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A framework for linking competitor ecological differences to coexistence

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Abstract

1. Not all ecological differences among competing species affect their ability to locally coexist. Rather, the differences that promote stable coexistence can be those which cause each species to experience stronger intraspecific than interspecific competition. Recent approaches have established how to detect the demographic signature of these competitive effects, but alone they cannot elucidate the ecological differences among species that yield these patterns.
2. Here, we present a unifying experimental and observational framework that identifies potential ecological differences among species shaping their responses to intra- and interspecific competition. We first describe a conceptual model establishing why the strength of intra- and interspecific competitive interactions should vary along environmental gradients related to species ecological differences. We then show how to apply the framework using *Enallagma* damselflies, a diverse group of predatory aquatic insects.
3. To determine how species responded to intra- and interspecific competition along environmental gradients, we experimentally manipulated the relative abundances of three species and replicated this across five lakes which varied in environmental conditions affecting larval damselfly per capita growth and mortality rates—key vital rates regulating their populations.
4. Results suggest *Enallagma* are ecologically differentiated in ways that in some communities can result in intraspecific competition exceeding interspecific competition. However, in many cases the opposite was true, or the effects of intra- and interspecific competition were equivalent via growth and mortality responses. Moreover, these effects tended to be weak and asymmetrical among competitors, which suggests that differential responses of larval growth and mortality to intra- and interspecific competition may not contribute strongly to the maintenance of *Enallagma* diversity. Different environmental factors appear to shape these demographic responses to competition, providing insight into the ecological mechanisms regulating damselfly assemblages.
5. This framework can be broadly applied to identify the ecological differences among species that may promote coexistence, advancing knowledge of the mechanisms underlying coexistence and overcoming some limitations of purely phenomenological approaches.

KEYWORDS
coexistence, competition, diversity, *Enallagma*, interspecific effects, intraspecific effects, niche

1 | INTRODUCTION

A fundamental goal of ecology is to understand if, how and why species diversity in communities is being maintained or only slowly lost (Chesson, 2000b; Dornelas et al., 2014; Hubbell, 2001; Hutchinson, 1959; MacArthur & Levins, 1967; Vellend et al., 2013). Critical to any mechanism promoting the maintenance of species diversity through stable coexistence are differences among species in how they interact with the environment (Gause, 1934; Hutchinson, 1959). One approach to understanding the maintenance of species diversity is therefore to identify "ecological differences" among species. Fulfilling this task, ecologists have exerted tremendous effort identifying differences among co-occurring taxa in communities (Chesson, 2000b; Siepielski & McPeek, 2010; Silvertown, 2004). Countless studies have revealed that species within the same trophic position frequently differ in their abilities to interact with competitors, predators, parasites and mutualists (Mittelbach, 2012). Similarly, species differ in their demographic responses to abiotic gradients such as temperature, precipitation, pH or salinity (Chesson, 2000b). Arguably, these differences in how species interact with the environment are taken to constitute various aspects of a species niche.

While ecological differences among species are a necessary criterion for the maintenance of diversity, not all ecological differences promote local coexistence (Adler, Fajardo, Kleinhesselink, & Kraft, 2013; Siepielski & McPeek, 2010). Rather, the key ecological differences that can promote coexistence are those that result in competitors interacting differently with the environment (e.g. consume different prey resources, vary in physiological sensitivity to environmental stress), such that intraspecific density dependence is stronger than interspecific density dependence (Adler, Hillerislambers, & Levine, 2007; Chesson, 2000b). When density-dependent intraspecific competition is stronger than interspecific competition, each species limits their own population growth rates more than their competitors (Adler et al., 2007; Chesson, 2000b). The resulting negative frequency-dependent demographic responses species would then exhibit can promote coexistence by preventing any one species from dominating in a community (Adler et al., 2007; Chesson, 2000b). Numerous studies have now taken this phenomenological approach and explicitly quantified how intra- and interspecific competition jointly vary to structure communities (Adler et al., 2018; Letten, Ke, & Fukami, 2017; McPeek, 2012).

Although these two approaches, identifying differences in how species interact with the environment and testing for intra- and interspecific competitive differences, are complementary, each has limitations. Whereas correlative studies of species associations with environmental variation often identify ecological differences among species, it is unclear whether these differences shape species' demographic responses to intra- and interspecific competition, and thus contribute to stable coexistence. By contrast, studies of species demographic responses to intra- and interspecific competitors can reveal the demographic signatures of ecological differences potentially promoting coexistence. However, this approach is inherently phenomenological and does not explicitly identify the underlying ecological mechanisms producing these effects (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Kraft, Godoy, & Levine, 2015; Letten et al., 2017). This is a familiar criticism of the phenomenological results provided by many well-known models (e.g. Lotka–Volterra models) upon which this latter approach is built, whereby the observed results are largely divorced from ecological mechanisms. Therefore, combining these two approaches may be a useful way of identifying what aspects of the environment shape the relative strength of species demographic responses to intra- and interspecific competition. Doing so would allow for a better understanding of what ecological differences among species may actually promote competitor coexistence.

Here, we present and demonstrate a framework that combines experimental and standardized observational studies to determine what ecological differences among species may shape intra- and interspecific competitive interactions. We first develop the conceptual context establishing why environmental heterogeneity and ecological differences among species may affect competitive interactions, and then proceed to explain the experimental–observational approach along with its caveats and potential pitfalls. We subsequently demonstrate how to apply this framework with a case study using an assemblage of predatory aquatic insects (*Enallagma* damselflies).

1.1 | A framework linking ecological differences, environmental variation and competitive interactions

1.1.1 | Conceptual context

Our goal here is to describe a conceptual framework explaining how environmental factors (e.g. abiotic conditions, species interactions) may shape the ecological mechanisms underlying competitive effects, and an experimental approach to test this model (Figure 1).

Because ecological differences are what cause species to experience stronger demographic responses to intra- than interspecific competition (Chesson, 2000b), this implies that the ecological factors that cause a species to have higher per capita population growth rates when rare must become limiting when that species is common (Siepielski, Hung, Bein, & McPeek, 2010). For example, coexistence of two species consuming two resources requires that each be better at consuming the resource that most limits its own population abundance (Letten et al., 2017; McPeek, 2018; Tilman, 1980, 1982). The feedback limiting per capita population growth imposed by negative frequency dependence can thus arise from differences in how

