

The evolution of size-dependent competitive interactions promotes species coexistence

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14 **Abstract**

15 1. Theory indicates that competing species coexist in a community when intraspecific compe-
16 tition is stronger than interspecific competition. When body size determines the outcome
17 of competitive interactions between individuals, coexistence depends also on how resource
18 use and the ability to compete for these resources change with body size. Testing coexis-
19 tence theory in size-structured communities, therefore, requires disentangling the effects of
20 size-dependent competitive abilities and niche shifts.

21 2. Here, we tested the hypothesis that the evolution of species and size-dependent competitive
22 asymmetries increased the likelihood of coexistence between interacting species.

23 3. We experimentally estimated the effects of size-dependent competitive interactions on so-
24 matic growth rates of two interacting fish species, Trinidadian guppies (*Poecilia reticulata*)
25 and killifish (*Rivulus hartii*). We controlled for the effects of size-dependent changes in the
26 niche at two competitive settings representing the early (allopatric) and late (sympatric) evo-
27 lutionary stages of a killifish-guppy community. We fitted the growth data to a model that
28 incorporates species and size-dependent competitive asymmetries to test whether changes
29 in the competitive interactions across stages increased the likelihood of species coexistence
30 from allopatry to sympatry.

31 4. We found that guppies are competitively superior to killifish but were less so in sympatric
32 populations. The decrease in the effects of interspecific competition on the fitness of killifish
33 and increase in the interspecific effect on guppies' fitness increased the likelihood that sym-
34 patric guppies and killifish will coexist. However, while the competitive asymmetries between
35 the species changed consistently between allopatry and sympatry between drainages, the
36 size-dependent competitive asymmetries varied between drainages.

37 5. These results demonstrate the importance of integrating evolution and trait-based interac-
38 tions into the research of how species coexistence.

39 *Keywords:* size-dependent competition, intra- and interspecific competition, coexistence, co-
40 evolution, size-dependent competitive asymmetry, intraguild predation.

41 Introduction

42 A persistent challenge in ecology is to understand how species can coexist when they overlap
43 in their resource use (Chesson, 2000). Whether two such species will coexist depends upon the
44 balance between the negative effect of competition over shared resources and the positive effect
45 of using some resources exclusively (Chesson, 2000; Siepielski & McPeck, 2010). For many
46 organisms, this balance depends upon the values of traits that determine the type of resource use
47 and the efficiency with which the resources are acquired and transformed into somatic growth,
48 survival, and offspring (Ellner *et al.*, 2016).

49 Body size is often a key trait influencing competitive ability and resource use (Werner &
50 Gilliam, 1984). For example, taller plants can access more sunlight and larger fish can forage more
51 efficiently and consume a wider range of prey sizes (Weiner, 1990; Young, 2004; Bassar *et al.*,
52 2016). In both cases, larger individuals are better competitors, a situation termed size-dependent
53 competitive asymmetry (Weiner, 1990). In size-structured communities, size-dependent competi-
54 tive asymmetries combine with competitive inequalities based on species' identity define the dif-
55 ferences in competitive effects between individuals on the same and other species across their
56 respective life cycles (Bassar *et al.*, 2016).

57 In addition to size-based competitive asymmetries, changes in body size can be associated
58 with changes in resource use (Hjelm *et al.*, 2003; de Roos & Persson, 2013; Aresco *et al.*, 2015;
59 Turner Tomaszewicz *et al.*, 2017). When this occurs, coexistence depends on how changes in
60 body size in each species influence resource use shifts, competitive asymmetries, and fitness,
61 particularly in the range of body sizes in which the species have the greatest overlap in resource
62 use (Loreau & Ebenhoh, 1994; Miller & Rudolf, 2011; Nakazawa, 2015; Bassar *et al.*, 2017b).

63 Testing theoretical predictions about coexistence in size-structured communities, however, is
64 an empirical challenge. Compelling tests require understanding two things: first, how body size
65 variation translates to competitive asymmetries and differences between the species in resource
66 use; and second, how these size-based interactions map to fitness effects across the life cycles
67 of the interacting species (Bassar *et al.*, 2017b; Chesson, 2000; Siepielski & McPeck, 2010). The
68 first requirement, separating individual effects of the confounded changes in resource use and
69 efficiency during ontogeny, can be met with careful experimentation (Inouye, 2001; Potter *et al.*,

70 2019).

71 The second requirement can only be met by integrating the demography of each species
72 with the knowledge acquired from the first requirement (Bassar *et al.*, 2017b). This is because,
73 while competitive interactions and resource use may change with ontogeny, the various stages
74 in the life cycle do not count equally towards fitness (Caswell, 2001). Reproductive value (per-
75 capita contribution of age- or size-class towards fitness), for instance, can change dramatically as
76 organisms grow or age (Caswell, 2001; Bassar, Travis & Coulson, 2017b)

77 A solution to these challenges is to develop demographic models of interacting structured
78 populations that can be readily parameterised by empirical data (Ellner *et al.*, 2016). These mod-
79 els allow researchers to evaluate how changes in the ecological interactions between the species
80 influences their fitness (Bassar *et al.*, 2016, 2017b,a). Applying such models requires devising
81 manipulative experiments that can measure, separately for each species, how trait variation influ-
82 ences resource use and competitive efficiency, and ultimately, the fitness consequences of trait
83 variation integrated across the life cycles of the organisms.

84 Here, we experimentally test how species- and size-dependent competitive asymmetries con-
85 tribute to the evolution of species coexistence in Trinidadian stream communities comprised of
86 Trinidadian guppy (*Poecilia reticulata*) and Hart's killifish (*Rivulus hartii*) a.k.a., KG communities
87 (Travis *et al.*, 2014). We executed a laboratory experiment that allowed us to parameterise a size-
88 structured demographic model for these species under two contrasting scenarios, representing the
89 beginning and endpoint of novel community formation (Travis *et al.*, 2014; Bassar *et al.*, 2017a).
90 Prior empirical work has demonstrated that coexistence between these species is an evolved prop-
91 erty, with coexistence more likely between established sympatric populations of each species than
92 between allopatric populations that first encounter each other (Bassar *et al.*, 2017a). However, it is
93 not clear whether the increased likelihood of coexistence is due to changes in competitive asym-
94 metries, changes in the resource niche use, or both. Specifically, we tested the hypothesis that
95 the evolution of stronger size-based competitive asymmetries in guppies increased the likelihood
96 of coexistence between both species in sympatry.

97 **Methods**

98 **Study system**

99 Each river that drains the Northern Mountain Range of the Caribbean island of Trinidad has a
100 replicated succession of fish communities. At low elevations, fish communities contain numerous
101 species (Gilliam *et al.*, 1993). Fish species diversity declines progressively upstream because
102 waterfalls impede the upstream movement of larger fish (Gilliam *et al.*, 1993). In lower stream
103 reaches, guppies and killifish co-occur with multiple predatory fish species (killifish-guppy-predator
104 communities, hereafter KGP communities). Above barrier waterfalls, guppies and killifish occur
105 without predators (killifish-guppy, or KG communities). Above these communities, killifish are the
106 only fish species found in the streams (killifish only, or KO communities). Life histories, behaviour,
107 morphology, and physiology evolve in both species as they adapt to these different communities
108 (Reznick & Endler, 1982; Ghalambor *et al.*, 2004; Auer *et al.*, 2018).

109 KG communities are thought to be formed when guppies are able to surmount barrier water-
110 falls and invade KO communities (Travis *et al.*, 2014). This encounter between KGP guppies and
111 KO killifish represents the first stage of KG community development with allopatric phenotypes.
112 Replicated experiments, wherein guppies from KGP communities were translocated over barrier
113 waterfalls into KO communities have shown that both species evolve genetically based trait differ-
114 ences that are consistent with those observed in comparative analyses of natural KG communities
115 (Reznick *et al.*, 1990, 2019; Walsh & Reznick, 2011). These evolutionary changes have been
116 observed over relatively short time periods (Reznick *et al.*, 2019). In this study, we consider sym-
117 patric phenotypes of killifish and guppies to be those from long-established KG communities that
118 have evolved together (Alexander *et al.*, 2006; Walter *et al.*, 2011). These phenotypes represent
119 the endpoint of the evolutionary interaction between the species in these locations (Bassar *et al.*,
120 2017a).

