taxonomic groups with differences in traits. However, testing this hypothesis has been challenging, in part because of methodological challenges that arise when comparing taxa that differ substantially in their morphology, development, and ecology. However, making these comparisons is essential to determine whether there are systematic differences in ontogenetic niche shifts within and across ecosystems.

Here I propose and apply a new multi-variate approach to examine patterns of ontogenetic niche shifts across functionally and taxonomically diverse set of species based on stable isotopes. Specifically, I calculated a set of metrics based on stable isotopes to describe how different aspects of the trophic niche of individuals changes during the ontogeny of consumer species. This approached allowed me to (1) describe and quantify diversity of trophic niche change patterns over ontogeny in multi-dimensional space, and (2) identify what aspects of ontogenetic shifts vary across taxa and functional groups. Results indicate a rich diversity of ontogenetic niche shifts patterns across species, but differences fell in predictable patterns across taxonomic and functional groups.

2 | METHODS

2.1 | Quantifying ontogenetic niche shifts using stable isotopes

The diet of consumers is a frequently used metric to identify functional differences among organisms because it indicates the trophic niche of individuals and is directly linked to the structure of food webs. However, measuring such differences in resource use is challenging, particularly when comparing consumers that differ substantially in size, feeding mode, and diets. For instance, while gut content analysis has been successfully used in predatory species (e.g. Post, 2003; Sánchez-Hernández et al., 2017; Woodward & Hildrew, 2002), this approach cannot be applied to consumers with sucking mouth parts, or when diet items cannot be recognised. This makes it infeasible to compare diet variation in predators with different feeding modes or to predators versus herbivores or detritivores. However, technological and statistical advances now allow us to use stable isotopes to quantify some of the fundamental characteristics of the trophic niche space occupied by species and even communities (Bearhop, Adams, Waldron, Fuller, & Macleod, 2004; Newsome, del Rio, Bearhop, & Phillips, 2007). While not without their own limitations, stable isotopes have been particularly useful in this context because they are tightly linked to diet. The ratio of heavy to light stable nitrogen isotope ($\delta^{15}N$) increases in a stepwise fashion with the trophic level of an organisms, while stable carbon isotopes ($\delta^{13}C$) primarily reflect the $\delta^{13}C$ in a consumer's diet (i.e. you resemble what you eat). Importantly, the variance in $\delta^{13}C$ and $\delta^{15}N$ isotope ratios among individual consumers can then be linked qualitatively to variation in the diet among individuals and thus represents an integrated measure of the trophic niche width of a species (Bearhop et al., 2004; Newsome et al., 2007).

This stable isotope approach is particularly useful for estimating the ontogenetic differences in the trophic position of species

(Hammerschlag-Peyer et al., 2011; Sanders, Vogel, & Knop, 2015; Zhao et al., 2014). Variation in stable isotopes signatures among individuals are closely related to estimates of diet variation from gut contents, but stable isotopes are often more sensitive (Araujo, Bolnick, Machado, Giaretta, & dos Reis, 2007; Quevedo, Svanback, & Eklov, 2009) and can be used to compare organisms with very different feeding modes (sucking versus chewing) and diets (e.g. predator versus herbivore). Importantly, stable isotopes change fast enough during development to quantify differences in diets among stages. Indeed, stable isotopes have been successfully used to capture ontogenetic changes in diet and trophic position of individuals and how it relates to consumer body size (e.g. Hentschel, 1998; Jennings, Pinnegar, Polunin, & Boon, 2001; Post, 2003; Power, Power, Caron, & Doucett, 2002; Xu, Zhang, & Xie, 2007). Finally, by measuring isotopic ratios across the full range of developmental stages of a consumer, I can extend current approaches for individual specialisation (Bearhop et al., 2004; Bolnick et al., 2003) and community niche metrics (Layman, Arrington, Montana, & Post, 2007) to calculate a complementary set of metrics that describe different aspects of how resource use differs across stages (Table 1). This allows me to identify general patterns of ontogenetic niche shifts across species with different feeding modes, morphologies, and trophic positions.

2.2 | Metrics for quantifying ontogenetic niche shifts

To estimate how ontogenetic stages of a consumer differ in their trophic niche, I used six quantitative metrics calculated from the variation in the $\delta^{15}N$–$\delta^{13}C$ signature of individuals from different stages (Table 1). Several of these metrics were originally used to describe entire communities with species as the reference points (Layman et al., 2007). I modified and applied them at the population level, where species represent *communities* and individuals within stages represent the measurement subunits. Rather than estimating the exact diets of individuals with stable isotopes (e.g. using mixing models (Phillips, Newsome, & Gregg, 2005)), this approach uses the variation in stable isotope ratios among individuals to calculate the metrics. This allowed me to use relative comparisons among species within communities while bypassing many of the methodological concerns associated with estimating niche width from individual diets based on mixing models (Matthews & Mazumder, 2004).

Each metric is aimed to look at different aspects of ontogenetic niche shifts. For instance, *SEAc* indicates how the trophic niche changes over ontogeny (e.g. whether it systematically expands or contracts), and its overlap between stage pairs (*P*) indicates overlap in resource use among stages (*P*), and *TS* determines how important size is for ontogenetic shifts in the trophic position of individuals. By comparing these coefficients across species and communities, we can identify how consistent ontogenetic niche shifts are across different species and different environmental conditions. Finally, using a range of metrics increases our ability to (a) detect ontogenetic niche shifts, (b) quantify how different aspects of the trophic niche of individuals (and thus their functional role) changes during ontogeny, and (c) determine how these patterns differ across species.

The standard ellipse area corrected for sample size of a given stage (*SEAc*) combines information from $\delta^{13}C$ and $\delta^{15}N$ values. This metric allows for an unbiased and robust comparison across data with different sample sizes (Jackson, Inger, Parnell, & Bearhop, 2011). All sample sizes in this study were above the minimum recommended for this method for all stage and species combinations. I calculated niche overlap (*P*) as the area of overlap of the *SEAc* of two stages within a given species. This was repeated for all stage pair combinations for each species.

