RESEARCH ARTICLE

Interactions between fitness components across the life cycle constrain competitor coexistence

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Abstract

1. Numerous mechanisms can promote competitor coexistence. Yet, these mechanisms are often considered in isolation from one another. Consequently, whether multiple mechanisms shaping coexistence combine to promote or constrain species coexistence remains an open question.

2. Here, we aim to understand how multiple mechanisms interact within and between life stages to determine frequency-dependent population growth, which has a key role stabilizing local competitor coexistence.

3. We conducted field experiments in three lakes manipulating relative frequencies of two *Enallagma* damselfly species to evaluate demographic contributions of three mechanisms affecting different fitness components across the life cycle: the effect of resource competition on individual growth rate, predation shaping mortality rates, and mating harassment determining fecundity. We then used a demographic model that incorporates carry-over effects between life stages to decompose the relative effect of each fitness component generating frequency-dependent population growth.

4. This decomposition showed that fitness components combined to increase population growth rates for one species when rare, but they combined to decrease population growth rates for the other species when rare, leading to predicted exclusion in most lakes.

5. Because interactions between fitness components within and between life stages vary among populations, these results show that local coexistence is population specific. Moreover, we show that multiple mechanisms do not necessarily increase competitor coexistence, as they can also combine to yield exclusion. Identifying coexistence mechanisms in other systems will require greater focus on determining contributions of different fitness components across the life cycle shaping competitor coexistence in a way that captures the potential for population-level variation.

KEYWORDS
competition, mating harassment, predation, species coexistence

1 | INTRODUCTION

Identifying the mechanisms that promote competitor coexistence is necessary to move beyond merely determining if, but also, how biological diversity is maintained or lost from communities (Letten et al., 2017; McPeek, 2012; McPeek & Siepielski, 2019; Tilman, 1987). A mechanistic understanding of coexistence would not only explain the properties of species that foster their local coexistence (McPeek, 2022; Tilman, 2000), but it would also provide insights about why species do not coexist—an equally worthwhile endeavour. Ultimately, at a regional scale, the balance between species coexisting and being lost is what shapes extant biodiversity—locally coexisting species make up only a fraction of species in communities (McPeek, 2017).

Local species coexistence is determined by the interplay of stabilizing effects and fitness differences (Chesson, 2000). Fitness differences are differences in species competitive abilities manifested as inequalities in average per capita population growth rates that predict which species would go locally extinct without stabilizing effects operating. Stabilizing effects are differences between species that cause them to experience reduced demographic effects of heterospecifics and intensify the effects of conspecific competitors (Chesson, 2000). When present, stabilizing effects give species a frequency-dependent demographic advantage when rare, preventing species loss (Chesson, 2000). Many studies have identified this phenomenological property of competitor assemblages (Adler et al., 2007, 2018; Chesson, 2000; McPeek, 2019, 2022). Critically, however, this negative frequency dependence does not only arise from competitive interactions (Chesson & Kuang, 2008; McPeek, 2022), as coexistence frequently involves interactions beyond resource competition (Chesson & Kuang, 2008; Gómez-Llano et al., 2021; Ishii & Shimada, 2012; Kishi et al., 2009; Kobayashi, 2019; McPeek, 2022; Shoemaker et al., 2020).

Indeed, multiple mechanisms can generate stabilizing effects among a set of ecologically similar species. For example, differences in predator susceptibility (Bried & Siepielski, 2019; Chesson & Kuang, 2008; Ishii & Shimada, 2012), resource use (Amarasekare, 2002; Bengtsson et al., 1994), phenology (Blackford et al., 2020; Usinowicz et al., 2017), and reproductive interactions (Gómez-Llano et al., 2021; Kishi et al., 2009; Kobayashi, 2019; Svensson et al., 2018). Such diverse mechanisms are thought to increase the potential for species to coexistence (Adler et al., 2010). However, mechanisms often act simultaneously (Chase et al., 2002; Kishi & Nakazawa, 2013; McPeek & Peckarsky, 1998), and these interactions can positively or negatively affect population growth and thereby promote or prevent species coexistence (Broekman et al., 2019). Yet, the relative contribution of different mechanisms towards species coexistence remains largely unknown (Broekman et al., 2019; Grether et al., 2022; Siepielski et al., 2011).

Differences in the relative contributions of mechanisms promoting species coexistence or loss may be more likely to occur in species with complex life cycles that experience abrupt ontogenetic habitat shifts. This is because different mechanisms can act within different habitats where different ecological opportunities are present (Wilbur, 1980) or major life history events occur (Gómez-Llano et al., 2021; Grether

et al., 2022). Understanding how mechanisms shaping coexistence interact across the life cycle is, therefore, necessary for a more complete understanding of how diversity is maintained in local communities (Moll & Brown, 2008; Polis et al., 1997, 2004). Yet, even though most species have complex life cycles (approximately 80% of animals; Werner, 1988), most studies have focused on a single life stage, or integrated across the life cycle, and thereby provided an incomplete view of how mechanisms unfold to shape local diversity (Moll & Brown, 2008; Nakashizuka, 2001). Decomposing the relative effects of different mechanisms can reveal how interactions between mechanisms across the life cycle can promote or prevent local species coexistence (Broekman et al., 2019; Shoemaker et al., 2020).

Damselflies are an ideal system to test these ideas because they have complex life cycles with an abrupt habitat shift from aquatic larvae to terrestrial adults where they experience different mechanisms that can affect their abilities to coexist. Larval mortality from predators is a key mechanism promoting species coexistence (Bried & Siepielski, 2019; McPeek, 1998; Stoks & McPeek, 2003), although foraging competition may also play a role (McPeek, 1998; Siepielski et al., 2011). In adults, reproductive interactions, such as mating harassment, can have a strong role in local species coexistence (Fincke, 1992; Grether et al., 2020). Critically, predation, competition, and mating harassment affect different fitness components (mortality, growth, and fecundity, respectively) that can interact to determine population growth rates (Stoks & Cordoba-Aguilar, 2012). Yet, it remains unknown how these various facets combine to promote or prevent local coexistence. To understand this, a demographic model determining their unique effects on fitness across the entire life cycle is required (Caswell, 1989; McPeek & Peckarsky, 1998).