121 Guppies and killifish use similar resources, which makes their coexistence a persistent puzzle.
122 There is some evidence suggesting that both fish species alter their resource use after gup-
123 pies have invaded KO streams. Guppies feed primarily on aquatic invertebrates, detritus, and
124 algae (Bassar *et al.*, 2010; Zandonata *et al.*, 2011; Fraser & Lamphere, 2013) but guppies from
125 KGP communities feed mostly on invertebrates, while guppies in KG communities are more gen-

126 eralist feeders (Zandona *et al.*, 2011). Moreover, dietary studies based on stomach contents have
127 shown little support for strong size-based niche shifts in guppies (Zandonà *et al.*, 2015). Killi-
128 fish, on the other hand, are mostly insectivorous (Fraser & Gilliam, 1992) and are thought to have
129 stronger size-based niche shifts than guppies (Travis *et al.*, 2014). Field observations have shown
130 that killifish prey on aquatic and terrestrial invertebrates (Owens, 2010; Murray *et al.*, 2018). But
131 there is no evidence of strong size-based niche shifts in killifish.

132 Theory shows that different patterns of size-based niche use between the species can lead
133 to coexistence only if guppies are better competitors than killifish in the region of the niche that is
134 shared between the species (i.e., aquatic invertebrates; Bassar, Travis & Coulson, 2017b). Mark-
135 recapture and experimental studies have shown that larger guppies are better intraspecific com-
136 petitors than smaller guppies and that guppies from KG communities are generally stronger in-
137 traspecific competitors than KGP guppies (Bassar *et al.*, 2013; Potter *et al.*, 2019).

138 **Demographic model**

139 Our experiment was designed to estimate the parameters describing the interactions between
140 individuals of distinct species and body sizes, parameters that feed directly into a size-structured
141 demographic model (Bassar, Travis & Coulson, 2017b). A model that allows us to map competitive
142 interactions across the life cycle onto the fitness of both species. The demographic model is an
143 integral projection model (IPMs) described in Bassar *et al.* (2016) and Bassar, Travis & Coulson
144 (2017b). A key advantage of these type of models is that they can be parameterised with individual
145 data on demographic rates, allowing the generation of theoretical predictions and interpretation of
146 experimental data (Bassar *et al.*, 2016, 2017b; Potter *et al.*, 2019). We briefly summarise the
147 salient features of the model here. More details can be found in Bassar *et al.* (2016) and Bassar,
148 Travis & Coulson (2017b).

$$n(z', t + 1) = \int [G(z', z) \cdot S(z) + D(z', z) \cdot M(z) \cdot B(z) \cdot S(z)] \cdot n(z, t) \cdot dz. \quad (1)$$

149 where $n(z, t)$ is a distribution describing the number of individuals of body size z at time t ,
150 $n(z', t + 1)$ is a distribution describing the number of individuals of z' at time $t + 1$. The functions
151 S, G, B, M , and D are demographic rates representing survival, growth, probability of reproduction,

152 litter size, and size of offspring in individuals as functions of body size z at time t .

153 If $V_i = [S_i, G_i, B_i, M_i, D_i]$ is the set of the linearised demographic rate equations for species i ,
 154 z_i is the body size of a focal individual of species i , and x_i represents the body sizes of intraspecific
 155 competitors, then an equation for any of the mean demographic rates of species i competing with
 156 species j and other members of species i can be expressed as:

$$V_i(z_i, N_i) = \beta_{i_0} + \beta_{i_z} \cdot z_i + \beta_{i_N} \cdot \int \alpha_{ii}(z_i, x_i) \cdot n_i(x_i, t) dx_i + \beta_{i_N} \cdot \int \alpha_{ij}(z_i, x_j) \cdot n_j(x_j, t) dx_j. \quad (2)$$

157 The first two terms ($\beta_{i_0} + \beta_{i_z} \cdot z_i$) describe the value of the demographic rate of an individual
 158 of species i and size z in the absence of competition. The parameter β_{i_N} describes the per-capita
 159 effect on the demographic rate V (e.g., somatic grow rates or survival) of an individual of species
 160 i and size z of an equal sized individual of the same species. The function $n(x, t)$ describes the
 161 distribution of sizes of competitors at time t and may be either from the same species, i , or from
 162 another species, j . The species- and size-dependent effects of intraspecific and interspecific com-
 163 petition on the demographic rates are calculated as interaction surfaces $\alpha_{ii}(z_i, x_i)$ and $\alpha_{ij}(z_i, x_j)$,
 164 respectively, which describe the competitive equivalence of individuals of size x_i or x_j on individu-
 165 als of size z_i . Overall, the interaction surfaces can be interpreted as the relative competitive effect
 166 of a competitor of species i (or j) of size x on an individual of size z of species i . For example,
 167 if $\alpha_{ij}(z_i, x_j) = 3$, it means that the competitive effect of a competitor of size x of species j on a
 168 size z individual of species i is equivalent to the competitive effects of three individuals of species
 169 i and size z (see Bassar, Travis & Coulson, 2017b).

170 The outcome of competition can be determined from the shape of the interaction surfaces.
 171 In turn, the shape of the interaction surface depends upon the resources that are used by each
 172 species and on the size-dependent ability of individuals to effectively compete for those resources.
 173 When individuals use different resources and larger or smaller individuals are better at acquiring
 174 and assimilating those resources, the interspecific interaction surfaces can be modelled as an
 175 exponential function of the size and species of competitors as:

$$\alpha_{ij}(z_i, x_j) = e^{\eta_{ij} + \phi_j(x_j - v) - \phi_i(z_i - v)} \cdot e^{\frac{-(\eta_{ij} + \rho_j(x_j - v) - \rho_i(z_i - v))^2}{2H^2}} \quad (3)$$

176 The expression $e^{\eta_{ij} + \phi_j(x_j - v) - \phi_i(z_i - v)}$ describes how the competitive effects change as a func-
177 tion of species identity and body size (i.e., the species-dependent and size-dependent competitive
178 asymmetry component). The expression $e^{\frac{-(\nu_{ij} + \rho_j(x_j - v) - \rho_i(z_i - v))^2}{2H^2}}$ describes the proportion of niche
179 overlap between individuals of each species as a function of their body sizes.

180 In the first expression, the parameter η_{ij} captures the relative species-dependent competitive
181 effect, which is simply the difference between the competitive effects of intraspecific competitors
182 (species i) and interspecific competitors (species j) at size v , which is a centring value chosen by
183 the researcher. Typically, v is a biologically meaningful size, such as size at birth. If $\eta_{ij} < 0$, the
184 competitive effect of species j on species i at size v is less than the competitive effect of species i
185 is on itself. The size-dependent competition coefficients ϕ_i and ϕ_j describe how the magnitude of
186 the effect changes with body size in each species (i.e., size-dependent competitive asymmetry).
187 When $\phi_i = 0$, the competitive effects of species i are said to be symmetric with respect to body
188 size of species i (i.e., body size plays no role in determining the competitive advantage of species
189 i). When $\phi_i > 0$, competition is considered asymmetric with respect to size, and larger individuals
190 have stronger competitive effects than smaller individuals. Conversely, when $\phi_i < 0$, competition
191 is asymmetric with respect to size such that smaller individuals have stronger competitive effects
192 than larger individuals. Overall, the η and ϕ parameters together describe the relative competitive
193 effects of one species on the other. The degree of interspecific competitive asymmetry is therefore
194 given by the difference between the effects of conspecific competitors on focal growth (across all
195 sizes) and the effects of heterospecific competitors on focal growth (across all sizes).