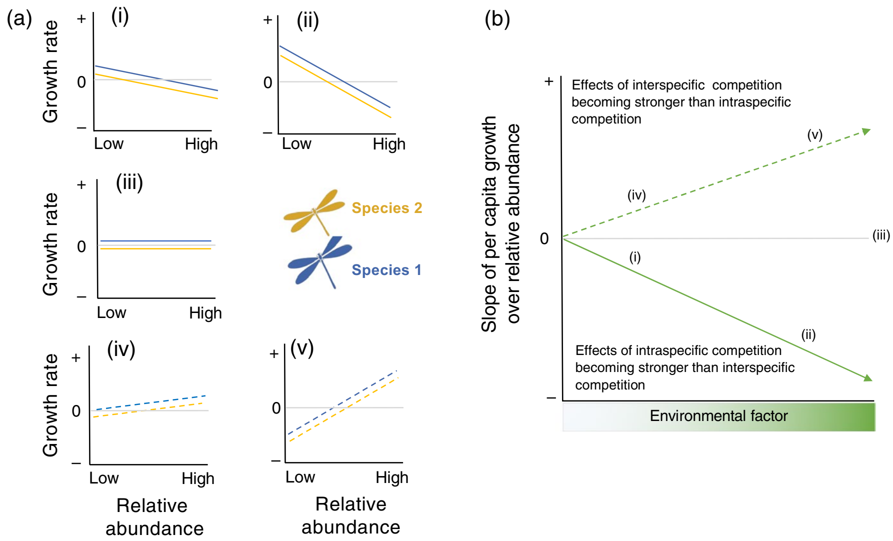

FIGURE 1 A conceptual framework to understand the ecological differences among competitor species shaping the potential for local coexistence. Panel (a) denotes variation in the outcomes of experimental manipulations of species relative abundances between a pair of competing species: (i and ii) demonstrate outcomes where species experience increasingly stronger intra-relative to interspecific competitive effects on per capita population growth rates. In this scenario, such demographic responses may facilitate species coexistence by preventing any one species from dominating; (iii) denotes an outcome where the effects of intra- and interspecific competitive effects are equivalent; (iv and v) demonstrate outcomes where species experience stronger inter-relative to intraspecific competitive effects. In this scenario, such demographic responses may result in competitive exclusion depending on which species has the strongest overall competitive effect. Panel (b) maps the slopes depicted in panel (a) across an environmental factor that potentially influences the outcomes of inter- and intraspecific competitive interactions. The solid green line depicts a situation in which an increase in an environmental factor is causing species to experience stronger intraspecific than interspecific competitive effects, and thus facilitates coexistence. Finding such associations can help to reveal potential ecological differences among species that mediate coexistence. For example, the environmental factor could be increased in the abundances of two limiting prey types that each competitor species uses. By contrast, the dashed green line depicts a situation in which an increase in an environmental factor is causing species to experience stronger inter- than intraspecific competitive effects, and thus may increase competitive exclusion

the environment shapes species responses to intra- and intraspecific competition via indirect resource competition (Chesson, 2000a; Germain, Mayfield, & Gilbert, 2018; HilleRisLambers et al., 2012; Lanuza, Bartomeus, & Godoy, 2018; Letten et al., 2017), or how it shapes direct intraspecific density dependence outside of resource limitation (McPeek, 2012), as well as other factors such as predators and parasites that emerge in richer community modules (Chesson, 2018; Chesson & Kuang, 2008; McPeek, 2012, 2018; Sommers & Chesson, 2019).

Therefore, there are two components underlying any mechanism of ecological differences that structure an assemblage of competitors: (a) the interspecific differences that exist among taxa (e.g. different limiting prey resources, susceptibilities to predators) affecting species demographies and (b) the intraspecific population regulation occurring within a particular species. Although much of community ecology has focused on identifying the differences among species that affect their abilities to engage in interspecific interactions (e.g. Chesson, 1991), it is important to remember that many species directly limit their own per capita demographic rates (McPeek, 2018) by mechanisms such as territoriality (Grether, Losin, Anderson, & Okamoto, 2009; Losin, Drury, Peiman, Storch, & Grether, 2016), feeding interference (Le Bourlot, Tully, & Claessen, 2014; Skalski & Gilliam, 2001; de Villemereuil & López-Sepulcre, 2011), cannibalism (Polis, 1981; Rudolf, 2007) and physiological responses to crowding (Glennemeier & Denver, 2002; McPeek, Grace, & Richardson, 2001).

Given the multitude of mechanisms shaping species demographic responses to intra- and interspecific competition, it is reasonable to suspect that the environmental factors shaping these competitive interactions should vary among communities. Indeed, local adaptation to environmental factors across the landscape can modify the strength of competitive interactions (Siepielski, Nemirov, Cattivera, & Nickerson, 2016). Therefore, we should expect the relative effects of intra- and interspecific competition to also vary among communities because of how species ecological differences cause them to respond differently to environmental heterogeneity (Figure 1b). Identifying these ecological factors provides insight into the underlying mechanisms causing intra- and interspecific responses to vary, which is a key determinant of local coexistence.

1.1.2 | Unified experimental–observational approach

One way to quantify the strength of the demographic effects of intra-relative to interspecific competition is to conduct pairwise competition experiments, where each species is manipulated to low and high relative abundances (Adler et al., 2007). When a species is manipulated to low relative abundance, it primarily experiences the demographic effects of interspecific interactions. By contrast, when a species is manipulated to high relative abundance, it primarily experiences the effects of intraspecific interactions. Therefore, if a species per capita population growth rate decreases as it becomes common, this would indicate that the effects of intraspecific competition reduce growth rates more than interspecific competition. If, however, a species per capita growth rate decreases as it becomes rare, this would imply that interspecific competition reduces growth rates more than intraspecific competition, which would hamper coexistence (Figure 1a). Thus, when both species in a given pair experience demographic advantages when rare (e.g. reciprocal slopes; Figure 1a), this condition can promote local coexistence. If only one species gains a demographic advantage when rare, this would imply that one species exerts a stronger competitive effect, regardless of which species is the recipient of competition.

The strength of these competitive responses can therefore be estimated as the slope of per capita population growth rates when species are established at low and high relative abundances. Larger negative values indicate stronger intraspecific effects, larger positive values imply stronger interspecific effects, and a slope of zero would suggest species respond identically to intra- and interspecific competition (Figure 1). Note that to estimate the individual strengths of intra- and interspecific competition, additional experimental manipulations (e.g. a response surface design) of both species in isolation are required (Hart, Freckleton, & Levine, 2018; Inouye, 2001). The experimental design we subsequently employed in our case study, though, is still sufficient to estimate demographic responses to intra- and interspecific competition. In the absence of being able to estimate per capita population growth rates, a limitation faced by many researchers for numerous study systems, it may be permissible to use other vital rates that shape population growth rates (e.g. per capita mortality, fecundity, individual somatic growth rates; Hart et al., 2018). In doing so, one must assume a linear correlation between a particular per capita demographic rate and per capita population growth rates.

When manipulative experiments of relative abundance are replicated in multiple locations along environmental gradients, this natural heterogeneity provides an opportunity to then understand how the environment may shape intra- and interspecific competitive effects (Figure 1b). These associations can help reveal the ecological differences among species potentially shaping coexistence (or exclusion; Figure 1). This can be accomplished by observing how demographic responses (changes in per capita rates) to relative abundance manipulations change along environmental gradients. Results from this approach can be statistically evaluated with a simple model:

$$y = \alpha + \beta_a a + \beta_E E + \beta_{aE} aE + \varepsilon$$

where y is per capita population growth rate (or a surrogate as above, e.g. per capita individual growth rate, mortality rates), α is the intercept, a denotes relative abundance, E is an environmental factor, aE is the interaction between relative abundance and an environmental factor, and ε is error; β_i are slope parameters estimated from the data. Importantly, these terms do not have to be linear functions of relative abundance and environmental factors; nonlinear regression approaches could also be used. In the context of pairwise competitive effects, this model can be implemented using familiar MANOVA type models, as there are two species and thus two vital rates (y_1 and y_2). The aE term is of particular interest because it captures how the effect of relative abundance depends on an environmental factor. Note, however, that it may be more straightforward to first assess whether there is a site effect (e.g. simply testing for spatial variation in competitive effects), rather than a particular environmental effect.

The above analysis is informative for understanding whether the effects of relative abundance vary among sites, or are potentially influenced by an environmental factor, but it does not test how the strength of competitive effects might vary with the environment. Quantifying how the strength of competitive effects varies along environmental gradients for species pairs requires estimating the correlation between different environmental factors and the slope of the difference in growth rates between low and high relative abundance treatments per species (Figure 1b).

