RESEARCH ARTICLE

Does the evolution of ontogenetic niche shifts favour species coexistence? An empirical test in Trinidadian streams

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Abstract

1. A major question in ecology is how often competing species evolve to reduce competitive interactions and facilitate coexistence. One untested route for a reduction in competitive interactions is through ontogenetic changes in the trophic niche of one or more of the interacting species. In such cases, theory predicts that two species can coexist if the weaker competitor changes its resource niche to a greater degree with increased body size than the superior competitor.

2. We tested this prediction using stable isotopes that yield information about the trophic position (δ^{15}N) and carbon source (δ^{13}C) of two coexisting fish species: Trinidadian guppies *Poecilia reticulata* and killifish *Rivulus hartii*.

3. We examined fish from locations representing three natural community types: (1) where killifish and guppies live with predators, (2) where killifish and guppies live without predators and (3) where killifish are the only fish species. We also examined killifish from communities in which we had introduced guppies, providing a temporal sequence of the community changes following the transition from a killifish only to a killifish–guppy community.

4. We found that killifish, which are the weaker competitor, had a much larger ontogenetic niche shift in trophic position than guppies in the community where competition is most intense (killifish–guppy only). This result is consistent with theory for size-structured populations, which predicts that these results should lead to stable coexistence of the two species. Comparisons with other communities containing guppies, killifish and predators and ones where killifish live by themselves revealed that these results are caused primarily by a loss of ontogenetic niche changes in guppies, even though they are the stronger competitor. Comparisons of these natural communities with communities in which guppies were translocated into sites containing only killifish showed that the experimental

communities were intermediate between the natural killifish–guppy community and the killifish–guppy–predator community, suggesting contemporary evolution in these ontogenetic trophic differences.

5. These results provide comparative evidence for ontogenetic niche shifts in contributing to species coexistence and comparative and experimental evidence for evolutionary or plastic changes in ontogenetic niche shifts following the formation of new communities.

1 | INTRODUCTION

Since the earliest description of character displacement (Brown & Wilson, 1956), ecologists have studied how trait evolution can facilitate resource niche shifts and enhance the prospects for co-existence (Lawlor & Smith, 1976; McPeek, 2017; Nosil, 2012; Schluter, 2000). However, nearly all of this effort has focused on adult traits, even though numerous animal taxa exhibit significant ontogenetic changes in the resource niche (Werner & Gilliam, 1984). These ontogenetic changes pose a challenge for understanding how dietary niche evolution contributes to coexistence (Bassar, Travis, et al., 2017).

Ontogenetic changes in resource use occur in one of three ways. First, in taxa like amphibians and holometabolous insects, there are discrete phases of the life cycle between which individuals shift their resource use and, often, their habitat (ten Brink et al., 2015). Second, in some taxa without discrete phases of the life cycle, discrete changes in resource use occur when animals pass a threshold body size (Cipriani et al., 2017; Graham et al., 2007). Third, in taxa like fish, reptiles, and many hemimetabolous insects, individuals change their resource use gradually as they grow (Aresco et al., 2015; Briones et al., 2012; Reñones et al., 2002; Wallace & Leslie, 2008; Werner & Gilliam, 1984).

Mathematical theory developed for this third situation predicts that differences between species in how they shift their resource niches with body size can promote stable coexistence. This happens when the species that is the weaker competitor shifts its niche with body size (or age) to a greater extent along the portion of the resource niche that the two species share (Bassar, Travis, et al., 2017; Miller & Rudolf, 2011; Nakazawa, 2011, 2015). This ontogenetic niche shift reduces the effect of competition on the competitively weaker species. However, despite the widespread occurrence of gradual ontogenetic changes in resource use, there are few empirical tests of this prediction (Bassar, Travis, et al., 2017; Nakazawa, 2015).

Finding communities where a weaker competitor shifts its niche to a greater degree than a superior competitor provides evidence that the two species are likely to coexist, but not for the processes that lead to this outcome. One possibility is that the changes in the resource niche with increased body size are immutable properties of the species. Under this hypothesis, species coexistence in these systems represents a fortuitous outcome of community assembly. An alternative hypothesis is that the differences in the resource niche change (either through evolutionary or plastic changes) during the process of community assembly, facilitating coexistence of the two species. The latter of these two hypotheses is central to ecological character displacement (Brown & Wilson, 1956), yet it is not clear if ontogenetic changes in resource use are sufficiently malleable to facilitate coexistence.

Stream communities on the Caribbean Island of Trinidad are an excellent system for testing these predictions. On the island, each river that drains the Northern Range Mountains has a replicated succession of fish communities, in which fish species diversity and predation risk declines progressively upstream (Gilliam et al., 1993). In lower stream reaches, guppies *Poecilia reticulata* and killifish *Rivulus hartii* are at low densities and co-occur with multiple predatory fish species (hereafter, killifish–guppy–predator, or KGP communities). Above barrier waterfalls, killifish and guppies live without predators (hereafter, killifish–guppy, or KG communities). Because there is little predation in these localities, guppies and killifish occur at higher densities (Reznick et al., 2001; Rodd & Reznick, 1997), which increases the effect of competition on fitness (Bassar et al., 2013). Even further upstream, killifish are the only fish species found in the streams (hereafter, killifish-only, or KO communities).

Communities containing only killifish and guppies (KG) have formed independently in different rivers following the colonization of KGP guppies into KO habitats (Alexander et al., 2006; Travis et al., 2014). During the formation of KG communities, both species have evolved different life histories from their respective KO and KGP ancestors (Reznick, 1982; Reznick & Endler, 1982a; Walsh et al., 2011; Walsh & Reznick, 2011). KG guppies have a more herbivorous diet than KGP guppies (Zandona et al., 2011), which translates into their exerting different effects on the community (Bassar et al., 2010, 2012; Bassar, Bryan, et al., 2017; Simon et al., 2017). While killifish have a greater reliance on terrestrial invertebrates in their diet than do guppies (Fraser et al., 1999), we know relatively little about how killifish diets change with body size in any community.

