Parent-offspring conflict, ecology, and life history diversification of livebearing fishes

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Major shifts in life history evolution—such as the transition from pre- to post-fertilization maternal provisioning in viviparous organisms—require complex morphological and physiological adaptations. The conditions under which these transitions arise remain largely unexplored. Theory postulates that parent-offspring conflict can drive diversification in maternal provisioning strategies, but while alternative hypotheses focusing on sexual selection and ecological adaptation have been proposed, neither have been evaluated comparatively. Livebearing fishes (Poeciliidae) have provided important insights into life history evolution due to variation in maternal provisioning strategies, mating systems, and ecology. Comparative analyses of temporal dynamics across 94 species revealed that repeated shifts from lecithotrophy (pre-fertilization provisioning) to matrotrophy (post-fertilization provisioning) preceded concomitant changes in sexual selection, establishing a previously missing causal link in the correlated evolution of life history and mating systems. Adaptive hypotheses of matrotrophy evolution were supported by correlations between ecological variables and the extent of post-fertilization provisioning. Consistent with theoretical models, matrotrophy was associated with environments exhibiting high primary productivity and low competition. In contrast, results did not support strictly conflict-driven scenarios of matrotrophy evolution. Bi-directional evolution along the lecithotrophy-matrotrophy continuum contradicted the expectation of intraspecific Red Queen dynamics with perpetual increases in post-fertilization provisioning. Our results demonstrate that parent-offspring conflict alone is not sufficient to explain the evolution of matrotrophy, but may play a role in conjunction with ecological mechanisms. We propose that natural selection mediated by resource availability counterbalances conflict-fueled—potentially maladaptive—increases in matrotrophy.

33 Evolutionary transitions in maternal provisioning strategies represent a primary axis of
34 reproductive life history variation in viviparous organisms (1, 2). Shifts from an ancestral strategy of
35 females providing all resources for embryonic development prior to fertilization (lecithotrophy) to
36 post-fertilization provisioning (matrotrophy) have been associated with the evolution of complex
37 physiological and morphological adaptations, including placental structures of apposed maternal and
38 embryonic tissues that facilitate nutrient transfer (3). Matrotrophy and placentas have evolved
39 repeatedly in viviparous animals, including multiple invertebrate (4-8) and vertebrate lineages (9-12).
40 Transitions along the lecithotrophy-matrotrophy continuum may have far reaching consequences,
41 shaping the evolution of other traits and patterns of biological diversification. The exacerbation of
42 parent-offspring conflict associated with the evolution of matrotrophy (13, 14) has been
43 hypothesized to impact patterns of sexual selection and promote speciation (15-18). What
44 evolutionary forces shape the evolution of matrotrophy consequently is a pivotal question in
45 evolutionary biology (19).
46 Two conceptual frameworks may explain the evolution of matrotrophy. *(1)* The viviparity-
47 driven conflict hypothesis postulates that matrotrophy evolves as a consequence of parent-offspring
48 conflict over the degree of maternal investment, leading to antagonistic coevolution between
49 maternal and embryonic traits that impact nutrient transfer during pregnancy (17, 20). This
50 hypothesis predicts positive feedback loops between matrotrophy and the strength of parent-
51 offspring conflict, and variation in maternal provisioning strategies is not expected to be related to
52 environmental variables (16, 19, 20). The viviparity-driven conflict hypothesis also predicts
53 correlated evolution between life history and sexual selection, because matrotrophy can facilitate
54 post-copulatory mate choice by females and weaken the importance of pre-copulatory sexual
55 selection and male courtship (15). While there is empirical evidence for correlated evolution between
56 matrotrophy and sexual selection (15), the causal relationship between life history evolution and

57 sexual selection remains unresolved. It has been assumed that shifts in maternal provisioning
58 strategies drive shifts in sexual selection, but the directionality of this relationship may just as likely
59 be reversed (21, 22). Evolution along a continuum of mating systems ranging from those
60 characterized predominantly by male coercion to those predominantly exhibiting male courtship and
61 pre-copulatory female choice may favor diversification in life history strategies, where females of
62 species exhibiting high rates of male coercion should be selected for reduced pre-fertilization
63 provisioning to avoid costs associated with genetically incompatible sires. *(2)* Matrotrophy may be a
64 consequence of adaptive evolution in response to ecological sources of selection. Matrotrophy has
65 been hypothesized to reduce locomotor costs associated with pregnancy (23-25). Specifically,
66 lecithotrophic females are expected to suffer from impaired locomotion throughout gestation, while
67 matrotrophic females with initially small embryos should avoid such costs at least in early stages of
68 pregnancy (26, 27). In addition, resource availability may shape evolution along the lecithotrophy-
69 matrotrophy continuum. Lecithotrophy is expected to be adaptive in environments with fluctuating
70 resource availability (27), whereas matrotrophy theoretically maximizes reproductive output when
71 resource availability is high and stable (28).