196 Following previous treatments of niche overlap (MacArthur & Levins, 1967), the resource
197 niche is modelled as a normal distribution along a resource axis, R (Bassar, Travis & Coulson,
198 2017b). The niche overlap, as a function of body size, is the overlap of the distributions of indi-
199 viduals with trait value z from species i and trait value x from species j . The parameter ν_{ij} is the
200 difference in the mean of the resource niche at size v ; and ρ_i and ρ_j describe how the mean of
201 the resource niche changes with body size in species i and j , respectively. H^2 is the variance
202 in the niche width. In our experiment described below, we assume that ν_{ij} , ρ_i , and ρ_j are zero.
203 In this case, the niche overlap term is unity for all sizes, meaning all individuals compete for the
204 same resource. When the experiment is carried out using a single resource – as in this study –
205 this allows researchers to fit the demographic model to the empirical data without confounding

206 changes in competitive effects with changes in resource use.

207 **Experimental design**

208 We were interested in asking whether there is evidence for differences in species- and size-
209 dependent competitive effects (η and ϕ 's) for killifish and guppies between the initial (allopatric)
210 and final stages (sympatric) of community development and whether these changes would lead
211 to a greater likelihood of coexistence. We estimated these parameters by performing an aquaria-
212 based response surface experiment (Inouye, 2001), in which we manipulated the number and size
213 distributions of fish in the treatments (Fig. 1). We measured somatic growth over a 28-day period
214 and fitted a version of equation 2 to those data. Because theory predicts that the two species
215 could coexist if guppies are better competitors for resources on the shared portion of the niche
216 (i.e., aquatic invertebrates), we fed the fish identical quantified rations of aquatic invertebrates
217 over the course of the experiment. We ran this experiment using guppies and killifish with al-
218 lopatric phenotypes (KO killifish and KGP guppies) and sympatric phenotypes (KG guppies and
219 KG killifish). The pairing of KO killifish with KGP guppies recreates the initial stages of the invasion
220 of a KO community by guppies from KGP communities. The pairing of KG killifish with KG guppies
221 represents the situation after each species has adapted to the other.

222 Each aquarium contained either two or four fish (Fig. 1). Within the two fish treatment, the
223 tanks contained either two guppies, two killifish, or one guppy and one killifish. Within the four
224 fish treatment, the tanks contained either four guppies, four killifish, three guppies and one killifish,
225 or one guppy and three killifish. Manipulating the sizes of fish in each tank produced different
226 combinations of competitor sizes and enabled the experiment to cover different portions of the
227 interaction surfaces. All fish were classified into four size classes ($\pm 2mm$): $10mm$, $14mm$, $18mm$,
228 and $22mm$. These size classes represent different life-history stages in guppies (10 and $14mm$ =
229 juveniles, $18mm$ = young adults, $22mm$ = older adult females; Reznick *et al.*, 2001) and juvenile
230 stages of killifish, which mature at approximately $35mm$ (Walsh & Reznick, 2008). Each aquar-
231 ium had either one or two size classes of fish, and sizes were paired so that each size category
232 competed against fish of all other size categories in the experiment (112 possible unique compe-
233 tition trials). Simulations and experimental studies have shown that this experimental design has

234 enough power to estimate the parameters of the interaction surfaces (Bassar *et al.*, 2017b; Potter
235 *et al.*, 2019). Some experimental trials were not possible because 22mm killifish tended to kill
236 guppies smaller than 18mm.

237 **Sampling and allocating fish to treatments**

238 We ran the experiment with fish from two different river systems, the Aripo and the Quare. These
239 systems represent independent origins of allopatric KGP guppies invading KO habitats to estab-
240 lish coevolved sympatric KG communities (Willing *et al.*, 2010; Walter *et al.*, 2011). In the Aripo
241 drainage, we collected guppies from KGP communities downstream from Haskins' Falls on the
242 Aripo River. We collected KG guppies and killifish from the Naranjo and Endler streams and KO
243 killifish from the upper reaches of the Naranjo stream. In the Quare drainage, we collected KGP
244 guppies from the main branch of the Quare River, adjacent to the pump-house on the Hollis Reser-
245 voir Road. We collected KG guppies and killifish from the El Campo and Quare 2 tributaries to the
246 Quare River and KO killifish from the upper reaches of each of these tributaries.

247 We performed our experiments during the dry season (February to June). We collected gup-
248 pies with butterfly nets and transported them to our field station in plastic bottles with medicated
249 water (0.15mL/L of Stress Coat®, Mars Fishcare, PA, USA; 0.075mL/L AmQuel Plus®, Kordon
250 LLC, CA, USA). Killifish were collected with hand nets and transported to the laboratory in Hefty®-
251 bags. In the laboratory, we treated all fish with a salt bath (sea salt 25g/l, 15min) to eliminate
252 ectoparasites and with antibiotics (0.187g/20L Tetracycline or 1.25g/20L Furan) to reduce the like-
253 lihood of bacterial infections.

254 At the beginning of the experiments, we assigned each fish to an appropriate size class based
255 on standard length (SL, $\pm 0.5mm$), measured its mass ($\pm 0.001g$), and classified it as male, female,
256 or juvenile. We used only females and juvenile guppies, and juvenile killifish in our experiment.
257 We did not use adult male guppies because they have little or no growth after maturity (14mm),
258 which limits our ability to evaluate the fitness consequences of the competitive environment. We
259 randomly assigned each individual to a size class and density treatment (Fig. 1). Before adding
260 them to their tanks, we marked individuals with a single subcutaneous injection of a coloured
261 elastomer (Northwest Marine Technology) for identification. We kept extra fish in glass tanks at

262 approximately two fish per litre of water to replace any fish that died during the experiment, and to
 263 maintain the density and size-structure treatment for the experimental fish.

264 Fish feeding and housing

265 We performed the competition trials in plastic tanks ($L \cdot W \cdot H : 26 \cdot 16 \cdot 17\text{cm}$) for 28 days and
 266 provided food to each tank once a day as a 1000 μL solution of *Artemia* nauplii (≈ 400 live larvae).
 267 We filled each tank with $\approx 4\text{L}$ of medicated water (0.15mL/L of Stress Coat, Mars Fishcare, PA,
 268 USA; 0.075mL/L AmQuel Plus®, Kordon LLC, CA, USA). On the first day of the experiment, we
 269 added $500\mu\text{L}$ of 10% Formalin to each tank to further reduce ectoparasites such as *Gyrodactylus*
 270 *spp.* and to avoid secondary bacterial infections. We performed water changes every other day
 271 by siphoning out up to 75% of the water, making sure to remove organic waste and excess food.
 272 Dead or missing individuals were replaced with another fish of the same species, community of
 273 origin, and size class to maintain the experimental treatment.