Experimental evidence suggests that ontogenetic changes in competitive ability and resource use may play a key role in the

coexistence of these two species in KG communities (Anaya-Rojas et al., 2021). For instance, intraspecific competitive ability in guppies is strongly dependent on body size (Potter et al., 2019). Recent laboratory experiments indicate that when both species are given the same food, guppies are the stronger competitor (Anaya-Rojas et al., 2021). Mathematical models that describe these interactions predict that in communities where guppies and killifish are the only fish species and where competition for resources is stronger (KG communities), the two species can coexist if killifish have stronger ontogenetic shifts in their resource niche than guppies (Bassar, Travis, et al., 2017).

Here, we use $\delta^{15}N$ and $\delta^{13}C$ stable isotopes to investigate whether ontogenetic changes in resource niche use, specifically trophic position and carbon source, have evolved to promote coexistence between killifish and guppies. Stable isotope analysis is an excellent method for investigating ontogenetic patterns of resource use because it integrates dietary data over long periods (Birkhofer et al., 2016; Boel et al., 2018; Krumsick & Fisher, 2019; Matthews et al., 2010; Matthews & Mazumder, 2004; Reñones et al., 2002). The ratio of heavy to light stable nitrogen isotope ($\delta^{15}N$) increases stepwise (~3‰) with the trophic level of a consumer because the two isotopes fractionate at different rates. The ratio of stable to unstable carbon isotope ($\delta^{13}C$) provides an estimate of the source of carbon in the diet (Boecklen et al., 2011).

In stream fish, $\delta^{15}N$ often increases with fish age or body size due to the tendency of older and larger individuals to shift their diets towards the consumption of prey occupying higher trophic levels (Winemiller, 1989). The $\delta^{13}C$ of stream fish can also increase with age/size if older or larger individuals shift their diets to more allochthonous resources (e.g. terrestrial insects: (Frossard et al., 2021; see Fletcher et al., 2015 for a counter-example). Such patterns are detectable when the d13C of algae in streams is lower than that of terrestrial vegetation, which can occur when the $\delta13C$ of dissolved inorganic carbon is lower than atmospheric carbon (Lancaster & Waldron, 2001).

We measured stable isotopes of $\delta^{15}N$ and $\delta^{13}C$ collected from wild populations of guppies and killifish to evaluate the general hypothesis that size-dependent shifts in the niche allow these two species to coexist. This general hypothesis makes two specific predictions. First, we expect to find evidence for ontogenetic niche shifts in killifish and perhaps guppies in communities where the potential for competition is the greatest (KG communities). Second, if both species shift their niches with increased body size, killifish should do so to a greater degree.

If this mechanism of coexistence is correct, it raises the question of whether differences between the species are present as a fortunate consequence of differences between guppies and killifish in general or whether they arise through either plastic or evolutionary changes in response to increased competition in KG communities. We took two approaches to evaluating this question. First, we compared the observed ontogenetic niche shifts in guppies and killifish in communities with high competition (KG) to the observed ontogenetic niche shifts in communities where they live with predators

(KGP) and competition is lower. For killifish, we also compared the ontogenetic niche shifts in KG communities to those where killifish experience high intra-specific competition (KO). If the ontogenetic niche shifts observed in KG communities are different than in other communities, then this provides comparative evidence for ecological character displacement reducing the effect of competition on each of the species.

Second, to evaluate the possible timescale over which these changes are taking place, we compared the communities from natural populations with experimental communities that vary in their time since formation to ask whether they are evolving towards the patterns observed in the natural KG communities. If ecological character displacement is an ongoing process that is shifting the ontogenetic niches of the species due to plasticity and/or via evolutionary changes, then we expect to see niche shifts that are intermediate between those observed in the communities of origin.

2 | MATERIALS AND METHODS

2.1 | Do killifish and guppies have ontogenetic shifts in the resource niche and is it larger in killifish?

To test the hypothesis that ontogenetic niche shifts contribute to coexistence between guppies and killifish in highly competitive communities, we collected guppies and killifish from three natural killifish/guppy communities (KG-nat) in the Guanapo, Aripo, and Quare drainages on the southern slope of the Northern Range Mountains on the island of Trinidad, West Indies (Table S1). We sought to collect individuals spanning the range of sizes observed at each site. We sampled all fish during the dry season of 2017 (February–June) following methods described elsewhere (Bassar, Simon, et al., 2017).

From each sampling site, we also collected aquatic grazing (*Thraulodes* spp.) and shredding (*Phylloicus* spp.) invertebrates to calibrate the fish isotopic values within each location. We measured guppy and killifish body size to the nearest 0.1 mm and wet weight to the nearest 0.01 g. We removed the visceral organs to eliminate stored lipids and lipid-rich reproductive tissue that represent very recent metabolic investments and not longer-term diet histories. Then, we dried the whole body of all fish and invertebrates at ~60°C for a minimum of 72 h, freeze-dried all samples, and ground them to a fine powder with a ball mill. For each sample, we measured the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic signatures using a Thermo Fisher Delta V Advantage Isotope Ratio mass spectrometer coupled to a Thermo Flash 2000 Organic Elemental Analyser. Isotopic reference materials (acetanilide; Stable Isotope Research Facility) were assayed at the beginning of each run and after every 10 samples. The average precision of standards for $\delta^{13}C$ and $\delta^{15}N$ was 0.04‰ and 0.12‰, respectively. All research was conducted with the approval of FSU's Animal Care and Use Committee, protocol number 1607.