TABLE 1 Metrics to describe different aspects of ontogenetic niche shifts within species, see Figure 1 for examples

Metric	Calculation details	Interpretation
SEAc	Standard ellipse area (SEA) of a stage corrected for sample size	Information on the trophic niche width of a stage
P	Average proportional overlap in SEA among consumer stages	Estimates average trophic niche overlap among consumer stages (= inverse of niche differences)
TS	Scaling coefficient of size versus $\delta^{15}N$	Information on whether and how trophic position scales with consumer size
TR	$\delta^{15}N$ range between average (centre of SEA) $\delta^{15}N$ of largest and smallest stage	Information on the total change in trophic position during ontogeny
DV	Variation (r^2) in $\delta^{13}C$ within a population explained by differences in stage	Information on how much of the diversity in resource use can be explained by consumer stage
DR	Maximal $\delta^{13}C$ range between average (centre of SEA) $\delta^{13}C$ of ontogenetic stages	Information on how much of the diet range can be explained by consumer stage
HA	Total area of convex hull encompassing all stage centroids	Information on total niche space occupied by stages of a consumer (ontogenetic trophic diversity)

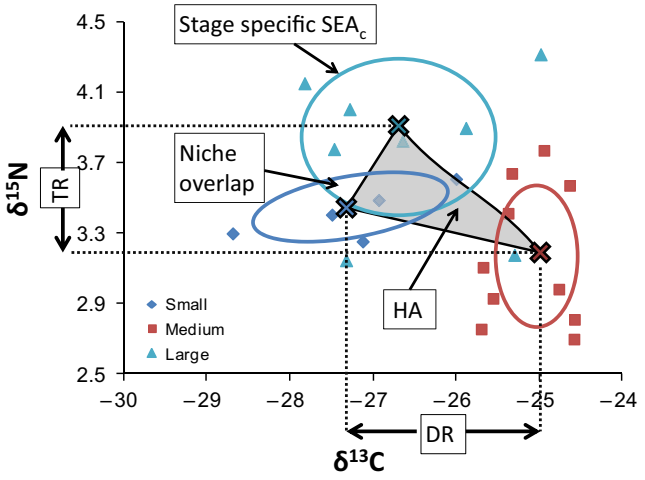

FIGURE 1 Example of how stable isotopes were used to calculate several metrics in Table 1 for quantifying ontogenetic functional diversity. Symbols represent stable isotope combinations of field-collected individuals in three different stages of *Notonecta* (x = ellipse centre) [Colour figure can be viewed at wileyonlinelibrary.com]

Note that *P* can be seen as an multi-stage expansion of the niche overlap metric calculated by Hammerschlag-Peyer et al. (2011), but it is based on the overlap in SEAc (instead of hull) and thus more robust to sample size and outliers. The hull area (*HA*) for a given species is the total hull area that includes the centroids of all stages (see Figure 1). All three metrics were calculated using the *SIBER* package in R (Stable Isotope Bayesian Ellipse in R) (Jackson et al., 2011).

The trophic scaling (*TS*) metric indicates how δ^{15}N scales with dry mass of consumers. A positive or negative value indicates whether trophic level increases or decreases with body size over ontogeny respectively, and the magnitude indicates how rapidly this change occurs along a size gradient. I first used general linear mixed model (GLMM) with δ^{15}N as dependent variable and dry mass, species identity and their interaction as fixed predictors, and sample location (pond) as random factor to test how trophic position scales with size and whether this relationship varies across species. I then extracted the species-specific regression coefficient for each species to obtain the *TS* metric.

The *DV* metric is based on δ^{13}C and provides information on how much of the variation in diet can be attributed to variation in ontogenetic stage. Unlike δ^{15}N, there is no clear expectation how δ^{13}C should change with size or developmental stage. Thus, I used δ^{13}C as dependent variable, and stage (see cluster analysis above) as categorical fixed factor instead of body size. I tested for significant effect of ontogenetic stage and species and their interaction with sample location as random effect using GLMM. I then extracted the explained variance (*DV*) from the model using the *broom* package in R (Robinson, 2014).

I performed all GLMM analyses in R with the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015) and the *car* package (Fox & Weisberg, 2011) to test for significance of main effects using Wald χ^2 statistics and type II tests. If a given species was sampled at multiple locations (ponds), I calculated the respective metrics for each location separately. Finally, to visualise differences in ontogenetic trophic niche pattern across species, I used NMDs ordination based on all size metrics outlined above (Table 1). To account for differences in units, metrics were standardised to a range between 0 and 1. Ordination was based on Euclidean distance matrix using the *vegan* package in R (Oksanen et al., 2012).

2.2.1 | Ontogenetic stages

Ontogenetic stages are challenging to determine and even more challenging to compare across species. However, several metrics and comparisons outlined above are group metrics and thus require distinct stages. Traditionally, ontogenetic stages are classified based on body morphology, ecology, or age/size. Furthermore, when comparing a wide range of taxa, species naturally differ in what qualifies as a change in morphology. For instance, tadpoles are often classified along a gradient of small morphological changes, while insects are often classified by moults (instars) which can vary dramatically across taxa and even within taxa (e.g. three moults in diving beetle larva versus five moults in backswimmer versus 11–15 in dragonfly larvae). Such differences would inherently bias any comparisons across species and confound our metrics with species specific differences in life histories. Thus, to make comparisons across species possible, I used a simple but ubiquitous metric: size (i.e. dry mass). Within a given environment, dry mass is generally well correlated with age and stage as individuals develop and grow (although there can be considerable variation under some conditions). Using this relationship, we can then sort individuals by mass and divide them into equal number of groups (= stages) across species (Figure S1).