274 Data analysis

275 Statistical model

276 We estimated the competition parameters in equation 2 using the somatic growth increment as
 277 a demographic rate (V). The somatic growth increment is an ideal demographic rate from which
 278 to estimate the effects of competition –both fish species of these size classes grow considerably
 279 over a 28-day period – and fitness is extremely sensitive to effects on somatic growth (Bassar
 280 *et al.*, 2013, 2017a). The demographic equation for somatic growth is a slightly modified version
 281 of equation 2 (Griffiths *et al.*, 2020). Our somatic growth increment equation for guppies was:

$$\ln\left(\frac{z'_G}{z_G}\right) = \beta_{0,G} + \beta_{z,G} \cdot \ln\left(\frac{z_G}{v}\right) + \beta_{z^2,G} \cdot \ln\left(\frac{z_G^2}{v^2}\right) +$$

$$\left[\beta_{N,G} + \beta_{zN,G} \cdot \ln\left(\frac{z_G}{v}\right)\right] \cdot \sum_{x_G}^{k_G} e^{\phi_G \cdot (x_G - v) - \phi_G \cdot (z_G - v)} + \quad (4)$$

$$\left[\beta_{N,G} + \beta_{zN,G} \cdot \ln\left(\frac{z_G}{v}\right)\right] \cdot \sum_{x_K}^{k_K} e^{\eta_{GK} + \phi_K \cdot (x_K - v) - \phi_G \cdot (z_G - v)} + \varepsilon(0, \sigma^2)$$

282 Where z'_G is the observed length of an individual guppy after the interval and z_G is the ob-
283 served length of the same guppy at the beginning of the experiment. The somatic growth incre-
284 ment typically decreases with increased length ($\beta_{z,G}$) and sometimes is slightly convex, which is
285 captured by the quadratic term, $\beta_{z^2,G}$. We also included other terms to the model ($\beta_{N,G}$ and $\beta_{zN,G}$)
286 that describes how individuals of distinct sizes respond to resource competition. The integrals in
287 equation 2 are replaced by summations in equation 4 because the populations in the experiment
288 are small and are better described in discrete terms rather than continuous functions. The indexes
289 on the summation thus represent individual guppies or killifish. The term $\varepsilon(0, \sigma^2)$ is a normal resid-
290 ual error term with mean of zero and variance σ^2 . An analogous equation was fitted to the killifish
291 data.

292 **Model fitting**

293 We estimated all parameters in equation 4 using a Bayesian modelling framework in Stan via the
294 *rstan* package in R 3.6 (Carpenter *et al.*, 2017). We fitted data for the Quare and Aripo drainages
295 separately. To allow comparisons between species and phenotypes within drainages, we fit mod-
296 els that included both species from allopatric and sympatric locations. We used dummy coding
297 to identify parameters for the distinct species and phenotypes. Posteriors were sampled from six
298 Hamilton Monte Carlo (HMC) chains, 8000 iterations, and a warmup of 5000 iterations. We used
299 informative priors for the guppy interaction surface parameters that we derived from similar exper-
300 iments on intraspecific competition using KGP and KG guppies (Potter *et al.*, 2019). For the rest
301 of the parameters, we used weakly informative priors, e.g., mean= 0 and SD= 5. For all models,
302 we verified that all four chains converged using the estimated potential scale reduction statistic
303 (\hat{R}) and visually checking the trace plots (Fig. S1-S6). Additionally, we evaluated each model's
304 behaviour by plotting the predicted vs observed values and the distribution of their residuals (Fig.
305 S7).

306 We modelled somatic growth increment with a normal error distribution and length centred at
307 $10mm$ (i.e., v). To facilitate the interpretation of the parameters describing the interaction surface,
308 beginning from near birth to older individuals, we set v equal to $10mm$ in both species. This es-
309 timates the difference between the species in their competitive abilities at $10mm$. We report the

310 means of the posterior samples of the parameters and the 95% Compatibility Interval (i.e., mean
311 [2.5%, 97.5% CI]). For comparisons between parameters, we estimated the difference between
312 the posterior samples and reported the mean differences, CI, and the Level of Support (LOS) of
313 the difference in the parameters. The LOS is estimated as the proportion of the posterior differ-
314 ence distribution greater or less than zero. We asked whether the species and size-dependent
315 competition parameters improved the overall fit of the growth models to the data by comparing
316 the models for each treatment with a null model assuming symmetric species and size-dependent
317 competition parameters ($\eta_{GK} = 0$; $\phi_G = \phi_K = 0$) using the function *compare()* from the rethink-
318 ing R package (McElreath, 2020). We chose the best model as the model with the lowest WAIC
319 (Watanabe Akaike Information Criterion) and highest weight.

320 For the statistical analyses, we used the growth data of any fish that began and completed
321 the experiment (776/891; 87%). Survival to the end of the experiment was higher in the Aripo
322 compared to the Quare (92% vs 82%), yielding slightly higher sample sizes in the Aripo compared
323 to the Quare. We replaced any fish that died during the experiment with a similar-sized fish. These
324 replacements were not used as dependent data for growth unless they were in the experiment for
325 more than 25 of the 28 days of the experiment. We used the size of the replacement fish to
326 calculate the weighted average size of competitors. To do so, we multiplied the body size of the
327 replaced and replacement fish by the number of days they were in the experiment and divided by
328 the total number of days in the experimental tanks.

329 **Comparisons of the change in the competitive asymmetries between communities**

330 We used the posterior samples of the parameters describing the interaction surfaces to ask how
331 the differences between the intraspecific and interspecific competitive effects of each species on
332 the other changed between allopatric (i.e., KGP guppies vs KO killifish) and sympatric phenotypes
333 (i.e., KG guppies vs KG killifish). For each species, we calculated the change in competitive
334 asymmetry by subtracting the difference in the intra- and interspecific interaction surfaces from
335 the allopatric trials (representing the initial conditions following the invasion of guppies) from the
336 difference in the intra- and interspecific interaction surfaces in the sympatric trials (representing the
337 competitive conditions in established KG communities). For example, for guppies, we calculated

338 the change in competitive asymmetry as (ΔCA):

$$\Delta CA = \ln \left(\frac{\alpha_{GG}(z_G, x_G)}{\alpha_{GK}(z_G, x_K)} \right)_{sym} - \ln \left(\frac{\alpha_{GG}(z_G, x_G)}{\alpha_{GK}(z_G, x_K)} \right)_{allo}, \quad (5)$$

339 where subscripts "sym" and "allo" denote the sympatric and allopatric comparisons, respec-
340 tively. The effect is independent of the size of the individual experiencing the competitive im-
341 pact (i.e., z_G), which can be seen by replacing the alphas with the parameters [$\alpha_{GK}(z_G, x_K) \rightarrow$
342 $e^{\eta_{GK} + \phi_K(x_K - v) - \phi_G(z_G - v)}$] and rearranging them:

$$\Delta CA = [(\phi_G - \phi_K)x - \eta_{GK}]_{sym} - [(\phi_G - \phi_K)x - \eta_{GK}]_{allo}, \quad (6)$$

343 Calculating the difference in competitive asymmetries in this way captures how the differ-
344 ences between the effects of intraspecific and interspecific competitors change from allopatric to
345 sympatric phenotypes. Positive values of ΔCA indicate that the effects of interspecific competi-
346 tion are stronger in sympatric phenotypes compared with allopatric ones, negative values of ΔCA
347 indicate that the effects of interspecific competition are weaker in sympatric phenotype, compared
348 with allopatric ones.

349 **How changes in competitive asymmetry alter predictions of coexistence**

350 We parameterised the model of Bassar, Travis & Coulson (2017b) using the posterior means of
351 the parameter from this study to illustrate how changes in the interaction surfaces between the two
352 communities alter predictions about species coexistence. We parameterised the model, assuming
353 that the only differences between the species are the values of the intra- and interspecific inter-
354 action surfaces. All other parameters were identical and based on KG guppies, as described in
355 Bassar, Travis & Coulson (2017b). Using parameters from a single species and changing only the
356 competition parameters isolates the effect of the change in the competition parameters on coex-
357 istence. Other differences between the species that may contribute to coexistence or competitive
358 exclusion will not be included.

359 We used the model to calculate the invasion exponent of each species in each community
360 type as the dominant eigenvalue of the matrix approximation of the continuous model (for de-

361 tails on these calculations, Bassar, Travis & Coulson, 2017b). Coexistence is predicted by mutual
362 invasibility, meaning that each species can invade a population of the other when the resident pop-
363 ulation is at its single species equilibrium (Siepielski & McPeck, 2010; Bassar *et al.*, 2017b). We
364 illustrate the predictions of the model by evaluating mutual invasibility over a range of ontogenetic
365 niche shift parameters (ρ) in both species. We varied ρ from no niche shift ($\rho = 0$) to a value
366 indicating moderate niche shifts ($\rho = 0.18$) between new-born individuals ($\approx 6mm$ SL) and larger
367 individuals ($\approx 25mm$ SL), as in Bassar, Travis & Coulson (2017b).