1.1.3 | Caveats and pitfalls

Several caveats are important for implementing this unified experimental–observational framework in field settings. First, it assumes that manipulations of relative abundance are performed at a relevant spatial scale whereby frequency dependence occurs (Amarasekare, 2003; Hart, Usinowicz, & Levine, 2017; Sears & Chesson, 2007) and that sufficient environmental heterogeneity exists within and among experimental locations which might differentially affect vital rates (Adler et al., 2007). It is also critical that there is feedback between limiting factors (e.g. prey abundances, nutrients) and manipulations of relative abundance. That is, experiments must be conducted such that perturbing one species to low relative abundance allows its limiting resources (and those of its competitors) to respond in turn.

Second, and following from the above, the total densities of species must be sufficient that competitive interactions are occurring, which can be challenging to determine given spatial and temporal variation in natural densities for most species (Mittelbach, 2012). That is, if species densities are so low that resource is not limiting, then responses to relative abundance would potentially be weakened if not absent. This is a limitation of such substitutive experimental designs, where total density is fixed (Goldberg & Scheiner, 2001; Underwood, 1986). Responses to relative abundance manipulations could also be weakened if density-dependent responses occurred with a time-lag greater than the duration of the experiment (e.g. if resources take more time to be depleted). Study system-specific knowledge can be important in determining relevant total densities (Mittelbach, 2012). In the absence of such knowledge, one potential solution is to simultaneously manipulate both relative and total abundances in a crossed factorial design, book-ending relevant extremes in natural total densities (Siepielski et al., 2010). Such an approach is also informative because it may be that species are ecologically equivalent, and thus do not respond to relative abundance manipulations. However, if density-dependent population regulation is important, species should still respond to manipulations of total abundance (Siepielski et al., 2010). Similarly, response surface designs could also be implemented (Hart et al., 2018; Inouye, 2001).

Third, for clarification, the present framework is concerned with what has been referred to as "variation-independent stabilizing mechanisms" focused on local species coexistence (Chesson, 2000b). These are mechanisms that shape the strength of intraspecific relative to interspecific competitive effects, but are not dependent on spatial environmental variation (e.g. local resource or habitat partitioning along a gradient), temporal environmental variation (e.g. storage effect type mechanisms) or relative nonlinearities to work (Chesson, 2000b; Sears & Chesson, 2007). The latter are all important mechanisms that can shape coexistence (Chesson, 2000b) and expansions of these mechanisms to the framework we outline would be a useful endeavour. Thus, while the framework we propose is not comprehensive, and does not allow for an exploration of all possible mechanisms underlying potential coexistence, it should still serve as a useful starting point that can be modified to accompany other mechanisms.

Fourth, this framework only works for fairly simple communities and relies on pairwise comparisons of competitive interactions. Indeed, because the competitive effects of interest here are by definition demographic responses that cause species to have differential effects on themselves relative to other species (Letten et al., 2017), this way of quantifying competitive differences can only be understood in the context of pairwise competitive interactions. Yet, real communities are often very complex, and multiple environmental conditions and interspecific interactions contribute to species differences that can shape their abilities to coexist (Chesson, 2018; McPeek, 2017, 2018). As a result, it may very well be that complex indirect interactions among community members via interaction chains and higher order interactions emerging from non-additive density responses are critical (Letten & Stouffer, 2019; Levine, Bascompte, Adler, & Allesina, 2017). In principal, the framework presented here could be extended to capture these higher order actions. Likewise, consideration of not only resource-based competitive interactions, but also of other species interactions (e.g. parasitism, predation, mutualism) that influence consumers and resources embedded within complex food webs will be important (Chesson & Kuang, 2008; McPeek, 1989, 2018; Sommers & Chesson, 2019).

Finally, while the framework we outline may experimentally identify the occurrence and strength of competitive effects, the correlation between competitive responses and environmental factors is not experimentally determined and direct causality cannot be inferred. Essentially, the framework we outline is perhaps best viewed as a "where-to-start inquiry". It allows researchers to identify whether species exhibit differences in responses to intra- and interspecific competition, and if so, what *might* be the underlying causal factors for those responses. Subsequent to this, if environmental factors are identified, experimental studies manipulating those factors would then be necessary (HilleRisLambers et al., 2012).

2 | MATERIALS AND METHODS

2.1 | Study system

We applied our framework to a field study with *Enallagma* damselflies. *Enallagma* are among the most diverse and abundant genera of odonates in North America, with 34 of the 38 species found as larvae in lakes and ponds with fish (McPeek, 1990, 1998; McPeek & Brown, 2000; Siepielski et al., 2010; Westfall & May, 2006). In our study region in the Ozarks and the Arkansas River Valley of the south-central United States, two to six species of *Enallagma* frequently co-occur is small areas (1-m^2 patches of macrophytes). These damselflies spend over 90% of their lives (ca. 11 months in temperate zones) as aquatic larvae in the littoral zone, feeding upon small invertebrates and being consumed by conspecifics and heterospecifics, larger predacious insects and especially fish.

Previous field experiments have shown that density-dependent growth (changes in body size) through competition for food resources contributes to the regulation of fish-lake damselfly assemblages, and ecological differences affecting growth rates among species are detectable using cage experiments (McPeek, 1990, 1998; McPeek et al., 2001; Siepielski & McPeek, 2013; Siepielski, Mertens, Wilkinson, & McPeek, 2011). Similarly, per capita mortality is also strongly density-dependent (see figure 2 of Siepielski et al., 2010) with different species exhibiting differences in predator-driven mortality rates (Bried & Siepielski, 2019). Although our experiment did not include fish predators, which are a major source of mortality for fish-lake *Enallagma* (McPeek, 1998; McPeek & Peckarsky, 1998), mortality arising from both intraguild predation and cannibalism is common and often density dependent in odonates (Van Buskirk, 1989; Fincke, 1994; Johnson, 1991; McPeek & Crowley, 1987). Thus, density- and frequency-dependent mechanisms via resource and interference competition, as well as intraguild and cannibalistic interactions, can regulate damselfly population growth rates (McPeek, 2008; McPeek & Peckarsky, 1998).

2.2 | Experimental approach

To determine whether each species gained a demographic advantage when rare, we experimentally manipulated the relative abundance of species and compared their per capita individual growth rates (changes in body size through time; hereafter, per capita growth rates; see below) and per capita mortality rates when at low versus high relative abundance. Because manipulating the relative abundances of all species would be prohibitive, we chose three: *E. exsulans*, *E. vesperum* and *E. traviatum*. We selected these species because their ranges broadly overlap (Westfall & May, 2006), they commonly co-occur in lakes where their ranges overlap, and their relative abundances vary among lakes implying that different ecological factors regulate their abundances.

During October 2017, we established 25 submerged cages (0.47 m high × 0.23 m wide × 0.23 m long, giving a bottom surface area of 0.052 m^2) in the littoral zone of each of five lakes. These five lakes were chosen because preliminary sampling of environmental factors in them (see below) indicated that they varied in a manner that could mediate competitive interactions among damselflies. Cages were constructed of 2.1-cm-diameter PVC pipe encased in mesh netting (0.6 × 1.2 mm mesh), which allowed prey to readily colonize cages and for all damselflies to experience similar local conditions (e.g. water chemistry and temperature), while excluding competitors and non-damselfly predators. At the end of the experiment, all cages contained natural prey (i.e. annelids, cladocerans, chironomids and ostracods). To provide a foraging structure for damselflies, we added the dominant macrophyte (*Justicia americana*) at natural densities to each cage after carefully removing any invertebrates.

We initiated damselfly treatments 10–20 October by randomly assigning two species of *Enallagma* to each cage and manipulating one species of each pair to low relative abundance (25%; five larvae/cage) and the other to high relative abundance (75%, 15 larvae/cage) and vice versa for all possible pairwise combinations. Total abundance (n = 20) was thus held constant across relative abundance treatments. Given the bottom surface area of the cages, this results in a total density of ~378 damselflies/m^2. This density is greater than the average of 132 ± 141 (*SD*) *Enallagma*/m^2 in the study region, and thus, it should be sufficient to detect density-dependent growth (Figure S1) and mortality responses (figure 2 of Siepielski et al., 2010), as numerous previous studies have found across a range of total densities, species and geographic locations ranging from CA to NH (McPeek, 1990, 1998; Siepielski et al., 2010; Siepielski, Nemirov, et al., 2016). Our manipulations of damselfly relative abundance should affect the level of prey resources in our experimental cages because prey items were readily capable of moving into them. Thus, if different *Enallagma* species consumed different prey (e.g. resource partitioning), then when a given species was rare more of those prey items should have been available.

The three species pairings × two relative abundances were each replicated four times in each lake. All damselflies placed in cages were from their local lakes and included the natural size variation present in each lake at the time the experiments were established. The remaining cage in each lake allowed us to determine possible damselfly trespassing rates (i.e. non-experimental animals infiltrated the cages. This was found to be low [two larvae across all control cages]). We replicated this same experimental design in five lakes. We concluded the experiment during 9–20 November, after 30 days (±1.2 *SD*), which is more than sufficient for detecting changes in *Enallagma* per capita growth and mortality rates in field conditions (McPeek & Peckarsky, 1998; Siepielski et al., 2010, 2011; Siepielski, Nemirov, et al., 2016).

Although we cannot estimate per capita population growth rates directly, both per capita growth and per capita mortality contribute to damselfly population regulation (McPeek & Peckarsky, 1998). We therefore used these latter demographic rates as response variables for measures of demographic performance that should affect population growth rates (Siepielski et al., 2010, 2011). Importantly, previous field enclosure experiments showed that food additions increase damselfly growth rates, implying that prey resources (in addition to feeding interference; McPeek & Crowley, 1987) are limiting to the growth of damselflies in fish lakes, and that they are likely drawing resource levels down at the scale of our experiments (McPeek, 1998). Per capita growth rates are also an important demographic rate for damselflies, because they determine the length of time larvae is exposed to their predators (McPeek & Peckarsky, 1998). Despite the absence of fish predators, mortality likely arose from both cannibalism, which is essentially an extreme form of interference competition, and intraguild predation (Van Buskirk, 1989; Fincke, 1994; Johnson, 1991; McPeek & Crowley, 1987). The threat of cannibalism can also generate strong stress responses—growth rates of *Enallagma* are upwards of 50% lower when conspecifics are present (McPeek et al., 2001). We acknowledge that other sources of mortality, especially from fish, can strongly affect damselfly population growth rates and thus their potential to coexist (McPeek & Peckarsky, 1998). In the *Discussion*, we return to this issue.

As in our previous studies (Bried & Siepielski, 2019; McPeek, 1990, 1998; Siepielski et al., 2010), growth and mortality rates for each species were calculated for each cage. Per capita growth rates for each species were calculated as [mean(ln(head width of recovered larvae)) − mean(ln(head width of initial sample))]/duration. This growth rate metric assumes a model of head width(t) = head width(0) $e^{(gt)}$, where g is the growth rate and is independent of the initial size of the individual, but may depend on species, environmental conditions and the density of competitors (McPeek, 1998). The initial samples of head width were from a subset of randomly chosen individuals not used in the cages. Head widths were measured using a compound microscope fitted with an ocular micrometre. Per capita mortality rate was estimated as: −(ln(number recovered) − ln(initial number))/duration.

2.3 | Standardized sampling of environmental gradients

At the five lakes used in the experiment, we measured environmental factors that previous studies have shown can either directly or indirectly affect damselfly growth and mortality rates (McPeek, 1990, 1998; McPeek et al., 2001; Siepielski & McPeek, 2013; Siepielski et al., 2011; Siepielski, Nemirov, et al., 2016; Table S1). The methods used here have been described elsewhere (references as above), so we only briefly describe them here. We estimated the density of macrophytes in 10 0.25-m^2 quadrats in the littoral zone, because they are an essential habitat for damselflies, providing refuge from predators and foraging substrate for "arboreal" larvae (Crowley & Johnson, 1992). Damselfly prey density on submerged macrophytes was estimated by taking six replicate prey samples with a 6-L box sampler (100-μm mesh). We also measured the density of fish predators by taking three standardized seine hauls (4.5 m × 1.5 m beach seine net with 5-mm mesh). Although fish were not included in our experimental cages, their potential indirect effects (e.g. reduced prey consumption) on growth rates should still be detectable via olfactory or visual cues (Siepielski, Fallon, & Boersma, 2016). Because various aspects of water chemistry can either directly or indirectly affect the movement of nutrients, oxygen and other abiotic factors within and between levels of the local food web (Corbet, 1999; Frolich Strong & Robinson, 2004), we characterized water chemistry (conductivity, pH, salinity) of each lake using a YSI probe (YSI ProPlus, YSI Incorporated), using the averages of three measurements from the sampling area. Finally, we estimated an overall index of lake productivity by measuring chlorophyll-*a* (hereafter chl-*a*) concentration (µg/ml) with a fluorometer (Turner Designs) after a standard ethanol digestion (Siepielski & McPeek, 2013), using the averages from two water samples.

To estimate the density of *Enallagma* (all species combined), we returned to lakes twice during the larval period (27 September–20 October 2016 and 20 October–20 November 2016). During each visit, larvae were sampled by taking 10 standardized 1-m-long dip net sweeps (28 cm net opening, 1 × 1 mm mesh) spread across a 60-m stretch of the littoral zone and stratified by dominant macrophytes. This method gives highly repeatable estimates of odonate densities (Crowley & Johnson, 1992; Stoks & McPeek, 2003). All captured odonates were preserved in 70% ethanol and later identified to species and measured in the laboratory. We used mean density over the two samples as an estimate of competitor density.

2.4 | Statistical analyses

In our experiment, two species were present in all cages, and thus, the growth and mortality responses are inherently multivariate. Therefore, we first used a MANOVA model to determine the effects of relative abundance, lake and their interaction on per capita growth and mortality rates for each species pairing. This analysis allowed us to determine whether, when paired together, species per capita growth and mortality rates responded to relative abundance manipulations, and whether these responses varied among lakes (e.g. Figure 1a). We then conducted simple linear regressions of per capita growth and mortality rates against relative abundance for each lake × species pairing (Levine & HilleRisLambers, 2009) to estimate the slope of growth and mortality rates in relation to relative abundance. In addition, we also built hierarchical models with a random intercept and slope for each lake by species by relative abundance combination. In principal, these models would allow for regularization, because estimates for each slope inform the estimates of the other slopes (Gelman, Hill, & Yajima, 2012). However, results from these more complicated models were qualitatively similar, and thus, we present results from the simpler analysis, acknowledging that such model estimates are likely to be noisy and may overestimate the variation among lakes and species combinations in slopes in relation to relative abundances. To assess how environmental variation can affect the relative strength of intra- and interspecific competition, we then conducted a simple correlation analysis between these estimated slopes and each of the environmental variables measured in each lake (e.g. Figure 1b). All analyses were conducted in program R version 3.3.3 (R Core Team, 2017).

3 | RESULTS

3.1 | Experimental manipulations of species relative abundances to infer competitive effects

Per capita growth rates for species pairs varied significantly among lakes for two of the three species pairs (Table 1; Figure 2); however, there was no consistent effect of relative abundance, nor a significant interaction between relative abundance and lake terms (Table 1). Across lakes, species growth rates were significantly different from each other (ANOVA, $F_{2, 237} = 40.09$, $p < 0.0001$): *E. vesperum* (mean growth rate = $0.008 \pm 1.8 \times 10^{-4}$ *SE*) had a higher per capita growth rate than *E. exsulans* (mean growth rate = $0.006 \pm 3.0 \times 10^{-4}$ *SE*; Tukey HSD, $p < 0.0001$) and *E. traviatum* (Tukey HSD, $p < 0.0001$), and *E. exsulans* had a higher per capita growth rate than *E. traviatum*

TABLE 1 Results of the MANOVA comparing *Enallagma* species per capita growth and mortality rates at low and high relative abundances for each of the three species pair combinations among five lakes in Arkansas (see Figure 2)

	Per capita growth rate				Per capita mortality rate			
Comparison and model terms	Wilk's λ	F	df	P	Wilk's λ	F	df	p
E. traviatum–E. vesperum comparison								
Lake	0.762	1.06	8.58	0.406	0.642	1.797	8.58	0.096
Relative abundance	0.922	1.218	2.29	0.31	0.982	0.257	2.29	0.774
Lake × relative abundance	0.678	1.555	8.58	0.159	0.841	0.651	8.58	0.731
E. exsulans–E. vesperum comparison								
Lake	0.19	9.403	8.58	<0.0001	0.476	3.254	8.58	0.003
Relative abundance	0.941	0.906	2.29	0.415	0.975	0.359	2.29	0.701
Lake × relative abundance	0.9	0.394	8.58	0.92	0.48	3.213	8.58	0.004
E. traviatum–E. exsulans comparison								
Lake	0.359	4.844	8.58	0.0001	0.59	2.181	8.58	0.042
Relative abundance	0.988	0.183	2.29	0.833	0.869	2.176	2.29	0.131
Lake × relative abundance	0.78	0.959	8.58	0.476	0.888	0.44	8.58	0.891

(mean growth rate = 0.005 ± 2.0 × 10^{-4} *SE*; Tukey HSD, p = 0.028). These results indicate per capita growth rates were variable among lakes and species, though differences in the effects of intra- and interspecific competition were largely absent or not detectable.

Per capita mortality rates for species pairs also varied among lakes for the same two species pairs as found for growth rates (Table 1; Figure 2). Unlike growth rates, however, across lakes species per capita mortality rates were not significantly different from each other (ANOVA, $F_{2,\,237}$ = 2.37, p = 0.095). Although no effect of relative abundance or interaction terms between lakes and relative abundance were apparent for *E. traviatum*–*E. vesperum* or *E. traviatum*–*E. exsulans* pairs (Table 1; Figure 2a,c), there was a significant lake × relative abundance interaction effect for *E. exsulans*–*E. vesperum* pairs (Table 1). Individual lake-level analyses showed that this effect was driven by one lake—Lake Wedington (MANOVA relative abundance term $F_{2,5}$ = 15.03, Wilks λ = 0.14, p = 0.077; all other MANOVA tests for relative abundance effects p > 0.12; Figure 2b). Individual species-level ANOVAs showed that this effect was driven by *E. exsulans* alone experiencing greater mortality when common (ANOVA $F_{1,6}$ = 19.24, p = 0.004), but no effect of relative abundance for *E. vesperum* (ANOVA $F_{1,6}$ = 1.25, p = 0.305). Overall, these results indicate that mortality rates varied among lakes, but were generally similar among species, with only a single instance of a species experiencing lower mortality when rare and only in one lake.

Comparisons of the individual slopes of each species per capita growth and mortality rates between low and high relative abundance manipulations showed considerable variation among lakes

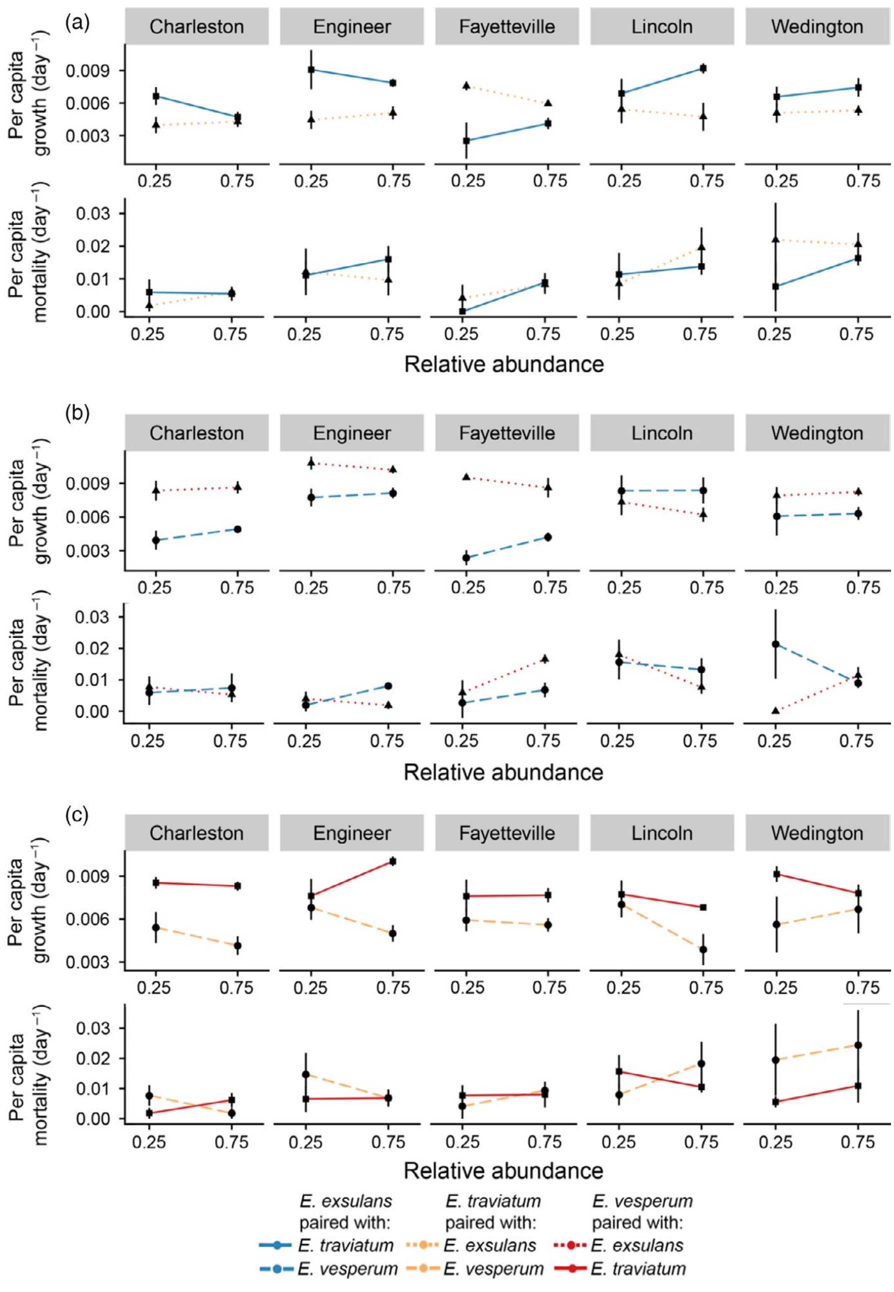

FIGURE 2 Per capita growth (top panels) and mortality (bottom panels) rates of *Enallagma* damselflies when experimentally manipulated to low (five individuals/cage = 0.25) or high (15 individuals/cage = 0.75) relative abundances among lakes. Each panel depicts the per capita growth rate (mean ± 1 *SEM* of individual growth rates (changes in body size through time)) or mortality rate of a species pair when both rare and common (a) *E. exsulans* with *E. traviatum*, (b) *E. exsulans* with *E. vesperum* and (c) *E. traviatum* with *E. vespersum* in each lake. To illustrate, the uppermost left panel shows *E. exsulans* and *E. traviatum* per capita growth or mortality rates in Lake Charleston, AR. When *E. exsulans* is at low relative abundance, *E. traviatum* is at high relative abundance, and vice versa

and species pairs, both in magnitude and sign (Figure 2), though confidence intervals of most slopes overlapped with zero (Figure S2). Although some species experienced a tendency for greater per capita growth or lower mortality when rare in some lakes when paired with some species, the effects were rarely reciprocal among a given pair of taxa in a given lake. That is, it was uncommon for both species when paired together to both experience demographic advantages (higher growth or lower mortality) where rare, which is a necessary condition for local coexistence. Instead, most slopes were opposing, but again the confidence intervals of these slopes largely overlapped with zero implying that intraspecific effects were largely the same as interspecific effects (Figure S2). Overall, these results indicate that per capita growth and mortality rate changes in response to relative abundance manipulations are both infrequent and variable in magnitude and direction.

3.2 | Examining how species competitive effects are shaped by environmental variation

Although the MANOVA and individual-level regressions (the regressions per species pairing per lake, Figures 2 and S2) detected infrequent, subtle and variable effects of relative abundance manipulations among species and lakes, we further investigated how these effects on per capita growth and mortality rates varied in relation to environmental differences among lakes (Figures 3 and 4). The slopes of per capita growth and mortality rates between low and high relative abundances simply provide an estimated effect size, albeit with much uncertainty (Figure S2) capturing the strength of competitive effects, and we can examine how this varies along different environmental factors. However, given the overall lack of statistical significance in most of these comparisons, we exercise

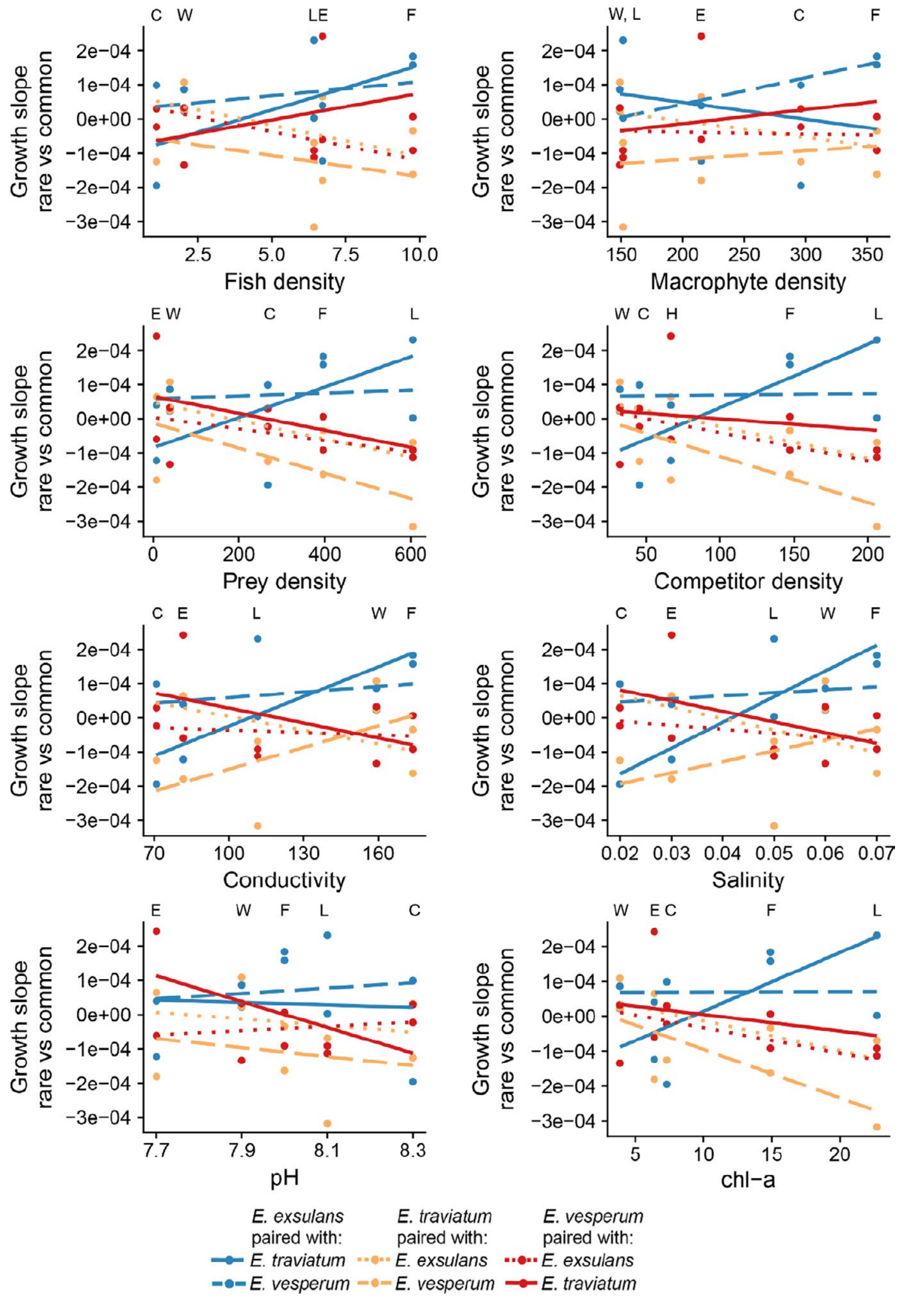

FIGURE 3 Relationships between the slopes of species per capita growth rates between low and high relative abundances among pairs of competing species across environmental factors. Colours correspond to the species per capita growth rate slope that is plotted and line texture denote the species it is paired with. Letters above plots denote each experimental lake (C = Charleston, E = Engineer, *F* = Fayetteville, L = Lincoln and W = Wedington). For example, the solid blue line shows the slope of *E. exsulans* when rare versus common when paired with *E. traviatum* (i.e. the slopes from Figure 2); the dotted yellow line shows the slope of *E. traviatum* when rare versus common when paired with *E. exsulans*. Negative values correspond with higher growth rates when rare, and positive values with higher growth rates when common. Regression lines are added only to help guide the reader. Correlation coefficients between the slopes and environmental factors are provided in Figure S3

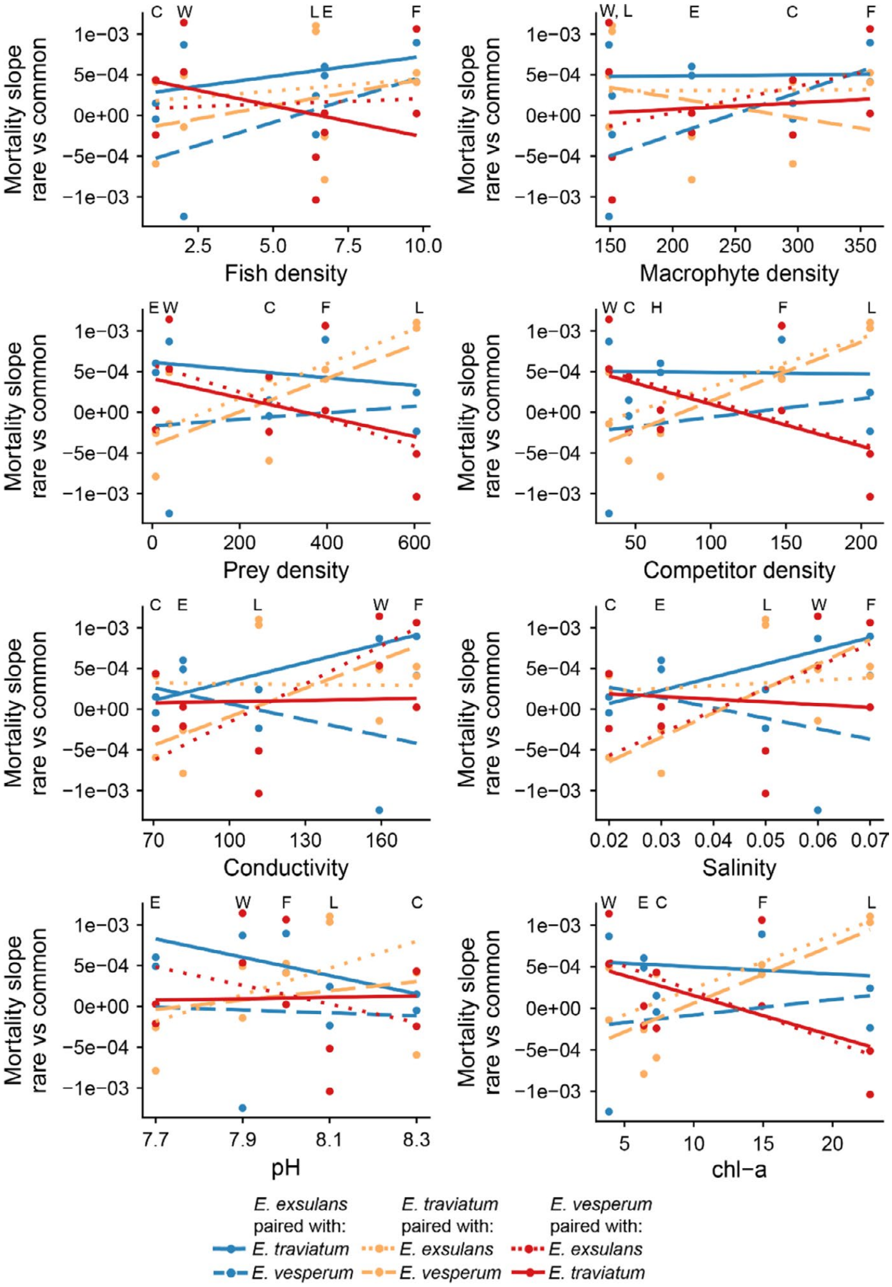

FIGURE 4 Relationships between the slopes of species per capita mortality rates between low and high relative abundances among pairs of competing species across environmental factors. Colours correspond to the species per capita growth rate slope that is plotted and line texture denote the species it is paired with. Letters above plots denote each experimental lake (C = Charleston, E = Engineer, *F* = Fayetteville, L = Lincoln and W = Wedington). For example, the solid blue line shows the slope of *E. exsulans* when rare versus common when paired with *E. traviatum* (i.e. the slopes from Figure 2); the dotted yellow line shows the slope of *E. traviatum* when rare versus common when paired with *E. exsulans*. Note, that because the response variable is mortality, positive slopes are expected if a species gains a mortality advantage when rare, then when common. Thus, negative values correspond with higher mortality rates when rare, and positive values with higher mortality rates when common. Regression lines are added only to help guide the reader. Correlation coefficients between the slopes and environmental factors are provided in Figure S3

caution in interpreting these results and consider it an exploratory analysis aimed at understanding how frequency-dependent growth and mortality *might* vary along environmental gradients, as well as an illustration of our conceptual framework (Figure 1).

Overall, correlations between frequency-dependent growth (Figures 3 and S3) and mortality (Figures 4 and S3) and environmental factors among lakes differed in both direction and magnitude among species pairs. In most cases, a given species growth or mortality response to relative abundance within a pair responded differently to different environmental factors. This is most apparent by comparing the same pairs of different taxa, where the growth or mortality slopes are often in opposing directions for the same environmental factors (Figures 3 and 4). However, there were also some instances where species responded similarly. For example, as prey density increased, most species tended to experience greater growth rates when rare (e.g. largely negative slopes in Figure 3). Similarly, as fish density increased, per capita mortality increased as a species relative abundance increased for most species' pairs (e.g. largely positive slopes in Figure 4). While growth and mortality rates of some species pairs showed similarity in their overall responses, most changes were nevertheless idiosyncratic. Thus, for at least some species, this analysis suggests differences in how species growth and mortality responses to relative abundance varied with environmental factors, implying differences in the ecology of these species that might shape competitive interactions.

4 | DISCUSSION

Coexistence theory focused on determining if species exhibit stronger population regulation because of intra-relative to interspecific competition has provided a compelling framework identifying whether species differ ecologically in ways that promote their coexistence. This is an important contribution, because it has spurred critical tests evaluating if species do coexist, which has long been assumed but rarely determined (Siepielski & McPeek, 2010). However, this body of work does not identify the ecological underpinnings of species differences that shape the effects of intra-relative to interspecific competition. Concomitant with this line of inquiry are studies of species associations with the environment, which measure aspects of species' ecological differences, but not whether these differences actually affect the strength of intra- and interspecific competition. The framework we outlined shows one way of combining these two approaches to move purely phenomenological studies of species competitive differences into one incorporating ecological underpinnings (Figure 1). Addressing this “why do species coexist” question, as opposed to simply “do they meet conditions facilitating coexistence” should help develop mechanistic insights into explaining the maintenance of species diversity.

Results from applying this framework to *Enallagma* damselfly assemblages indicate that, on average, intra- and interspecific competitive effects tend to be equivalent, at least through the contribution of larval per capita growth and mortality rates. Despite finding some instances of negative frequency dependence among competing species, indicating stronger intra-relative to interspecific competition, we found none where this pattern was reciprocated within a pair in the same lake. If only one of a pair of species exhibits a demographic advantage when rare, this alone would not contribute to reducing competitive exclusion, and the species with the strongest competitive effect could eventually dominate. Obviously, results from these experiments do not include processes acting during other life stages (egg, early instars, adult). However, no density-dependent effects on growth and mortality have been detected during these shorter life stages (McPeek, 2008).