Using these groups to calculate the metrics outlined above allows us to compare patterns of ontogenetic niche shift across species using on common criteria regardless of taxonomy. Note, that this method is scaled to the size range of a given species. Thus, it is important that we capture the whole life cycle with full size/ stage range of a given species to make unbiased comparisons. For the species used here, this grouping method adequately describes developmental stages and also captures big jumps (e.g. between instars) that can occur in some species (Figure S1). Note, absolute values of metrics (Table 1) need to be interpreted carefully since they depend on the absolute number of groups chosen for a given study. Instead, the focus should be on relative differences across species which is generally robust and independent of the number of groups chosen. Based on the natural history of species, I present results based on five groups/stages, which provided the best fit to capture natural *stage* differences across very different species and provided enough resolution to detect differences. Using different group sizes (3–7) did not change the results qualitatively (see Results), indicating that the results present here are robust to specific assumptions.

2.3 | Study species

The goal of the study was to compare patterns of ontogenetic niche shift across a broad range of species. For this purpose, I focused

on species that were abundant, co-occurred, and had overlapping cohorts so that all developmental stages were present at the same time. Collecting all developmental stages at the same time assured that differences in stable isotope signatures were not driven by changes in environmental conditions over time (e.g. abiotic conditions or community composition). I identified 13 species that met these criteria, including three tadpole species (three genera, two families: *Hyla versicolor*, *Acris crepitans*, and *Rana* (*Lithobates*) *sphenocaphala*), four predatory hemipteran species (four genera, three families: *Notonecta indica*, *Buenoa scimitar*, *Belostoma sp.*, *Pelocoris sp.*), larvae from five dragonfly species (five genera, one family: *Erythemis simplicicollis*, *Libellula incesta*, *Plathemis lydia*, *Pachidiplax longipennis*, *Tramea carolina*), and one predatory beetle species (*Cybister fimbriolatus*). All species differ considerably in their biology, including life histories, habitat use, behaviour, feeding mode, and body morphology across and within orders, allowing me to examine ontogenetic niche shifts across diverse set of species. Mean and range of dry mass for each species are shown in Figure 2 and cover up to >3 orders of magnitude from smallest to largest individual (0.017 to 38 mg). Note that all species have a terrestrial part of their life cycle, but here I only focus on the aquatic habitat where all stages have access to the same resources and are part of the same community.

2.4 | Sample collection

I collected 2,272 individuals from 13 species from three locations (ponds) in South East Texas: Nick's Pond in Steven F. Austin Experimental Forest (31.509376, −94.761019), DC108-1 in Davy Crocket National forest (31.20547196, −94.99097256) and New Pond at CBFS of Sam Houston University (30.746377, −94.473880). All ponds are fish free, but only the last two are permanent (i.e. never dried out completely in past 10 years) while Nick's Pond is temporary and dries out every year.

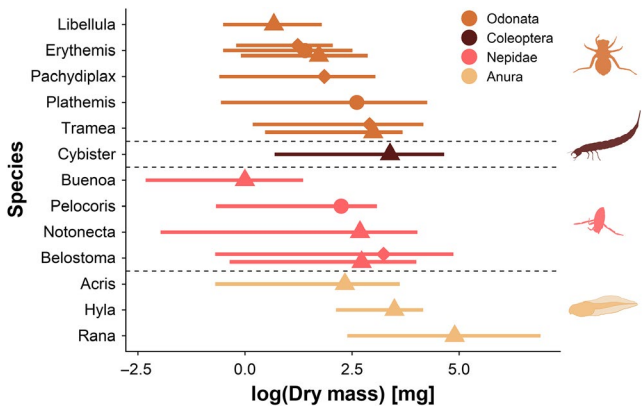

FIGURE 2 Mean and full size range of individuals from 13 different species used in stable isotope analyses. Colours indicate taxonomic group, different symbols represent one out of three sample locations. Note that some species were collected from multiple sites. Dashed lines indicate transitions between taxonomic groups [Colour figure can be viewed at wileyonlinelibrary.com]

All individuals of a species at a given site were collected during a single day or within 2-week period depending on their respective abundances. Overall, I found no systematic influence of sample date on the relationships between body size and stable isotopes. Consequently, I pooled dates within a given location. All but three species were collected from the same site (DC 108-1), and three species were additionally collected from one or two other sites (Figure 2). Details for locations and collection dates are given in Table S1.

2.5 | Sample preparation

Collected individuals were immediately frozen and stored at −33°C until further processing. I first photographed each individual and used Image J to measure body length. Individuals were dried at 65°C for 72 hr, allowed to cool off in an airtight desiccation chamber before they were weighed to obtain dry mass. All samples were analysed by the UC-Davis Stable Isotope Facility following their standard preparation guidelines. Individuals larger than 1.2 mg were homogenised with an amalgamator to obtain *c.* 1 mg sample for the isotope analysis. I used whole body samples, as it is infeasible to obtain sufficient mass of specific tissues (or body parts) for most size classes. Following previous studies (Sanders et al., 2015), we combine multiple individuals (two to 10 depending on species) of similar weight of the very smallest sizes to get the minimum total dry mass necessary for stable isotope analysis, and used average mass for all further analyses. This was done for 268 out of 1,603 samples. Pooling multiple individuals will not change metrics based on stage means (besides increasing confidence due to larger sample size), but could reduce intra-stage variation and related metrics (e.g. SEAc). However, inspection of stage-specific variance showed that variation in first stage that included pooled individuals was not consistently smaller than variation in any other staged (see Results). Furthermore, there was no correlation between *SEAc* and mean number of individuals pooled per sample (Kendall's rank correlation tau = −0.015, p = 0.9342), indicating that variance in isotopes was not reduced by pooling individuals. Isotope rates for C and N were obtained simultaneously and reported in δ units and used to calculate all metrics in Table 1. All procedures were in compliance with ethical guidelines for animal use and approved by the Institutional Animal Care and Use Committee (IACUC Protocol no. A09022601).