368 Results

369 Are competitive interactions between guppies and killifish asymmetric and size- 370 structured?

371 Yes, resource competition within and between guppies and killifish depends strongly on the species
372 identity of their competitors (η) and on body size (ϕ , Table 1). Incorporating the parameters that
373 describe species and size-dependent competition into the growth models increased the fit of the
374 models to the data compared with models that did not include these effects ($\Delta WAIC > 10.9$
375 for all four models, Table 2). At $10mm$ (SL), there was strong and consistent support for killi-
376 fish exerting weaker species-dependent competitive effects on guppies than guppies on them-
377 selves (all $LOS_{\eta_{GK} < 0} > 97\%$, see Table 1 and Fig. 2b). At the same time, small ($10mm$ SL)
378 guppies exerted a stronger competitive effect on killifish than a killifish of equal size on themselves
379 ($-\eta_{GK} = \eta_{KG} > 0$). For both species, larger individuals were stronger competitors (Table 1,
380 Fig. 2a: $\phi > 0$, i.e., positive size-dependent competitive effects for both species). The level of
381 support for positive size-dependent competitive asymmetry ($\phi > 0$) was larger than 94% in all but
382 allopatric killifish from the Aripo drainage ($LOS_{\phi_K > 0} = 88.4\%$, Table 1).

383 Is there evidence for the evolution of changes in the competitive asymmetry be- 384 tween guppies and killifish following guppy invasion?

385 Yes, for both guppies and killifish, the level of interspecific competitive asymmetry was smaller
386 between sympatric phenotypes – representing coadapted communities– than between allopatric

387 phenotypes –representing the initial invasion of guppies into killifish populations ($LOS_{\Delta CA < 0} >$
388 99.3%, Fig. 3a and 4a). Contrary to the Aripo system, in the Quare system the level of interspecific
389 competition increases with the size of competitors, suggesting that sympatric killifish outside the
390 body size range of guppies have stronger competitive effects than guppies. Although the greatest
391 change occurred in the largest size classes of competitors (middle and right columns in Fig. 3 and
392 4), the change in the interspecific differences in competitive asymmetry was consistent across all
393 sizes.

394 In both competitive settings, the competitive asymmetries across all sizes favoured guppies.
395 First, guppies exerted larger competitive effects on conspecifics compared to those exerted by
396 killifish on guppies across all but the largest body sizes (Fig. 3). Second, the effect of interspecific
397 competition of guppies on killifish was greater than the effect of intraspecific competition between
398 killifish (Fig. 4).

399 Although the direction of change in species-dependent competitive asymmetries (following
400 guppy invasion, i.e., from allopatric to sympatric communities) was consistent, the magnitude of
401 this change differed between drainages (Fig. 2). In both drainages, co-evolved, sympatric killifish
402 were stronger competitors to guppies than the allopatric killifish, but this effect was stronger in
403 the Quare drainage compared to the Aripo (Quare $\Delta\eta_{GK} = 2.628$ [0.81, 4.434]; Aripo $\Delta\eta_{GK} = 0.316$
404 [0.017, 0.637]; Fig. 2b).

405 There was a difference between the drainages in how the association between body size and
406 competitive effect changed between allopatric and sympatric phenotypes ($\Delta\phi_G = \phi_{G,sym} - \phi_{G,allo}$
407 and $\Delta\phi_K = \phi_{K,sym} - \phi_{K,allo}$). In the Aripo drainage, competitive effects increased with body size
408 to a greater extent in sympatric fish than in allopatric fish ($\Delta\phi_K = 0.05$ [0.009, 0.085]; $\Delta\phi_G = 0.03$,
409 [0.004, 0.057]). By contrast, in the Quare drainage, there was no clear difference in how competitive
410 effects changed with body size between sympatric and allopatric phenotypes ($\Delta\phi_K = -0.128$,
411 [-0.270, 0.072]; $\Delta\phi_G = -0.017$, [-0.050, 0.072]).

412 **How much do these changes in competitive asymmetry shift predictions about co-** 413 **existence in guppies and killifish?**

414 The two species IPM model of Bassar, Travis & Coulson (2017b), when parameterised with the
415 interaction surfaces from these experiments, suggests that coexistence is slightly more likely be-
416 tween the sympatric phenotypes of both species than the allopatric phenotypes (Fig. 5). In gen-
417 eral, throughout most of the parameter space defined by the size-dependent niche shifts in each
418 species, the model predicts that guppies will exclude killifish. However, the area in which coex-
419 istence is possible expands from the allopatric to the sympatric phenotype combinations (Fig. 5).
420 In the Aripo and Quare drainages, the percentage of parameter space in which coexistence is
421 predicted to increase from allopatry to sympatry (Aripo: 6.6% to 8.3%; Quare: 0% to 12.2%). In
422 both drainages, the region where killifish can exclude guppies also expands (Aripo: < 1% to 19%;
423 Quare: 0% to 2.5%). Coexistence between these species is predicted to occur above the diagonal,
424 where killifish shift their resource use with increased body size to a greater degree than guppies.

425 **Discussion**

426 In this study, we quantified scenarios of intra and interspecific competition at two stages of the
427 formation of a new fish community. We described the degree of competitive asymmetry between
428 the initial (allopatric phenotypes) and final stages (sympatric phenotypes) of a guppy-killifish com-
429 munity formation, following the up-stream invasion of guppies into killifish habitats. In both stages
430 of the KG community development, guppies tended to be stronger competitors than killifish. How-
431 ever, we found that guppies and killifish became more equal competitors in sympatry. This change
432 in the degree of competitive asymmetry increased the likelihood of coexistence of these species
433 in sympatry. The decrease in the competitive asymmetry between the allopatric and sympatric
434 populations was due to changes in both species and size-dependent competitive asymmetries.

435 The different pattern of size-dependent competitive asymmetries between the two drainages
436 suggests that there are several routes to achieve the same effect across the life cycle of guppies
437 and killifish. In the Aripo drainage, the change in competitive asymmetry among small competitors
438 was moderate compared to the change in larger competitors (Fig. 3A and 4A). In contrast, in the

439 Quare drainage, the change in competitive asymmetry was much greater for smaller compared to
440 larger competitors (Fig. 3D and 4D). Integrated across the entire life cycle of the guppies and the
441 juvenile stages of killifish, the effect on the ability of each species to invade the other was similar;
442 changes in competitive asymmetry led to an expanded region of coexistence and a region where
443 killifish could exclude guppies, depending on the degree of ontogenetic niche shifts in each of the
444 species (Fig. 5).

445 As predicted, the competitive advantage of guppies over killifish in allopatric and sympatric tri-
446 als indicates that killifish should have stronger ontogenetic niche shifts than guppies in both newly
447 founded and established KG communities (Balfour *et al.*, 2003; Reichstein *et al.*, 2013; Bassar
448 *et al.*, 2017a,b). There is some support for these predictions from niche occupancy from existing
449 data. Guppies in KG communities have a broader resource use than guppies from KGP commu-
450 nities (Bassar *et al.*, 2010; Zandona *et al.*, 2011). Killifish rely more on terrestrial invertebrates
451 than aquatic ones (Fraser *et al.*, 1999; Owens, 2010) and it seems that as they grow larger, killifish
452 increase their consumption of terrestrial prey (Dough Fraser *pers. comm.*), but currently there is
453 no empirical data supporting this claim. Additionally, we do not currently know how differences in
454 resource use at the species level or across sizes within a species map to the fitness of the two
455 species.

