

ARTICLE

Freshwater Ecology

Evidence consistent with local adaptation to predation shaping stabilizing effects underlying local coexistence

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Abstract

Trait divergence in resource use and susceptibility to predation can promote local competitor coexistence if such divergence generates demographic advantages when species are rare, producing frequency-dependent stabilizing effects. These effects may vary spatially as populations experience different ecological conditions shaping species interactions. Here, we examine how population-specific differences in competitive and predator–prey interactions among damselfly larvae are associated with variation in the strength and occurrence of stabilizing mechanisms underlying coexistence. Using field transplant experiments, we compared growth and mortality rates between local and transplanted damselfly populations to assess whether stabilizing effects differed across population–environment contexts. We observed population-specific differences in growth rates in one species, but found no evidence that resource competition generated stabilizing effects. By contrast, fish predation imposed strong frequency-dependent mortality generating stabilization, and the occurrence and magnitude of this effect differed between local and nonlocal populations. However, the direction and strength of these differences varied between species: In one species, frequency-dependent predation effects were marginally reduced, whereas in the other, they were effectively absent. These asymmetries suggest that population-specific responses to predators, potentially driven by local adaptation, may influence coexistence outcomes, even under similar ecological settings. A laboratory experiment revealed no differences in predation rates imposed by fish on local versus nonlocal damselfly prey, indicating that observed field patterns are unlikely to arise from predator local adaptation to prey alone. Collectively, our results highlight how spatial variation in species interactions can generate heterogeneity in stabilizing processes, while underscoring the challenges of disentangling ecological and evolutionary mechanisms in natural systems.

KEYWORDS

adaptation, coexistence, competition, damselfly, predation, stabilization

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INTRODUCTION

Population differentiation in response to environmental conditions, such as through local adaptation, can not only promote (Bassar et al., 2017; Hart et al., 2019; Lankau, 2011; Le Gac et al., 2012; Zhao et al., 2016) but also constrain the maintenance of species diversity in a given area (i.e., local species coexistence) (Lankau, 2011; Nadeau et al., 2021; Pastore et al., 2021; Urban et al., 2012; Urban & De Meester, 2009). Indeed, evolutionary change rarely occurs uniformly at the species level. Instead, populations of species often evolve and locally adapt differently in response to variable abiotic conditions and species interactions (Hargreaves et al., 2020; Hereford, 2009; Thompson, 2005; Wadgyman et al., 2022). Consequently, understanding ecological processes at the population level is necessary to determine whether and how divergence contributes to species coexistence (Gómez-Llano et al., 2023; Lankau, 2011; McPeck, 2017; Urban et al., 2008).

Local species coexistence is shaped by the balance between stabilizing effects and fitness differences (Chesson, 2000). Stabilizing effects give species a demographic advantage when rare and promote coexistence. By contrast, fitness differences reflect the difference between species in their average per capita population growth rates and can lead to competitive exclusion and thus constrain coexistence (Chesson, 2000). At the population level, evolutionary divergence among competitors has the potential to promote species coexistence via stabilizing effects if trait differences cause species to experience stronger demographic consequences of intraspecific than interspecific interactions (Adler et al., 2007; Chesson, 2000; MacArthur, 1958; MacArthur & Levins, 1967). For instance, population divergence can promote species coexistence through differences in resource use (Schoener, 1974), predator susceptibility (Chesson & Kuang, 2008), mutualistic interactions (Johnson & Bronstein, 2019), or phenology (Blackford et al., 2020)—each of which can generate a stabilizing effect (Chesson, 2000). Such stabilizing effects could arise because competitors have coevolved via character displacement or because populations have evolved in response to other local environmental conditions (Bassar et al., 2017; Germain et al., 2018; Schluter & McPhail, 1992). Population divergence can also shape species fitness differences, such as competitive abilities and sensitivity to competition (Sakarchi & Germain, 2023), and thereby affect species coexistence (Germain et al., 2020; Hart et al., 2019).

While many studies suggest that local population differentiation promotes coexistence, it can also constrain or prevent coexistence (HilleRisLambers et al., 2012; Pastore et al., 2021). For example, the coevolutionary history of

competitor species could lead to local niche convergence and competitive similarity, increasing the likelihood of exclusion (Fox & Vasseur, 2008; Lancaster et al., 2017; McPeck, 2017; Pastore et al., 2021). Alternatively, local divergence in niche use might increase competitive fitness differences if such niche evolution causes one species to use an inferior resource (Chen & Pfennig, 2020; Lankau, 2011). Similarly, not all species evolve in response to the same sets of conditions, and some species may evolve, and others may not. Such asymmetries in evolution may limit the potential for local species coexistence. Indeed, the ecological consequences of evolution for community structure differ when only one or multiple species are evolving (Vanvelk et al., 2024).

One group for which population differentiation might play an important role in shaping local coexistence are damselflies in the genus *Enallagma*. Damselflies have limited dispersal abilities (Conrad et al., 1999, 2002; McPeck, 1989; Purse et al., 2003) and lakes often differ in environmental features shaping demographic performance and stabilizing effects (Gómez-Llano et al., 2023; Ousterhout et al., 2019; Siepielski et al., 2016). This system therefore provides an opportunity to investigate whether population-specific responses to local conditions are associated with key processes underlying coexistence. We focus here on frequency-dependent stabilizing effects because some degree of stabilization is necessary to promote long-term local species coexistence (Chesson, 2000). We also have a well-developed understanding of stabilizing effects in this system (Bried & Siepielski, 2019; Gómez-Llano et al., 2023; Ousterhout et al., 2019; Siepielski et al., 2011). While there is spatial variation in stabilizing effects damselflies experience (Bried & Siepielski, 2019; Gómez-Llano et al., 2023; Ousterhout et al., 2019; Siepielski et al., 2010), our previous work found that larvae mortality from fish predation generates a stabilizing effect that promotes local damselfly coexistence (Bried & Siepielski, 2019; Gómez-Llano et al., 2023). Such spatial variation could arise from differences in environmental conditions (e.g., predator or prey densities) as well as through potential local adaptation to these conditions. By contrast, we found no evidence for divergence in resource use shaping competition among species (Bried & Siepielski, 2019; Gómez-Llano et al., 2023; Ousterhout et al., 2019). Although damselflies are food-limited and engage in resource competition (Grether et al., 2022; McPeck, 1998), growth advantages when rare have not been detected locally in *Enallagma* (Grether et al., 2022). Nonetheless, population differentiation in resource use could still influence demographic performance and coexistence outcomes under different ecological contexts, such as during initial colonization (Bassar et al., 2017).

Here, we ask whether population-specific responses, consistent with local adaptation in competitive and predator–prey interactions, shape stabilizing effects contributing to local species coexistence among damselflies. We test the hypothesis that stabilizing effects generated through predation from a shared fish predator should be stronger among local than nonlocal species pairs. This stronger stabilization could arise if populations differ in traits mediating detection by predators, such as camouflage or behavior. Because bluegill (*Lepomis macrochirus*), the dominant fish predator in this system, is a highly visual predator capable of forming search images based on repeated encounters with common prey (O'Brien et al., 1976), locally adapted individuals may experience reduced predation when rare, but lose this advantage when common and predators focus on them. Such frequency-dependent predation driven by predator search images can generate stabilizing effects that maintain prey diversity (Ishii & Shimada, 2010). Although we previously found no stabilization underlying competition for shared resource use (Bried & Siepielski, 2019; Gómez-Llano et al., 2023; Ousterhout et al., 2019), we nonetheless investigate whether growth rates exhibit a signature of potential local adaptation that contributes to local stabilization.

To test these ideas, we transplanted two common damselfly species to nonlocal lakes, controlling for total and species relative abundances and measuring growth rates, shaped by competitive interactions, and mortality rates, mediated by fish predation (Bried & Siepielski, 2019; Gómez-Llano et al., 2023). Together with a previous study performing the same experiment but in local lakes, we asked whether frequency-dependent larval growth rates and mortality rates differ between local and nonlocal assemblages. Given the importance of fish predation in mediating local species coexistence, we also evaluated whether fish generate higher mortality on local or nonlocal damselflies. Lastly, we quantified differences between local and nonlocal lakes in environmental features to which populations could have adapted, and thus could explain between-lake differences in growth and mortality rates. Much like how classic transplant experiments among single species are used to infer local adaptation (Kawecki & Ebert, 2004), this design allows us to evaluate whether demographic patterns consistent with local adaptation are associated with variation in stabilizing effects among competing species.

MATERIALS AND METHODS

Study system

Enallagma damselflies are a diverse genus of predatory insects commonly found in freshwater systems across

North America. In lakes across Northwest Arkansas, where this study took place, *Enallagma exsulans* and *Enallagma traviatum* are two of the most common co-occurring species (Ousterhout et al., 2019). In this region, *Enallagma* spend several weeks as eggs, approximately 11 months as aquatic larvae, and around 1 week as flying adults during summer. During the aquatic larval stage, damselflies are littoral zone generalist predators that consume animals smaller than them, including other damselflies, and serve as prey sources, mainly for fish (McPeck, 1998).

Predation by fish is the primary source of mortality in *Enallagma* damselflies, accounting for up to 80% of larval mortality (Bried & Siepielski, 2019; McPeck, 1990). As such, it accounts for much of the local population regulation in damselflies (Gómez-Llano et al., 2023; McPeck & Peckarsky, 1998). Moreover, fish predation appears to be the main source of stabilizing effects in these species in these lakes (Gómez-Llano et al., 2023). Cannibalism also occurs among conspecifics, and intraguild predation among competitors, but has no detectable role in promoting local damselfly species coexistence (Gómez-Llano et al., 2023; Grether et al., 2022).

Enallagma also engage in direct and indirect competition (Grether et al., 2022; McPeck, 1998). Competition for limiting food resources among larvae, as well as reproductive interactions of adults, has been widely observed in this system (Gómez-Llano et al., 2023; Johnson, 1991; Johnson et al., 1987; McPeck, 1990, 1998). Field experiments elevating food resources increase individual somatic growth rates (i.e., increased biomass), which are density-dependent (McPeck, 1998). However, we recently showed that larval resource competition and adult reproductive interactions have a limited role in generating stabilizing effects in these species (Gómez-Llano et al., 2023). Thus, mortality from a shared fish predator and, to a limited extent, competition for limiting food resources are key fitness components that shape damselfly population growth rates (Gómez-Llano et al., 2023; McPeck & Peckarsky, 1998). Given this knowledge, we evaluated how potential local adaptation may shape stabilizing effects via predation by fish and through resource competition.

Experimental methods and statistical analysis

This study builds upon previous research that examined the effects of different mechanisms underlying damselfly species coexistence (Gómez-Llano et al., 2023). In that work, performed in October 2020, we also studied *E. exsulans* and *E. traviatum* in their local lakes, which

we review below because the experimental setup is quite similar. The study presented here complements that previous experiment, and its transplant design across lakes (i.e., nonlocal environments) provides an opportunity to test whether demographic patterns consistent with local adaptation are associated with differences in the occurrence or strength of stabilizing effects. In the previous experiment, we placed 11 submerged PVC cages (47 cm length $\times$ 23 cm wide $\times$ 23 cm height) covered in nylon mesh (1 mm opening) in the littoral zone of three lakes in Northwest Arkansas: Bob Kidd (lat: 35.97, long: -94.36), Fayetteville (lat: 36.133, long: -94.13), and Lincoln (lat: 35.99, long: -94.41). The mesh openings allowed small prey to enter the cages but prevented damselflies from escaping or entering cages. We added the dominant macrophyte of each lake at natural densities to each cage and allowed all cages to be colonized by natural local prey for 1 week before damselflies were introduced.

Next, we used a substitutive series design that held the total density of both species combined constant while manipulating their relative abundance by randomly assigning each cage to one of two treatments: *E. exsulans* common (75%) and *E. traviatum* rare (25%) or *E. exsulans* rare (25%) and *E. traviatum* common (75%). Each treatment had five replicate cages in each lake. In each lake, we left one cage empty to detect possible intrusion from nonexperimental damselflies, which we did not find. We collected damselfly larvae with a D-frame dip net and introduced 40 damselflies to each cage giving a total density of approximately 370 damselflies/m², which is within the range of natural damselfly densities in this study region (Ousterhout et al., 2019). We also introduced one approximately 65 mm bluegill fish—the dominant fish predator in our study region—to each cage, caught using a 4.5 $\times$ 1.5 m seine net (5 mm mesh). All macrophytes, damselflies, and fish were collected in the same lakes in which the experiments took place. The experiment lasted 15 days, which is a sufficient period to detect differences in growth and mortality rates in response to frequency manipulations (e.g., Gómez-Llano et al., 2023). We then collected all surviving larvae and preserved them in 70% ethanol for measurement. We also collected 30 individuals of each species in each lake immediately before the experiment began and preserved them in 70% ethanol for initial size measurements. We photographed all preserved individuals above a standardized 1 cm grid and measured head width using ImageJ (Schneider et al., 2012). Head width is strongly correlated with body mass (McPeck, 1990).

Using this experimental framework, we then examined the frequency-dependent effects of competition and fish predation on damselflies in their local lake

(Gómez-Llano et al., 2023). Although density-dependent effects can also occur and have different effects on different fitness components (Jolliffe, 2000), the critical test for quantifying stabilizing effects is to determine whether species limit themselves more than they limit other species. That is, whether species have a fitness advantage over the competing species when rare (i.e., low relative frequency). Thus, frequency manipulations are key to quantifying this stabilizing effect (Adler et al., 2007). The substitutive design we employed is appropriate for detecting stabilization (Adler et al., 2007; Broekman et al., 2019), but it does not allow us to separately estimate the absolute magnitude of intra- and interspecific effects (see Hart et al., 2018; Inouye, 2001). Rather, it allows us to estimate how mortality and growth rate in each species respond to the intensity of the effects of intra- and interspecific competitors. Additionally, this design does not allow us to estimate the effect of competition in the absence of predation. Although this aspect is a limitation of the current study, we note that estimates of growth and mortality rates of the same species in the same lakes, but in the absence of fish predators, found no frequency dependence in growth or mortality rates (Ousterhout et al., 2019). Therefore, no stabilizing effects due to competition could be detected in the absence of predation. Regardless, it is important to consider that the effects on growth estimated in our study can only be interpreted as their combined effect with fish predation (e.g., Siepielski et al., 2010), as well as possible cannibalism and intraguild predation.

To test whether potential local adaptation affected stabilization through growth and mortality, we expanded on this initial experimental setup. We used the same experimental cage setup we previously used but conducted transplants of damselfly populations between lakes to use nonlocal damselflies (Figure 1). It is important to note that the previous experiments were conducted in October 2020 (Gómez-Llano et al., 2023) while the current experiments with nonlocal individuals were conducted during April–May 2021, which has important implications for interpretability of the results (see below). By comparing local and nonlocal performance in growth and mortality rates, we can determine whether those demographic rates are consistent with a signature of how local adaptation shapes stabilizing effects by combining both transplant experiments (capturing the potential effects of local adaptation) and a frequency manipulation (capturing the stabilizing effect). As before, we placed 11 cages in each lake following the previous methodology, then we collected 230 individuals of each species of damselfly from each lake (hereafter source lake) and introduced them in cages at a different lake (hereafter experimental lake). The rest of the

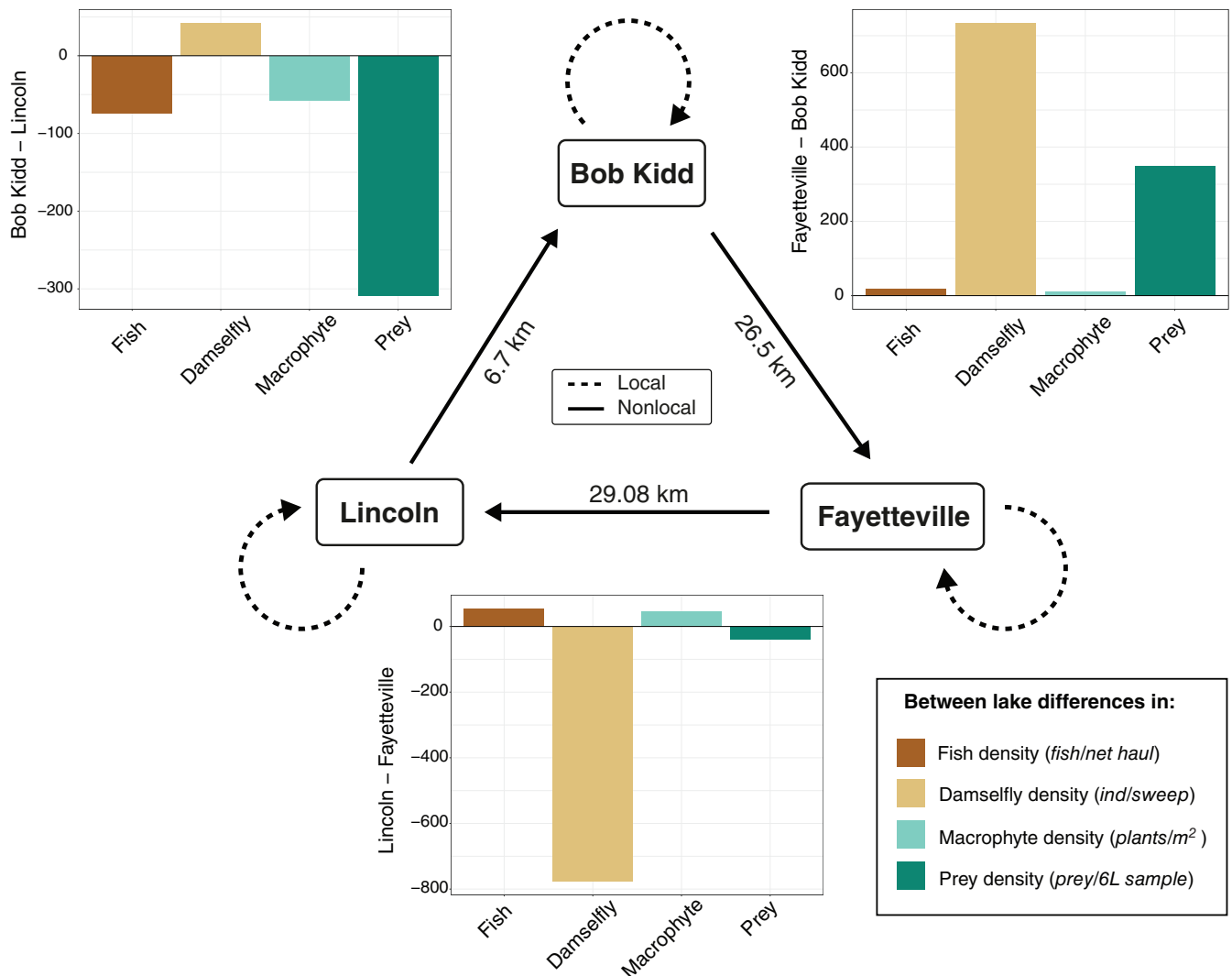


FIGURE 1 Differences in environmental features between local and nonlocal lake pairings of the transplant experiment. The central panel shows the locations of damselfly species in their local lakes (curved dashed lines) with destinations of transplant experiments between lakes (solid lines) with the base of the arrow showing the source lake and arrowhead the experimental lake. The distance between lakes is shown along the body of the arrow. Even though some lakes are separated by relatively short distances, there were large differences in environmental variables between lakes. Differences between lakes (local–nonlocal) in predator fish, prey, damselfly, and macrophyte densities are shown in the inset figures for each local–nonlocal lake pairing. Thus, the panels show if nonlocal individuals are moved to environments with higher or lower densities of fish, damselflies, plants, and prey.

experiment (total abundance, species relative frequencies, duration, preservation) follows the same methodology as the previous experiment except one important detail. In this study, prey, macrophytes, and fish are from the local lake, whereas damselflies are from a different lake (i.e., nonlocal). This design allowed us to determine the frequency-dependent effect of competition and predation on nonlocal damselflies.

Unfortunately, extreme weather conditions destroyed some cages and complete reciprocal transplants could not be completed. Instead, damselfly growth and mortality from every source lake were estimated in their local and one nonlocal lake, which is a sufficient experimental

design to detect potential local adaptation (e.g., Hoeksema & Forde, 2008). Specifically, individuals from Lake Lincoln were transplanted to Bob Kidd Lake, individuals from Bob Kidd Lake to Lake Fayetteville, and individuals from Lake Fayetteville to Lincoln Lake (Figure 1). Importantly, the distance between the three lakes is greater than the typical dispersal ability of damselflies (<1 km) (Conrad et al., 1999, 2002; McPeck, 1989; Purse et al., 2003).

Because of the logistical demands associated with conducting large-scale field transplant experiments, experiments with nonlocal and local individuals were conducted in different years (April–May 2021 and

October 2020, respectively). As a result, environmental conditions (e.g., temperature, resource availability) and larval size distributions likely differed between sampling periods. These temporal differences mean that comparisons between local and nonlocal populations necessarily incorporate variation in both population origin and seasonal environmental context. Importantly, however, within each experiment individuals interacted under natural field conditions and at comparable developmental stages typical of the periods in which they naturally interact. Thus, although this design does not allow strict isolation of population origin from seasonal environmental variation, combining the two experiments provides a rare opportunity to evaluate how population-specific demographic responses and stabilizing effects manifest in realistic local versus nonlocal community contexts. We therefore interpret differences between local and nonlocal treatments cautiously, focusing on whether demographic patterns are consistent with population-specific responses that could contribute to variation in stabilizing effects across lakes, rather than as definitive evidence of local adaptation per se.

We estimated growth rate as $(\text{mean}(\ln(h_r)) - \text{mean}(\ln(h_i)))/t$, where 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, assuming that $h(t) = h(0)e^{gt}$, with g the growth rate. We estimated mortality rate as $-((\ln(n_r) - \ln(n_i)))/t$, where n_r is the number of individuals recovered at the end of the experiment, n_i the initial number of individuals, and t the duration of the study. Many previous studies have estimated mortality and individual growth rates in this way (Bried & Siepielski, 2019; Gómez-Llano et al., 2023; McPeck, 1990, 1998; Ousterhout et al., 2019; Siepielski et al., 2010, 2011).

We used MANOVA to evaluate the fixed effects of transplant treatment (local or nonlocal), experimental lake (i.e., the lake in which the experiment was conducted), and frequency treatment (common or rare), combining both species in two separate models with growth or mortality as the response variable; replicate cage was included as a random effect. Our primary goal was to assess whether population origin was associated with differences in stabilizing effects across lakes. In principle, population-specific responses consistent with local adaptation could manifest as a three-way interaction among transplant treatment, source lake, and experimental lake. However, higher order interactions are often difficult to interpret biologically. We therefore adopted a two-part analytical approach focused on interpretable lower order interactions.

First, we interpret a transplant $\times$ experimental lake interaction as evidence that demographic performance differed among populations across environments. If

individuals originating from a given lake exhibited higher growth or lower mortality in their native environment relative to nonlocal populations, this pattern would be consistent with local adaptation, although not definitive given potential environmental and temporal differences among experiments. Because individuals in our study were transplanted to only one nonlocal lake, a main effect of transplant treatment could similarly indicate consistent differences between local and nonlocal populations, which we interpret cautiously as population-specific demographic divergence rather than unequivocal evidence of local adaptation.

Second, a significant transplant $\times$ relative abundance interaction would indicate that the strength of frequency dependence (i.e., the stabilizing effect) varied with population origin. Together, interactions involving transplant treatment and experimental context therefore allow us to assess whether stabilizing effects differ between local and nonlocal community contexts and whether such differences are consistent with population-specific responses that could influence coexistence. Because multivariate results could be driven by a single species, we subsequently conducted species-specific ANOVAs for growth and mortality using the same model structure to clarify the contribution of each species to overall patterns.

Environmental measures

While we do not identify the precise biological underpinnings of potential local adaptation, and instead focus on its demographic signature, we nevertheless surveyed lakes to determine how they differed. In each lake, during the same months and year, we measured four ecological components that likely shape aspects of damselfly growth and mortality rates (Siepielski et al., 2010): predator fish density, damselfly prey density, damselfly density, and macrophyte density, using methods briefly described below and in more detail in previously published studies (Siepielski et al., 2010, 2011). Fish, especially centrarchids, are the main predators of damselfly larvae (Bried & Siepielski, 2019; McPeck, 1990), competition and prey availability strongly limit damselfly growth rate (McPeck, 1990, 1998; Siepielski et al., 2011, 2016), and macrophytes are essential habitats for larvae that provide refuge against predators, foraging opportunities, and space to avoid interference competition (Crowley & Johnson, 1992).

We estimated fish density using a 4.5×1.5 m seine net (5 mm mesh) and counted all the fish collected in three hauls. To estimate prey density, we took six water samples in submerged macrophytes with 6 L box samples (100 μm mesh). We estimated damselfly density with

repeated 1 m long sweeps through macrophytes using a D-frame dip net (28 cm opening, 1 mm mesh). To estimate macrophyte density, we counted macrophytes in ten 0.25 m² quadrants following the shoreline. These methods have been thoroughly described elsewhere and shown to provide reliable and replicable estimates of the focal ecological components (Crowley & Johnson, 1992; Siepielski et al., 2010; Stoks & McPeck, 2003). We found substantial differences in these ecological components among the lakes (Figure 1).

Predator preference for local versus nonlocal damselflies

Given the central role of fish predation in generating a stabilizing effect (Bried & Siepielski, 2019; Gómez-Llano et al., 2023), we wanted to investigate whether mortality rates imposed by fish differed between local and nonlocal damselfly prey when both co-occurred. To determine this, we conducted a short-term laboratory-based predator choice experiment during April and May 2023.

For each of the three lakes in our main study, we placed five local individuals and five nonlocal individuals of the same damselfly species in 18.9 L containers (36 cm height × 26 cm diameter) filled with dechlorinated tap water. This generated a density of approximately 200 damselflies per m² of bottom surface area, which is within the natural range of damselflies in our study region (Ousterhout et al., 2019; Figure 1). Each container was stocked with macrophytes and one bluegill (mean length = 85.7 ± 10.8 mm SD) from local lakes. Therefore, local damselflies experienced local predators and local macrophytes, but nonlocal damselflies did not. Although this design combines local vegetation and predators, our goal was ultimately to ask how mortality rates change between local and nonlocal prey. All trials only included one damselfly species at a time. Each local to nonlocal lake pairing was the same as our field transplant experiment (Figure 1; $n = 20$ replicates per lake pair). We differentiated local versus nonlocal individuals by removing part of one midleg (either left or right for local and nonlocal, altered between the first and last 10 replicates of the experiment). Containers were placed in a temperature-controlled room (~20°C) with natural lighting conditions provided by a window. Damselflies were allowed to acclimate to these conditions for 24 h without fish. The experiment began after fish were introduced into containers and ran for 48 h.

To analyze predator preference, we used a linear mixed-effects model. We used mortality rate as the response variable and included damselfly species, treatment (local or nonlocal), lake, and all interactions as fixed factors. We included fish length as a covariate because

larger fish can consume more damselflies, and fish lengths in these experiments were somewhat larger than those used in our field studies. Replicate was included as a random effect. For the results from the linear mixed-effects model, we present a full contrast table for mortality rate testing differences between local and nonlocal individuals in each lake combination and species. All analyses were performed in R statistics (R Development Core Team, 2018), using the packages “lme4” (Bates et al., 2015), “emmeans” (Lenth, 2019), and “car” (Fox et al., 2012).

RESULTS

Growth rates

Across lakes and treatments, *E. exsulans* grew faster (2.3×) than *E. traviatum* (paired t -test $t_{58} = 4.480$, $p < 0.0001$). MANOVA indicated that there was no frequency × transplant effect on growth rates (Pillai = 0.085, $F_{2,50} = 2.351$, $p = 0.105$). There was also no main effect of frequency (Pillai = 0.079, $F_{2,50} = 2.151$, $p = 0.127$); thus, neither species gained a growth rate advantage when rare. However, there was a significant effect of transplant (Pillai = 0.221, $F_{2,50} = 7.127$, $p = 0.001$) along with a significant transplant × lake effect (Pillai = 0.359, $F_{8,102} = 2.797$, $p = 0.007$) where growth rates generally declined when nonlocal, and this effect depended on lake (Figure 2).

However, individual ANOVAs for some factors differed between the species, indicating that the effects were species-specific (Figure 2). Specifically, the effect of transplant × lake was only statistically significant for *E. exsulans* ($F_{4,52} = 5.4691$, $p = 0.0009$), not *E. traviatum* ($F_{4,52} = 1.904$, $p = 0.123$). By contrast, only *E. traviatum* experienced a statistically significant main effect of transplant ($F_{1,52} = 11.662$, $p = 0.001$), not *E. exsulans* ($F_{1,52} = 0.182$, $p = 0.671$). Across lakes, growth rates for nonlocal *E. traviatum* individuals were 89.5% lower than those for local individuals, but no consistent differences were apparent in *E. exsulans*. Individual MANOVAs on a lake-by-lake basis showed variable effects of transplant (Appendix S1: Table S1), where individual species ANOVAs also showed this effect (a reduction in growth when nonlocal) occurred mainly for *E. traviatum*; *E. exsulans* increased its growth rate when nonlocal in one lake (Appendix S1: Table S1).

Mortality rates

Across lakes and treatments, *E. traviatum* had a higher (1.4×) mortality rate than *E. exsulans* (paired t -test

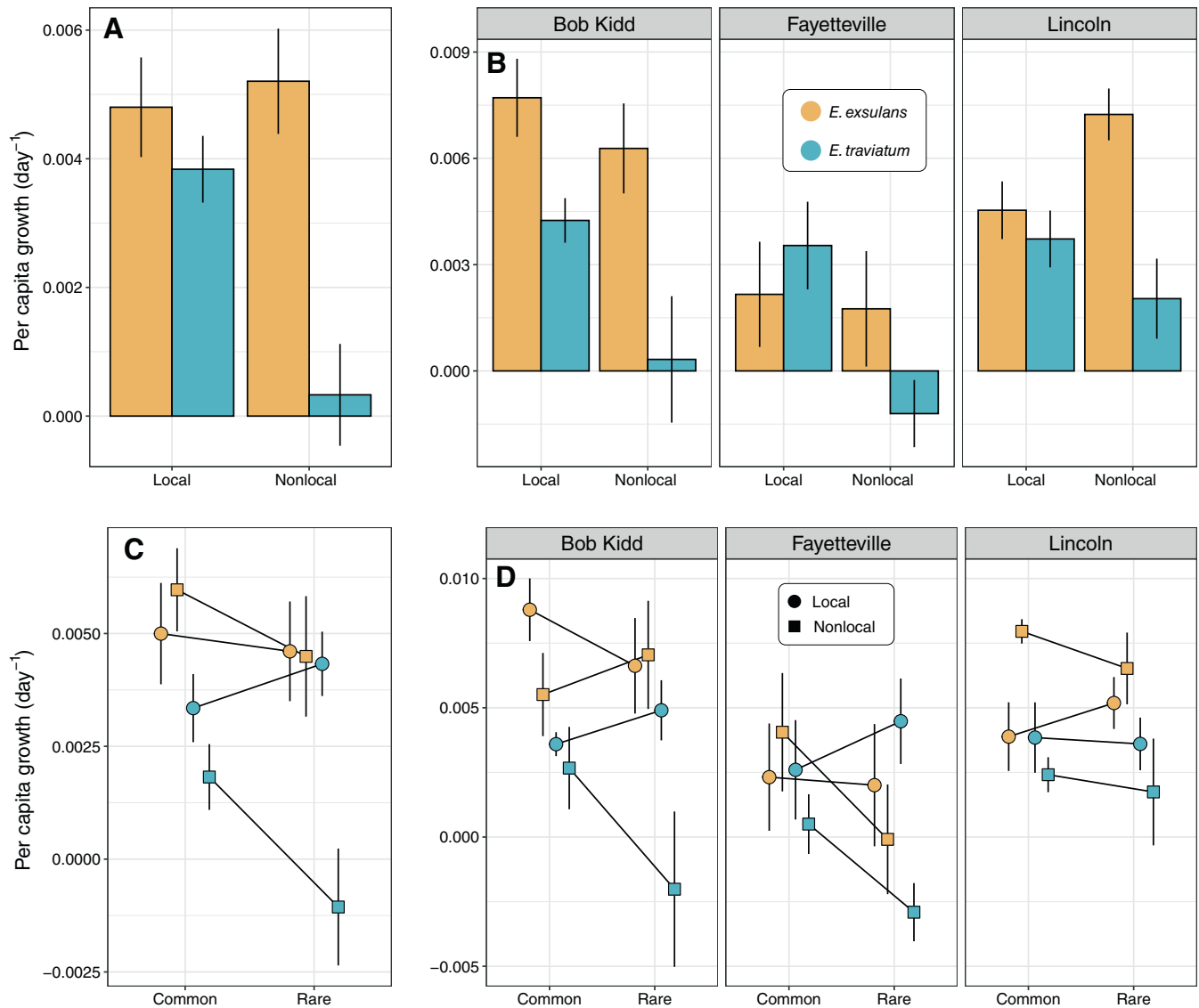


FIGURE 2 Effects of transplant (local or nonlocal) and frequency (common or rare) manipulations on individual growth rates of damselflies (mean $\pm$ SE). Comparison of growth rates between local and nonlocal individuals (A) averaged across populations and (B) for each population separately, pooled across frequencies. Frequency dependence in individual growth rates (growth rate when common and rare) (C) averaged across populations and (D) for each population separately. Lakes listed at the top of panels (B) and (C) designate the local lake (see Figure 1 for which populations were transplanted as nonlocal). We estimated growth rate as $\text{mean}(\ln(h_r)) - \text{mean}(\ln(h_i))/t$, where 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, assuming that $h(t) = h(0)e^{gt}$, with g the growth rate.

$t_{58} = 2.266$, $p = 0.027$). MANOVA indicated there was a significant effect of frequency $\times$ transplant (Pillai = 0.241, $F_{2,50} = 7.958$, $p = 0.009$), indicating that the effect of frequency depended on transplant (Figure 3). Specifically, the effect of frequency is only statistically significant for local individuals (Pillai = 0.415, $F_{2,27} = 9.607$, $p = 0.007$), not transplanted individuals (Pillai = 0.108, $F_{2,26} = 1.575$, $p = 0.226$). These same patterns were apparent in the individual species ANOVAs. The effect of frequency was only statistically significant in local (*E. exsulans*: $F_{1,28} = 18.242$, $p = 0.0002$; *E. traviatum*: $F_{1,28} = 10.014$, $p = 0.003$), not nonlocal comparisons

(*E. exsulans*: $F_{1,28} = 0.034$, $p = 0.854$; *E. traviatum*: $F_{1,28} = 3.269$, $p = 0.08$) (Figure 3). Across lakes and treatments, the mortality rate when common was 40% higher than when rare in *E. traviatum* and 61% higher when common than rare in *E. exsulans*.

There was also a significant transplant $\times$ lake effect (Pillai = 0.317, $F_{8,102} = 2.409$, $p = 0.020$) where mortality rates generally increased when nonlocal. Thus, across both species, there is evidence consistent with patterns expected under local adaptation. However, the individual species ANOVAs indicated that some of these overall effects were species-specific. The effect of transplant $\times$ lake was only

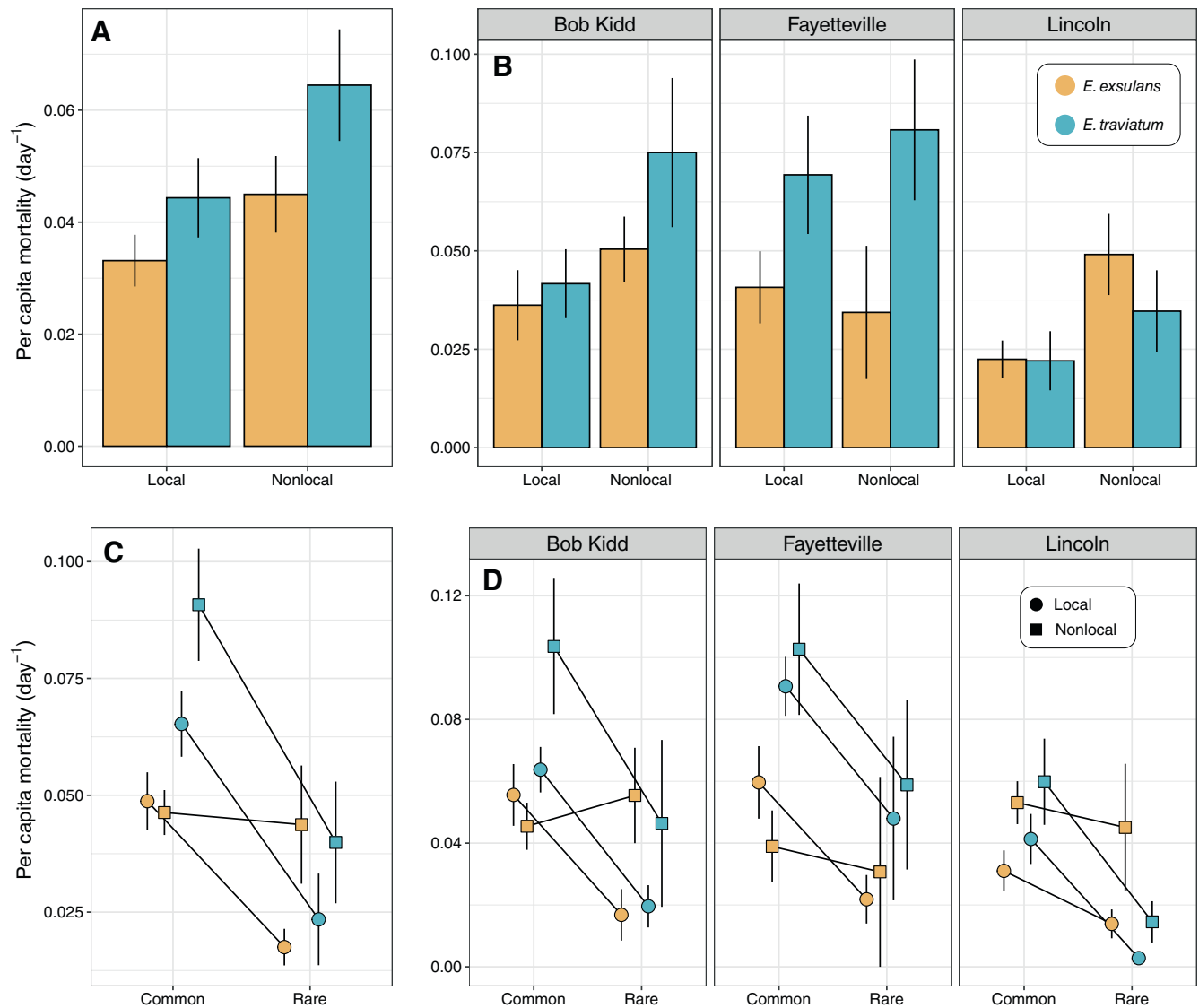


FIGURE 3 Effects of transplant (local or nonlocal) and frequency (common or rare) manipulations on per capita mortality rates of damselflies (mean $\pm$ SE). Comparison of mortality rates between local and nonlocal individuals (A) averaged across populations and (B) for each population separately, pooled across frequencies. Frequency dependence in mortality rates (per capita mortality rate when common and rare) (C) averaged across populations and (D) for each population separately. Lakes listed at the top of panels (B) and (C) designate the local lake (see Figure 1 for which populations were transplanted as nonlocal). We estimated mortality rate as $-(\ln(n_r) - \ln(n_i))/t$, where n_r is the number of individuals recovered at the end of the experiment, n_i the initial number of individuals, and t the duration of the study.

statistically significant for *E. triviatum* ($F_{4,51} = 4.371$, $p = 0.004$), not *E. exsulans* ($F_{4,51} = 0.910$, $p = 0.465$). In *E. triviatum*, nonlocal individuals had 67% higher mortality than local individuals. Although *E. exsulans*' nonlocal individuals also had slightly higher mortality than local individuals, this difference was not statistically significant.

Predator preferences for local or nonlocal damselfly prey

We found no predator preference (difference in mortality rates) for local over nonlocal prey in our laboratory

experiment in either *E. triviatum* or *E. exsulans* (Table 1A, Figure 4A). This lack of statistical difference in mortality rates between local and nonlocal individuals was consistent across lakes for both species (Table 1B, Figure 4B).

DISCUSSION

Understanding how species do or do not coexist is an enduring problem at the interface of community ecology and evolutionary biology. Studies increasingly reveal that coexistence is not a property of species per se, but instead

TABLE 1 Contrast table from linear mixed model results of a laboratory experiment of fish predator preference for local or nonlocal damselflies across lakes (A), and for local or nonlocal damselflies in each lake (B).

Species and treatment	Source lake	Estimate	SE	p
(A) Across lakes				
<i>E. exsulans</i> , local versus nonlocal		0.098	0.05	0.057
<i>E. traviatum</i> , local versus nonlocal		−0.086	0.04	0.078
(B) Each lake				
<i>E. exsulans</i> , local versus nonlocal	Bob Kidd	0.049	0.08	0.55
	Fayetteville	0.165	0.08	0.069
	Lincoln	0.08	0.08	0.37
<i>E. traviatum</i> , local versus nonlocal	Bob Kidd	−0.104	0.08	0.22
	Fayetteville	−0.118	0.08	0.14
	Lincoln	−0.036	0.08	0.67

Abbreviations: *E. exsulans*, *Enallagma exsulans*; *E. traviatum*, *Enallagma traviatum*.

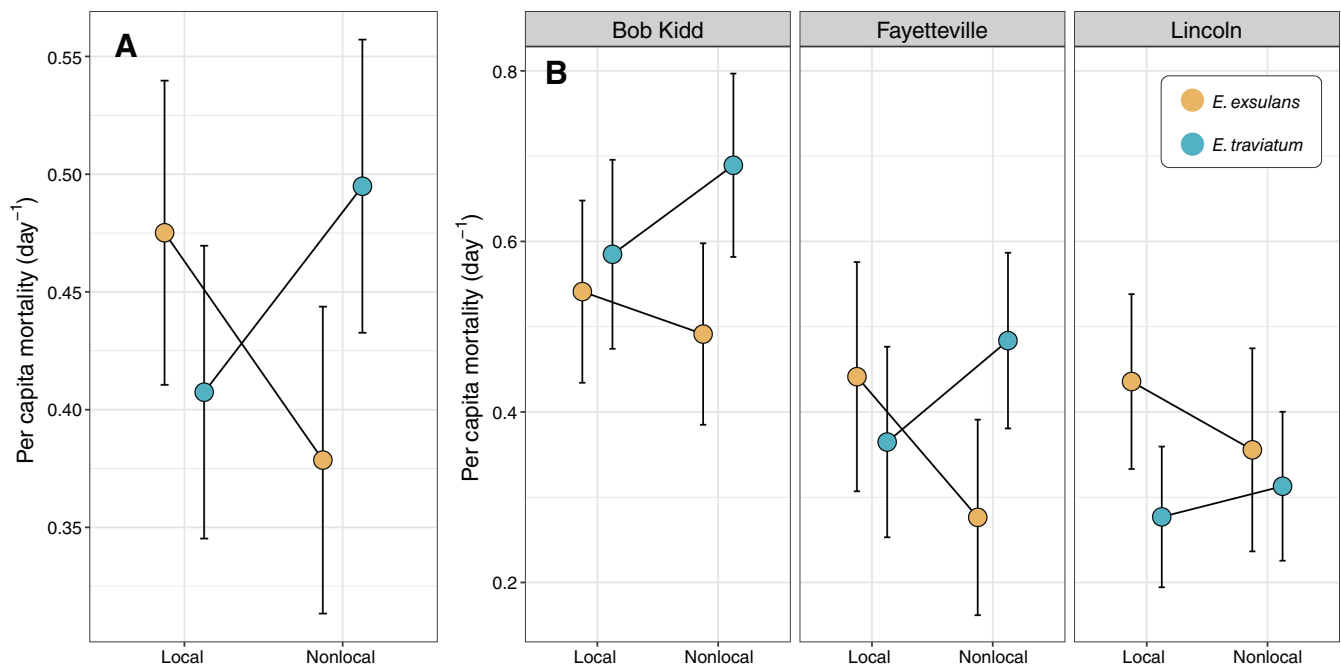


FIGURE 4 Comparison of mortality rates (A) between local and nonlocal damselfly prey and (B) per lake from the predator choice experiment in the laboratory (mean ± SE).

occurs at the population level. That is, populations of some species may locally coexist, but other populations of the same species may not coexist (Bried & Siepielski, 2019; Germain et al., 2020; Gómez-Llano et al., 2023; Hart et al., 2017). Here, we used an experimental approach to show that frequency dependence in mortality rates shaping stabilizing effects is likely strengthened by population-specific responses consistent with local adaptation to predation. However, we also found that these effects were asymmetrical between

species. It is important to note that our local and nonlocal experiments were conducted in different seasons and thus environmental and developmental differences may contribute to the observed patterns. As a result, while the demographic differences we observed are consistent with local adaptation shaping stabilizing effects, they cannot be interpreted as definitive evidence of adaptation. Nevertheless, the patterns provide valuable insight into how population-level variation may influence coexistence under natural conditions.

Is there evidence consistent with local adaptation?

Our results provide evidence consistent with local adaptation, but the patterns differed between species and the fitness components used. Growth rates were generally lower for nonlocal than local populations among lakes, consistent with prior work using complete reciprocal transplant experiments, where the local and transplant experiments were conducted simultaneously (Siepielski et al., 2016). However, in the present study the local advantage was found only in *E. traviatum*, not *E. exsulans*. While our experiment does not allow us to rule out a contribution of phenotypic plasticity or learning, such as damselflies developing search images for their local prey, previous work has shown genetic variation in damselfly growth rates and found little evidence for maternal effects (Shama et al., 2011). Notably, growth rates did not increase when damselflies were transplanted to lakes with higher prey densities (e.g., Bob Kidd damselflies in Lake Fayetteville; cf. Figures 1 and 2), indicating that reduced growth rate was not simply due to low prey availability. Instead, nonlocal damselflies were perhaps less adapted to capturing local prey items or differ in their digestive physiology to allow them to process nonlocal prey items (McPeck, 2004; Siepielski et al., 2016; Tye et al., 2020).

Mortality rates also showed evidence consistent with local adaptation, being generally higher for nonlocal damselflies, although consistently elevated only for *E. traviatum*. For *E. exsulans*, mortality rates both declined and increased when nonlocal, the latter implying some degree of potential mismatch to their local conditions. This contrasts with previous evidence of widespread local adaptation in prey to local predator regimes (Ruxton et al., 2019). Although we did not conduct predator-free experiments, and so cannot rule out other causes of elevated mortality, our prior studies conducted in many of the same lakes comparing predator presence and absence strongly imply fish predation as the cause of mortality (Gómez-Llano et al., 2023; Ousterhout et al., 2019) and therefore driving selection and adaptive evolution (Benkman, 2013; Siepielski et al., 2020). Although traits that shape susceptibility to predation are heritable (Swaegers et al., 2017), they can also exhibit plasticity, particularly coloration (Johansson & Nilsson-Örtman, 2013). Indeed, predation often drives local adaptation in plasticity (Boys et al., 2025; Reger et al., 2018), which may shape local coexistence (e.g., Turcotte & Levine, 2016).

Lakes differed in ecological factors potentially underlying growth and mortality differences between local and nonlocal populations (Figure 1). Although the number of lakes precluded statistical analyses linking these

ecological factors to differences in growth and mortality rates among lakes (Hereford, 2009; Siepielski et al., 2016), some patterns are noteworthy. Growth rates in Bob Kidd and Lincoln were similar, but relatively lower in Fayetteville, which had the highest damselfly larval density, while Bob Kidd and Lincoln had similar densities. This pattern is consistent with previous research that showed competition is a leading cause of reduced growth rates (Johnson, 1991; McPeck, 1990; Siepielski et al., 2011). Moreover, mortality was lowest at Lincoln, the lake with the highest fish density, and similar between Bob Kidd and Fayetteville. Although this might seem counterintuitive, fish predation selects for reduced damselfly activity as a predator avoidance mechanism (Siepielski et al., 2020; Swaegers et al., 2017). Stronger selection under high fish density could lead to stronger evolutionary responses (Caruso et al., 2017; Siepielski et al., 2020), consistent with our observation of this population showing the greatest increase in mortality rates when transplanted.

Our field experiments indicate that damselfly responses to local and nonlocal predators are population-specific and consistent with local adaptation that may generate performance trade-offs. However, contrary to expectations, our predation trial experiment did not show stronger predation on nonlocal damselflies. This discrepancy between lab and field experiments suggests the patterns we observed are not simply tied to the interactions between fish and damselflies alone. Although selection by fish does drive adaptive evolution in traits conferring a local fitness advantage (Boys et al., 2025; Siepielski et al., 2020), we suggest that what matters is how this selection and subsequent adaptive evolution manifests in the local environment. For example, bluegill are highly visual predators (O'Brien et al., 1976), so the differences in damselfly traits mediating predation are likely only functional in the field where the environments also differ (e.g., water turbidity; Miner & Stein, 1996) and not found in the common garden conditions where this effect is not recreated.

While we found evidence consistent with local adaptation in damselflies, a key finding is that the effects were only consistently found for one species (*E. traviatum*). Meta-analyses of local adaptation including studies with multiple species often find differences among species in the occurrence or extent of local adaptation (Briscoe Runquist et al., 2020; Hargreaves et al., 2020; Hereford, 2009), but there has been little discussion as to why this pattern exists and its ecological consequences. At present, it is unclear why such asymmetries exist among the species studied despite them occupying the same lakes. The lack of evidence for consistent local adaptation for *E. exsulans* suggests that it may be under

some constraint, that it only recently arrived and so has not yet locally adapted, or that environmental differences among lakes are simply insufficient to drive any divergent selection. Although distances between populations are greater than those damselflies typically disperse (Conrad et al., 1999, 2002; McPeck, 1989; Purse et al., 2003), some gene flow must occur to establish new populations. Gene flow could constrain local adaptation (e.g., Kirkpatrick & Barton, 1997), but could also add genetic variation potentially enhancing local adaptation over longer timescales (Aitken & Whitlock, 2013; Garant et al., 2007). Given the ecological differences among lakes and the potential for local adaptation, it may simply be that one species is potentially evolving at a faster rate than the other, a common occurrence found even among closely related species (Hendry & Kinnison, 1999; Kinnison & Hendry, 2001; Sanderson et al., 2023). Regardless, this asymmetry has implications for the strength and occurrence of stabilizing effects and the potential for local species coexistence.

Does potential local adaptation shape stabilizing effects?

If we consider growth rate, the answer is no, given that growth rates do not contribute to a stabilizing effect even if they exhibited a signature consistent with local adaptation. Thus, traits mediating growth rates are likely differentiating in a way that is not shaped directly by competitive interactions among these species, even if these species could be locally evolving in ways that shape fitness differences (Chesson, 2000). Despite the intuitive appeal that local adaptation should generate stabilizing resource-based niche differences, other studies suggest that species might evolve to locally coexist largely by reducing competitive fitness differences (Hart et al., 2019) or even evolve in ways that destabilize coexistence (Hausch et al., 2017).

Considering predation, the answer is more nuanced, as the effects of potential local evolution on stabilizing effects differed between species. For *E. traviatum*, nonlocal individuals experience higher mortality rates and a subtle weakening of stabilizing effects compared to local individuals. For *E. exsulans*, nonlocal individuals had anywhere between slightly higher, lower, or no differences in mortality rates when rare and common. Both species must experience a stabilizing effect to yield local coexistence. Thus, the effect of potential local adaptation shaping stabilizing effect through predation seems to predominately be driven by how this stabilizing effect is lost in one species when transplanted.

Although we have focused on stabilizing effects, we acknowledge that stabilizing effects are only one component of species coexistence, and changes in fitness differences could also play a role. Stabilizing effects are necessary for coexistence because without them competitive exclusion is expected (Adler et al., 2007; Chesson, 2000). Potential trait differences that influence frequency-dependent interactions, such as predator avoidance or body size, could also generate fitness differences independent of relative abundance, and in our system local populations sometimes had consistently lower mortality across frequencies. While we do not have estimates of population growth rates, we do know that mortality is a key component (Gómez-Llano et al., 2023; McPeck & Peckarsky, 1998). Thus, fitness differences are likely present and the changes in mortality rates we observed between local and nonlocal populations across experimental frequencies may reflect this to some extent. Directly estimating fitness differences in field experiments is logistically challenging (see Adler et al., 2007), and so ultimately, we focused on determining whether stabilizing effects were operating, while interpreting population-specific patterns as consistent with a role for local adaptation in shaping local coexistence. These results therefore highlight that local adaptation may shape the demographic context for coexistence, but the overall outcome may also depend on unmeasured fitness differences that could reinforce or counteract these effects (Germain et al., 2020; Hart et al., 2019).

CONCLUSIONS

Our results suggest that population-specific responses associated with local environmental conditions, consistent with local adaptation, can contribute to shaping stabilizing effects underpinning local coexistence. Unlike many studies emphasizing resource competition, we found no evidence that divergence in resource use generated stabilizing effects, even though growth rates exhibited some population-specific differences consistent with local adaptation. These findings suggest that demographic signatures consistent with local adaptation need not translate directly into mechanisms promoting coexistence and may instead be uncoupled from stabilizing effects. That is, demographic rates like growth rate may show evidence consistent with local adaptation, but this same demographic rate does not necessarily have a role in shaping local coexistence. We did, however, uncover a key role for predation in generating stabilizing effects, with local populations often experiencing stronger frequency-dependent mortality patterns than nonlocal

populations, even when evidence for population-specific responses to shared predators differed between species. Such asymmetries in how locally interacting species respond to predation may therefore play an important role in shaping local coexistence. More broadly, our results highlight the importance of evaluating how population differentiation across landscapes is shaped by species interactions across trophic levels (e.g., predator–prey) and not merely within trophic levels (e.g., competition) to influence coexistence. Advancing this understanding will require continued theoretical development and carefully designed experiments that integrate ecological and evolutionary processes within and across trophic levels.

AUTHOR CONTRIBUTIONS

Miguel Gómez-Llano and Adam M. Siepielski conceived the idea, performed the analysis, and wrote the main draft. All authors contributed to field and lab-based experiments as well as input on revising the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Gómez et al., 2026) are available from Dryad: <https://doi.org/10.5061/dryad.612jm64m5>.

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SUPPORTING INFORMATION

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

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