3 | RESULTS

3.1 | Change in trophic level over ontogeny

The trophic level, indicated by $\delta^{15}N$, differed across species (χ^2 = 1,317.02, p < 0.0001) and generally changed with dry mass (χ^2 = 88.25, p < 0.0001), but the magnitude and even direction of this relationship between body mass and trophic level (*TS*, Table 1) was highly species specific (species*dry mass: χ^2 = 973.20, p <

0.0001). Out of the 13 species, six species showed a positive scaling relationship (indicating increase in trophic position with size/stage), while the remaining species either showed no clear directional relationship, or even a negative trend, indicating a decrease in the trophic level with size over their ontogeny (Figure 3, Figure S2). Only predators (but not all predators) increased in trophic position with body mass, while tadpoles showed either no, or a weak negative trend.

Trophic range (*TR*) varied considerably across and within functional groups but was on average lowest in dragonfly and beetle species (Figure 3). Trophic range was only very weakly positively correlated with trophic scaling (Figure 3, Figure S8), indicating that species with a relatively narrower total *TR* can still experience a higher shift in trophic position over ontogeny than species with wider trophic range (e.g. *Buenoa* versus *Notonecta*). It also indicates that both measured very different aspect of ontogenetic niche shifts.

3.2 | Variation in diet composition and across stages

Diet (measure via $\delta^{13}C$) of individuals varied across species (χ^2 = 1,899.10, $p < 0.0001$) and developmental stages (χ^2 = 44.63, $p < 0.0001$, Figure S3). However, how much of the intraspecific variation could be explained by differences in developmental stage was contingent on species identity (species*stage interaction: χ^2 = 229.67, $p < 0.0001$), ranging from as little as 5% up to as much as 43% (Figure 4). Differences between stages were largest in two of the three herbivore species, indicating that $\delta^{13}C$ ratio can change just as much or even more in herbivores than in predators in this system. Within species, variation in diet across stages also differed across sites (Figure 4). Absolute range in $\delta^{13}C$ (*DR*) was positively correlated with *DV* and largely followed the same patterns, with some notable exceptions. *DV* but not *DR* varied across sites in *Erythemis*, while *Pelocoris* had a wide diet range (*DR*), but stage identity explained little of the total difference across individuals, probably due to large variation within stages (Figure 5).

3.3 | Stage-specific trophic niche width and niche overlap between stages

The *SEAc*, a metric for trophic (isotopic) niche width of a given species in the $\delta^{13}C$ and $\delta^{15}N$ space, varied substantially across species (χ^2 = 204.28, $p < 0.0001$), ranging from *SEAc* = 0.488 (*Tramea*) to *SEAc* = 6.190 (*Pelocoris*). Standard ellipse area was generally larger in nepid predators and smallest in dragonflies (Odonata). Standard ellipse area also differed across stages but this difference was species specific (species–stage interaction: χ^2 = 95.76, $p < 0.0001$; Figure 5). Some species such as the diving beetle (*Cybister*) or dragonfly larvae (*Libellula*), showed very similar *SEAc* across stages, while others, such as the nepid predators *Pelocoris* and *Notonecta*, showed up to 3-fold differences in *SEAc* between stages. Overall, the size of *SEAc* did not change consistently across stages (χ^2 = 7.04, p = 0.134), i.e. the final stage could have the largest, intermediate, or smallest trophic niche depending on species identity (Figure 5).

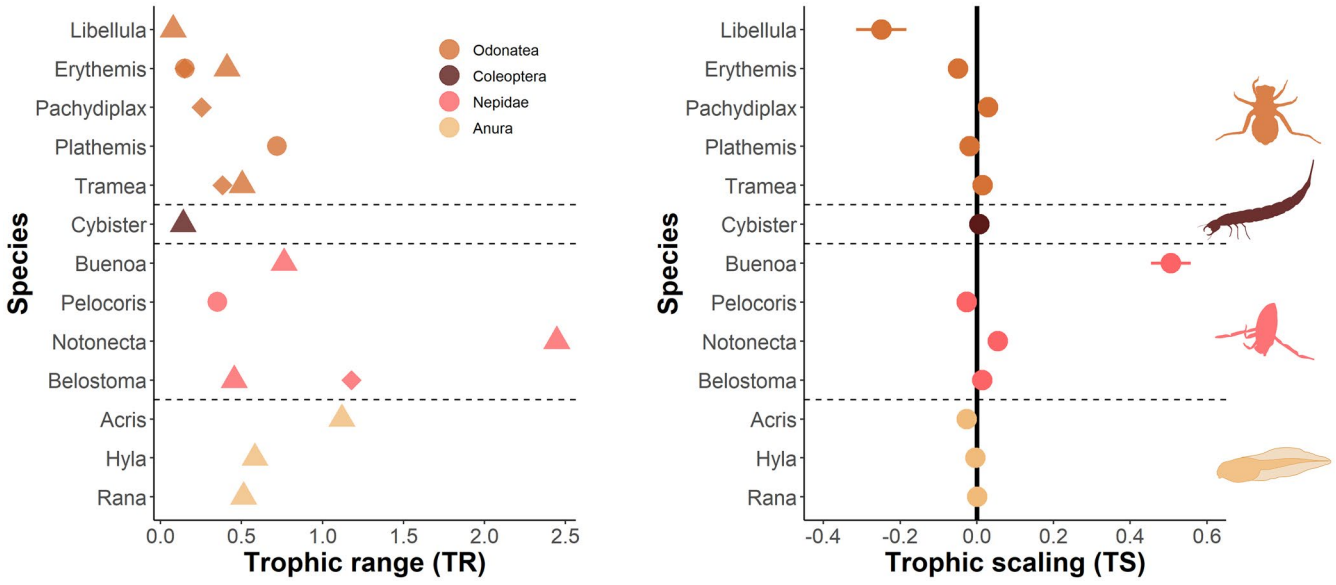

FIGURE 3 Differences in trophic range (*TR*) and trophic scaling (*TS*) across taxa. *TR* indicates largest differences in trophic height ($\delta^{15}N$) across stages. *TS* indicates how trophic height changes with dry mass of individuals within a given species, positive values indicate positive slope and this increase in trophic height with size, negative values indicate a decline. Colour indicates taxonomic groups, and symbol shapes represent three different sample locations. *TS* values show species specific mean (±1*SE*) model estimates while accounting for differences in sample location. See methods and Table 1 for more details on metrics [Colour figure can be viewed at wileyonlinelibrary.com]