72 Livebearing fishes of the family Poeciliidae have become an iconic model system for testing
73 hypotheses about the evolution of reproductive strategies (29). Poeciliids have undergone
74 remarkable diversification in levels of post-fertilization maternal provisioning [with independent
75 origins of matrotrophy in different clades (15, 19, 30)], as well as male mating strategies and sexual
76 selection [ranging from mating systems dominated by male coercion to systems dominated by pre-
77 copulatory female mate choice (15, 31, 32)]. In addition, species in this family are broadly distributed
78 throughout the Americas, found in a wide variety of ecological contexts, and have a well-resolved
79 phylogeny (33-35), facilitating comparative analyses that contrast alternative hypotheses about the
80 evolutionary origins of matrotrophy. Research on poeciliid fishes has been instrumental for the

advancement of our theoretical and empirical understanding of matrotrophy (19, 27, 36), and there is circumstantial evidence supporting various predictions of both the viviparity-driven conflict and adaptive hypotheses of matrotrophy evolution. Intra-specific analyses have shown that the evolution of matrotrophy is associated with parent-offspring conflict (37, 38), and a comparative study documented the predicted correlation between matrotrophy and sexual selection (15). Furthermore, pregnancy in poeciliids is associated with locomotor costs expected under the adaptive hypothesis (39, 40), and there is evidence that matrotrophy increases streamlining (41) and is favored in high predation environments requiring efficient escape responses (42). Finally, maternal provisioning also responds to resource availability (43, 44), and matrotrophy is associated with significant costs when resources fluctuate (45).

Here, we used phylogenetic comparative analyses of 94 species spanning the family Poeciliidae to test predictions of the viviparity-driven conflict and adaptive evolution hypotheses to gain insights into ultimate drivers of matrotrophy evolution: *(1)* The viviparity-driven conflict hypothesis predicts correlated evolution between life history and sexual selection, but the causal relationship remains unclear. We used phylogenetic time-series analyses to test whether life history evolution drives sexual selection, or vice versa. *(2)* The viviparity-driven conflict hypothesis predicts that positive feedbacks lead to continuous increases in matrotrophy through evolutionary time. We used ancestral state reconstruction to evaluate the directionality of matrotrophy evolution during the diversification of poeciliids. *(3)* The adaptive hypothesis of matrotrophy evolution predicts correlations between ecological variables and the degree of matrotrophy. We used phylogenetic path analyses to test whether variation in abiotic and biotic environmental variables relevant to locomotor costs and resource availability predict variation along the lecithotrophy-matrotrophy continuum.

Results

105 ***Evolution of matrotrophy shapes sexual selection, not vice versa***

106 A prior study documented correlated evolution of matrotrophy and sexual selection in poeciliid
107 fishes (15), but the causal relationship was not resolved. Three hypotheses could explain correlated
108 evolution: *(1)* Shifts along the lecithotrophy-matrotrophy continuum (driven by parent-offspring
109 conflict or ecological selection) may drive the evolution of sexual selection (15, 16); *(2)* evolution in
110 patterns of sexual selection along a continuum from male coercion with cryptic female choice to
111 male courtship with pre-copulatory female choice may favor different maternal provisioning
112 strategies and impact parent-offspring conflict (21, 38); or *(3)* the same (or correlated) environmental
113 factors may exert selection on multiple traits, causing correlated phenotypic evolution without
114 pleiotropic interactions among trait suites.

115 These alternative hypotheses result in different predictions about time-lags between shifts in
116 the evolution of matrotrophy and sexual selection, which can be contrasted by explicitly testing the
117 relative timing of evolutionary shifts in the two traits across a phylogenetic tree. We quantified
118 variation along the lecithotrophy-matrotrophy continuum based on embryonic mass changes during
119 development [resulting in a matrotrophy index (30)] and variation in sexual selection based on the
120 degree of sexual dimorphism [resulting in a sexual selection index (31)]. Analyses of evolutionary
121 time-lags across 250 trees revealed the strongest support for the model in which shifts in
122 matrotrophy preceded shifts in sexual selection (mean Akaike weight: 0.430; 95% CI: 0.411 – 0.450).
123 The null model (no lag between the two traits) received significantly lower support (mean Akaike
124 weight: 0.312; 95% CI: 0.304 – 0.320), and the model assuming that shifts in sexual selection
125 preceded shifts in matrotrophy had the lowest support (mean Akaike weight: 0.258; 95% CI: 0.244 –
126 0.272). These results support the previously held assumption that evolution in matrotrophy mediates
127 subsequent changes in sexual selection (15), rejecting the alternative hypothesis that sexual selection
128 was a key driver of life history diversification.