456 In a previous study, Fraser & Lamphere (2013) found that allopatric (KO) killifish are stronger
457 competitors than allopatric (KGP) guppies. In contrast to their study, we found that KGP guppies
458 are better competitors than KO killifish. These differences are mainly the result of distinct exper-
459 imental approaches. First, Fraser & Lamphere (2013) performed their experiment with similarly
460 sized individuals of the two species, particularly guppies from the larger end of their natural size
461 distribution. This restricts their results to only part of the range of sizes in which guppies and
462 killifish partly share a niche, in particular the part in which competition for resources might not be
463 so strong or where killifish may be stronger competitors than guppies. The range of body sizes
464 used in this study captures most stages in the life history of guppies and the initial stages in the life
465 history of killifish (Reznick *et al.*, 2001; Walsh & Reznick, 2008), in which these species are more
466 likely to compete for resources (Travis *et al.*, 2014). Our results are therefore a better representa-
467 tion of the effects of resource competition and allow us to derive more robust conclusions about
468 the changes in competition among guppies and killifish in the region where their niches overlap.

469 A caveat to our study is that we performed the experiments with wild-caught individuals. Thus,
470 a combination of phenotypic plasticity, experience, and genetic differences may each explain a
471 significant part of the variation in competitive asymmetries of the fish used in this study. The
472 ideal experiment should use second generation (F2) laboratory-bred individuals to separate the
473 plastic and genetic differences underlying the differences in competitive ability and test the effects
474 of competition on multiple life-history traits (e.g., survival and reproduction).

475 The evolution of size-competitive asymmetries increases the likelihood of coexistence, but
476 only in relatively small areas of parameter space defining size-dependent niche shifts (Fig. 5).
477 This suggests that KG guppies should still exclude KG killifish. Their demonstrable co-existence
478 means that other ecological mechanisms must be acting. One possibility is that temporal or spatial
479 variation may interact with size-structured interactions (e.g., competition and predation) to favour
480 coexistence via storage effects and nonlinear effects competition on fitness (Warner & Chesson,
481 1985; Chesson, 2000; Kuang & Chesson, 2010). In the wild, guppies and killifish experience
482 pronounced wet and dry seasons that change their resource landscape completely (Travis *et al.*,
483 2014). During the wet season, aquatic prey items are drastically reduced while terrestrial prey
484 items increase (Owens, 2010), a pattern that might offer a benefit to killifish. Indeed, guppy mor-
485 tality is much higher in the wet season than the dry season, whereas the reverse is true for killifish
486 (Travis *et al.*, 2014).

487 A second possibility is based on the fact that guppies and killifish each consume neonates of
488 their own and the other species (Fraser & Gilliam, 1992; Fraser & Lamphere, 2013). The extent to
489 which intraguild predation enhances the likelihood of coexistence depends on whether predatory
490 effects are themselves symmetric between species (Bassar *et al.*, *unpublished data*). In this case,
491 we do not yet know whether one species is a more voracious predator of the other and whether
492 this component of the interaction evolves after initial contact as well.

493 Regardless of the mechanisms, this study demonstrates that the effects of body size on
494 competition and niche differences between the species are likely to play an influential role in the
495 evolution of coexistence. Size-based variation in these coexistence mechanisms is one way that
496 individual differences can alter species coexistence through non-linear effects of competition on
497 fitness (Hart *et al.*, 2016). Given the ubiquity in nature of size-based interactions and their impor-
498 tant ecological effects, understanding such interactions ought to be a priority for understanding

499 coexistence (or the lack thereof) in natural communities.

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506 **Author Contributions**

507 RDB developed the models, and RDB and JT conceived of the experiments with input from
508 DNR. JMA, TP, AB, SC, NF performed the experiments. JMA and RDB analysed the results. JMA,
509 RDB, and JT wrote the manuscript, and all authors contributed to the final draft.

510 **Data Availability Statement**

511 The full data and the code will be deposit in Dryad.

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Table 1: Parameter estimates of the models.

Parameter	Aripo								Quare							
	Allopatric				Sympatric				Allopatric				Sympatric			
	mean	SD	2.50% (CI)	97.50% (CI)	mean	SD	2.50% (CI)	97.50% (CI)	mean	SD	2.50% (CI)	97.50% (CI)	mean	SD	2.50% (CI)	97.50% (CI)
Guppy																
β_0	0.397	0.03	0.337	0.456	0.328	0.037	0.255	0.401	0.423	0.024	0.377	0.47	0.318	0.034	0.25	0.385
β_z	-0.762	0.073	-0.909	-0.619	-0.575	0.096	-0.761	-0.387	-0.859	0.068	-0.994	-0.727	-0.591	0.087	-0.761	-0.413
β_{z^2}	0.355	0.054	0.25	0.462	0.253	0.068	0.12	0.386	0.385	0.058	0.271	0.499	0.279	0.087	0.107	0.45
β_N	-0.073	0.009	-0.089	-0.056	-0.038	0.01	-0.057	-0.019	-0.081	0.007	-0.095	-0.068	-0.034	0.011	-0.056	-0.012
β_{zN}	0.084	0.016	0.054	0.115	0.035	0.02	-0.002	0.074	0.107	0.013	0.081	0.132	0.028	0.022	-0.017	0.071
σ	0.04	0.003	0.035	0.046	0.055	0.004	0.048	0.063	0.037	0.003	0.032	0.042	0.046	0.004	0.039	0.055
Killifish																
β_0	0.39	0.033	0.324	0.455	0.695	0.032	0.631	0.758	0.17	0.028	0.119	0.232	0.559	0.055	0.451	0.667
β_z	-0.707	0.076	-0.861	-0.559	-0.976	0.09	-1.153	-0.799	-0.322	0.123	-0.573	-0.091	-0.863	0.148	-1.153	-0.569
β_{z^2}	0.249	0.068	0.114	0.382	0.418	0.069	0.283	0.552	0.157	0.125	-0.081	0.402	0.295	0.095	0.106	0.482
β_N	-0.06	0.009	-0.078	-0.042	-0.096	0.009	-0.114	-0.079	-0.002	0.003	-0.009	0.000	-0.085	0.014	-0.113	-0.058
β_{zN}	0.078	0.016	0.047	0.109	0.06	0.017	0.027	0.093	-0.007	0.006	-0.019	0.006	0.085	0.029	0.029	0.144
σ	0.038	0.003	0.032	0.045	0.048	0.004	0.042	0.056	0.062	0.005	0.054	0.073	0.053	0.005	0.044	0.065
Interaction surface																
ϕ_G	0.02	0.01	0.000	0.039	0.05	0.009	0.032	0.069	0.038	0.011	0.017	0.06	0.022	0.014	-0.005	0.049
ϕ_K	0.02	0.017	-0.013	0.053	0.067	0.01	0.048	0.086	0.19	0.082	-0.005	0.325	0.062	0.021	0.019	0.102
η_{GK}	-0.506	0.121	-0.761	-0.285	-0.191	0.096	-0.379	-0.003	-3.091	0.927	-4.893	-1.277	-0.463	0.139	-0.732	-0.184

Table 2: Fit statistics for growth models of guppies and killifish. Including the interaction surface parameters increased model fit (lower WAIC) and model weight.

Model	WAIC	SE	dWAIC	dSE	pWAIC	weight
Aripo allopatric						
with	-670.6	39.76	0	NA	22.8	1
without	-623.6	34.38	47	17.35	16.7	0
Aripo sympatric						
with	-728.9	49.11	0	NA	30.8	1
without	-690.8	33.34	38.1	27.48	19.9	0
Quare allopatric						
with	-692.4	24.54	0	NA	17.8	1
without	-617.9	30.45	74.5	21.8	17.2	0
Quare sympatric						
with	-448.4	26.46	0	NA	17.2	1
without	-437.6	22.55	10.9	9.28	12.9	0

641 **Figure 1.** Schematic representation of the design of the experiment. Each coloured cell rep-
642 represents an aquarium, in which we manipulated the density (high and low: orange and blue cells,
643 respectively) and frequency of guppies (G) and killifish (K) across a range of body sizes. Within
644 each aquarium, each fish acted as a competitor (X-axis) and as a focal fish (y-axis).