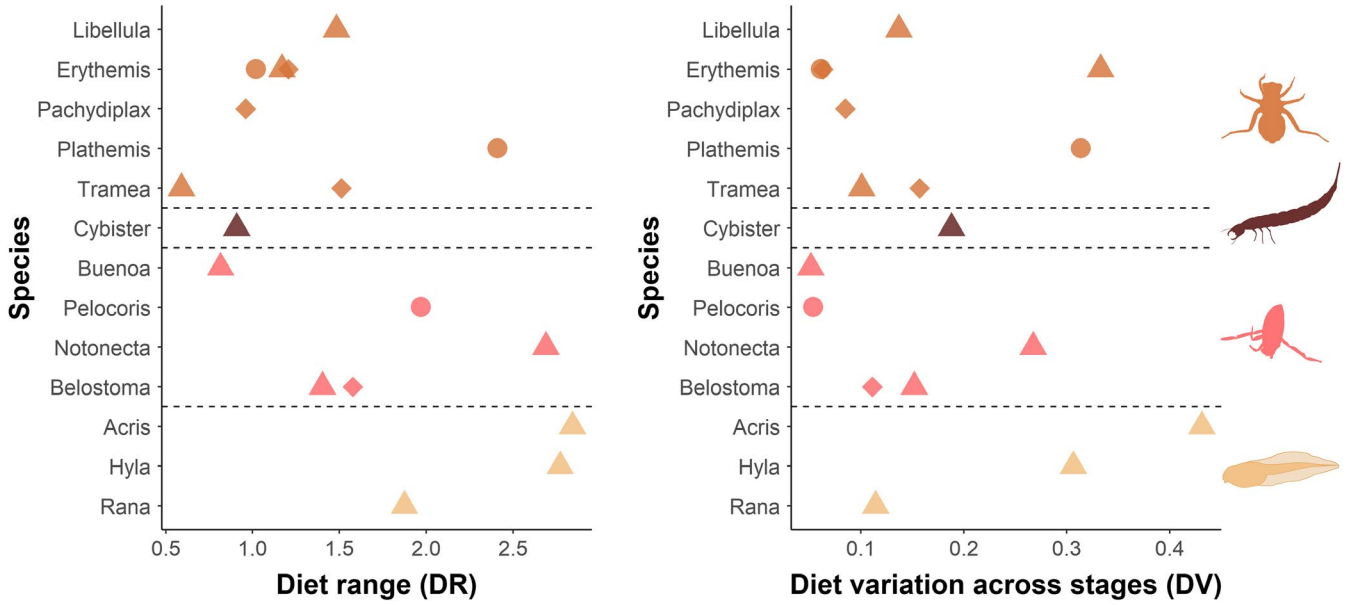

FIGURE 4 Differences in diet range (*DR*) and diet variation (*DV*) across taxa. *DR* indicates largest differences in $\delta^{13}C$ across stages. *DV* indicates how much of variation in $\delta^{13}C$ across individuals within a species can be explained by stage identity. See Table 1 and methods for more details on each metric. Colour indicates taxonomic groups, and symbol shapes represent different sample locations [Colour figure can be viewed at wileyonlinelibrary.com]

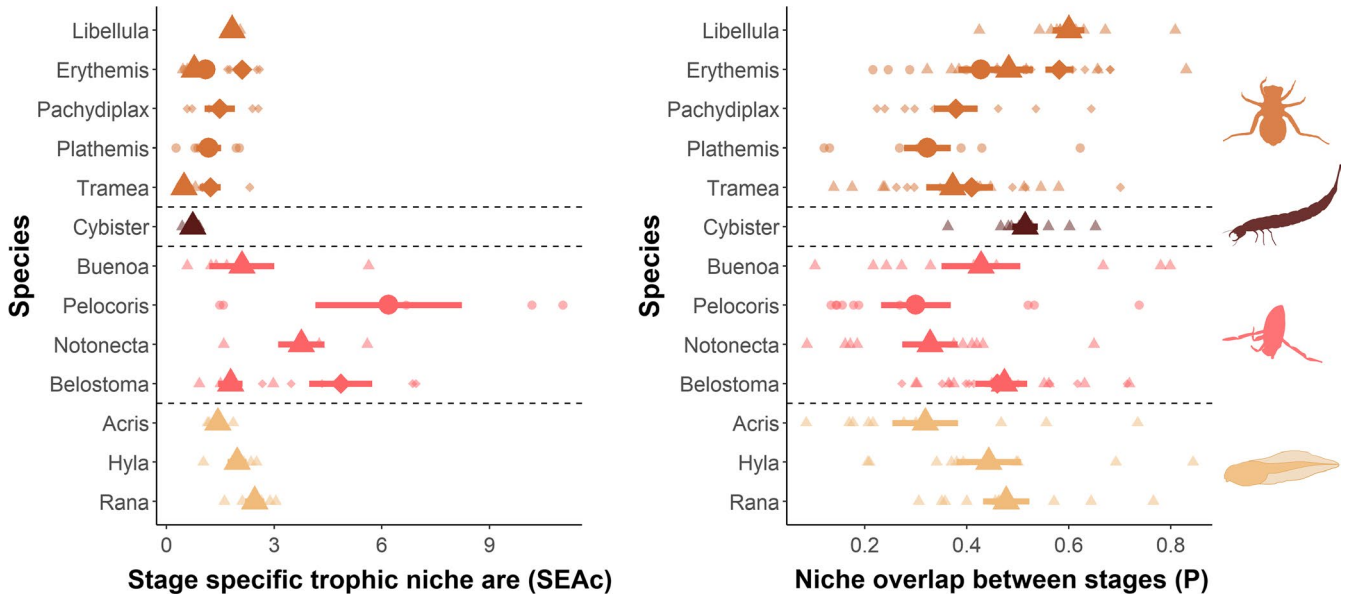

FIGURE 5 Stage-specific trophic niche (standard ellipse area, *SEAc*) and overlap in trophic niche (*P*) for 13 different species. Large symbols indicate mean values (±1 *SE*) averaged across all stages within a given species (small symbols). Colours indicate taxonomic groups, and symbols represent different sample locations. See Table 1 and methods for more details on metrics [Colour figure can be viewed at wileyonlinelibrary.com]