129

130 ***Matrotrophy has evolved bi-directionally during the diversification of poeciliids***

131 A critical assumption of the viviparity-driven conflict hypothesis is that there are positive feedback-
132 loops between parent-offspring conflict and matrotrophy (19). Matrotrophy evolution within species
133 should therefore be characterized by Red Queen dynamics (46). Following the emergence of
134 matrotropy, coevolution of maternal and embryonic traits that impact nutrient transfer during
135 pregnancy are expected to continuously increase post-fertilization provisioning (20). Consequently,
136 the viviparity-driven conflict hypothesis predicts that lecithotrophy is the ancestral provisioning
137 strategy in the family Poeciliidae, and that unidirectional evolutionary changes have occurred from
138 lecithotrophy toward matrotrophy.

139 Ancestral state reconstructions (ASR) were used to compare inferred ancestral states of
140 matrotrophy to variation in matrotrophy observed in extant taxa. ASRs across 250 trees
141 demonstrated that lecithotrophy is not the ancestral provisioning strategy (Fig. 1A), challenging
142 previous assumptions about matrotrophy evolution in poeciliids (19). The inferred ancestral state
143 was clearly toward the matrotrophic end of the spectrum (with a net weight gain during
144 development) and distinctly above the levels of post-fertilization provisioning observed in most
145 extant taxa (Fig. 1B). This does not mean that matrotrophy evolved prior to lecithotrophy, but
146 rather that the common ancestor of extant poeciliids had already evolved some degree of post-
147 fertilization provisioning. More importantly, examining the direction of shifts in post-fertilization
148 provisioning strategies between all nodes and their descendants revealed that reductions of
149 matrotrophy were just as common as increases in matrotrophy (Fig. 1C). The bidirectionality of
150 matrotrophy evolution does not support the central prediction of the viviparity-driven conflict
151 hypothesis that matrotrophy should continue to increase throughout diversification.

152

153 ***Ecological variables are correlated with matrotrophy evolution***

154 Ecological selection related to locomotor performance and resource acquisition are the two leading
155 adaptive hypotheses for diversification of maternal provisioning strategies. The locomotor cost
156 hypothesis predicts that matrotrophy should evolve in ecological contexts that select for high
157 locomotor efficiency, for example under high water flow conditions or in habitats with high
158 predation risk (42, 47). Alternatively, matrotrophy may be favored in environments with high and
159 stable resource availability (28). If ecologically-mediated natural selection contributed to the
160 diversification in maternal provisioning strategies, we would predict correlations between the
161 matrotrophy index and ecological variables associated with locomotor performance, resource
162 availability, or both.

163 We contrasted a series of hypotheses about the hierarchical relationships among different
164 abiotic and biotic environmental variables and matrotrophy using phylogenetic path analysis (48).
165 Environmental predictor variables included metrics of hydrology (based on the topography of each
166 species' range) and predation (number of predatory fish species overlapping each species' range),
167 which are both relevant in the context of the locomotor cost hypothesis (42, 47). In addition, we
168 used metrics of climate (temperature and precipitation patterns in each species' range), average net
169 primary productivity (NPP), and competition (number of poeciliid species overlapping each species'
170 range), which are relevant in the context of the resource availability hypothesis (28). The
171 matrotrophy index and environmental predictor variables were combined in model sets representing
172 18 different hypotheses about putative relationships among the variables (Fig. S1). Model selection
173 identified two models with average $\Delta CIC_c < 2$ across the 250 trees (Fig. S2), including NPP,
174 competition, and predation as predictor variables for variation in matrotrophy. Both models
175 indicated that NPP positively correlated with competition ($r = 0.325$, 95% CI = 0.324 – 0.326 for
176 both supported models), which in turn was negatively correlated with matrotrophy (top model: r = -

177 0.030, 95% CI = -0.034 – -0.025; secondary model: r = -0.077, 95% CI = -0.081 – -0.075). In
178 addition, there was a positive relationship between NPP and matrotrophy (top model: r = 0.024,
179 95% CI = 0.022 – 0.025; secondary model: r = 0.023, 95% CI = 0.021 – 0.024). Simultaneously
180 visualizing the effects of NPP and competition on matrotrophy indicated that high levels of
181 matrotrophy occurred when NPP was high and competition was low (Fig. 1D). This finding is
182 consistent with the predictions of theoretical models that emphasize resource availability (28). In the
183 best supported model, NPP was also positively correlated with predation (r = 0.184, 95% CI =
184 0.183 – 0.185), which was negatively correlated with matrotrophy (r = -0.082, 95% CI = -0.087 – -
185 0.078). Notably, however, the directionality of the relationship between predation and matrotrophy
186 was opposite to the predictions of the locomotor cost hypothesis, which posits that matrotrophy
187 should enhance locomotor performance and be favored in high-predation environments (42).
188 Although the effects sizes in the path analyses were relatively small, they were nonetheless
189 significantly different from zero, indicating that ecology has played a role in matrotrophy evolution.
190