We mathematically adjusted the fish $\delta^{13}C$ values based on their variation in lipid content following established methods (Kiljunen et al., 2006). Then, we corrected the $\delta^{13}C$ and $\delta^{15}N$ values of each

fish at each location by subtracting the mean carbon and nitrogen isotopic signal of invertebrates for each location (Figures S1 and S2). This resulted in Δ^{15}N and Δ^{13}C representing the difference between the isotopic values between the fish and the invertebrates. These values were then used in the analyses. Hereafter, we analysed and discuss the variation in the resulting differences as the variation in the relative carbon source (Δ^{13}C) and relative trophic position (Δ^{15}N) following Birkhofer et al. (2016).

To test our hypotheses, we used a linear mixed model to estimate how trophic position (Δ^{15}N) and carbon source (Δ^{13}C) of the fish depended on species, body size and community using the LME4 package (Bates et al., 2015) in R 4.0 (RCoreTeam, 2020). We centered the linear model on 10 mm standard length so that the intercept term and the main effects of species × community correspond to the mean Δ^{15}N and Δ^{13}C of a 10 mm fish (standard length). Guppies and killifish are both 6 to 7 mm at birth so at this size they have likely grown enough beyond their hatching size for their isotopic signatures to no longer resemble those of their mothers. We initially included random effects of drainage and species within drainage on both the intercept and slopes (body size) of the models. The drainage random effect was intended to capture variation between drainages that is common between the species. The species within drainage random effect accounts for multiple measures of each species (individuals) within a drainage. For both the carbon source and trophic position, these maximal random effect models did not converge, so we reduced the models to include only the random effects on the intercepts (Matuschek et al., 2017). We then evaluated whether the body size slopes of each species differed from zero and differed between the species using t-tests and Satterthwaite's degrees of freedom as calculated in the LMERTEST package (Kuznetsova et al., 2017).

2.2 | Are the differences in the trophic niches in the KG communities due to character displacement in KG-nat communities?

To test the hypothesis that the ontogenetic niche shifts in the high competition (KG-nat) sites were products of plastic and/or evolutionary adjustments that facilitate coexistence, we also collected guppies, killifish and baseline invertebrates from locations where the two fish species also live with predators (KGP). Both species live at lower densities in these sites and experience less resource competition. Both species are also known to have evolved genetically based differences in their life histories, behaviour, morphology and physiology between these sites (Auer et al., 2018; Endler, 1978; Ghalambor et al., 2004; Houde, 1997; Langerhans & DeWitt, 2004; Palkovacs et al., 2011; Reznick et al., 1996; Reznick & Endler, 1982b; Seghers, 1974; Seghers & Magurran, 1995; Walsh & Reznick, 2008, 2011). For killifish, we also collected individuals from paired sites where killifish are the only species of fish and intraspecific competition is the most intense (KO).

Our sampled KGP and KO communities were located downstream and upstream, respectively, of the KG-nat communities used above (see Table S1). Fish and invertebrate baselines were collected on the same dates as the KG-nat sites and processed identically. We formally tested our hypothesis using a linear mixed model in which we included body size, community, and the interaction between community and body size as fixed effects. We initially included random effects of drainage, community (KGP, KG-nat, KO) within drainage, and species within drainage and community on both the intercept and slopes (body size) of the models. As above, this random effect structure accounts for spatial variation between drainages and habitats as well as multiple measures of each species within sites. For trophic position, the maximal random effect model converged but did not explain a significant amount of variation in the data (LRT: $\chi^2_6 = 8.67, p = 0.193$), so we reduced the models to include only the random effects on the intercepts (Matuschek et al., 2017). The maximal model with random effects on the intercepts and slopes (body size) for carbon source converged with the random slopes explaining significant variation in the data (LRT: $\chi^2_6 = 34.49, p < 0.001$) so we report results from this maximal model. Analyses were performed in the LME4 package (Bates et al., 2015) in R 4.0 (RCoreTeam, 2020). We then used contrasts to ask whether there was evidence for differences between the ontogenetic niche shifts of guppies or killifish in KG-nat communities compared with the other communities where the species occur. We conducted these contrasts separately for each fish species and compared the intercepts and slopes using t-tests for guppies and omnibus F-tests for killifish. For all tests, we calculated Satterthwaite's degrees of freedom and p-values using the LMERTEST package (Kuznetsova et al., 2017).

2.3 | Is there evidence for ongoing plastic or evolutionary changes in ontogenetic niche in experimental communities?

Finally, we asked whether there was evidence of ongoing plastic or evolutionary changes in experimental communities. These experimental communities represent intermediate points between the initial and final states of community formation. We collected guppies and killifish from four experimental introductions of guppies from KGP communities into KO communities. These communities were initiated in 1976 (a tributary of the Aripo river, Endler, 1980), 1981 (El Cedro, Reznick & Bryga, 1987), and two in 2009 (two tributaries in the Guanapo Reznick & Travis, 2019; Travis et al., 2014, Table S2). These older and newer introductions were pooled so that we included a set of 'new' introductions and 'old' introductions. Below, we refer to these as KG-new and KG-old, respectively. Three (two new and one old) of these experimental communities occur in the same drainages, but different streams, as some of our natural sites (Guanapo and Aripo). The other (El Cedro; see Table S2 for details) is a tributary to the Guanapo River. To facilitate comparing these experimental communities to KO communities in the same streams, we also sampled KO communities upstream of the experimental communities. For the El Cedro, we also collected guppies and killifish from the KGP community within the El Cedro River, downstream of the introduction site. Overall, this means

that our comparisons are comprised of paired communities within each stream and drainage. All fish and invertebrate baselines were collected on similar dates as the other sites and processed in an identical manner.