Trophic niche overlap (*P*, the inverse of niche differences) across stage, ranged from 30 to 60% on average across species. The niche overlap of stage pairs could vary substantially (Figure 5). For instance, in *Pelocoris*, the trophic niche (*SEAc*) of the final stage was completely nested within the niche of stage 2, while the niche of the final stage in backswimmer (*Notonecta*) did not overlap (i.e. stage specific $p = 0$) with any another stage (Figure S4). Across all species, niche overlap decreased with increasing difference in size/stage across species ($\chi^2 = 18.40$, $p < 0.0001$, Figure S5), but the strength of this relationship was again species specific (species–stage interaction: $\chi^2 = 27.33$, $p = 0.007$) (Figure S6).

3.4 | Trophic niche diversity

The *HA* given by the centroids of each stage-specific ellipse indicates the ontogenetic *trophic diversity* within a species (see methods, Figure 1, Table 1): A relatively small area would indicate that

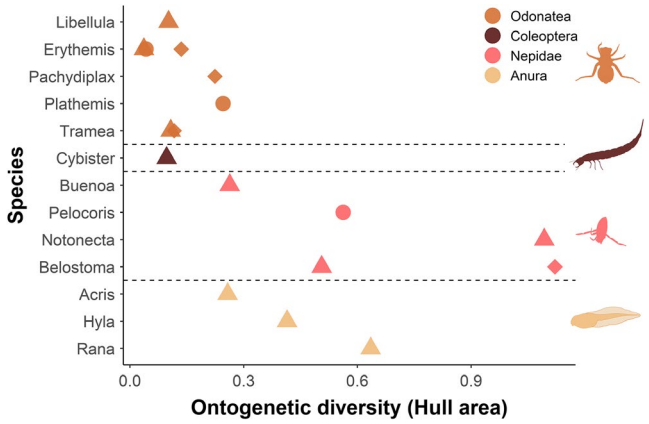

FIGURE 6 Ontogenetic trophic niche diversity indicated by hull area (*HA*) across 13 species. Small area indicates very similar trophic niches of stages within species. See Table 1 for details on *HA*. Colours indicate taxonomic groups, and symbol shapes indicate locations [Colour figure can be viewed at wileyonlinelibrary.com]

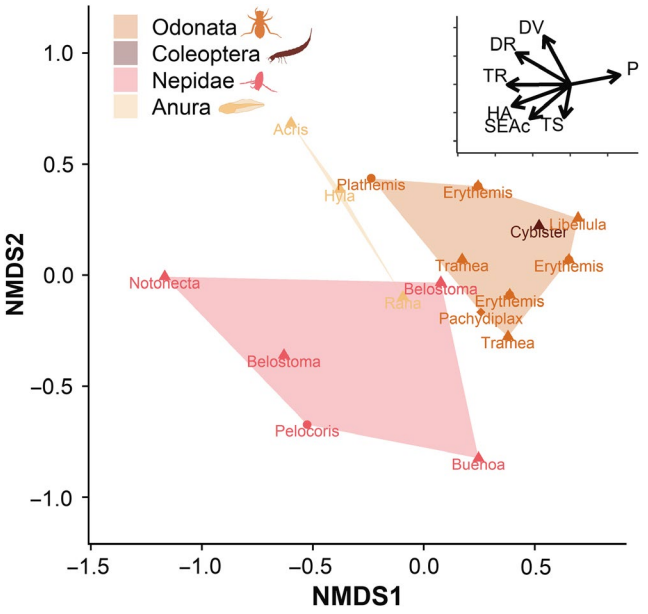

FIGURE 7 Locations of 13 species in multivariate space based on seven ontogenetic niche shift metrics (Table 1). Colours indicate taxonomic groups, and symbols different locations. Hull areas include all species within a given taxonomic group with more than one species. Insert shows vector loading (relative importance) for each standardised ontogenetic niche shift metric (Table 1) in relation to the two non-metric multidimensional scaling (NMDS) axes. NMDS Stress = 0.153 [Colour figure can be viewed at wileyonlinelibrary.com]

the trophic (isotopic) niche is similar across stages, while a larger area would indicate that each stage occupies a distinct trophic niche (Figure S7). Overall, species varied in ontogenetic diversity (*HA*); dragonfly predators had generally smaller *HA* than herbivorous tadpoles, and predatory Nepidae showed the largest differences in trophic niche across stages (Figure 6, Figure S7).

3.5 | Multi-variate patterns of ontogenetic niche shifts across species

Most traits of the ontogenetic niche shifts very only weakly (or un-) correlated with each other (16 out 21 possible pairwise trait correlations were not significant [before adjusting for multiple comparisons]) Figure S8). Furthermore, all ontogenetic niche shift metrics showed either no or only very weak correlations with any species-level body size metrics (i.e. mean-, maximum-, or minimum-dry mass of a species; Table S2).