191 **Discussion**

192 Shifts from pre- to post-fertilization maternal provisioning represent a major axis of life history
193 evolution in viviparous organisms (1, 2), with cascading effects for the evolution of complex traits,
194 sexual selection, and speciation (16, 49, 50). We used phylogenetic comparative analyses of 94
195 livebearing fishes in the family Poeciliidae to contrast hypothesized mechanisms driving the
196 evolution of post-fertilization maternal provisioning. A key assumption of the viviparity-driven
197 conflict hypothesis is a positive feedback-loop between parent-offspring conflict and matrotrophy,
198 resulting in a co-evolutionary arms-race between maternal and offspring traits (19, 20). Conflict
199 mechanisms—by definition—are therefore only sufficient to explain the evolution of matrotrophy if
200 post-fertilization maternal provisioning increases through time. Our analyses indicated that decreases

201 in levels of matrotrophy were just as common as increases (Fig. 1C). Such bi-directional evolution
202 along the lecithotrophy-matrotrophy continuum has been documented in other viviparous taxa (e.g.,
203 47, 51) and parallels secondary losses of obligate viviparity in fishes and reptiles (52, 53). The
204 standard model of linear life history evolution from oviparity to lecithotrophic viviparity to
205 matrotrophic viviparity (e.g., 17) therefore needs reevaluation to acknowledge that the evolution of
206 these traits is much more complex and dynamic than generally appreciated. Our results demonstrate
207 that evolutionary mechanisms other than parent-offspring conflict must have played a role in the
208 diversification of maternal provisioning strategies of poeciliids.

209 Correlations between ecological variables and matrotrophy support adaptive hypotheses of
210 matrotrophy evolution. Phylogenetic path analysis identified three biotic variables that were
211 associated with variation in matrotrophy (resource availability, competition, and predation), all of
212 which are well-documented drivers of life history diversification in animals (54-56). While the
213 relationship between matrotrophy and predation was opposite to the predictions of the locomotor
214 cost hypothesis, high levels of matrotrophy coincided with low competition and high resource
215 availability (Fig. 1D). This finding is consistent with the Trexler-DeAngelis model (28), which
216 predicts matrotrophy evolution in environments with abundant and stable resources.

217 There are two caveats that highlight the inconsistencies between existing conceptual
218 frameworks and empirical data associated with matrotrophy evolution. *(1)* Although viviparity-
219 driven conflict alone cannot explain matrotrophy evolution due to repeated evolutionary transitions
220 towards lower levels of post-fertilization provisioning ($\Delta MI < 0$ in Fig. 1C), we cannot exclude the
221 possibility that viviparity-driven conflict played a key role in repeated transitions towards
222 matrotrophy [$\Delta MI > 0$ in Fig. 1C (15, 30)]. *(2)* There is clear empirical evidence that high levels of
223 matrotrophy are disadvantageous when resources are scarce or unpredictable, impacting both
224 offspring size and maternal body condition (45, 57). But while models suggest that matrotrophic

225 provisioning should outcompete a lecithotrophic strategy when resource availability is high (28), key
226 assumptions of the model do not hold up to empirical scrutiny (57), and we still lack any empirical
227 evidence indicating that matrotrophy provides fitness benefits over lecithotrophy under those
228 conditions (19).