645

646 **Figure 2.** Estimated species- and size-dependent competitive asymmetry parameters. In a),
647 values greater than zero indicate positive size-based competitive asymmetry. In b), η_{GK} indicate
648 that individual killifish have a smaller competitive effect on guppies than guppy of them selfs at
649 10mm.

650

651 **Figure 3.** Change in competitive asymmetry for guppies. Panel a) shows the change in
652 competitive asymmetry from allopatry to sympatry. Panels b), c), e), and f) show slices of the in-
653 teraction surface for a “focal” 10mm guppy competing against either other guppies (red) or killifish
654 (black) of all sizes. Values less than 1 mean that the competitive asymmetry favours the 10mm
655 guppy, and values greater than one means favours the competitor. Shaded areas represent the
656 95% CI, and percentages are the level of support that $\Delta CA > 0$.

657

658 **Figure 4.** Change in competitive asymmetry for killifish. Panel a) shows the change in com-
659 petitive asymmetry from allopatry to sympatry. Panels b), c), e), and f) show slices of the interaction
660 surface for a “focal” 10mm killifish competing against either other killifish (black) or guppies (red)
661 of all sizes. Values less than 1 mean that the competitive asymmetry favours the 10mm guppy,
662 and values greater than one means favours the competitor. Shaded areas represent the 95% CI,
663 and percentages are the level of support that $\Delta CA > 0$.

664

665 **Figure 5.** Predictions from IPM (Integral Projection Model) on species coexistence. The X-
666 and y- axes represent how much guppies and killifish, respectively, shift their niches with increased
667 body size. Light grey areas are those where guppies and killifish can coexist stably.

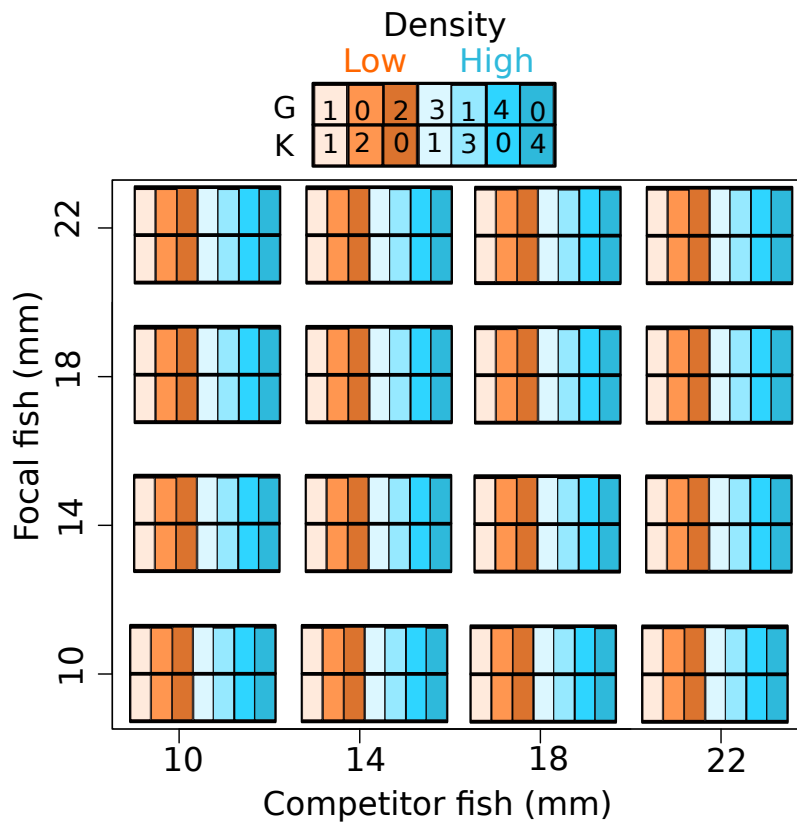


Figure 1:

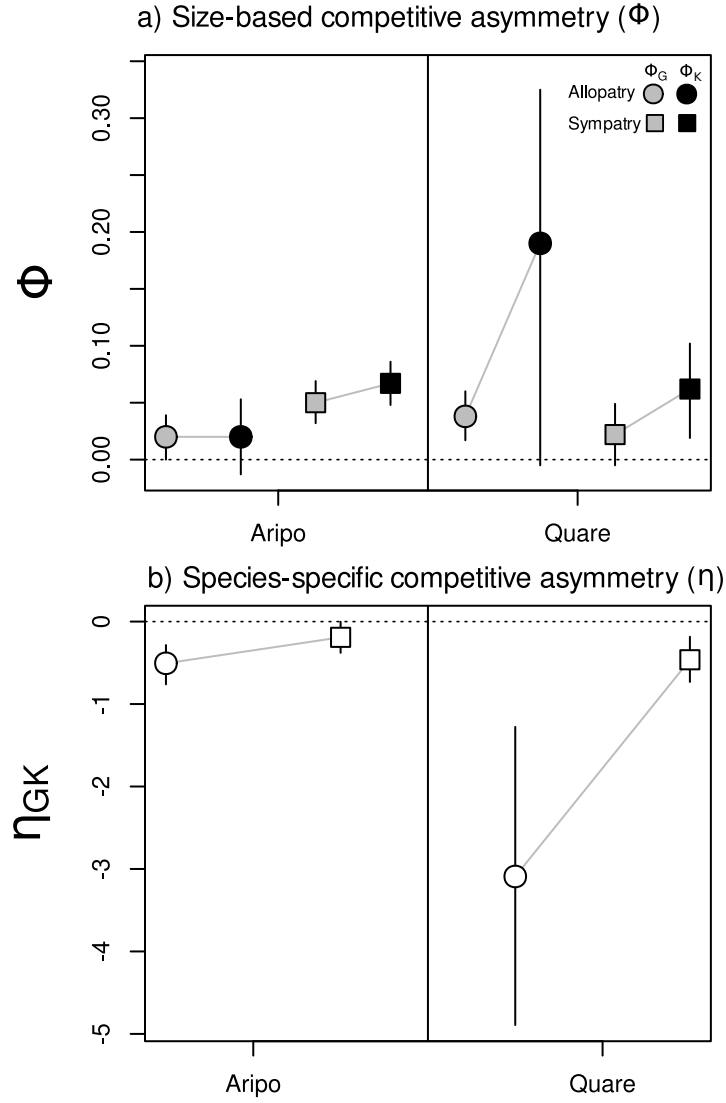


Figure 2:

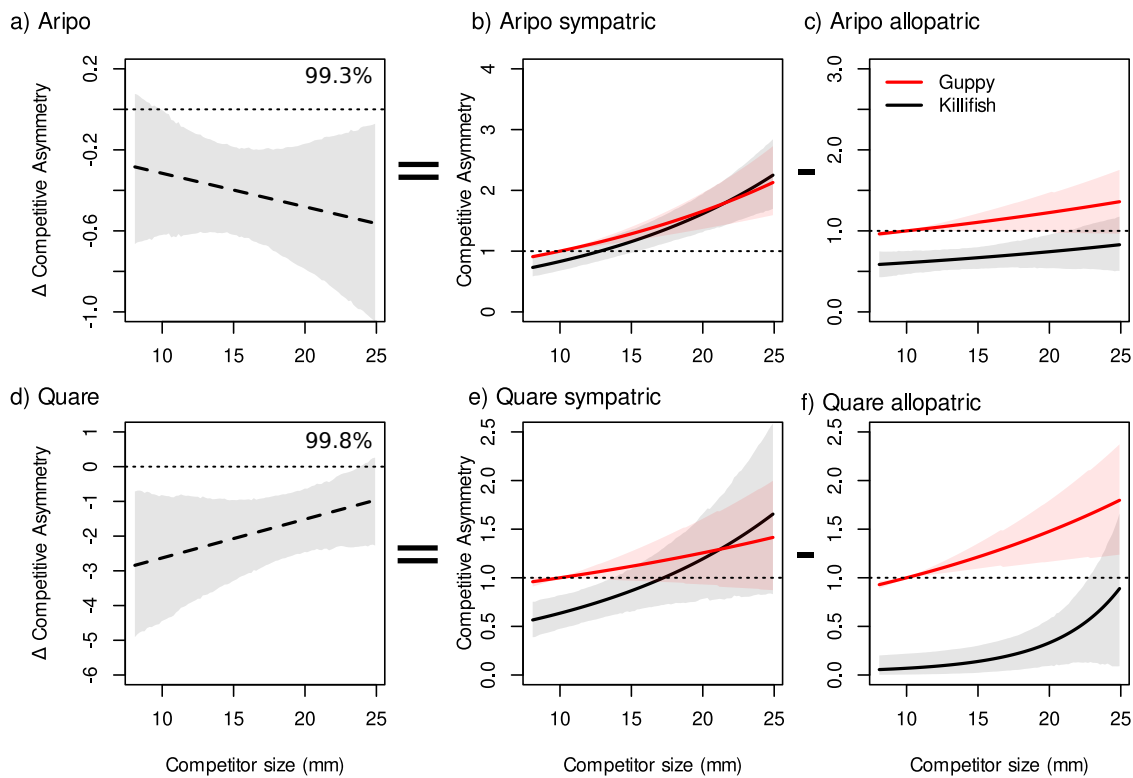


Figure 3:

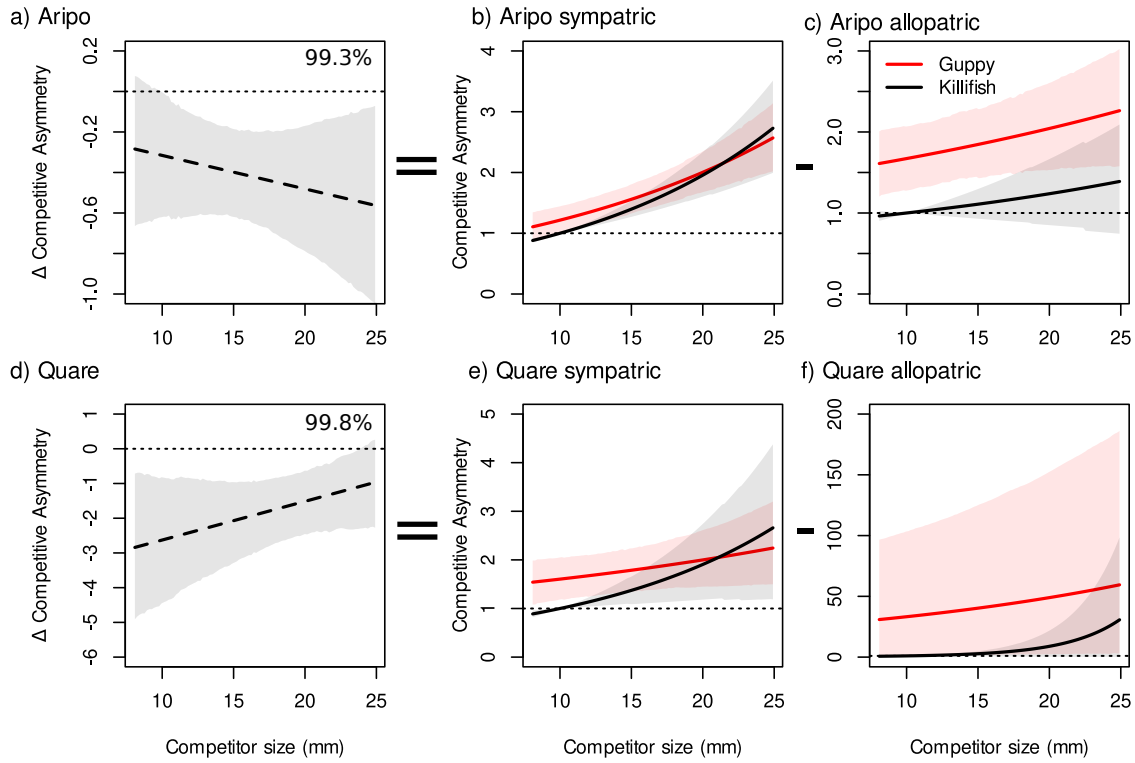


Figure 4:

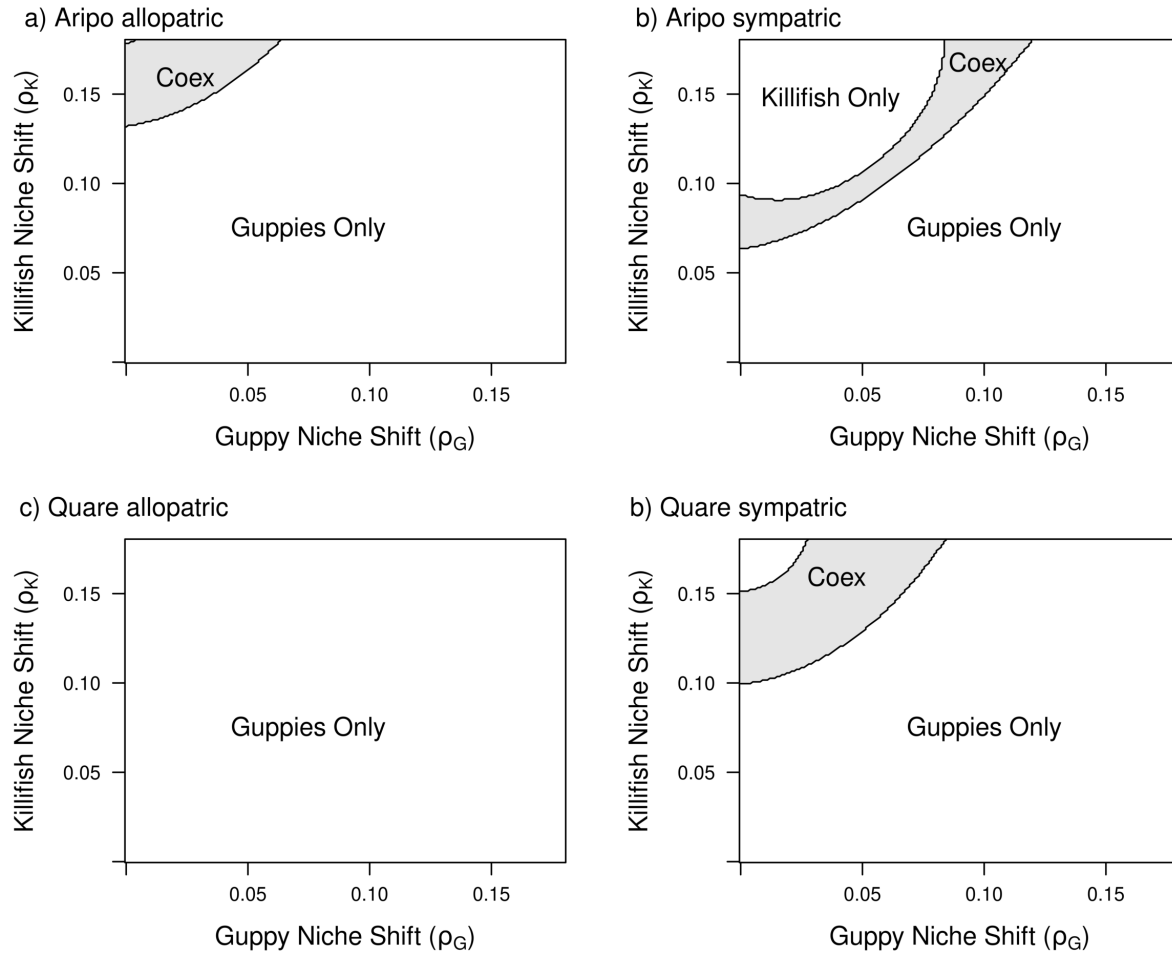


Figure 5: