



# What Drives Life-History Variation in the Livebearing Fish *Poeciliopsis prolifica*? An Assessment of Multiple Putative Selective Agents

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Life-history traits are directly linked to fitness, and therefore, can be highly adaptive. Livebearers have been used as models for understanding the evolution of life histories due to their wide diversity in these traits. Several different selective pressures, including population density, predation, and resource levels, can shape life-history traits. However, these selective pressures are usually considered independently in livebearers and we lack a clear understanding of how they interact in shaping life-history evolution. Furthermore, selective pressures such as interspecific competition are rarely considered as drivers of life-history evolution in poeciliids. Here we test the simultaneous effects of several potential selective pressures on life-history traits in the livebearing fish *Poeciliopsis prolifica*. We employ a multi-model inference approach. We focus on four known agents of selection: resource availability, stream velocity, population density, and interspecific competition, and their effect on four life-history traits: reproductive allocation, superfetation, number of embryos, and individual embryo size. We found that models with population density and interspecific competition alone were strongly supported in our data and, hence, indicated that these two factors are the most important selective agents for most life-history traits, except for embryo size. When population density and interspecific competition increase there is an increase in each of the three life-history traits (reproductive allocation, superfetation, and number of embryos). For individual embryo size, we found that all single-agent models were equivalent and it was unclear which selective agent best explained variation. We also found that models that included population density and interspecific competition as direct effects were better supported than those that included them as indirect effects through their influence on resource availability. Our study underscores the importance of interspecific competitive interactions on shaping life-history traits and suggests that these interactions should be considered in future life-history studies.

**Keywords:** resource availability, interspecific competition, density, life history, poeciliids, stream velocity

## INTRODUCTION

Life-history traits can be highly adaptive (Roff, 2002; Chapuis et al., 2017), and can evolve in response to a variety of selective pressures, both biotic and abiotic (Johnson and Bagley, 2011). Some demonstrated selective agents known to affect the evolution of life histories are population density (Reznick et al., 2002, 2012), predation (Martin, 1995; Johnson and Belk, 2001; Reznick et al., 2001; Roff, 2002; Chapuis et al., 2017), resource availability (Reznick and Yang, 1993; Grether et al., 2001; Roff, 2002; Pérez-Mendoza et al., 2014; Zani and Stein, 2018), and other environmental effects, such as water flow, elevation, toxicity, etc. (Badyaev and Ghalambor, 2001; Ghalambor et al., 2004; Zúñiga-Vega et al., 2007; Riesch et al., 2010, 2014; Johnson and Bagley, 2011; Banet et al., 2016; Heins and Baker, 2017; Santi et al., 2019). The family Poeciliidae has a staggering diversity in reproductive adaptations and heterogeneity in life-history traits, emerging as a model system for life-history research (Pollux et al., 2009). A wealth of knowledge has been accumulated in several species of this family (Pollux et al., 2009; Johnson and Bagley, 2011), however, most studies tend to focus on a single selective factor, although it is clear that life-history traits can be affected and shaped simultaneously by several factors (Moore et al., 2016).

Studies that have examined how several factors affect life-history traits in poeciliids have shown that life histories respond in a predictable and repeatable way to certain selective agents, but not to all of them (Moore et al., 2016). For example, in several livebearing fish species predation drives life-history evolution in a predictable and repeatable manner, but resource availability has less consistent effects (Johnson and Belk, 2001; Reznick et al., 2001; Moore et al., 2016). However, the response to other selective factors can depend on the population studied (Moore et al., 2016). For some populations, it is clear that several pressures may be acting in concert (Johnson, 2002; Moore et al., 2016), whereas in others one factor may be dominant. Nevertheless, we still have a lack of studies that allow us to draw general predictions about responses to several selective pressures, and which selective pressures have primacy in wild populations.

Here, we evaluate several hypotheses about the relative importance of biotic and abiotic factors in shaping four life-history traits using a multi-model inference approach in a species of livebearing fishes (Johnson and Bagley, 2011). We focus on four well known life-history traits: superfetation (number of simultaneous broods carried by a female), individual embryo size, number of embryos (across all broods; Frías-Alvarez and Zúñiga-Vega, 2016), and reproductive allotment. We build specific hypotheses of how each factor could affect the evolution of the life-history traits using the wealth of knowledge available for poeciliids (Johnson and Bagley, 2011). However, some selective agents have only received modest consideration in this type of study (interspecific competition and stream velocity; Johnson and Bagley, 2011). Given this modest inclusion, it is unknown how important interspecific competition and stream velocity are in comparison to other more commonly studied selective agents in livebearers. Thus, we model four hypothetical drivers of life-history variation: resource availability, population density,

stream velocity, and interspecific competition (see **Table 1** for hypotheses), each of which is a potential agent of life-history evolution in livebearing fishes (*Poeciliidae*; Johnson and Bagley, 2011). We compare these putative selective agents to evaluate the relative importance of each on the evolution of life histories of *Poeciliopsis prolifica* and test if the effect of each selective agent is in accordance with previous hypotheses (**Table 1**).

## MATERIALS AND METHODS

### Study System and Collection Sites

*Poeciliopsis prolifica* is distributed through northwestern Mexico on the Pacific slope from the Rio Yaqui, Sonora south to near Las Varas, Nayarit (Miller et al., 2005). Populations exist under a variety of environmental conditions that include differences in fish density, stream velocity, fish community structure, and habitat characteristics. This provides a range of selective conditions under which populations might evolve local adaptations. We collected 298 *P. prolifica* females using hand-held seine nets (1.3 m × 5 m; 8 mm mesh size) from 12 populations (**Figure 1**) during the dry season (**Table 2**; Permits FAUT-0117, DGOPA/1864/210205/-0765, and DGOPA-005/16). All individuals were euthanized and preserved in alcohol following guidelines of the ethics committee of Brigham Young University (although Ethics Committee approval is not required according to national law in Mexico).

For each locality, we quantified four environmental parameters that represent four putative selective agents: interspecific competition, resource availability, stream velocity, and population density (**Table 2**). All selective agents are predicted to affect life-history traits, either directly or indirectly (Johnson and Bagley, 2011). In this study, we assume that these four selective agents are unmeasured factors that are correlated with measurable environmental characteristics. To characterize the selective agent we attempt to identify environmental parameters that are correlated with the unmeasured true selective agent. We then estimate the correlation between observed characters and unobserved factors through path analysis.

We estimated relative population density of *P. prolifica* by calculating the average number of *P. prolifica* fish observed per seining attempt, a standardized catch per unit effort (CPUE) found to be positively correlated with actual population density (Johnson, 2002). CPUE can allow comparison of localities with different seining efforts and has been used in several studies as a proxy to population density (Kobza et al., 2004; Cruz et al., 2020). We estimated interspecific competition as the number of co-occurring species of the same genus. *P. prolifica* can co-occur with up to three species of the same genus: *P. viriosa*, *P. latidens*, and *P. presidionis* (Mateos et al., 2002; Miller et al., 2005). Thus, competition will have four factors from no competitors to three co-occurring competitors (0,1,2,3). To our knowledge there are no published accounts of the degree of similarity or the niche overlap among these four species. However, general accounts of these four species indicated that they are ecologically similar—they all inhabit the mid-water column in streams and small rivers, they are similar in body form,

**TABLE 1** | Potential effects of the four putative selective agents on the life history of *P. prolifica*.

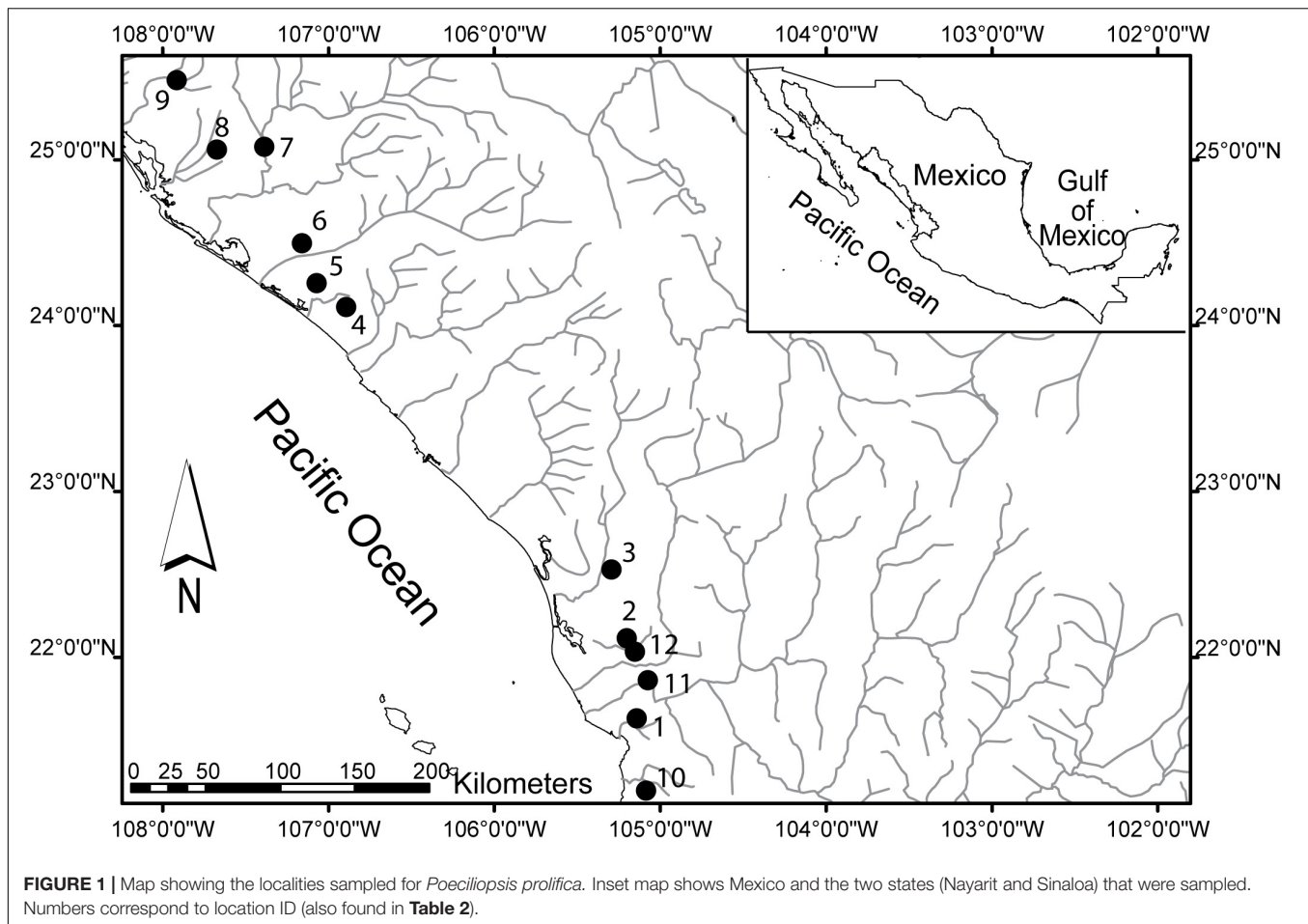
Selective Agent	Path ID <sup>a</sup>	Effect on life history	Prediction	Rationale	References
Resources (R)	1	Direct	An increase in resources will result in an increase in number of embryos and reproductive allocation, but a decrease in superfetation and embryo size	Higher resources should result in greater body condition and thus greater investment in reproduction. An increase in number of embryos should result in a reduction in the size of each individual embryo (trade-off between number and size of offspring). Partitioning a large reproductive bout into smaller broods (superfetation) is less necessary if resources are abundant	Reznick and Yang, 1993; Zúñiga-Vega et al., 2010; Johnson and Bagley, 2011
Population density (D)	2	Direct	An increase in population density will result in an increase in superfetation and embryo size, but a decrease in number of embryos and reproductive allocation	Higher population density may increase competition for other environmental factors, such as habitat and not through resource availability. Competition should still negatively affect body condition and result in lower investment in reproduction. Both superfetation and large offspring size are advantageous in competitive environments	Johnson and Bagley, 2011
	5	Indirect through resources	An increase in population density will result in an increase in superfetation and embryo size, but a decrease in number of embryos and reproductive allocation	Higher population density increases competition for resources resulting in lower resources per individual, which causes lower body condition and lower investment in reproduction. If resources are scarce, superfetation may reduce peak cost of reproduction by partitioning a large reproductive bout into smaller broods	Reznick et al., 2002, 2012; Zúñiga-Vega et al., 2010; Johnson and Bagley, 2011
Interspecific competition (C)	3	Direct	An increase in competition will result in an increase in superfetation, number of embryos and reproductive allocation, but a decrease in embryo size	Higher interspecific competition causes a pressure for higher reproduction to compete and coexist. Life history acts as a tradeoff for competition that allows coexistence. Simply said there is a trade-off between competitive abilities and reproduction	Hutchinson, 1957; Levine and Rees, 2002; Kneitel and Chase, 2004; Leibold et al., 2004; Calcagno et al., 2006; Chapuis et al., 2017
	6	Indirect through resources	An increase in competition will result in an increase in superfetation and embryo size, but a decrease in number of embryos and reproductive allocation	Higher interspecific competition increases overall density that in turn decreases resources. As resources are lower per individual this causes low body condition and lower investment in reproduction. Superfetation is beneficial when resources are scarce	Scott and Johnson, 2010; Wilson, 2013
Stream velocity (S)	7	Direct	An increase in stream velocity will result in an increase in superfetation, number of embryos and reproductive allocation, but a decrease in embryo size	Fast flow environments result in more streamlined body shapes that should increase superfetation, allowing reproductive effort to be higher or at least unchanged. More embryos should result in a reduction in the size of each individual embryo	Zúñiga-Vega et al., 2007, 2010; Johnson and Bagley, 2011