Here, we quantify how different mechanisms, each contributing a possible stabilizing effect, combine across the life cycle to shape the potential for local species coexistence. To accomplish this, we performed replicated field experiments among three populations manipulating species relative frequencies in larvae and adults of two *Enallagma* damselfly species, to estimate the fitness effect of three mechanisms that can affect population growth rates in a frequency-dependent way. Specifically, we estimated the effect of fish predation on larval mortality, the effect of resource competition on larval growth rate (as manifested under the threat of predation), and the effect of mating harassment on female fecundity. We then used these fitness component estimates to parameterize a demographic model that incorporated carry-over effects across the life cycle (McPeek & Peckarsky, 1998) and determined the relative effect of each fitness component towards stabilizing population growth rates.

2 | MATERIALS AND METHODS

2.1 | Study system

Enallagma is a speciose genus of damselflies commonly found across North American lakes, including our study region of Northwest Arkansas, USA. Our goal in this study was not to develop an

understanding of coexistence among all *Enallagma* species. Rather, we aimed to characterize the mechanistic basis for potential local coexistence or species loss among two competing *Enallagma* species. As such, we focused on two of the most common co-occurring species in our study area: *E. exsulans* and *E. traviatum* (Ousterhout et al., 2019). *Enallagma* spends several weeks as eggs, about 11 months as aquatic larvae, and roughly 1 week as flying adults during the summer. Both larvae and adults are generalist predators, and larvae are primarily predated upon by fish.

Previous work has shown that fish predation can account for up to 80% of *Enallagma* mortality, and mortality rates increase as damselfly densities or species frequency increase (Bried & Siepielski, 2019; McPeek, 1990, 1998). Although fish predation is the dominant source of mortality, it can also arise from cannibalism and intraguild predation (Johnson, 1991; McPeek & Crowley, 1987; Van Buskirk, 1989). *Enallagma* also engages in direct and indirect intraspecific and interspecific competitive interactions, as increasing damselfly densities decreases their individual growth (change in body mass) rates (Johnson, 1991; Johnson et al., 1987; McPeek, 1990, 1998). Moreover, *Enallagma* are food-limited, since adding food increases their growth rates (McPeek, 1998). Thus, mortality from shared predators and competition for shared prey regulate their local abundances, and mortality and growth rate are key fitness components that shape their population growth rates (McPeek & Peckarsky, 1998).

Interactions during the adult life stage also have the potential to affect population growth rates in a frequency-dependent way. Damselflies often experience strong mating harassment and interspecific reproductive interference that can reduce female fecundity (Gómez-Llano et al., 2018; Gosden & Svensson, 2009; Grether et al., 2017, 2022). Male damselflies chase and attempt to clasp and mate with females, even of the wrong species (Corbet, 1999). Mating harassment from conspecific and heterospecific males is costly for females due to the energetic demands, physical damage, aggressive behaviours, and loss of foraging time (Grether et al., 2020; Sirot & Brockmann, 2001; Takahashi & Watanabe, 2010). Thus, if females experience more mating harassment from conspecifics than heterospecifics, we would expect a decrease in female fecundity when conspecifics males are common and increase when rare, thereby stabilizing species coexistence (Gómez-Llano et al., 2021; Kobayashi, 2019; Zhang & Hanski, 1998).

Given the above understanding, we estimated the contribution of stabilizing mechanisms shaped by competition, predation, and mating harassment indirectly through their effects on different fitness components. If these species differ ecologically in ways that reduce competition for resources (e.g., consume different limiting prey resources), this would be expressed in mutual, negative frequency-dependent growth rates. Similarly, if species differ in ways that shape their susceptibility to predators (e.g., they differ in coloration or behaviour), they would exhibit mutual, negative frequency-dependent mortality rates. Lastly, if species differ in their susceptibilities towards mating harassment, this too would be reflected in mutual negative frequency-dependent fecundity. This framework, therefore, allows us to investigate the mechanism underlying potential coexistence by evaluating each fitness component.

2.2 | Experiments to estimate larvae growth and mortality

To estimate frequency dependence in larval growth and mortality rates, we used a field experiment, following previous studies (Bried & Siepielski, 2019; McPeek, 1998; Ousterhout et al., 2019; Siepielski et al., 2010). We placed 11 submerged cages (47 cm length × 23 cm wide × 23 cm height) in the littoral zone of each of the three lakes: Fayetteville (Lat: 36.133, Long: −94.13), Bob Kidd (Lat: 35.97, Long: −94.36) and Lincoln (Lat: 35.99, Long: −94.41). The distance between lakes (>6 km) is greater than damselfly dispersal abilities (<1 km) (Conrad et al., 1999, 2002; Purse et al., 2003). Cages were made of 2.1 cm PVC pipe covered with mesh (1 mm opening), allowing damselfly prey to enter the cages. In each cage, we introduced the dominant macrophyte species at natural densities to provide foraging and hiding substrates for damselflies. We submerged cages for 1 week to allow natural colonization of damselfly prey items.

After this period, we used a substitutive series design where we held total combined density (density of both species) constant and randomly assigned cages to one of two treatments manipulating each species frequency: *E. exsulans* common (75%) and *E. traviatum* rare (25%) or *E. exsulans* rare (25%) and *E. traviatum* common (75%) ($n = 5$ replicates per treatment) and one empty cage. In the experimental cages, the total density was set at 40 damselflies (approx. 370 damselflies/m^2; within the natural range of damselfly densities that facilitates detecting density-dependence growth and mortality; Ousterhout et al., 2019). Although density-dependent effects can occur and affect different fitness components (Jolliffe, 2000), the critical test for detecting stabilizing effects is to determine if species limit themselves more than they limit others, thus frequency manipulations are a key way to quantify stabilizing effects (Adler et al., 2007). The empty cage was used to detect any intrusion by non-experimental damselflies—we found none.