Combining all ontogenetic niche metrics (Table 1) into a multi-variate analysis revealed a diversity of ontogenetic niche shift patterns across species that would not be apparent when using just a single metric (Figure 6). Furthermore, species clustered into distinct, largely non-overlapping taxonomic/functional groups. Tadpole species generally showed more differences in diet (δ^{13} C) than predators (i.e. large *DV*, *DR*). Predators were largely split in two non-overlapping groups: one group that included all nepid species, and one group that included all odonate species and the only beetle species. The first predator group (Nepidae) exhibited low niche overlap between stages (low *P*), largely driven by large changes in trophic height (*TS*, *TR*), and showed more individual variation within stages (*SEAc*), while the other predator group (Odonata) showed high overlap among stages (high *P*), small trophic range shifts (*TR*,*TS*) and more diet variation across stages (*DV*) (Figure 7). This general pattern was robust and not influenced by cluster size (i.e. number of stages) (Figure S9).

4 | DISCUSSION

Ontogenetic niche shifts are ubiquitous in nature, but we know little about how they differ across species. However, this knowledge is essential to predict the dynamics of populations and communities, and how they respond to environmental change (Miller & Rudolf, 2011; Nakazawa, 2015; De Roos & Persson, 2013; Rudolf & Rasmussen, 2013a). By taking a multi-variate approach, I revealed that species can differ substantially in which aspect of the trophic niche changes and how it changes during ontogeny. Interestingly, species still fell within distinct taxonomic groups in multivariate space. Overall, these results emphasise the diversity of ontogenetic niche shifts possible in natural communities, and suggest that differences in phylogeny, traits, and functional roles could help explain variation across species in natural communities.

4.1 | Diversity of ontogenetic niche shifts patterns

Thirty-five years ago, Werner and Gilliam (1984) reviewed the concept of ontogenetic niche shifts, pointing out that ontogenetic niche shifts are ubiquitous and important, yet were largely ignored in community ecology. Importantly, the authors also emphasised early on that the patterns of ontogenetic niche shifts vary across species. Consistent with this observation, I found that patterns of niche shifts varied substantially across species. As expected, I found that niche overlap (inverse of degree of niche shift) generally declined

with increasing stage/size differences across species, but this trend varied considerably across species and could even be completely absent. Similar differences in niche overlap have been highlighted in fish (Hammerschlag-Peyer et al., 2011). Such differences in niche overlap have important consequences for a population dynamics (Miller & Rudolf, 2011; Nakazawa, 2015) and its extinction risk (Rudolf & Lafferty, 2011).

Although important, niche overlap is only one aspect of an ontogenetic niche shift. By taking a multi-variate approach, I found that ontogenetic niche shifts are complex and can differ in more than just one aspect and how these aspects are related to each other. Using more complementary metrics inherently provides more information and therefore also more power to identify differences in ontogenetic niche shift patterns that would be missed otherwise. For instance, some species showed little difference in some traits, but big differences in other traits (e.g. x versus y axis in Figure 7).

The multi-variate approach also allows one to test predictions and identify potential trade-off or constraints of ontogenetic niche shifts. If ontogenetic niche shifts are driven by constraints or trade-offs, we might expect strong positive or negative correlations among certain niche shift traits. For instance, it has been suggested that specialist species should show a lower degree of ontogenetic niche shifts compared to generalists (Hammerschlag-Peyer et al., 2011; Werner & Gilliam, 1984). In contrast, I found that species with large stage-specific trophic niche (*SEAc*, indicating more intra-stage trophic niche variation) typically also had higher ontogenetic niche diversity (*HA*) and lower niche overlap among stages. Thus, species that would be considered generalist were not more likely to share resources across stages than more specialised species in this system. Furthermore, most traits of the ontogenetic niche shifts very only weakly (or un-) correlated with each other. These results do not support the idea of strong constraints or trade-offs. Instead they emphasise the (largely unexplored) diversity of ontogenetic niche shifts patterns possible in natural communities.

4.2 | Ontogenetic niche shifts, functional groups, and species traits

Trait differences across species are increasingly used to describe differences in their niches (e.g. location and/or dimensions in multivariate space) (McGill, Enquist, Weiher, & Westoby, 2006), including trophic (isotope) niches (Fitzgerald, Winemiller, Sabaj Pérez, & Sousa, 2017). For instance, habitat use or body size can be linked to location and *size* of a trophic niche (Boukal, 2014). But what species traits drive *changes* in the niche (e.g. change in location, size) during the life of an organism? Body size is often a key trait to differentiate among trophic niches of species, at least within a functional group (Sánchez-Hernández et al., 2019; Sanders et al., 2015; Woodward & Hildrew, 2002). Consequently, I expected that mean body size, or at least the range of body sizes (smallest to largest stage) would be linked to the degree of ontogenetic niche shifts. In contrast, I found that body size was a poor predictor of similarities or differences in ontogenetic niche shifts across species. For example, trophic level increased, decreased, or remained largely unchanged with body size in both herbivores and predators. Body size could also not explain differences across or within taxonomic/functional groups (e.g. *Plathemis* versus *Plecoris* or *Belostoma* versus *Notonecta* versus *Buenoa*). Indeed, all ontogenetic niche shift metrics showed either no or only very weak correlations with any species-level body size metrics. Note, individual body size was still clearly linked to the ecological niche of individuals within species; body size at the species level just did not explain differences between species in how the trophic niche changed during ontogeny.

Differences in ontogenetic niche shifts were, however, not random across species. Instead, the 13 species clearly grouped into three distinct taxonomic groups that differed in their functional role and traits: two non-overlapping predator groups, and one smaller group with all tadpole species. The differences between groups appear consistent with some fundamental trait differences between these groups. For instance, nepids pierce their prey, odonates engulf their prey, and tadpoles ingest prey (via scraping). Previous work suggests that predators with piercing mouth parts are much less gape limited than predators that engulf their prey and therefore could show different ontogenetic niche shifts (Nakazawa et al., 2013). In contrast, tadpoles should not be gape limited based on their *scraping* feeding mode. Overall, odonates showed much small trophic niche ranges (*TR*) and negative or weak increases in trophic position with size (*TS*), and higher niche overlap across stages than nepids. Furthermore, tadpoles' trophic positions either did not increase with size/stage or decreased. Overall, this confirms the idea that feeding mode plays a key role in driving ontogenetic niche shift patterns (Nakazawa et al., 2013).

Besides feeding modes, other factors, including behavioural traits may also play a role in generating differences in ontogenetic niche shifts (Sánchez-Hernández et al., 2019). For instance, early stages of *Notonecta* stay in very shallow, densely vegetated parts of the pond margin (likely to reduce risk of predation by conspecifics and other predators) while older, larger stages forage freely throughout the rest of the pond and in the open, deep water (Sih, 1982). While larvae of some odonate species can show some micro-habitat segregation (e.g. along a water depth gradient), these differences are usually much smaller and more continuous (e.g. *Plathemis*, *Tramea*) or absent (e.g. *Pachidiplax*, *Erythemis*) (Wissinger, 1992). Such differences in habitat use across stages would explain why *Notonecta* exhibited the largest *TR* and *DR*, and one of lowest average niche overlap among stages and largest trophic diversity (*HA*), while dragonflies (e.g. *Pachidiplax*, *Erythemis*) showed a narrow diet range and small trophic diversity (*HA*). These and other differences in morphology and behaviour could help explain why patterns of ontogenetic niche shift differed between predator and tadpole groups. This does not imply that species within each group cannot deviate from these general patterns, but if these traits are well preserved within taxonomic groups this would still result in general differences across taxonomic or functional groups, as observed in this study. If such patterns hold true across a diverse range of taxa and systems, phylogenetic and trait-based approaches could provide some general

guidelines of what patterns of ontogenetic niche shifts we could expect in a given species.

One key advantage of the approach I used here is that it allows one to compare very different functional groups that fundamentally differ in their feeding mode and functional role (predators, herbivores, detritivores, scavengers). Tadpoles are often classified as herbivores. However, some tadpoles showed similar or even larger changes in trophic level ($\delta^{15}N$) or diet ($\delta^{13}C$) than some predator species. This pattern is consistent with previous study (Schriever & Williams, 2013), which found that some tadpole species switch from plant based diet to detritus, and diets with higher animal items over their ontogeny. This would result in concurrent shift in stable isotope space in tadpoles while predatory salamander did not show clear ontogenetic niche shift (Schriever & Williams, 2013). However, the decrease in trophic level in *Acris* tadpoles is opposite to this trend, suggesting that other types of diet shift may occur in different tadpole species. When considering all aspects of the ontogenetic niche shift, tadpoles did appear to fall outside of the two insect predator clusters, but differences between tadpole species were similar to differences between tadpoles and some predator species. Future studies with a larger species pool of tadpoles and other herbivores are needed to confirm whether this pattern is representative across other taxa and systems and what traits could explain these patters.

4.3 | Quantifying ontogenetic niche shifts

The metrics presented here have many advantages for describing niche shifts, but it is important to consider the much discussed limitations of isotopes (Hoeinghaus & Zeug, 2008; Newsome et al., 2007), and interpret the results in the context of a species' biology (Fink, Reichwaldt, Harrod, & Rossberg, 2012). For instance, the earliest stages of a species (e.g. recently hatched, newborn individuals) will initially carry the stable isotope signature of their mothers. Depending on the biology, this signature may persist for some time (some tadpole species continue to *feed* on egg yolk after hatching) or may be quickly lost. In both scenarios the trophic signature still accurately represents the *diet* (energy) source of the organism, but it does not reflect the realised trophic interaction, i.e. individuals with mother's signature did not actually consume those resources themselves. Furthermore, differences in environmental conditions across habitats or time periods (e.g. resource diversity and abundance) can alter intraspecific variation and ontogenetic niche shifts patterns (Costa-Pereira, Araújo, Olivier, Souza, & Rudolf, 2018a; Costa-Pereira, Rudolf, et al., 2018b). Similarly, taxon-specific differences in isotopic turnover rates (Vander Zanden, Clayton, Moody, Solomon, & Weidel, 2015), or tissue content could influence stable isotope metrics. Since individuals spend time within a given stage, these differences are more likely to affect short-term diet switches within a stage than the ability to detect diet shifts between stages. Regardless, these factors should be considered when they are known, especially when comparing very different taxonomic groups (e.g. birds versus invertebrates). Ideally, the stable isotope analyses presented here would be complemented with data from realised feeding interactions (Fink et al., 2012; McCoy, Barfield, & Holt, 2009), but depending on the system this is often not possible for all species and can be biased by feeding mode and require different techniques (e.g. visual inspection of items versus DNA analysis).

While continuous data can outperform binned data in size-spectra analyses (Edwards, Robinson, Plank, Baum, & Blanchard, 2017), certain metrics simply cannot be calculated with continuous data and require grouping individuals in distinct ontogenetic stages. I used a binning approach that was intentionally set up to treat all species equally regardless of their different life histories and morphology. Ideally, the size of the bins should capture the biology of the species involved and should be accompanied by a sensitivity analysis. Analyses based on too large bin sizes will have lower resolution and thus less power to detect differences across stages. Similarly, too many small bins will reduce the sample size in each bin, and thus either reduce the confidence for estimates, or require much bigger sample sizes. It also runs the risk of splitting biologically similar stages into arbitrary subunits which is not meaningful. Fortunately, I found that results were qualitatively not sensitive to which bin size was chosen. Furthermore, for metrics that could be calculated with continuous body size data, the results were qualitatively the same with binned data, indicating that it does not introduce a systematic bias. Until we have new complementary approaches, the methods outlined here therefore serve as a useful tool to describe ontogenetic niche shift patterns in natural communities across a diverse range of taxa and functional groups. Such patterns are sorely needed to guide future empirical work and develop theory to study how ontogenetic niche shifts influence the structure and dynamics of natural communities.

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DATA AVAILABILITY STATEMENT

All data and code for this project are available online at Dryad (Rudolf, 2019): https://doi.org/10.5061/dryad.rxwdbrv4d

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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