We combined the data from the experimental streams with the data from the natural communities to test the hypothesis that the slopes of the stable isotope data with body size in each species in the experimental communities were different from the natural communities. We then used a linear mixed model to test whether the slopes of the stable isotopes against body size were different between the experimental and natural communities. We included species, body size, community and the interaction between community as fixed effects. We initially included random effects of drainage, community (KGP, KG-new, KG-old, KG-nat, KO) within drainage, and species within drainage and community on both the intercept and slopes (body size) of the models. This random effect structure accounts for spatial variation between drainages and habitats as well as multiple measures of each species within sites. For carbon source, the maximal random effect model did not converge, so we reduced the model to include only the random effects on the intercepts (Matuschek et al., 2017). The maximal model with random effects on the intercepts and slopes (body size) for trophic position converged but did not explain significant variation in the data (LRT: $\chi^2_6 = 5.30, p = 0.506$) so we report results from the reduced model without the random effects on the slopes (Matuschek et al., 2017). Analyses were performed in the LME4 package (Bates et al., 2015) in R 4.0 (RCoreTeam, 2020). We tested whether there was a significant amount of variation in the slope parameters as a function of all five community types using omnibus F-tests of the slope parameters for each species. Intermediacy of the experimental communities was judged visually from the plots of the estimated marginal means when the omnibus F-tests were significant.

2.4 | Missing data

In three sites, we were unable to collect information on the isotope values of either a grazer or shredder baseline species due to limited abundance during collection. In these cases, we used the baseline isotope values from the corresponding KG or KO site in that location for the missing values. This should introduce minimal error because KG and KO sampling sites are adjacent to each other, often separated by tens of meters or less, and the baselines have similar values between communities (ANOVA: baseline × community; δ^{15}N: $F_{2, 13.88} = 0.261, p = 0.773$ and δ^{13}C: $F_{2, 24} = 1.313, p = 0.287$). We had no missing invertebrate values in KGP communities.

3 | RESULTS

3.1 | Do killifish and guppies have ontogenetic shifts in the resource niche, and are these shifts larger in killifish?

In the natural sites where guppies and killifish are the only fish and the potential for competition is the highest (KG-nat), killifish had a significantly larger ontogenetic niche shift in trophic level with increased body size compared with guppies ($t_{157.8} = 2.72, p = 0.007$; Figure 1a). Killifish had an ontogenetic niche shift such that larger individuals feed at higher trophic levels ($t_{157.1} = 7.27, p < 0.001$; Figure 1a) and guppies did not ($t_{157.7} = -0.73, p = 0.465$; Figure 1a). The two species did not differ in the trophic level of the smallest-sized individuals (10 mm standard length; $t_{5.2} = 0.828, p = 0.444$; Figure 1a).

In these same sites, we found no evidence that killifish had a significantly larger shift in the carbon source with increased size than guppies ($t_{157.7} = 0.599, p = 0.557$; Figure 1). This was despite the individual species estimates showing killifish had an ontogenetic niche shift in the carbon source with increased size ($t_{157.1} = 4.47, p < 0.001$; Figure 1) and guppies did not ($t_{157.5} = 0.666, p = 0.506$; Figure 1). We also found no evidence that small guppies and killifish differed in their carbon source ($t_{2.77} = 2.42, p = 0.100$; Figure 1) which would be evidence for a whole scale difference in the resources that are used between the species.
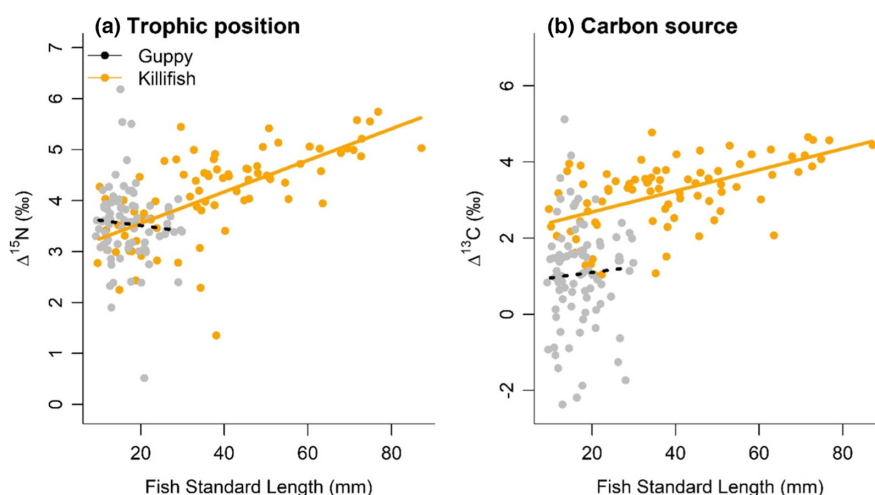

FIGURE 1 Trophic position (a) and carbon source (b) for different sized guppies and killifish in the KG-nat sites. Points are the observed values independent of the best linear predictor of the random effects and the lines are the fitted lines from the linear mixed model. Solid lines and dashed lines represent significant ($p < 0.05$) and non-significant slopes ($p > 0.05$). Equivalent figures for all sites from the global model are included in the online supplement.

3.2 | Are the differences in the trophic niches in the KG communities due to character displacement in KG-nat communities?

We further tested whether the observed differences in KG-nat communities were fortuitous characters of the species or whether these differences potentially resulted from competitive interactions within the communities (i.e. character displacement), and if so, which species changes its resource niche upon contact. We tested this by comparing the isotope signatures of guppies and killifish in sites with the highest potential for competition (KG-nat) to paired sites where competition is expected to be low for both species (KGP) and where intra-specific competition is expected to be high for killifish (KO).