<sup>a</sup>Path ID numbers correspond to those shown in **Table 4** and **Figure 2**.

and they are omnivorous, consuming plant, and animal matter (Miller et al., 2005). Furthermore, we collected these species in the same microhabitat and it has been shown that *P. prolifica* body shape converges with that of its congeners when co-occurring due to interspecific competition (Roth-Monzón et al., 2020). Hence, we conclude that due to previous evidence, their close phylogenetic relationship, and ecological similarity there is high potential for competitive interactions. We used number of co-occurring species as an indicator of level of interspecific competition in our analysis. We chose number of co-occurring species to focus on answering the effect of the addition of species in life-history traits. Furthermore, it is a known measure that has affected *P. prolifica* (Roth-Monzón et al., 2020). Additionally, number of competitors is a general measure that can characterize interspecific competition throughout several years. We found no piscivorous predators in the localities sampled. However, in all locations, we found another species of livebearer (*Poecilia*

*butleri*). We also found one location with a very low density (only 16 individuals collected) of an introduced livebearer (*Gambusia affinis*).

We use stream slope to characterize stream velocity. We calculated stream slope in ArcMap 10.6 (Environmental Systems Research Institute [ESRI], 2014), as the difference between upper elevation and lower elevation of a 2-km segment of stream for each locality sampled. It is known that stream velocity increases as stream slope increases, thus this indirect measure should be a good proxy for stream velocity (Gore and Banning, 2017). We recognize that there is variation among sites in the number of pools and riffles, regardless of the overall slope across the focal 2-km segment of the stream. Frequently, poeciliids use pools of stagnant water for foraging activities and social interactions (Mazzoni et al., 2011). However, these pools are highly dynamic, some of them dry out, and new ones are constantly formed. Thus, our proxy for stream velocity does not represent these



changing microhabitats, which may be temporarily available to fish depending on the amount of daily precipitation or water runoff, but instead represents an estimate of the general water velocity that fish experience all throughout the year. Individuals that inhabit a steep river may indeed search for pools, but they certainly deal with fast currents when moving among pools. In contrast, individuals that inhabit a stream that runs through a plain landscape will never experience fast water currents, not even when moving between pools. Therefore, selection for more streamlined phenotypes with enhanced swimming abilities, which in turn impose constraints on reproductive allotment (Zúñiga-Vega et al., 2010), must be overall stronger in streams located in steep terrains than in streams located in relatively plain areas.

We estimated resource availability measuring canopy cover with a hand-held densiometer. Canopy cover is an indicator of primary productivity (Grether et al., 2001; Zimmermann and Death, 2002; Kiffney et al., 2004; Schiesari, 2006). High canopy cover indicates lower primary productivity that has been correlated with lower secondary productivity such as invertebrates, thus being a reliable measure of resources in a stream (Grether et al., 2001; Zimmermann and Death, 2002; Kiffney et al., 2004; Schiesari, 2006). Canopy cover has been a good proxy for resource availability in other studies with

streams similar to ours (Grether et al., 2001; Collins et al., 2015). Two populations had missing data on canopy cover (localities four and seven); to avoid the exclusion of these in the analysis we used aerial images from Google Earth to calculate percent cover in ImageJ. This approach has been used before and found to strongly correlate with field measurements of canopy cover (Inskeep et al., 2011). In our localities, we also found a strong correlation between our field measurements of canopy cover and our calculations of canopy cover from aerial images ( $R^2 = 0.76$ ,  $P = 0.010$ ). To understand if competition, resources, stream slope, and population density covaried, we conducted a pairwise correlation tests. We found no significant correlations among these putative selective agents (**Table 3**).

### Life-History Traits

We quantified four different life-history traits: superfetation (number of simultaneous broods carried by a female), individual embryo size, number of embryos (across all broods; Frías-Alvarez and Zúñiga-Vega, 2016), and reproductive allotment. We choose these traits because the four selective pressures of interest are thought to affect them, and clear predictions can be made of their effects (see **Table 1**). We classified embryo development stage using the 11-stage scale developed by Haynes



**TABLE 2** | Sample size, selective agents, and collection year for all twelve locations in the study.

Location ID	Collection year	Sample size	Number of competitors	Canopy cover (%)	Stream slope (km)	Population density (CPUE)
1	2007	44	2	100	7.5	7.38
2	2007	21	1	41	2.5	17.75
3	2007	39	3	37	9	21.71
4	2007	16	1	98	3.5	3.5
5	2007	17	1	100	5.5	4.14
6	2007	36	1	82	4.5	42.2
7	2007	29	0	82	22.5	41.29
8	2007	35	1	100	2.5	16.36
9	2007	19	1	100	3	9.86
10	2015	21	1	69	7	6.31
11	2015	11	2	36	1	27
12	2015	10	0	69	0	24.14

Population density is measured as catch per unit effort. Location ID corresponds to map in **Figure 1**.

(1995). We defined a brood as all the embryos that share the same developmental stage (Haynes, 1995). We measured individual embryo size by drying an entire brood of offspring in a desiccating oven for 48 h at 55°C and dividing the brood dry mass by the number of embryos in the brood. To avoid non-independence in individual embryo size due to the fact that females can have more than one brood, we only considered the brood at the most advanced developmental stage of each female for the calculation of individual embryo size. We obtained female somatic dry mass by drying the female soma (minus the intestinal tract and offspring) for 48 h at 55°C. For reproductive allocation, we used the total dry mass of all broods of each female relative to somatic dry mass of the female following Tomkins and Simmons, 2002.

To account for the effect of maternal body size differences on each life-history trait, we adjusted each trait by an analysis of covariance (ANCOVA). We adjusted individual embryo size by including maternal somatic dry mass and developmental stage as covariates, to obtain comparable “size-free” and “stage-free” least squares means for analysis. We only adjusted superfetation, number of embryos, and reproductive allocation by using maternal somatic dry mass as a covariate. To meet assumptions of normality for the ANCOVAs, we used the following transformations on the life-history traits: superfetation and total number of embryos were square root transformed, whereas embryo size and reproductive allocation were log

transformed. Hence, the comparison among populations were done using the adjusted least squares means generated by the ANCOVA models allowing us to compare “size-free” and “stage-free” life-history traits.

Before using the adjusted life histories in a model selection approach, we tested for population differences in all four life-history traits by employing a multivariate analysis of covariance (MANCOVA). Likewise, we included maternal somatic dry mass and stage of development as covariates in the MANCOVA. We found significant differences among the 12 populations of *P. prolifica* in all life-history traits ( $F_{11,1136} = 14.75, P \leq 0.001$ ), so we proceeded with the model selection approach using the adjusted least squares means. All of these analyses were implemented in R software (R Core Team., 2020).

## Model Selection

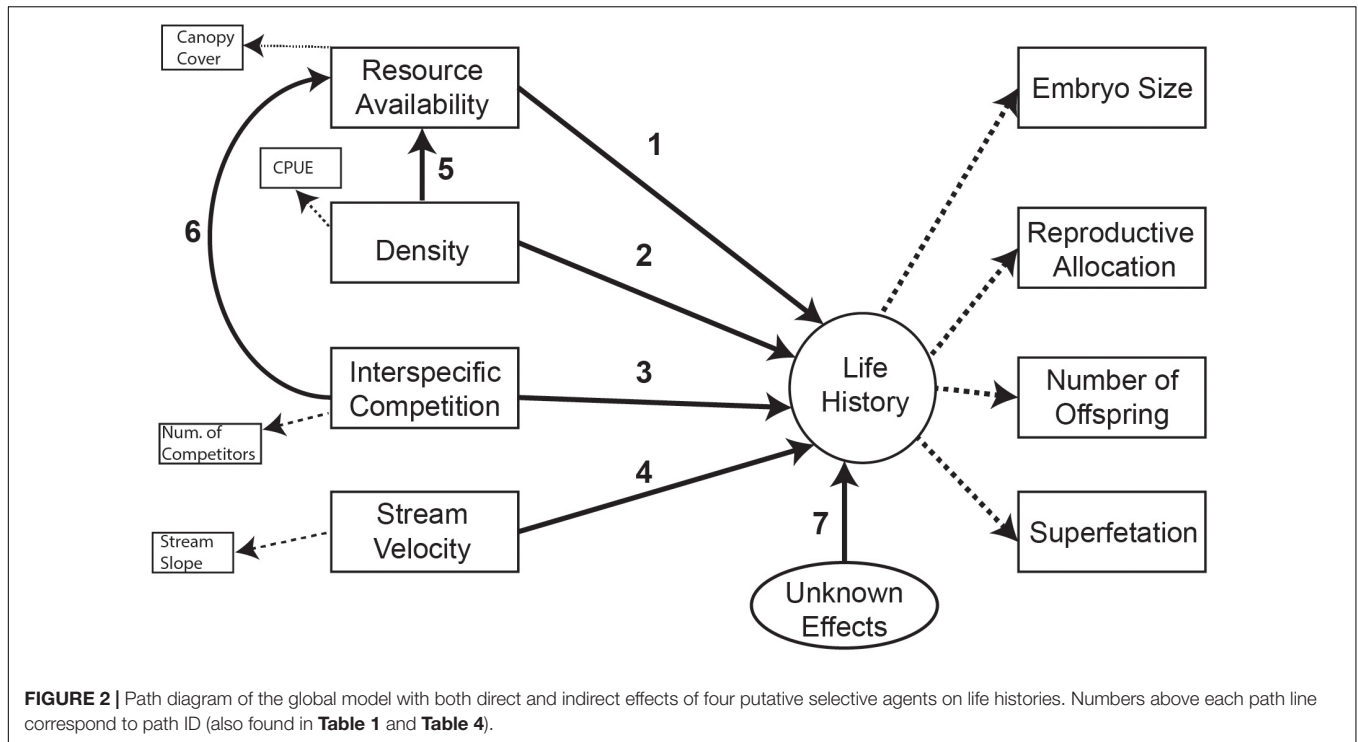
We generated a set of 14 candidate models that represent competing biological hypotheses of the way the four putative selection agents could act to shape life-history traits (**Figure 2**, **Table 4**, and **Supplementary Figure 1**). We did not include all possible interactions between factors because we wanted to include only those that represent plausible hypotheses taken from theory (**Table 1**). We used a structural equation modeling approach (i.e., path analysis) because it allowed us to assess both direct and indirect effects of the selective agents. Assessing indirect effects is important in our study because some selective agents (e.g., competition and population density) are usually only considered in previous studies as acting through indirect effects (Scott and Johnson, 2010; Reznick et al., 2012).

We know that life-history traits can co-vary and its theory suggests that it may evolve as an integrated suite of traits (Fisher, 1930; Reznick, 1985). This assumption is important as it affects whether life histories can be evaluated as a collective strategy or if each life-history trait should be considered separately. To assess this assumption we used a confirmatory factor analysis that allowed us to test if a single factor (i.e., a single life-history variable) could adequately summarize all four life-history traits measured (Burnham and Anderson, 2002). During this confirmatory analysis, we found a negative error for reproductive

**TABLE 3** | Pairwise correlation coefficients with *P*-values of the four putative selective agents.

Environmental variable	Competition	Resources	Stream slope	Population density
Competition		0.20	0.67	0.53
Resources	−0.39		0.79	0.27
Stream Slope	−0.14	0.09		0.23
Population density	−0.20	−0.35	0.37	

Values below the diagonal are correlation coefficients, and values above the diagonal are the corresponding *P*-values.



allocation. We determined that the negative error was due to sample variance (Van Driel, 1978; Chen et al., 2001), thus we restricted the error to a small positive number (0.01) following Van Driel (1978). Fixing the error term as a small positive number allowed us to continue running a factor analysis and retain the potential for error in the measurement of reproductive allocation. We found that three of the four life-history traits appear to behave as an integrated suite of traits in *P. prolifica*, as they all had a positive association and loadings greater than 0.50 in the

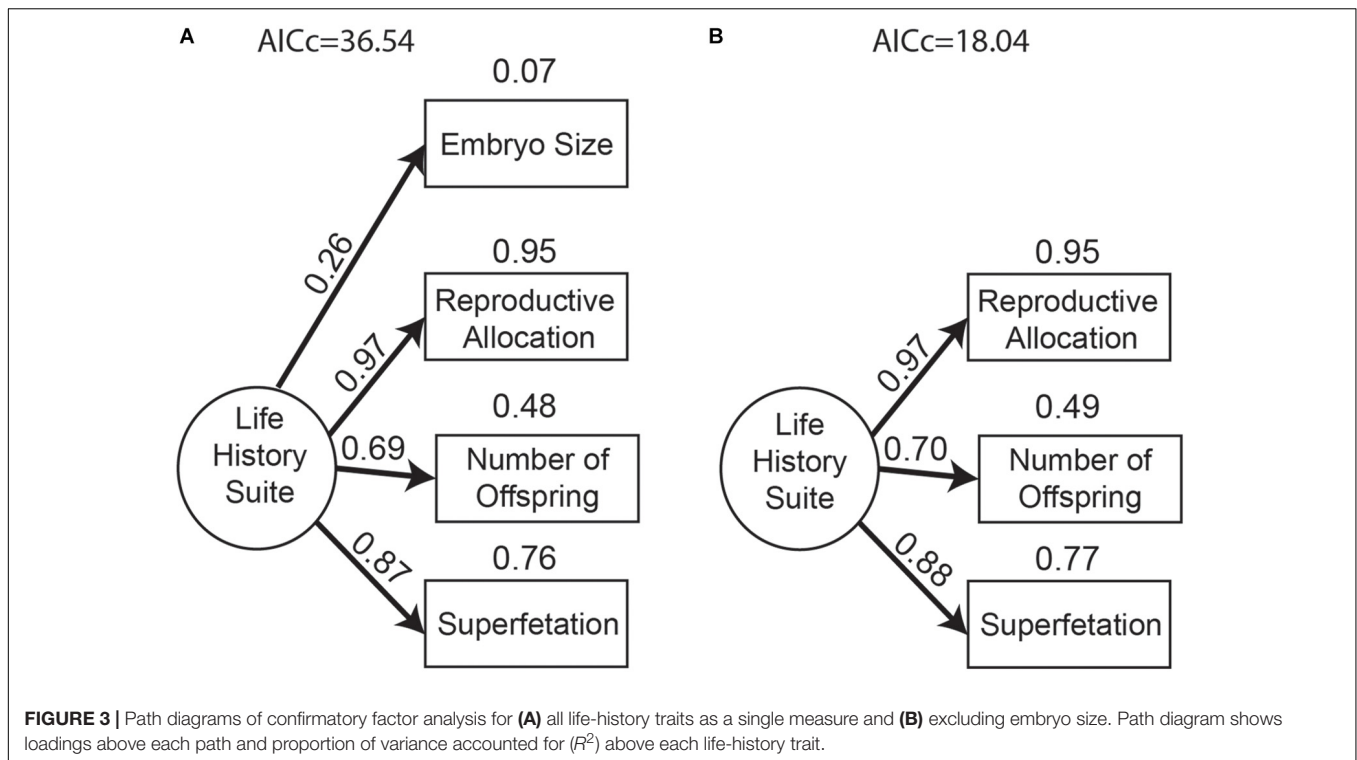
calculated life-history suite (**Figure 3**), corroborating the idea that certain life-history traits evolve in an integrated fashion (Fisher, 1930; Reznick, 1985). These three correlated life-history traits were number of embryos, reproductive allocation, and superfetation and, hence, our life-history suite is a combination of these three variables in such a way that large positive values of this variable correspond to females that produce many embryos, high reproductive allocation, and several simultaneous broods. In turn, large negative values of our life-history suite indicate females with the opposite set of traits (fewer embryos, low reproductive allocation, and fewer simultaneous broods). In contrast, embryo size had a small loading and very little variation explained by this life-history suite. Thus, our life-history suite was not a good reflection of embryo size, so for all the models we treated embryo size separately. We therefore proceeded to test the different hypotheses through a multi-model inference approach with two life histories measures as response: the life-history suite (which is a combined measure of number of embryos, reproductive allocation, and superfetation) and embryo size alone.

We ran all 14 candidate models in path analysis using the software Amos (Arbuckle, 2013). All models were run using a maximum likelihood estimator. For each model, we generated an Akaike Information Criteria score (corrected for small sample sizes; AICc). We used AICc scores to identify models that best fit the data. Models in which AICc scores differ by less than two are generally considered indistinguishable (Burnham and Anderson, 2002; Burnham et al., 2011). We also calculated the model-averaged standard total effect for each selective agent using all 14 models and their associated AIC weights. The model-averaged standard total effect represents the amount of change

**TABLE 4 |** List of the *a priori* 14 candidate models of the effect of the four putative selective agents.

Selective agents <sup>a</sup>	Model	Paths
R	1	1,7
D	2	2,7
C	3	3,7
S	4	4,7
RD	5	1,2,7
RD	6	1,5,7
RD	7	1,2,5,7
RC	8	1,3,7
RC	9	1,6,7
RC	10	1,3,6,7
RCD	11	1,2,3,7
RCD	12	1,5,6,7
RCD	13	1,2,3,5,6,7
RCDS	14	1,2,3,4,5,6,7

<sup>a</sup>Selective agents are abbreviated as follows: R, resources; D, population density; C, competition; S, stream velocity.



in either the life-history suite or embryo size given a standard deviation unit change in each of the selective agent included in the models.

## RESULTS

Population density and interspecific competition alone were the best predictors of number of embryos, reproductive allocation, and superfetation in *P. prolifica*. For this life-history suite, the two models with population density and interspecific competition alone as direct effects had lower AICc scores than all other models. However, it was not possible to distinguish between these two models as they differed by less than two AICc score units (Table 5). For embryo size, all models that included a single selective agent had the lowest AICc values and were equivalent in terms of AICc (Table 6).

Although the two models with population density and interspecific competition alone were undistinguishable based on AICc scores for the life-history suite, they differed in the strength of their effects on life histories. Population density had a stronger effect than interspecific competition (Figure 4), but both models revealed a positive influence of these two environmental factors on the life-history suite. In other words, increasing population density or interspecific competition results in an increase in all three life-history traits (number of embryos, RA, and superfetation).

For embryo size, all selective pressures, except interspecific competition, had the predicted effect from theory (Table 1 and Figure 5). This means that embryo size increased as population density increased (Figure 5A), and decreased as resources

and stream gradient increased (Figures 5B,D). In contrast, interspecific competition had a positive effect on embryo size (Figure 5C). This said, the model-averaged standard total effect was generally low for all four selective agents suggesting the strength of these selective pressures was overall weak on embryo size (Figure 5).

**TABLE 5** | List of the *a priori* 14 candidate models of the effect of the four putative selective agents on the life-history suite with corresponding AICc values,  $\Delta$ AICc, and AICc weight (W).

Selective agents <sup>a</sup>	Model <sup>b</sup>	Paths	AICc	$\Delta$ AICc	W
<b>D</b>	<b>2</b>	<b>2,7</b>	<b>31.08</b>	<b>0</b>	<b>0.416</b>
<b>C</b>	<b>3</b>	<b>3,7</b>	<b>31.37</b>	<b>0.29</b>	<b>0.360</b>
S	4	4,7	33.29	2.21	0.138
R	1	1,7	34.22	3.14	0.086
RC	9	1,6,7	45.92	14.84	<0.001
RD	5	1,2,7	46.91	15.83	<0.001
RC	8	1,3,7	47.33	16.25	<0.001
RC	10	1,3,6,7	48.95	17.87	<0.001
RD	6	1,5,7	49.02	17.94	<0.001
RD	7	1,2,5,7	49.06	17.98	<0.001
RCD	11	1,2,3,7	60.97	29.89	<0.001
RCD	12	1,5,6,7	63.18	32.1	<0.001
RCD	13	1,2,3,5,6,7	63.38	32.3	<0.001
RCDS	14	1,2,3,4,5,6,7	86.03	54.95	<0.001

*Bolded model are the best models according to the AICc for the life-history suite. <sup>a</sup>Selective agents are abbreviated as follows: R, resources; D, population density; C, competition; S, stream velocity.*

*<sup>b</sup>Model numbers correspond to those shown in Table 3.*

**TABLE 6** | List of the *a priori* 14 candidate models of the effect of the four putative selective agents on embryo size with corresponding AICc values,  $\Delta$ AICc, and AICc weight (W).

Selective agents <sup>a</sup>	Model <sup>b</sup>	Paths	AICc	$\Delta$ AICc	W
<b>R</b>	<b>1</b>	<b>1,7</b>	<b>10.46</b>	<b>0</b>	<b>0.245</b>
<b>D</b>	<b>2</b>	<b>2,7</b>	<b>10.46</b>	<b>0</b>	<b>0.245</b>
<b>C</b>	<b>3</b>	<b>3,7</b>	<b>10.46</b>	<b>0</b>	<b>0.245</b>
<b>S</b>	<b>4</b>	<b>4,7</b>	<b>10.46</b>	<b>0</b>	<b>0.245</b>
RD	6	1,5,7	17.43	6.97	0.008
RD	5	1,2,7	18.76	8.3	0.004
RC	8	1,3,7	19.29	8.83	0.003
RC	9	1,6,7	20.35	9.89	0.002
RD	7	1,2,5,7	20.91	10.45	0.001
RC	10	1,3,6,7	20.91	10.45	0.001
RCD	12	1,5,6,7	28.42	17.96	<0.001
RCD	11	1,2,3,7	29.43	18.97	<0.001
RCD	13	1,2,3,5,6,7	31.84	21.38	<0.001
RCDS	14	1,2,3,4,5,6,7	40.77	30.31	<0.001

*Bolded model are the best models according to the AICc for embryo size.*

<sup>a</sup>Selective agents are abbreviated as follows: R, resources; D, population density; C, competition; S, stream velocity.

<sup>b</sup>Model numbers correspond to those shown in **Table 3**.

## DISCUSSION

Overall we found mixed results, for embryo size selective agents were indistinguishable in their ability to predict life-history variation as in a previous study with the livebearing fish *Brachyrhaphis rhabdophora* (Johnson, 2002). However, for the other three life-history traits studied two selective agents independently, competition and population density, were equally likely to explain the variation in *P. prolifica*.

As interspecific competition increased, we found an increase in number of embryos, reproductive allocation, and superfetation. These results are consistent with theoretical predictions suggesting that poor competitive abilities can be compensated by a large reproductive effort (Hutchinson, 1957; Levine and Rees, 2002; Kneitel and Chase, 2004; Leibold et al., 2004; Calcagno et al., 2006; Chapuis et al., 2017). Hence, our findings indicate that *P. prolifica* may have low competitive abilities, but is likely better at reproduction. However, we did not measure competitive abilities which will be needed to confirm the hypothesis of a trade-off between reproduction and competitive abilities (Kneitel and Chase, 2004; Calcagno et al., 2006). Nevertheless, a trade-off is the most likely explanation for the observed positive association between the life-history suite and interspecific competition, otherwise a decrease in number of embryos and reproductive allocation would be expected (Scott and Johnson, 2010). Furthermore, interspecific competition was also positively associated with embryo size, meaning that for *P. prolifica* an increase in interspecific competition causes an increase in all four life-history traits, which also supports a trade-off between competitive ability and reproduction. Noticeably, the fact that intense competition can increase both number and size of offspring indicates that the common trade-off between these two life-history traits, which has been

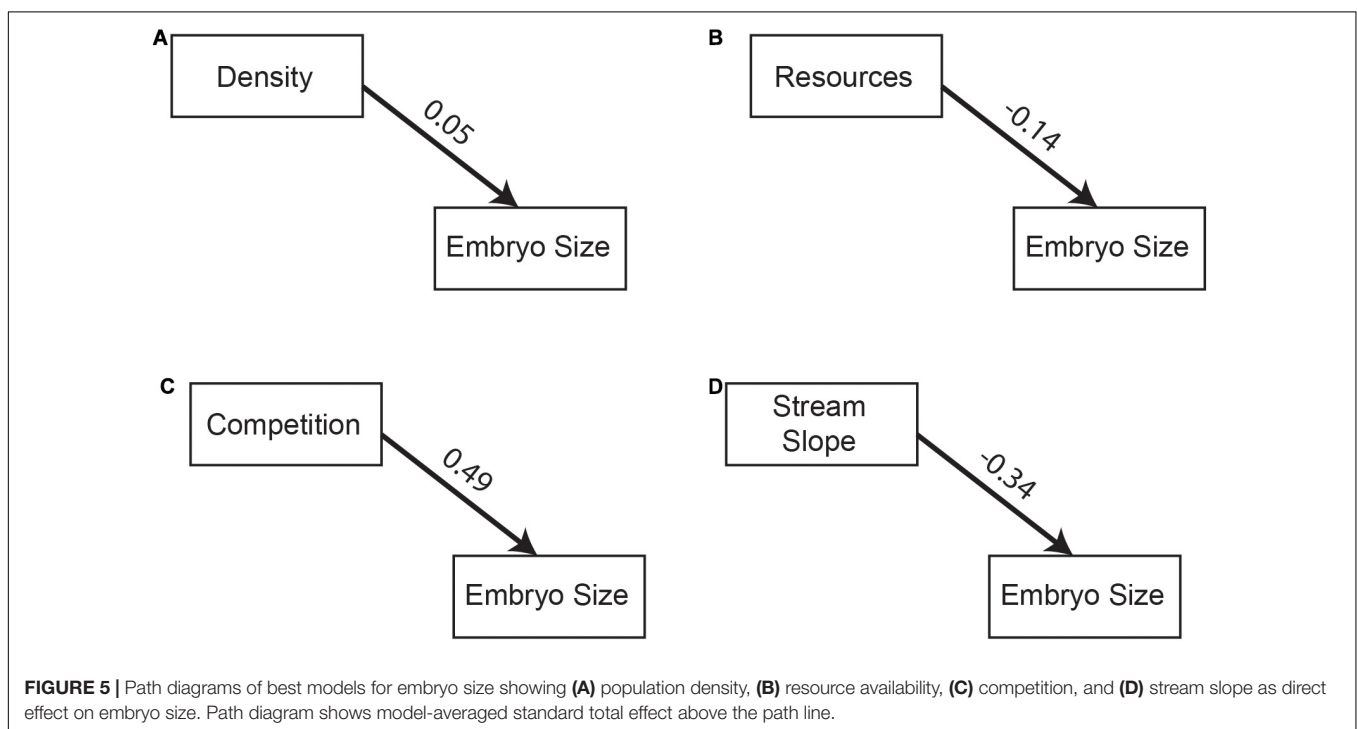
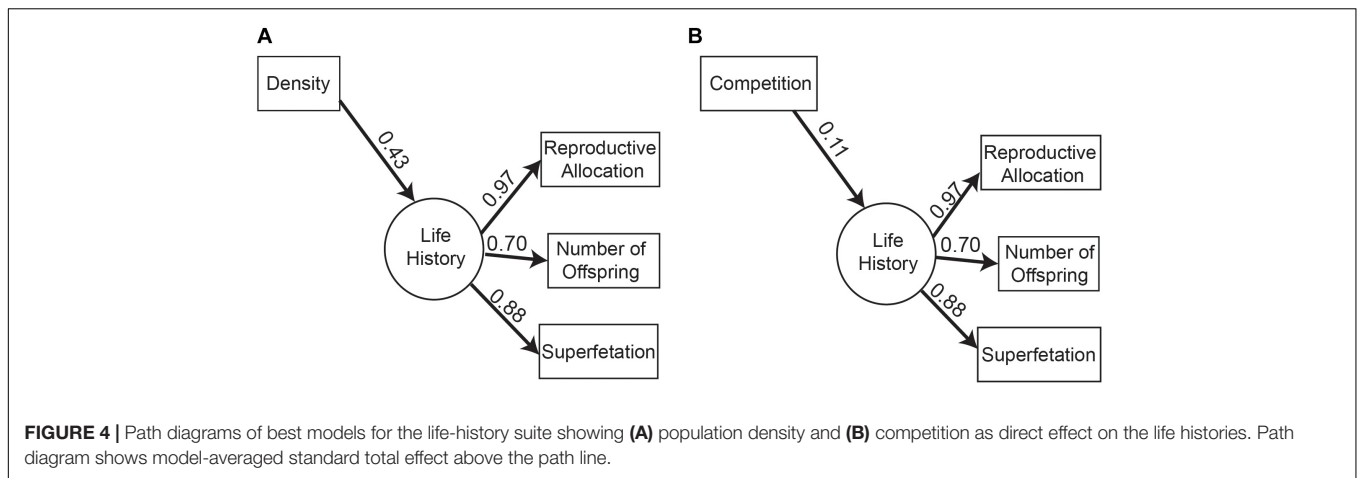
previously documented in other poeciliids (e.g., *Poeciliopsis gracilis* and *P. infans*; Frías-Alvarez et al., 2014), does not occur in *P. prolifica*.

Population density was also positively associated with each of the life-history traits evaluated here (reproductive allocation, number of embryos, superfetation, and embryo size). However, for embryo size the effect of population density was small (**Figure 5**). Nevertheless, results are still somewhat puzzling for the three other life-history traits in that increasing population density is expected to result in a decrease in number of embryos and in reproductive allocation (Johnson and Bagley, 2011; Moore et al., 2016). Higher population density should result in a reduction in per capita resource availability, resulting in lower reproductive allocation and number of embryos, but higher superfetation (**Table 1**). Two possibilities could account for our observations. First, competition in our system may not be through competition for available food resources as appears to be the case in other studies (Reznick, 1989; Reznick et al., 2002). In other words, life-history traits in *P. prolifica* may be shifting to improve competitive ability in a context different from competition for resources, such as microhabitat (**Table 1**). Second, most studies examining the effects of population density on life history have been conducted in species that lack superfetation (e.g., Smith, 2007; Reznick et al., 2012). The ability to carry multiple broods simultaneously in *P. prolifica* might confer advantages that alter the effect of population density on life history (Zúñiga-Vega et al., 2017). For example, higher superfetation is related to higher reproductive allocation in other livebearing fishes (Zúñiga-Vega et al., 2017), and it has been suggested that superfetation allows these species to overcome morphological constraints in terms of reproductive investment (Frías-Alvarez and Zúñiga-Vega, 2016; Zúñiga-Vega et al., 2017). Thus, it is possible that species that superfetate can have more offspring without the typical trade-off relative to non-superfeting species (Olivera-Tlahuel et al., 2015). This could allow for the positive relationship between population density and the life-history traits observed in our study.

Resource availability was not a good predictor of the life history suite, despite the fact this is a known selective agent for other poeciliids (Zúñiga-Vega et al., 2010; Johnson and Bagley, 2011). One possibility is that food resources are simply not limiting in this system and therefore play a lesser role in shaping life histories. Moreover, food resources availability can change through time (Reznick and Yang, 1993) and can be affected by several abiotic factors (i.e., substrate disturbance, stream velocity, etc., Zimmermann and Death, 2002; Hall et al., 2015) and it is possible that when we sampled did not capture the effects of resource availability. Another explanation could be that canopy cover, although a useful surrogate for primary productivity in streams, does not adequately reflect the resource dynamics in this system. If so, then future studies could focus on the inclusion of different measures to construct a more direct estimate of resource availability.

We were similarly surprised to find that stream velocity did not predict life history in our system, given that *P. prolifica* is a superfeting species and stream velocity is known to affect this life-history-trait in other superfeting poeciliid fish species





(Zúñiga-Vega et al., 2007, 2010). One possible reason for this is that our use of stream slope may not capture the actual water velocity that these populations encounter. It is possible that *P. prolifica* females spend their majority of time in pools, rather than in the current where stream slope would be a better predictor of flow rate (Croft et al., 2003). Thus, measuring water velocity in the particular pool where individuals are observed could better account for the stream velocity that the species is experiencing. Additionally, stream velocity is a complex measure that can vary in time and space, especially depending on space complexity and heterogeneity (Lake, 2000; Palmer et al., 2010). Several measures may be needed to truly account for stream velocity variability, and basic information about species-specific microhabitat preferences could aid in considering what is the best measure for a particular species. It is also important to note

that the effect of stream velocity on superfetation has not been conclusive, as some studies have found positive effects (Zúñiga-Vega et al., 2007) while others have found no effect (Frías-Alvarez and Zúñiga-Vega, 2016; Zúñiga-Vega et al., 2017). More research will be needed to understand how generally stream velocity can affect life histories. Finally, stream velocity is potentially a gradient in each population due to spatial heterogeneity. This gradient may cause individual fish to experience high variability in the direction and magnitude of selection. Adaptation to stream velocity could only occur in environments that are consistent in streamflow allowing selection time to act. Furthermore, the effect of stream velocity may not be detectable on those populations that experience gradients (either spatially or temporally) with a single point in time and several collections will be needed to reflect this variability.

The effect of all selective pressures on embryo size were small in *P. prolifica*. It is unclear why this is the case. It is possible that the selective agents that we examined here are simply weak in their ability to shape embryo size. Alternatively, embryo size may be a trait with little variation among populations such as has been previously observed in other poeciliids (e.g., *Poecilia butleri*; Zúñiga-Vega et al., 2011), perhaps as a result of genetic constraints. Despite the modest responses of offspring size to the putative selective agents, the pattern of change observed here was consistent in the direction predicted by theory for all selective agents (Table 1).

We found that the effect of interspecific competition was generally weaker than the effect of population density in predicting life history. This supports a body of theory that argues that intraspecific competition in general should be stronger than interspecific competition (Chesson, 2000, 2013; Adler et al., 2018). Although this was true for the majority of life-history traits examined here, this was not the case for embryo size where interspecific competition was stronger than the effects of population density. We note that studies which consider interspecific competition as a selective pressure on life histories of livebearers are uncommon (Scott and Johnson, 2010; Chapuis et al., 2017). Hence, our findings point to a promising area for future research, especially in understanding the interplay of ecological interactions both within and among species.

Finally, it is interesting to note that both population density and interspecific competition best explained our data when included as direct effects on life histories. Usually, when competition (both intraspecific and interspecific) is considered in life-history research, it is usually explained in terms of its indirect effect on life history mediated through food resource availability (Reznick and Yang, 1993; Scott and Johnson, 2010; Johnson and Bagley, 2011; Wilson, 2013). However, this was not the case in our study. Several possibilities could account for this result. First, food resource availability may not be as important in our system as in others; and it is possible that competition could be acting through some other environmental variable, such as habitat use. Second, this could simply be an artifact of the model selection framework used in our analysis. Models with indirect effects required more parameters, and consequently these models are penalized for the inclusion of additional parameters. Hence, the models may not be favored not because indirect effects are unimportant, but because they are not sufficiently important to offset the cost of including them in the model. When comparing models with direct and indirect effects at comparable nesting (models 5 vs. 6, 8 vs. 9, and 11 vs. 12), most were indistinguishable (Table 4 and Table 5), so penalization for number of parameters may play an important aspect on preference for direct and indirect effects. Finally, it is

possible that competition indeed has a strong direct effect on life history in *P. prolifica*. If this is the case, we need to consider how competition could act as a direct selective agent on life histories, an area where we still lack a strong theoretical foundation to make predictions.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## ETHICS STATEMENT

The animal study was reviewed and approved by the Brigham Young University Ethics Committee.

## AUTHOR CONTRIBUTIONS

AJR-M, JJ, and MB conceived the study and interpreted the data analysis. AJR-M and JJZ-V collected all samples and processed samples. AJR-M collected and analyzed the data, and wrote the first draft of the manuscript. All authors contributed to manuscript corrections, editing, and improved the final manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2020.608046/full#supplementary-material>

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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