229 We propose a novel paradigm of matrotrophy evolution that addresses existing caveats by
230 emphasizing interactions between conflict-driven and ecological mechanisms of selection.
231 Specifically, natural selection mediated by resource availability may counterbalance evolutionary
232 trends driven by parent-offspring conflict. Under low resource conditions, incipient matrotrophy
233 comes with substantial costs (28, 45), preventing the escalation of coevolutionary arms-races
234 between maternal and offspring traits, and thus, the evolution of matrotrophy is impeded. Under
235 favorable conditions with stable and abundant resources, matrotrophy may not actually provide a
236 selective advantage over lecithotrophy. Rather, increases in post-fertilization provisioning may be
237 rendered selectively neutral (or merely less maladaptive) under relaxed resource constraints, allowing
238 parent-offspring conflict to fuel increases in matrotrophy. Bi-directional evolution along the
239 lecithotrophy-matrotrophy continuum could be a simple consequence of a shifting balance between
240 ecological selection favoring lecithotrophy and conflict-driven increases in matrotrophy, in a manner
241 similar to how natural selection counter-balances sexually selected traits evolving under Fisherian
242 runaway scenarios (58, 59). The suggested paradigm is consistent with evidence of ecological sources
243 of selection modulating the outcomes of conflict in other contexts, including sexual conflict (60, 61)
244 and sibling conflict (62, 63). Consequently, we may have to consider that matrotrophy is not actually
245 adaptive [see (57)], but that maladaptive increases in post-fertilization provisioning may spread in
246 populations when selection against it is weak. The notion that matrotrophy—as a widespread life
247 history phenomenon—may be a maladaptive trait is also consistent with the observation that
248 evolutionary conflicts commonly cause deviations from adaptive peaks (64). Escalation of parent-

249 offspring conflict under relaxed constraints is readily possible, because fish eggs have an ancestral
250 ability to acquire organic molecules from the environment through active transport (65); *i.e.*,
251 conditions facilitating potentially maladaptive increases in matrotrophy are present in poeciliids and
252 do not have to evolve *de novo*.

253 A more rigorous understanding of matrotrophy evolution in the future will require the
254 exploration of interactive effects among evolutionary mechanisms. Combining theoretical models
255 and microevolutionary analyses will allow comparative evaluation of hypotheses about organismal
256 performance under different environmental conditions to explicitly determine the conditions that
257 are conducive to the spread of post-fertilization provisioning under adaptive and maladaptive
258 evolutionary scenarios. The grand question for future research is whether natural selection alone can
259 explain the evolution of post-fertilization provisioning (if there is a consistent—yet
260 unknown—adaptive benefit to matrotrophy), or whether matrotrophy evolution is a consequence of
261 a shifting balance between adaptive and potentially maladaptive evolutionary processes.
262

263 **Methods**

264 ***Taxon sampling and phylogenetic framework***

265 Our analyses included 94 species (Table S1), encompassing representatives of all major genera in the
266 family Poeciliidae. These species span a geographic range from the eastern United States south to
267 Argentina, including Caribbean islands (Fig. S3). The phylogenetic framework used for analyses
268 came from previously published studies with a similar taxon sampling (15, 31). In brief, sequences
269 for six mitochondrial (*12S*, *COI*, *CytB*, *ND2*, *tRNAvalu*, and *tRNAleu*) and 11 nuclear genes (*Beta*
270 *Actin*, *CCND1*, *ENC1*, *GLYT*, *MYH6*, *RAG1*, *Rhodopsin*, *RPS7*, *SH3PX3*, *T36*, and *XSRC*) were
271 obtained from GenBank, aligned, and maximum likelihood phylogenetic analysis was conducted
272 using RAxML-HPC version 8 (66) on the CIPRES computer cluster (San Diego State University,

San Diego, CA, USA). The resulting best scoring tree was highly consistent with previously published phylogenetic hypotheses for the family Poeciliidae (15, 34, 35). Phylogenetic trees were time calibrated with three calibration points spanning the depth of the phylogeny (see 31 for details), including a primary fossil calibration associated with the split separating the outgroup (*Fundulus*) from all poeciliids (55-99 Ma; 67) and a secondary fossil calibration separating *Heterandria formosa* from the genus *Poecilia* (9.3-19 Ma; 68). In addition, the formation of Laguna de Catemaco (Mexico), a crater lake with several endemic species, was used as a constraint on the age of the endemic *Poeciliopsis catemaco* (0.5-2.0 Ma; 69). Even though bootstrap support values on the best scoring tree were generally strong, phylogenetic comparative methods described below were conducted across 250 trees drawn at random from the bootstrap replicates to account for phylogenetic uncertainty.

Matrotrophy, sexual selection, and ecological variables

Matrotrophy index: The extent of post-fertilization maternal provisioning was quantified using the matrotrophy index (MI, ln-transformed for all analyses). The matrotrophy index is the ratio of offspring mass at birth to the mass of the egg at fertilization (19). Offspring of lecithotrophic species typically lose 25-55% of the initial egg mass during development (MI < 0.75), while continuous nutrient transfer from mother to offspring during gestation in matrotrophic species leads to MI > 1, with some species giving birth to offspring that are up to 100 times heavier than the initial egg (19, 30). Matrotrophy levels for all species included in the analysis were obtained from previously published studies (15, 70).

Sexual selection index: Variation in sexual selection within poeciliids was quantified using a morphology-based sexual selection index, which quantifies the degree of sexual dimorphism in body shape and multiple fin traits that reflect variation in female choice and male mating strategies (31). The index describes variation along a previously established continuum of poeciliid mating systems

297 (32, 71, 72), ranging from species characterized by long gonopodia and coercive mating tactics
298 (negative index scores) to species with short gonopodia and courtship [positive index scores (31)].
299 *Hydrology, climate, and net primary productivity*: Assembly of hydrological and climate variables
300 associated with each species' range was based on georeferenced occurrence points. We obtained
301 73,398 locality points from multiple sources (http://fishnet2.net/, http://gbif. org/, primary
302 literature), representing the known distributions for all 94 species included in our study. We first
303 removed duplicate points and retained a maximum of 100 randomly sampled localities within the
304 native range of each species, which is sufficient to capture environmental variation even in wide-
305 ranging species (73). We further verified that all data points for a given species were at least 1 km
306 apart to match the spatial resolution of environmental data. Any locality that did not meet this
307 criterion was either removed for species with <100 localities or replaced by another randomly drawn
308 locality for species with >100 localities. For all locality records, we then extracted values for 19
309 climatic (Worldclim: http://worldclim.org/) and three hydrological variables (elevation, slope and
310 compound topographic index; Hydro1k: https://lta.cr.usgs.gov/HYDRO1K/) as well as an
311 estimate of net primary productivity (https://lpdaac.usgs.gov/) at a spatial resolution of ~1 km^2 (30
312 arcsec) in ArcMap version 10.2.2 (ESRI Inc, Redlands, CA, USA). For each species, we calculated
313 the median value for all 23 variables. Climatic and hydrological variables were then subjected to
314 separate phylogenetic principal component analyses (pPCA) using a correlation matrix, as
315 implemented in the PHYTOOLS package in R (74). In addition to the estimate of net primary
316 productivity associated with each species' range, we retained two pPCA axes accounting for 66 % of
317 variation in hydrology (Table S2) and three pPCA axes accounting for 81 % of variation in climate
318 (Table S3).
319 *Competition and predation*: Quantifying the actual biotic interactions for a large number of
320 species distributed across the vast geographic scale included in this study is virtually impossible, and

321 we developed two simple, objectively quantifiable metrics to approximate levels of competition and
322 predation. We assumed that competitive interactions for the focal species primarily occur with other
323 species of the family Poeciliidae (75, 76) and that the intensity of competition is a function of the
324 number of coexisting species. Hence, we first analyzed overlap of distributional ranges to
325 characterize patterns of sympatry [defined as range overlap values greater than zero (77)]. We
326 created geo-referenced distributional range maps for each species by generating a convex hull
327 around each species' known occurrence points (see above) using ArcMap. The resulting species-
328 specific distributions were then intersected to determine the total number of competitor species
329 exhibiting a range overlap with a focal species. Similarly, we created a metric estimating the levels of
330 predation by determining the total number of piscivorous fish species exhibiting a range overlap
331 with a focal species. To do so, we obtained 271,148 locality points (http://gbif. org/) of 7,170
332 species across 1602 genera and 26 families in the superclass Osteichthyes that coincide with the
333 distribution of poeciliids. Since distributional polygons of some focal species overlapped with
334 marine habitats (particularly in poeciliid species occurring along the Gulf of Mexico and in both
335 island and mainland localities), we first removed species primarily inhabiting marine environments as
336 well as non-native species, retaining 5019 native freshwater species in 853 genera (Table S4). To
337 identify potential predators, we conducted a genus-level literature search of dietary habits using
338 relevant monographs (78-82), supplemented by the primary literature when necessary. We retained
339 131 genera that included species with evidence for piscivory (867 species, 73,421 locality points).
340 Values for the number of competitors and predators were square-root-transformed prior to analyses.
341

342 ***Analytical approaches***

343 *Evolutionary time-lag analysis*: We used the MVMORPH package in R (83) to evaluate the causal
344 relationship underlying the previously documented correlated evolution of matrotrophy and sexual

345 selection. MVMORPH implements Ornstein–Uhlenbeck models to test whether one trait follows the
346 optimum of a second trait with a detectable time-lag. We used the matrotrophy index and the sexual
347 selection index as focal traits, contrasting a null model (no detectable lag) to a model that assumes
348 shifts in matrotrophy lag behind shifts in sexual selection (i.e., sexual selection drives matrotrophy
349 evolution) and a model that assumes shifts in sexual selection lag behind shifts in matrotrophy (i.e.,
350 matrotrophy drives evolution of sexual selection). Analyses assuming a unique adaptive optimum
351 (OU1 model) yielded identical results to assuming multiple optima (OUM model). Analyses were
352 conducted across 250 random trees. Models were compared based on their average Akaike weights
353 calculated with a finite sample correction (84).

354 *Ancestral state reconstruction*: Ancestral state reconstructions of matrotrophy index were
355 conducted using PHYTOOLS (74). Inferences of ancestral states were averaged across 250 random
356 trees. To evaluate the directionality of matrotrophy evolution between each node and its
357 descendants, we extracted trait reconstructions for each node of the tree and calculated ΔMI as the
358 observed (tip) or inferred (node) matrotrophy values subtracted from the values of its most recent
359 ancestral node.

360 *Phylogenetic path analysis*: We investigated hypotheses about the hierarchical relationships
361 among abiotic and biotic environmental factors and matrotrophy using phylogenetic path analysis as
362 implemented in the R package PHYLOPATH (85). We developed 18 models based on *a priori*
363 hypotheses about the effects of climate, hydrology, competition, and predation, as well as
364 interactions between predictor variables relevant in the context of the locomotor cost and resource
365 limitation hypotheses of matrotrophy evolution (Fig. S1). Phylogenetic path analysis was run across
366 250 random trees. PHYLOPATH implements model selection with covariance inflation criterion [CIC_C
367 (86)]. Models with an average $\Delta CIC_C < 2$ were considered equally supported (87). Joint effects of net
368 primary productivity and competition were visualized using non-parametric thin-plate spline

regression to create a surface of matrotrophy variation (88). Estimation of matrotrophy surfaces was performed using the FIELDS package in R (89) (smoothing parameter $\lambda = 0.005$).

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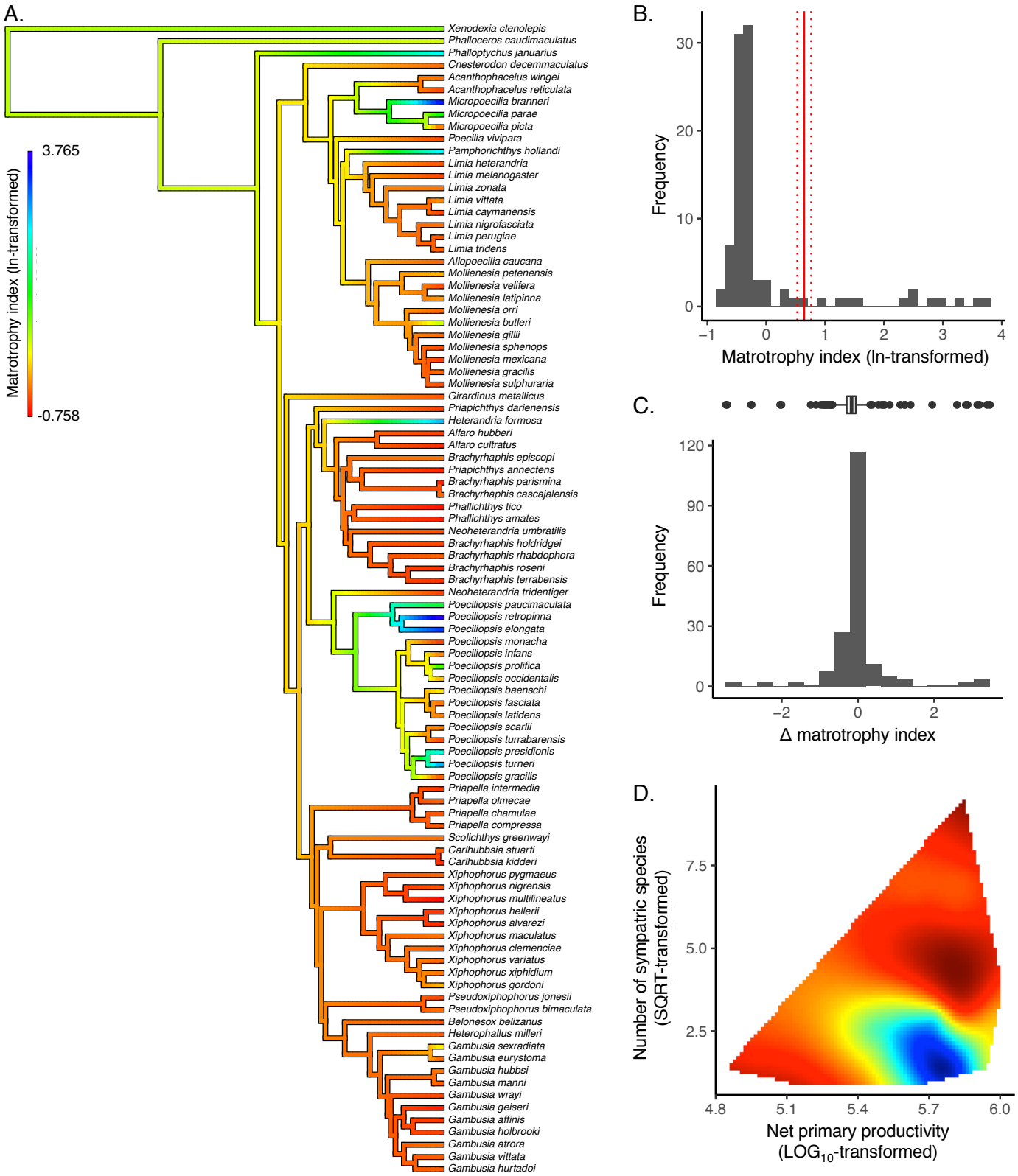
A.
Xenodexia ctenolepis
Phalloceros caudimaculatus
Phalloptychus januarius
Cnesterodon decemmaculatus
Acanthophacelus wingei
Acanthophacelus reticulata
Micropoecilia branneri
Micropoecilia parae
Micropoecilia picta
Poecilia vivipara
Pamphorichthys hollandi
Limia heterandria
Limia melanogaster
Limia zonata
Limia vittata
Limia caymanensis
Limia nigrofasciata
Limia perugiae
Limia tridens
Allopoecilia caucana
Mollienesia petenensis
Mollienesia velifera
Mollienesia latipinna
Mollienesia orri
Mollienesia butleri
Mollienesia gillii
Mollienesia sphenops
Mollienesia mexicana
Mollienesia gracilis
Mollienesia sulphuraria
Girardinus metallicus
Priapichthys darienensis
Heterandria formosa
Alfaro hubberi
Alfaro cultratus
Brachyrhaphis episcopi
Priapichthys annectens
Brachyrhaphis parismina
Brachyrhaphis cascajalensis
Phallichthys tico
Phallichthys amates
Neoheterandria umbratilis
Brachyrhaphis holdridgei
Brachyrhaphis rhabdophora
Brachyrhaphis roseni
Brachyrhaphis terrabensis
Neoheterandria tridentiger
Poeciliopsis paucimaculata
Poeciliopsis retropinna
Poeciliopsis elongata
Poeciliopsis monacha
Poeciliopsis infans
Poeciliopsis prolifica
Poeciliopsis occidentalis
Poeciliopsis baenschi
Poeciliopsis fasciata
Poeciliopsis latidens
Poeciliopsis scarlii
Poeciliopsis turrabarensis
Poeciliopsis presidionis
Poeciliopsis turneri
Poeciliopsis gracilis
Priapella intermedia
Priapella olmecae
Priapella chamulae
Priapella compressa
Scolichthys greenwayi
Carlhubbsia stuarti
Carlhubbsia kidderi
Xiphophorus pygmaeus
Xiphophorus nigrensis
Xiphophorus multilineatus
Xiphophorus hellerii
Xiphophorus alvarezi
Xiphophorus maculatus
Xiphophorus clemenciae
Xiphophorus variatus
Xiphophorus xiphidium
Xiphophorus gordoni
Pseudoxiphophorus jonesii
Pseudoxiphophorus bimaculata
Belonesox belizanus
Heterophallus milleri
Gambusia sexradiata
Gambusia eurystoma
Gambusia hubbsi
Gambusia manni
Gambusia wrayi
Gambusia geiseri
Gambusia affinis
Gambusia holbrooki
Gambusia atrora
Gambusia vittata
Gambusia hurtadoi
3.765
-0.758
Matrotrophy index (ln-transformed)
B.
Frequency
Matrotrophy index (ln-transformed)
C.
Frequency
Δ matrotrophy index
D.
Number of sympatric species (SQRT-transformed)
Net primary productivity (LOG10-transformed)

582 Fig. 1. A. Best-scoring maximum likelihood tree of 94 species in the family Poeciliidae. The ancestral
583 state reconstruction of matrotrophy is mapped onto the phylogeny, with red colors depicting
584 lecithotrophy and blue colors matrotrophy (as indicated by the color scale of ln-transformed
585 matrotrophy index values). B. Frequency histogram of the distribution of matrotrophy index values
586 in extant poeciliid species. The solid red line represents the average ancestral state reconstruction for
587 the matrotrophy index across 250 random trees with dotted lines indicating the 95% confidence
588 interval for the estimate. C. Frequency histogram depicting the relative change in matrotrophy index
589 between all nodes and their descendants. D. Landscape of matrotrophy variation as a function of net
590 primary productivity and competition. Colors correspond to variation in matrotrophy, as indicated
591 in the color scale of panel A.