Although this substitutive design is appropriate and sufficient for detecting stabilization (Adler et al., 2007; Broekman et al., 2019), it has limitations. Namely, it does not allow us to separately estimate the absolute magnitude of intra- and interspecific effects (see Hart et al., 2018; Inouye, 2001). Instead, it only allows us to assess how each species' mortality and growth rate respond to the relative intensity of the effects of intra- and interspecific competitors. Therefore, if species demographic advantages decline as they become common (e.g., lower growth or higher mortality), this would imply that the species differ in ways that stabilize coexistence (Adler et al., 2007; Chesson, 2000)—detecting this was the goal of our study. Additionally, because predation can weaken competition (e.g., reducing total

density; Chase et al., 2002), our ability to isolate the direct effect of competition is limited. However, it is important to note that the effects of competition are also manifested under the effects of predation. Thus, while this design cannot allow us to parse the isolated contribution of competition, it does allow us to understand the relative contributions of mechanisms reducing competition and generating a putative stabilizing effect. Therefore, the growth responses observed here can only be interpreted in light of their combined effect with predation from fish, as well as possible cannibalism and intraguild predation. In the *Discussion*, we return to this point and discuss results from a previous study using the same experimental design in the same species and lakes, except no fish were present (Ousterhout et al., 2019).

We collected larvae using a D-frame dip net; 30 individuals per species were preserved in 70% ethanol for initial size measurements (see below), and the remaining individuals were used to stock the experimental cages. In each cage, we introduced one bluegill fish (*Lepomis macrochirus*, standard length ~65 mm), the dominant predator in these lakes (Bried & Siepielski, 2019; Ousterhout et al., 2019).

The experiment was performed in October 2020, when damselflies were between their fifth and sixth instar (11 total instars). After 15 days, we collected all surviving larvae from cages and preserved them in 70% ethanol for measurement. We measured head width, which is strongly positively correlated ($R^2 > 0.90$) with damselfly body mass (McPeek, 1990), from photographs via ImageJ (Schneider et al., 2012). Photographs were taken above a standardized 1 cm grid.

Following previous studies (Bried & Siepielski, 2019; McPeek, 1990, 1998; Ousterhout et al., 2019), the growth rate was estimated as $\mathrm{mean}(\ln(h_r)) - \mathrm{mean}(\ln(h_i))/t$, were h is the head width of the recovered (h_r) and initial larvae (h_i) and t is the duration of the experiment in days. This model assumes that $h(t) = h(0)e^{gt}$, with g the growth rate (McPeek, 1998). Mortality rate was estimated as $(\ln(n_r) - \ln(n_i))/t$, where n is the number of individuals recovered at the end of the experiment (n_r) and the initial number of individuals (n_i) and t is the duration of the study. These fitness components are the response variables in this experiment.

Because we measured two fitness components in each cage, we used a multivariate general linear model with growth and mortality rates as the response variables, and the effects of lake, frequency, species, and all interactions, as explanatory factors. While this model can reveal a significant effect of the explanatory factors, to distinguish if the effects are in growth or mortality rate, or both, we used individual linear models of growth and mortality rates with the same model structure. Tukey post-hoc tests were used to make pairwise comparisons among lakes.

2.3 | Experiments to estimate mating harassment and fecundity

To test the role of mating harassment causing negative frequency dependence in female fecundity, we performed a field experiment in

which we set up 20 mesh cages (37 cm × 37 cm × 37 cm) in each of the same three lakes as the experiments with larvae. We performed this experiment in June and July (the reproductive season) of 2020 (Bob Kidd and Fayetteville) and 2021 (Lincoln). Fully mature males and females of similar age (age class 2; Siva-Jothy & Tsubaki, 1994) were caught via aerial nets. Cages were placed in the vegetation along the shoreline where adults perch and reproduce. In these cages, we introduced one female of each species and manipulated male species frequency as in the larvae experiment: *E. exsulans* common (75%, 3 males) and *E. traviatum* rare (25%, 1 male), and *E. traviatum* common and *E. exsulans* rare (within the natural density ranges). To identify mating attempts, each male was individually marked by applying a unique fluorescent colour powder to the claspers. Although *E. exsulans* females can show colour polymorphism (Paulson, 2011) we only found the 'green' morph in our lakes.

After 24 h in these cages, we recovered the females and used a UV light (Esco lite 51 Led UV light) to search for powder traces on the female's prothorax, indicating a mating attempt. As each male was uniquely marked, we were able to measure the minimum number of mating attempts received by each female. This method has been used successfully on other damselfly species to quantify mating attempts (Gómez-Llano et al., 2018, 2020), although it can underestimate the intensity of harassment, as costly non-clasping behaviours (i.e., chasing and fighting) or multiple claspings by the same male are undetected. In damselflies, heterospecific mating attempts can be equally as costly for females as conspecific mating attempts (Drury et al., 2015; Drury & Grether, 2014; Grether et al., 2017). Therefore, we used total mating attempts (combined number of mating attempts of con- and heterospecific males) as our estimate of mating harassment. We report conspecific and heterospecific mating attempts separately in the Supplemental Materials. We allowed living females to oviposit in 150 mL plastic cups lined with wet filtered paper for 24 h in the lab. After this period, we removed the females and covered the filters with filtered lake water for 2 days to allow eggs to melanise, then counted the number of melanized eggs (i.e., female fecundity). Because mature females of age class two are likely to have mated previous to the start of the experiment, we analysed the fecundity of all females irrespective if they mated or not during the experiment. It is important to note that female fecundity (and any fitness component) will be affected by conditions females experienced outside the cages, but any systematic difference in female fecundity between frequency treatments would reflect conditions within the cages. This is, if female fecundity is affected by sexual conflict, we expect females exposed to high frequency of conspecific males (i.e., common treatment) to have less fecundity than females exposed to a low frequency of conspecific males (i.e., rare treatment). Males and females were used for a single mating trial.

We analysed the number of mating attempts with a Poisson distribution, and female fecundity using a negative binomial model. We used lake, frequency, species, and all possible interactions as fixed factors. Female fecundity was collected mainly from Fayetteville ($n = 69$ females), with relatively few collected from Bob

Kidd ($n = 17$ females) and, due to logistical constraints, none from Lincoln. Analyses were performed using the packages 'LME4' (Bates et al., 2015), 'CAR' (Fox et al., 2012), 'MASS' (Venables & Ripley, 2013) and 'EMMEANS' (Lenth, 2019) in R (R Development Core Team, 2018). Permit from the Arkansas Fish and Game Commission (permit number: 082220221).

2.4 | Demographic model partitioning fitness components

To estimate the relative contributions of growth, mortality, and fecundity on per capita population growth rates, we used our experimental data to parameterize a population demographic model constructed for damselflies (McPeek & Peckarsky, 1998). In this model, larval growth and mortality rates, and female fecundity combine to determine population growth. We parameterized the model to estimate the population growth rate when rare and common in each lake. Then, to test the relative effects of each fitness component, we kept two of the three fitness components constant (set as the mean value when common and rare) and calculated how population growth rate when rare and common varied exclusively by the focal fitness component. For example, to test the effect of larval mortality, we used the measured larval mortality when common and rare from our experiments, and the mean values of larval growth rate and adult fecundity as a constant in both frequencies. To provide an estimate of uncertainty in population growth, we ran the model using the mean ± 1 standard error. Using the sampling error from the individual parameters of the model gives us an estimate of uncertainty in the model outcomes (Bowler et al., 2022).

In this model, population growth (λ) is defined by the number of adult females produced per female in the previous generation, given by:

$$\lambda = e^{-mD}HE, \tag{1}$$

where m is the larval mortality rate per day, D is the duration of the larval stage, H is the proportion of eggs that hatch, and E is the number of female eggs laid during the female adult lifespan (Figure 1). In our adult experiment, female fecundity was obtained from 1 day of oviposition, to estimate lifetime fecundity we used adult longevity estimates for congeneric females (E. borealis, 8 days) (Hecker et al., 2002; Robb & Forbes, 2006). Assuming equal sex ratio in oviposition (as is typical for damselflies; Fincke, 1986), the number of female eggs laid during a female lifespan is $E = (eggs \times 8)/2$. As in McPeek and Peckarsky (1998), we assume that all eggs hatch ($H = 1$), providing a measure of maximum fecundity. Importantly, variation in hatching success would not affect the conclusions of our model unless there is density-dependent hatching success, which has not been reported (McPeek, 2008). Because we were unable to gather fecundity from Lincoln, we used the mean fecundity between Fayetteville and Bob Kidd as our best approximation.

We do not have an estimate for D in our lakes. However, both species are found co-occurring during the larval and adult stages, with no indication of phenological differences. Therefore, we set D as 123 days
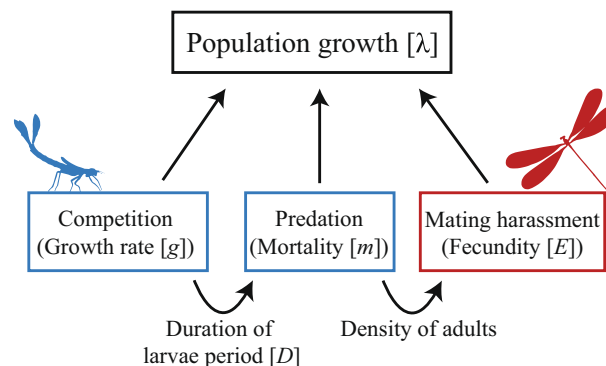

FIGURE 1　Different mechanisms in both larvae (blue) and adults (red) can promote or prevent species coexistence by affecting fitness components (individual growth rate [g], mortality [m] and fecundity [E]) that determine population growth (λ). Importantly, competition, predation and mating harassment can affect each other and have carry-over effects across life stages.

during which larvae can grow and be predated upon following previous studies (McPeek & Peckarsky, 1998). This duration corresponds with existing estimates of the period between eggs hatching and larvae becoming inactive during the winter and then re-emerging and growing until adulthood (McPeek & Peckarsky, 1998). Regardless of the absolute value of D, what is critical is that D can increase or decrease with the growth rate (g), and this rate can vary between species. Using common treatments as a reference value ($D = 123$ when common), the duration of the larval period when rare is

$$D_r = D - \left(D \times \left(1 - \left(\frac{g_c}{g_r} \right) \right) \right), \tag{2}$$

where g is the growth rate when common (g_c) and rare (g_r).

3 | RESULTS

3.1 | Larvae experiments

The multivariate general linear model showed a significant effect of lake and frequency on growth and mortality rates. Thus, we used individual linear models to disentangle the effects on growth and mortality rates. We found that growth rates varied among lakes, but there were no significant ($p > 0.05$) effects of frequency, species nor any interactions (Figure 2; Table S1). Across frequencies, *E. exsulans* had slightly higher, but not statistically significant, growth rates than *E. traviatum* (Figure 2a). Post-hoc analysis showed that damselflies from Bob Kidd had the highest growth rate, which was significantly different from Fayetteville but not Lincoln, and there were no significant differences between Fayetteville and Lincoln (Table S1).

Mortality rate also varied among lakes, and there was a strong effect of frequency—both species experienced ~35% lower mortality when rare than when common (Figure 2). Importantly,
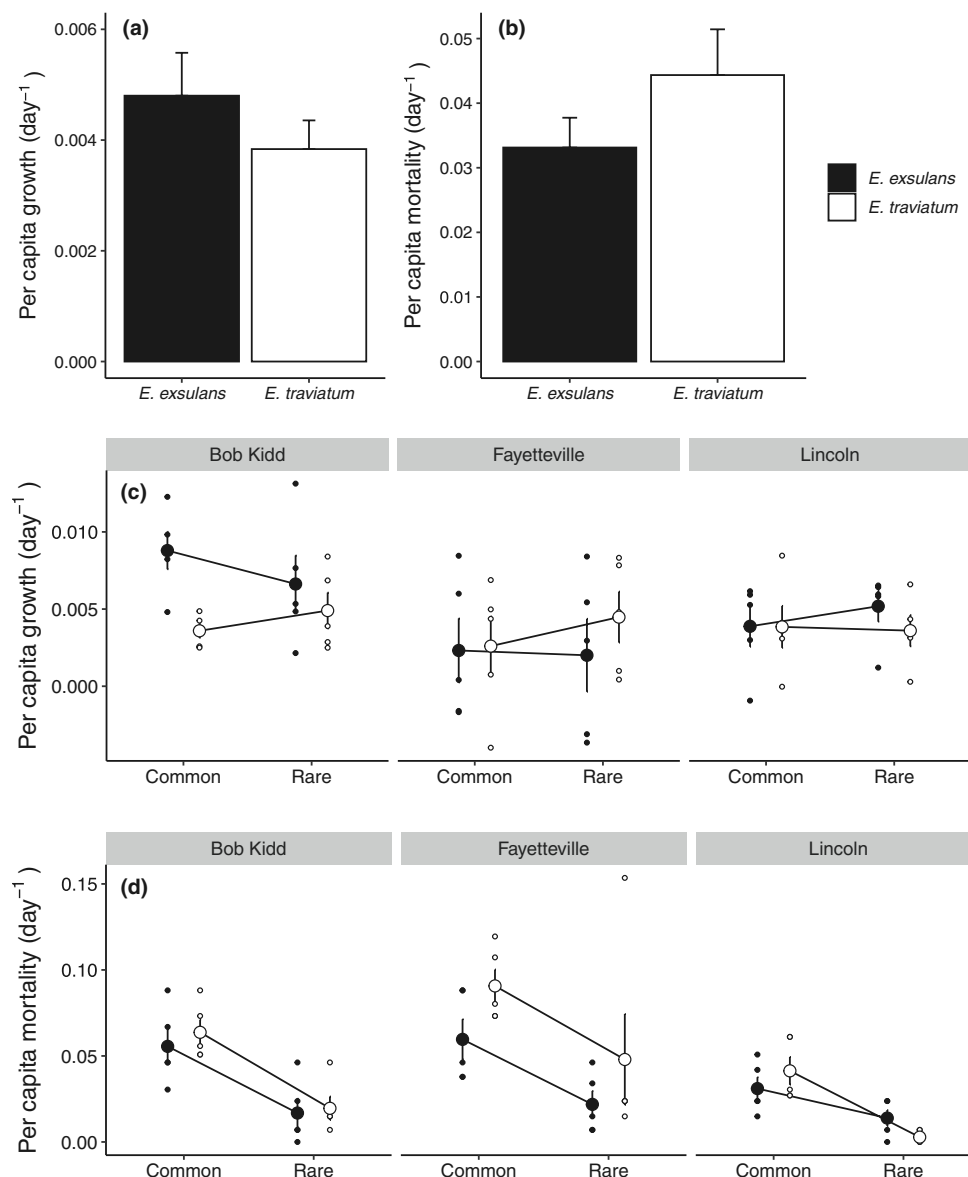
FIGURE 2 Growth and mortality rates among species and lakes. *Enallagma exsulans* showed higher larval growth rate (a) and lower mortality than *E. traviatum* (b), although these differences were not statistically significant; shown are mean values averaged across lakes ±1 standard error around the mean. We found no differences in growth rate when common or rare in either species (c). However, mortality was consistently higher when common than when rare in both species across all lakes (d). In (c) and (d), small dots show estimates per cage, and large dots and error bars show means ±1 standard error.

however, all the two and three-way interactions were non-significant. Across frequencies, *E. exsulans* had lower, but not statistically significant, mortality rates than *E. traviatum* (Figure 2b). Damselflies from Fayetteville had the highest mortality rate, which was significantly different from Lincoln but not Bob Kidd, and there were no significant differences between Lincoln and Bob Kidd (Table S1).

3.2 | Adult experiments

We found no significant effect of lake, species, frequency, nor any interaction on the number of total mating attempts (Figure 3a;

Table S2). When we analysed conspecific and heterospecific mating attempts separately, we found a significant effect of frequency as females experienced more conspecific mating attempts when common and more heterospecific mating attempts when rare (Table S3; Figure S1).

We found a marginal effect of frequency on female fecundity ($p=0.057$), with females having ~19% higher fecundity when rare than when common (Figure 3b). There was a significant lake×species interaction, with *E. traviatum* having higher fecundity in Fayetteville than in Bob Kidd, but no difference between lakes in *E. exsulans* (Figure 3b). There was no significant effect of lake, species, nor the other two (lake×frequency, frequency×species) or three-way interactions (Table S2).
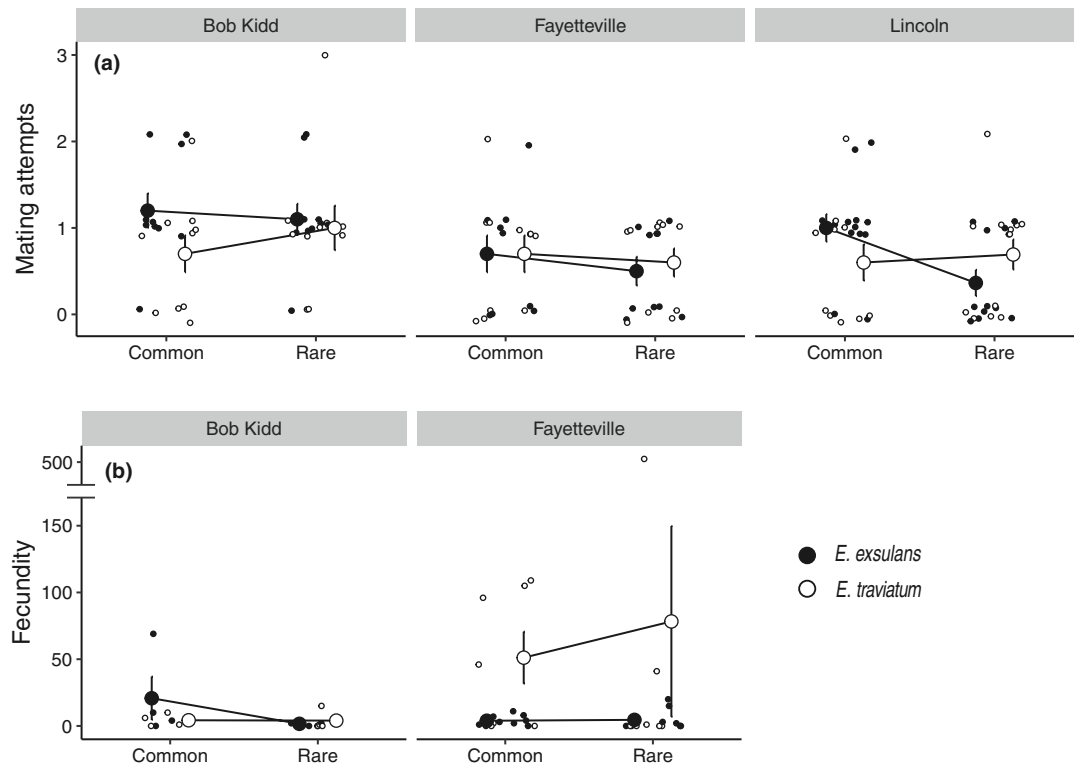
FIGURE 3 We found no frequency-dependent mating attempts in either species (a). *Enallagma traviatum* female fecundity was higher in Fayetteville than in Bob Kidd but no difference was found in *E. exsulans* (b). Small dots show the estimates per cage, and large dots and error bars show the means ±1 standard error. Note broken *Y* axis in (b). In the Supporting Information, we report results for conspecific and heterospecific mating attempts separately.

3.3 | Demographic model

We found that population growth rates in *E. traviatum* increased when rare and decreased when common in all lakes except Fayetteville. However, *E. exsulans* decreased when common and increased when rare in all lakes except Bob Kidd (Figure 4). Together, these results indicate that these commonly co-occurring species are likely not stably locally coexisting in at least two of the three lakes, as the only lake where both species population growth rates increased when rare was Lincoln.

Our decomposition of λ allowed us to establish why the stabilization of coexistence seems to break down. Namely, the beneficial effect of reduced larval mortality when rare was offset by the negative effects of larval growth and female fecundity, suggesting negative interactions within and between life stages constraining coexistence (Figure 4; Table S4). Intriguingly, unlike mortality, neither the effect of larvae growth nor fecundity alone consistently determined increased or decreased population growth rates, regardless of species, lake, or frequency. This suggests a limited demographic effect of larvae competition and mating harassment.

4 | DISCUSSION

Determining the mechanistic basis for coexistence is a challenging problem, especially for species with complex life cycles that

experience ontogenetic habitat shifts where multiple mechanisms can act in different life stages. We quantified the effect of different mechanisms as captured via their contributions to shaping fitness components that can determine population growth. Our decomposition of the fitness components underlying frequency dependence in population growth demonstrates that interactions between fitness components within and between life stages seem to largely constrain local species coexistence, but this effect varies across populations. Collectively, our results paint a complicated picture of how demographic forces combine to shape the abilities of species to locally coexist, and in doing this, allow us to understand why species do not coexist.

Our results are consistent with the idea that coexistence and the underlying mechanisms shaping it are not fixed properties of species. Rather, species coexistence may or may not occur in a given location (Bried & Siepielski, 2019; Germain et al., 2020), as the contribution of different mechanisms varies among species and populations. Several studies have reached this same conclusion regarding the population-specificity of coexistence; however, these studies are typically conducted with different species in different locations, not the same species assemblages (but see Germain et al., 2020). Thus, it remains unclear whether spatial variation in the potential for local coexistence is because of observing different species in different locations, or because of differences among the same set of species, as shown here.
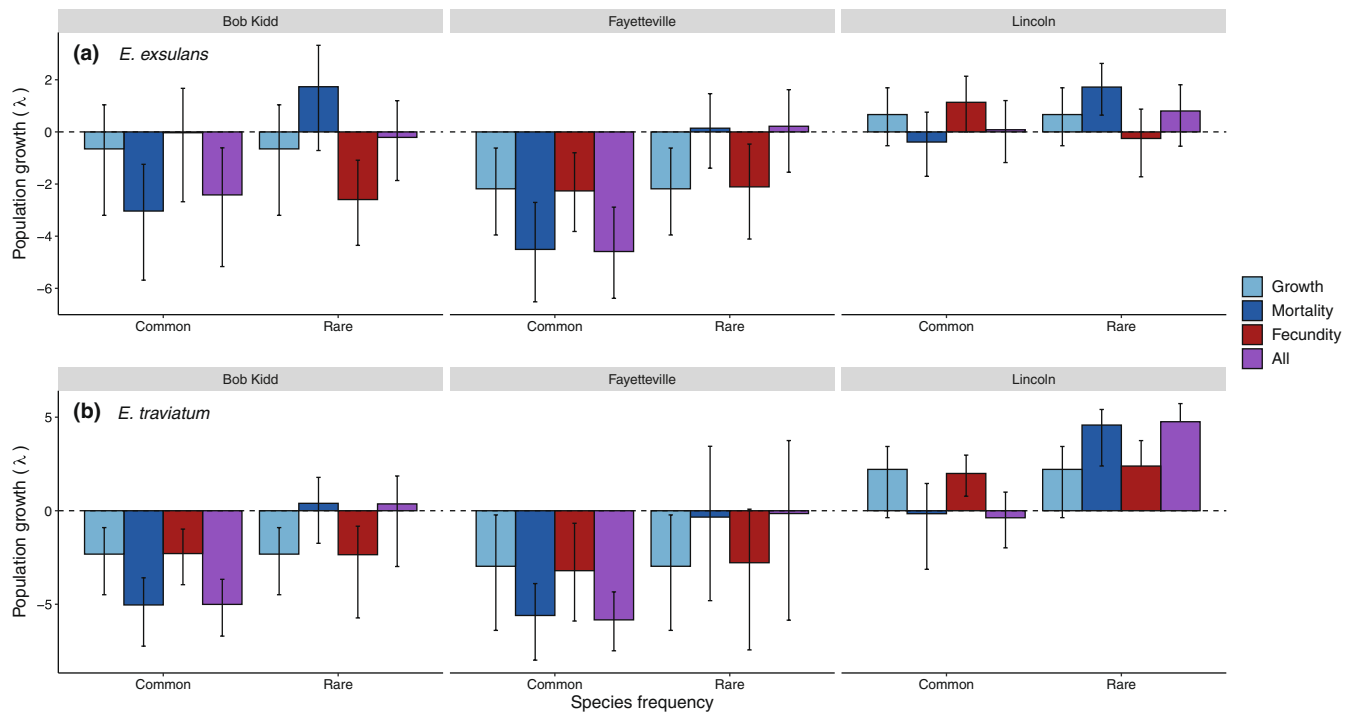
FIGURE 4 Relative and combined effects of larval growth and mortality, and female fecundity on per capita population growth (λ) when common and rare (shown on a natural logarithmic scale). Population growth of *E. exsulans* decreased when common and increase when rare in all lakes except Bob Kidd (a). *E. traviatum* decreased when common and increased when rare in all lakes except Fayetteville (b). The dashed line depicts no effect on population growth. Note different ranges on Y axes showing substantial differences between species and lakes. Upper and lower bounds were obtained by parametrizing the model using the estimated mean ± 1 standard error of each fitness component. Note the missing lower bounds of λ in *E. traviatum* in Lincoln depicting population extinction.

While we do not have estimates of equalizing mechanisms that can reduce competitor fitness differences in population growth (Adler et al., 2007; Chesson, 2000), the absence of stabilizing effects on per capita population growth for most of the populations studied indicate that local coexistence is unlikely. At least one species had negative population growth rates when rare in most locations, which was indicative of local demographic sinks. Importantly, although there was a large degree of uncertainty on the estimates of population growth from our model, we found no evidence of positive population growth rate in both species when rare. As such, the presence of these species is perhaps explained by ongoing, albeit likely infrequent, dispersal in a metacommunity (Leibold et al., 2004). Regardless, even though our study area covered only a fraction of the geographic distributions of these species, we detected considerable heterogeneity in the potential for local coexistence via stabilizing effects operating. Consequently, the potential for coexistence must be viewed on a population-by-population basis, highlighting the importance of geographic context in understanding the maintenance and loss of species diversity (Chesson, 2000; Germain et al., 2020; Hart et al., 2017).

Notably, the putative absence of local coexistence between these species in most locations is likely not attributable to resource competition alone. If resource competition were the driving force, we expected to observe evidence for positive frequency-dependent individual growth rates, but we did not observe this pattern. That

said, our experimental design does not allow us to infer whether competition is occurring, because we manipulated species frequencies and not total densities. Numerous studies, however, have shown that damselflies do compete for limiting prey resources – increasing their densities consistently causes individual growth rates to decline, and adding food causes them to increase (*reviewed in* Grether et al., 2022). While our estimates of competitive effects could be underestimated because predation reduced damselfly densities and the potential strength of resource competition (e.g., Chase et al., 2002), no consistent negative frequency dependence in growth rates was found in identical experiments with the same species in the same lakes but in the absence of fish (Ousterhout et al., 2019). Moreover, no consistent evidence of a positive frequency-dependent mortality rate was observed in those same experiments, indicating that no mortality (e.g., via cannibalism or intraguild predation) through competitors among species was occurring that could generate exclusion (Ousterhout et al., 2019). Fish predation could also be directed at larger individuals, affecting our estimates of individual growth rate (McPeek, 1990; Siepielski et al., 2020). Indeed, in Fayetteville, several replicates had negative growth rates, consistent with size-selective predation (Brooks & Dodson, 1965). Such selection is known to reduce the strength of intraspecific competition (Siepielski et al., 2020), which could therefore weaken stabilizing effects depending on how such selection might also affect interspecific competition. Regardless, this simply means that competitive effects are

likely overridden by predation being the dominant forces regulating population growth rates (Grether et al., 2022; McPeek, 2008; McPeek & Peckarsky, 1998).

While we cannot detect absolute competitive effects, it is perhaps somewhat surprising that we found no evidence for resource partitioning despite prior evidence for competition for limiting prey resources. The diversity of prey resources in the littoral zone where damselflies dwell is astounding—hundreds of different prey species abound (Thorp & Covich, 2009). However, the lack of evidence for resource partitioning is widespread, and damselflies are thought to be generalist consumers, consuming prey in proportion to their relative abundance (Corbet, 1999; Thompson, 1978). Aside from one study comparing different damselfly genera (Siepielski et al., 2011), no experimental field study, including many different *Enallagma* species pairs in geographically disparate lakes across eastern North America, has ever detected an effect of species frequencies shaping growth rates (McPeek, 1998; Ousterhout et al., 2019), including studies where total density was also manipulated so that more intense competition could be maintained (Bried & Siepielski, 2019; Siepielski et al., 2010). It may simply be that trade-offs in the ability to use and acquire different prey are simply insufficient to favour partitioning in resource use (Abrams & Chen, 2002; Chesson, 2000; Germain et al., 2021).

The only detectable differences consistently generating stabilizing effects seem to be susceptibility to fish predation. Meyer and Kassen (2007), also noted that in the absence of any kind of resource specialization, predation can be the dominant feature promoting stabilization. Interestingly, although mortality generated a stabilizing effect, neither growth rates nor fecundity exhibited positive frequency dependence that could destabilize the potential for overall stabilization (Broekman et al., 2019). Instead, the predicted species loss observed here seems to arise because of the interactive effects of various fitness components shaping per capita population growth rates across the life cycle. Indeed, in species with complex life cycles, mechanisms affecting different fitness components can interact across the life cycle and generate carry-over effects, affecting coexistence outcomes. Therefore, studying mechanisms in only one life stage can lead to a partial and possibly erroneous picture of how the mechanisms combine to affect coexistence (Broekman et al., 2019; Gómez-Llano et al., 2021; Kishi & Nakazawa, 2013; Miller & Rudolf, 2011; Moll & Brown, 2008; Schreiber & Rudolf, 2008). Shoemaker et al. (2020) also found that the interactive effects between predation and environmental variation could lead to species exclusion. Like our study, this understanding could only be achieved by decomposing the contribution of different forces affecting the potential for coexistence (Shoemaker et al., 2020).

While we developed a comprehensive decomposition of the fitness effect of different mechanisms stabilizing coexistence, we acknowledge our study is incomplete. We focused our efforts based on a detailed understanding of the natural history of this system (e.g. Grether et al., 2022; Siepielski et al., 2022), but there are likely other mechanisms that can affect fitness components and

population growth in our species, such as adult predation by birds (Kuchta & Svensson, 2014; Outomuro & Johansson, 2015) and parasitism (Åbro, 1982; Gómez-Llano et al., 2020). However, our study likely captured the main factors determining population growth (see McPeek, 2008; McPeek & Peckarsky, 1998; Thompson et al., 2011). For example, using our model, *E. exsulans* would have to produce 146% more eggs in Bob Kidd and 49% more in Fayetteville when rare to cause positive population growth, in contrast to a reduction of larval mortality rate of only 32% in Bob Kidd and 12% in Fayetteville when rare. We also lack temporal replication, and it may be that the effect of the different fitness components varies temporally, so that both species occasionally experience stabilization, which over the long run would still result in species loss (Haney et al., 2015). Regardless, our results predict species loss across most locations, attributable to the combination of different fitness components among locations, highlighting the complexity of inferring coexistence outcomes.

The frequent observation of ecologically similar species in small local areas is often the motivating basis (the 'paradox'—Hutchinson, 1961) for studies focused on the maintenance of species diversity. As noted by Simha et al. (2022), perhaps we should be surprised to encounter what we perceive as high diversity, since the focus on understanding species diversity has been cast in the light of what drives species exclusion, namely competition. In nature, species, including the species studied here, do compete, but they also interact with predators, parasites, pathogens, and mutualists, all against a milieu of varying abiotic factors. We fully agree with the view that we must move away from a seemingly paradoxical view of diversity distorted by a caricature of nature as one dominated by competition alone (McPeek, 2022; Simha et al., 2022). However, given our results, we disagree with the idea that we should develop a mindset assuming that species are coexisting as the default (Simha et al., 2022), as there is no reason to make any kind of assumption; rather, it must be empirically evaluated (Siepielski & McPeek, 2010).

Community ecologists have developed an ever-enriching theoretical and empirical edifice that expands beyond competition (Godoy et al., 2018; Gómez-Llano et al., 2021; McPeek, 2022; Shoemaker et al., 2020), increasing our mechanistic understanding of coexistence. Our results contribute to this by showing that the fitness effects of individual mechanisms per se do not matter. Rather, what matters is how they combine, and that they combine differently in different species and in different populations, to shape potential local coexistence. Although the presence of multiple mechanisms would seem to afford a greater opportunity for species to differ in ways that promote coexistence, we have shown they can also constrain coexistence, highlighting the importance of integrating population and community ecology to understand the maintenance of species diversity.

AUTHOR CONTRIBUTIONS

Miguel Gómez-Llano and Adam M. Siepielski conceived the idea. Miguel Gómez-Llano, Wade Boys, Taylor Ping, Simon Tye and Adam M. Siepielski performed the experiments. Miguel Gómez-Llano

conducted the analyses and wrote the first draft of the text with substantial help from all the authors.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.6m905qg4k (Gómez-Llano et al., 2023).

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SUPPORTING INFORMATION

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

Table S1: Results from the multivariate general linear model comparing growth and mortality rates in *E. exsulans* and *E. traviatum* at two different relative species frequencies across three lakes (A). Results from separate linear models for larval growth and mortality rates (B). Post-hoc analysis of lake in growth and mortality rates (C).

Table S2: Results from generalized linear model of total mating attempts (A) and female fecundity (B) in *E. exsulans* and *E. traviatum* at two different relative species frequencies across three lakes. (C) Tukey post-hoc analysis of the estimated differences in female fecundity between lakes in each species.

Table S3: Results from generalized linear model of conspecific mating attempts (A) and heterospecific mating attempts (B) in *E. exsulans* and *E. traviatum* at two different relative species frequencies across three lakes.

Table S4: Estimated relative demographic effects of larval growth rate (*g*), larval mortality (*m*), female fecundity (*E*) and the added effects of all fitness components on population growth (*λ*) in for *E. exsulans* and *E. traviatum* when common and rare in each of the three lakes.

Figure S1: Females of both species experience more mating attempts from conspecifics when common than when rare (A), but more heterospecific mating attempts when rare (heterospecifics are common) than when common (heterospecifics are rare) (B). Small dots show the estimates for each experimental cage, and large dots and error bars show the means and ±1 standard error around the mean. Black dots represent *E. exsulans* and white dots *E. traviatum*.