We found no evidence that the trophic position of the smallest guppies was different between KGP and KG-nat communities ($t_{12.1} = 0.450$, $p = 0.660$; Figure 2 and Figure S3). However, in contrast to KG-nat communities, guppies that live with predators (KGP communities) had a significantly larger ontogenetic shift in trophic position compared with guppies that live only with killifish ($t_{397.6} = 3.61$, $p < 0.001$; Figure 2 and Figure S3). In contrast, we found no evidence for a difference in the carbon source guppies use as they grow between the communities ($t_{41.3} = 0.653$, $p = 0.517$; Figure 2 and Figure S4) We did, however, find evidence that small guppies in KG-nat sites used less enriched carbon sources than small guppies in KGP communities ($t_{5.94} = 2.74$, $p = 0.034$; Figure 2 and Figure S4).
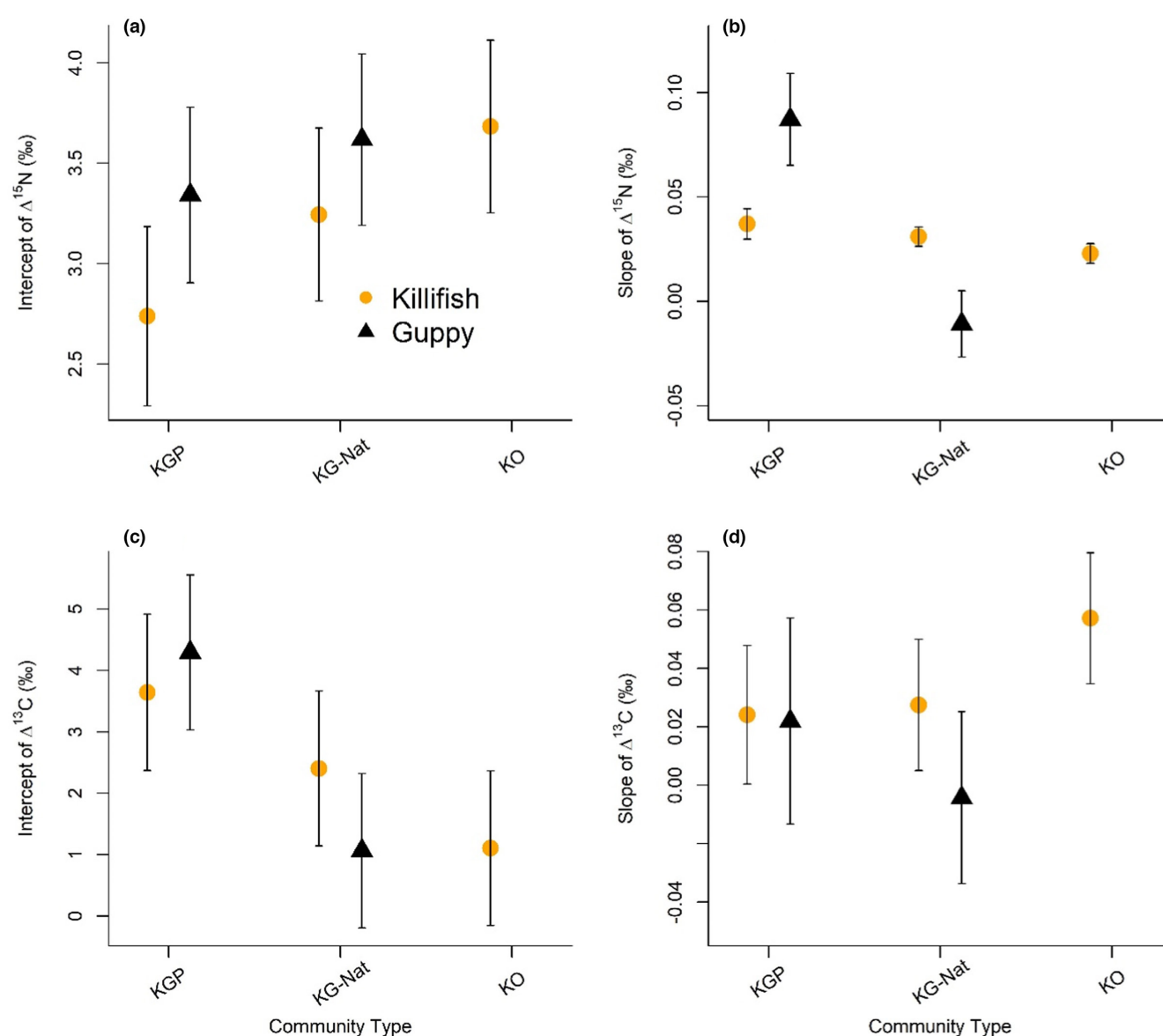

FIGURE 2 Estimated values of trophic position (a and b) and carbon source (c and d) for small body sizes (10 mm; a and c) and the estimated slopes of body (b and d) of guppies and killifish from the three natural community types. Estimates were taken from the model including all natural sites and all species. Points are the estimated marginal means and error bars are the standard errors.

In contrast to guppies, ontogenetic changes of killifish in KG-nat communities did not differ from killifish in other communities for trophic position (KGP and KO) ($F_{2,397.3} = 1.56$, $p = 0.212$; Figure 2 and Figure S3) or carbon source ($F_{2,5.05} = 1.24$, $p = 0.365$; Figure 2 and Figure S4). We did not find evidence that the trophic position of all sizes of killifish was lower in KG-nat sites compared with the other sites ($F_{2,12.5} = 1.16$, $p = 0.344$; Figure 2 and Figure S3) nor did we find evidence for a difference between all sizes of killifish across the communities for their carbon source ($F_{2,6.08} = 2.28$, $p = 0.182$; Figure 2 and Figure S4).

Together these results suggest that when guppies from communities with predators (KGP) invade previously killifish only (KO) communities to form KG communities, guppies undergo a dramatic

shift in ontogenetic changes in trophic position and killifish undergo a smaller, albeit significant ontogenetic shift in their carbon source.

3.3 | Are the populations in the experimental communities evolving towards the patterns observed in the natural KG communities?

The ontogenetic changes in trophic position in killifish in the old (KG-old) and new introduction experiments (KG-new) were no different from those displayed by killifish in the natural communities ($F_{4,806.2} = 1.31$, $p = 0.264$; Table S2, Figure 3 and Figure S3). Neither did we find evidence that the trophic position of the smallest sizes
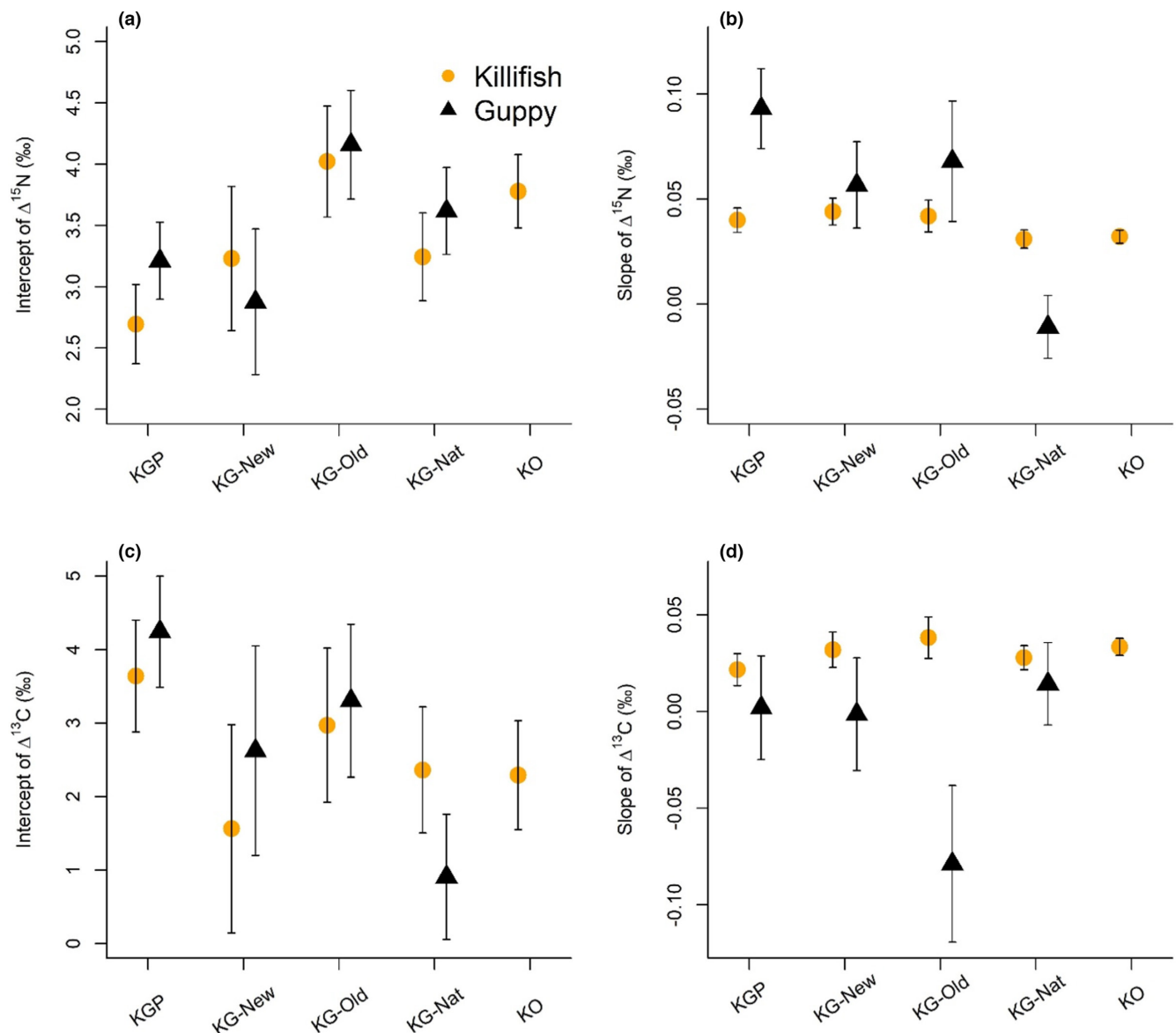

FIGURE 3 Estimated values of trophic position (a and b) and carbon source (c and d) for small body sizes (10 mm; a and c) and the estimated slopes of body (b and d) of guppies and killifish from the three natural communities and experimental communities. Estimates were taken from the global model including all sites and all species. Points are the estimated marginal means and error bars are the standard errors.

of killifish was different between the experimental communities and the natural communities ($F_{4,18.6}$ = 2.12, p = 0.119; Table S2, Figure 3 and Figure S3). Neither the change in carbon source with increased body size of killifish ($F_{4,806.3}$ = 0.567, p = 0.687; Figure 3 and Figure S4) nor the carbon source of the small killifish ($F_{4,8.26}$ = 0.797, p = 0.558; Figure 3 and Figure S4) was different between the experimental and natural communities.

In contrast, the change in the trophic position with increased size in guppies depended heavily on the community type ($F_{3,807.9}$ = 6.95, p = 0.0001; Figure 3 and Figure S3). The increase in trophic position with body size in guppies from the old and new introductions was intermediate between the patterns observed in KGP and those observed in KG-nat (Figure 3 and Figure S3). We did not find evidence that the guppies in the experimental communities differed from the natural sites in the trophic position of the smallest sizes ($F_{3,18.4}$ = 1.41, p = 0.271; Figure 3 and Figure S3), with the newer introductions more resembling guppies in KGP and the older introductions more resembling natural killifish and guppy communities (KG-nat). There were also no differences between the old or new introductions and the KG-nat natural sites for the change in their carbon source with increased body size in guppies ($F_{3,808.6}$ = 1.39, p = 0.243; Figure 3 and Figure S4). We also did not find evidence for the smallest-sized guppies in the introductions differing from the natural sites ($F_{3,8.53}$ = 3.54, p = 0.064; Figure 3 and Figure S4), but the experimental sites were intermediate between the sites with predators (KGP) and natural killifish guppy sites (KG-nat). This is not surprising, given that guppies in the natural sites show no ontogenetic shift in carbon source. The changes in guppies between KGP communities and the experimental communities are in the same direction as the differences between KGP and KG-nat communities.

4 | DISCUSSION

We used stable isotopes of nitrogen and carbon to ask whether ontogenetic niche shifts contribute to species coexistence in Trinidadian fish communities and whether there is evidence for the evolution of these shifts as new communities form. Our results revealed four important results. First, in high-competition communities (KG-nat), killifish have more pronounced ontogenetic niche shifts in trophic position than guppies, as predicted by mathematical theory (Bassar, Travis, et al., 2017). Second, the lack of ontogenetic niche shifts in the trophic position of guppies in these communities was in stark contrast to the strong ontogenetic niche shift in guppies in low competition sites that contain predators (KGP communities). This, combined with the little change in the ontogenetic niche shift for trophic position of killifish across all three natural communities suggests that these size-dependent coexistence mechanisms are mediated by plastic or evolutionary changes in the ontogenetic trophic niche of guppies. Third, the results for the carbon source showed little difference between guppies across community types. Instead, killifish decreased their ontogenetic niche shift in communities with guppies (KG-nat) compared with communities with only

killifish (KO). Fourth, in some instances, the trophic niche differences between guppies and killifish in the experimental introductions of KGP guppies into KO communities appear to be moving towards patterns that resemble natural KG communities and away from patterns in the KGP communities. Together these results show that differences in the ontogenetic niches of these two species are consistent with coexistence theory and, counterintuitively, it is the stronger competitor, guppies, that changes its niche more strongly during the formation of new communities.

The stronger ontogenetic niche shift for trophic position in killifish is consistent with the prediction that for these species to coexist, the weaker competitor, in this case, killifish, should display a stronger niche shift with body size (Anaya-Rojas et al., 2021; Bassar, Travis, et al., 2017). The comparisons with guppies and killifish in other communities suggest that it is guppies, and not killifish, that are changing their trophic position upon the formation of these communities. The observed change in trophic position in guppies between KGP and KG communities is the loss of the ontogenetic niche shift, which means larger guppies are feeding at the same, lower trophic position as smaller guppies. These results are consistent with other studies showing guppies that live with killifish in the absence of other predators consume more algae and detritus and fewer invertebrates in their diets than guppies that live with killifish and other predators (Bassar et al., 2010, 2012; Zandonà et al., 2011, 2015).

Given that guppies are much stronger competitors than killifish when they overlap in size, it is a puzzling why guppies, the stronger competitor, exhibit a change in ontogenetic niche shift from KGP to KG communities but killifish, the weaker competitor, do not. We posit that this shift may be a direct result of the lower productivity, lower diversity in potential food, and higher densities of guppies in KG communities (Travis et al., 2014). When KGP guppies invade KO communities, their populations grow rapidly to extraordinary densities (Reznick et al., 2020; Reznick & Travis, 2019; Travis et al., 2014). At the same time, the population density of killifish declines substantially (Fraser & Lamphere, 2013; Goldberg et al., 2022), which suggests that the greatest pressure on resource availability to guppies comes from the guppies themselves (Abrams, 2012; Reznick et al., 2019). The rapid population growth often causes the depletion of preferred food, which then selects for dietary expansion (Araújo et al., 2007; Bassar et al., 2012; Prati et al., 2021). The trophic niche shift documented here is consistent with this scenario. Feeding at a lower trophic level when resources are limited has been observed in other fish communities (Boel et al., 2018; Krumsick & Fisher, 2019; Matthews et al., 2010). However, if the differences in the ontogenetic niche shift of guppies between KGP and KG communities were solely due to such plastic adjustment of the trophic niche to the environment, then the experimental communities which all have high guppy densities but differ in their duration since introduction should be identical to the natural communities with guppies and killifish. Instead, the experimental communities are intermediate (Figure 3).

Another hypothesis for this phenomenon is that the niche shift of guppies in KG communities is a by-product of an increased intensity

of intraspecific competition, independently of the actual productivity of the KG habitat (Arim et al., 2010; Potter et al., 2019; Prati et al., 2021; Svanbäck et al., 2008; Young, 2004). Several lines of evidence align with this hypothesis. For instance, the intra- and interspecific competitive ability of KG guppies is greater than that of KGP guppies (Anaya-Rojas et al., 2021; Potter et al., 2019). Natural KG guppies have also evolved physiological adaptations to low resource availability, such as lower metabolic rates and a slower pace of life, as in other organisms adapted to competitive environments (Auer et al., 2018, 2020; Bozinovic et al., 2009; Pettersen et al., 2020). KG-nat guppies have evolved broader diets than KGP guppies, including an increased reliance on low-quality food (Bassar et al., 2010, 2012; Zandonà et al., 2011). The KG-nat guppies also display patterns of gene expression in digestive enzymes associated with a nutritionally deficient diet (Sullam et al., 2015) and a microbiome distinct in composition and function from that of KGP guppies (Evans et al., 2022). These changes in guppy diet represent part of our proposal (Travis et al., 2014) that their evolution in this community is in part driven by an interaction between ecology and evolution. One source of selection on guppies in KG communities is their having depleted their environment of some invertebrate resources after having attained high population densities.

Our results comparing natural KGP, KG and KO communities also revealed that the ontogenetic niche shift of killifish in their carbon source became more similar to guppies when killifish and guppies live together (KG) compared with when killifish are the only species present (KO) (Figure 2). On first inspection, these results seem to run counter to the theoretical prediction from mathematical theory that selection should act to separate the two species in their ontogenetic niche shifts in communities with high competition. Yet, at the same time, all sizes of guppies used carbon sources that were less enriched compared with killifish (Figure 2c). The use of different sources of carbon between the species is consistent with observations that, in KG communities, the two species display significant habitat partitioning, with killifish relying more on riffles and guppies relying more on pools (Goldberg et al., 2022). Using different habitats may generate diets based ultimately on different sources of carbon, for example, autochthonous vs. allochthonous bases, which would readily facilitate coexistence.

Such a broadscale shift across all sizes of guppies should also allow the two species to coexist (Bassar, Travis, et al., 2017), but it alone does not explain why all sizes of killifish become more similar in the use of their carbon sources when they live with guppies compared with when they live only with other killifish. As noted above, one effect of guppies is to decrease the densities of killifish when guppies and killifish are the only fish in the community. One possibility is that the decline in the ontogenetic niche shift of killifish may also be caused by a decrease in intra-specific competition for killifish in KG communities. This is supported by the observation that the ontogenetic niche shift of killifish in KG communities was not different from the ontogenetic niche shift of killifish in KGP communities where competition is also low (Figure 2d). The largest ontogenetic niche shift observed in killifish occurred in communities where

killifish experienced the highest level of intra-specific competition. In contrast to guppies, there may be strong selective pressures on killifish to increase their ontogenetic niche shifts when intra-specific competition is high. This would have the effect of reducing the per-capita effect of competition on killifish in these communities.

The limitations of stable isotope data suggest that the divergence in carbon use patterns should be interpreted cautiously. This is because, at first glance, one might argue that guppies shift their carbon use towards less enriched sources from KGP to KG because those more enriched sources are simply not available. The reliance of larger killifish on those more enriched sources, whether in KGP or KG communities (Figures 1–3), demonstrates that those sources are, in principle, available to guppies. That KG guppies do not appear to use them, while KGP guppies and killifish in all communities do, supports the interpretation that the shift in KG guppies towards less enriched carbon sources is a response to the increased competition with killifish.

Our analyses of trophic position and carbon source of two species across communities also revealed interesting trends across these communities that are independent of the fish. For instance, the difference between the fish and the baseline invertebrates in trophic position increased, and in carbon source declined, as the fish communities became simpler (KGP to KG to KO in Figure 2a,c). Importantly, these trends were apparent in both fish species and the species of invertebrates used as baselines in these comparisons were the same between the communities. One possibility here is that the invertebrates used as baselines are themselves providing different functional roles in these different communities containing different fish species. Another possibility is that these trends have nothing to do with biotic interactions but rather occur due to the physiographic differences in the streams themselves. Communities with predators tend to be lowland rivers, whereas killifish/guppy communities and killifish-only communities occur along the slopes of the Northern Range Mountains. This explanation seems unlikely to be general as killifish/guppy communities and killifish-only communities are often separated only by a few hundred meters or less, yet the isotope signatures differ as much as the communities with predators (Figure 2a,c), which are often several kilometres away.

Overall, our results point towards size-dependent differences in the trophic niche as a potentially powerful and underappreciated mechanism of species coexistence. Of course, how powerful this mechanism is must be judged in comparison with other coexistence mechanisms. Such comparisons are challenging because they require quantifying the effects of each mechanism on fitness in the context of a parameterized mathematical model. Such modelling efforts are possible (Bassar, Travis, et al., 2017), but are beyond the scope of the present study. Some of these other coexistence mechanisms are simple and others are complex. An example of a simple mechanism is the difference in the size-dependent or size-independent competitive ability of the two species (Anaya-Rojas et al., 2021; Potter et al., 2019). An example of more complex mechanisms is the temporal storage effect and relative nonlinearity of fitness (Chesson, 2000). These latter two mechanisms require temporal

fluctuations in environmental conditions and can act in conjunction with size-dependent changes in the resource niche and competitive ability. Understanding the role of these size-dependent interactions in fluctuating environments is an outstanding challenge. More challenging still is understanding whether and how the evolutionary process contributes to shaping these mechanisms. Endeavouring to do so represents a new and exciting twist on classical theories of character displacement.

AUTHOR CONTRIBUTIONS

Joseph Travis, Ronald D. Bassar and David Reznick conceived the research. Jaime M. Anaya-Rojas, Joshua F. Goldberg, Joseph Travis, Leighton King and Ronald D. Bassar collected the data. Jaime M. Anaya-Rojas and Blake Matthews performed the stable isotope analyses. Ronald D. Bassar, Jaime M. Anaya-Rojas and Joseph Travis performed the statistical analyses. Jaime M. Anaya-Rojas, Ronald D. Bassar and Joseph Travis wrote the paper's first draft, and all authors contributed to the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare that we have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.k6djh9wbg (Anaya-Rojas et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Sampling sites and number of fish used for each of the five community types.

Table S2. Parameter estimates for the five different communities from the global model. Intercepts are centered at 10 mm standard 1 length for guppies and killifish. Parameters that are significantly different than zero ($p < 0.05$) are highlighted in bold.

Figure S1. Site specific raw nitrogen isotopic signal of the baselines and consumers (fish).

Figure S2. Site specific raw carbon isotopic signal of the baselines and consumers (fish).

Figure S3. Effects of body size on the relative trophic position (site corrected $\Delta^{15}N$) of 17 guppies and killifish from the five community types.

Figure S4. Effects of body size on the carbon source (site corrected $\Delta^{13}C$) of guppies and 27 killifish from the five community types.