While the overall patterns suggest that these species respond similarly to relative abundance manipulations, they do show that the species are ecologically different. Mortality rates varied among lakes but were generally similar among species; however, we did find that the species differed in their average per capita growth rates (*E. vesperum* > *E. traviatum* > *E. exsulans*). In our analysis, there were also some suggestions that species differed in how their growth and mortality rates responded to frequency manipulations, and how these responses varied along environmental gradients. Such findings indicate that these species differ in their abilities to interact with other species, themselves and the environment. The differences in growth rates presumably arose because the species vary in their prey attack rates, conversion efficiencies or physiological stress responses to themselves or their competitors—all factors that previous experiments have established differ among *Enallagma* species (McPeek, 2004; McPeek et al., 2001; Stoks & McPeek, 2006). Thus, these results show that these species are ecologically different in ways that ecologists frequently identify as being important mediators of competition, though these apparent differences are not those that seem to contribute to local coexistence in this case (Chesson, 2000b; Leibold & McPeek, 2006; Siepielski & McPeek, 2010).

Taken at face value, our exploratory analysis examining the relationship between growth and mortality responses to relative abundance manipulations and environmental gradients can provide some insight into how ecological differences may nonetheless drive species’ responses to intra- and interspecific competition. Although most of these associations were idiosyncratic, there were some instances where species responded similarly. For example, as prey density increased, most species tended to experience greater growth rates when rare (Figure 3). Similarly, as fish density increased, per capita mortality increased as a species relative abundance increased for most species’ pairs (Figure 4). For most of these comparisons, though, any growth or mortality advantages when rare were rarely reciprocal, and never occurred across all lakes for a given species. It may simply be that the range of environmental conditions in our experimental lakes was not sufficient enough to allow species to gain any demographic advantages when rare (Bried & Siepielski, 2019), or that any advantages may be so subtle that stochastic processes simply play a more important role (Siepielski et al., 2010; Svensson, Gomez-Llano, Torres, & Bensch, 2018). Ultimately, further experimental work is necessary to more definitively understand what environmental factors might contribute to the weak negative frequency dependency observed in this system, and thus reveal any potential ecological differences mediating coexistence.

Although our experiment focused on the role of resource competition and potential mortality responses through cannibalism and intraguild predation, it did not capture the effects of other species interactions, such as predation by consumers in other trophic levels (Chesson, 2018; Chesson & Kuang, 2008; McPeek, 2012, 2014, 2018; Sommers & Chesson, 2019). Indeed, mortality driven by predation by fish is an important determinant of *Enallagma* population regulation (McPeek, 1990, 1998). In a recent experiment, we found that some *Enallagma* species experience lower mortality in response to their shared fish predator when rare in one location but not in another (Bried & Siepielski, 2019). Thus, these results suggest that *Enallagma* can be ecologically differentiated among populations in ways shaping survivorship in response to a shared predator, which should promote their coexistence. Clearly, in order to understand if and how competitors may coexist, the ideal experiment will fully capture all of the ecological factors that mediate a species long-term low-density growth rate (Chesson, 2000b). And no species’ demography is likely shaped by a single factor, interaction or process in nature. Extending this framework beyond competition is thus a necessary step (McPeek, 2018).

A benefit of this framework is that the reciprocal rare species advantage required for coexistence can be viewed both within and across localities. Although we did not find evidence for a reciprocal rare species advantage within a lake, some pairs of taxa exhibited reciprocal growth rate or mortality advantages when rare across different lakes. The absence of these reciprocal competitive effects within lakes may mean that each of the species is somewhat locally maladapted to environmental conditions that vary among these lakes (e.g. prey resources), which can affect density-dependent per capita growth rates (Siepielski, Nemirov, et al., 2016). Previous experimental work has shown that the strength of density-dependent intraspecific competition in *Enallagma* weakens as populations are increasingly maladapted to local conditions (Siepielski, Nemirov, et al., 2016). Thus, if the strength of interspecific competition was to increase with maladaptation, the effect could be a reduction in the strength of intra-relative to interspecific competition, which could lead to competitive exclusion. Alternatively, it may be that the species not exhibiting a growth or mortality advantage when rare was more limited by resources, consumption or stress responses to conspecifics, or other factors that were not as limiting for the other species at a given lake. It may also be that the natural densities of *Enallagma* varied enough that our standardized relative abundance manipulations affected them differently. Indeed, as noted earlier one caveat to the implementation of our framework is that a single total density treatment was sufficient to detect competitive effects. Given that our previous studies of several species in geographic locations ranging from California to New Hampshire have consistently found negative density dependence occurring it is reasonable to assume competition is occurring here, but further experimental manipulations of total abundance are warranted (Siepielski et al., 2010).

In addition to the above possibilities, it may simply be that local coexistence does not occur. Instead, the spatial scale of "coexistence" may be more regional (Amarasekare, 2003; Hart et al., 2017) and occur in a metacommunity context (Leibold & Chase, 2017; Leibold et al., 2004; Shoemaker & Melbourne, 2016). Some sites may serve as source populations, where growth or mortality advantages for different species buffer them from local extinction (Pulliam, 1988). However, if this is the case, local factors may not be promoting local coexistence among species, and in the absence of any dispersal, the species with the highest per capita population growth rate would likely eventually come to dominate (McPeek & Gomulkiewicz, 2005). Similarly, the single species (within a pair) positive frequency dependence in per capita effects we occasionally observed indicates locally stronger inter- than intraspecific competitive effects. Theoretical models (M'Gonigle, Mazzucco, Otto, & Dieckmann, 2012) have suggested that this kind of positive frequency dependence may be an important mechanism maintaining diversity in ecologically similar species such as *Enallagma*. However, positive frequency dependence would lead to the loss of diversity at the local scale where species interactions are most important, but promote it at a regional level via priority effects (M'Gonigle et al., 2012).

Regardless, the mixture of advantages, disadvantages and no demographic effects when rare that we observed is not uncommon. For example, at a single location Levine and HilleRisLambers (2009) grew 10 annual plants in mixed-species assemblages and estimated per capita population growth rates for each under relative abundance manipulations. They found that four species showed significant decreases in per capita population growth rates with increasing relative abundance, three had increasing per capita growth rates with increasing relative abundance, and three showed no significant change. Similarly, Kraft et al. (2015), also at a single location, conducted a field experiment in which 18 annual plant species were pitted against one another in pairwise combinations and found that only 12 of 102 pairwise species comparisons resulted in potential coexistence. In fact, in most cases negative frequency dependence was absent or particularly weak. A recent meta-analysis, however, found that intraspecific effects are frequently much stronger than interspecific effects, at least among plants where this has been best studied (Adler et al., 2018). Collectively, such results point to the need for a much more expansive view of the make-up of species assemblages in local communities (Leibold & McPeek, 2006; McPeek, 2017; Siepielski et al., 2010; Svensson et al., 2018). There is no a priori reason to suspect that all species are locally coexisting (McPeek, 2017).

Other recent studies have also sought to develop more mechanistic insight into the ecological factors underlying competitor coexistence. For example, Letten et al. (2017) showed how Chesson's coexistence theory (Chesson, 2000b) can be mapped onto classic niche theory on the basis of mechanistic resource-based models (e.g. the R^* approach). Adler et al. (2013) developed an insightful approach examining how species functional traits, which affect their interactions with the abiotic and biotic environment, might contribute to shaping species coexistence (Kraft et al., 2015). A next step would be to fully integrate studies of species functional traits and the environmental conditions that affect the strength of intra- and interspecific competition in order to determine what ecological differences mediate coexistence. This feedback between the environment and species traits that promote coexistence is ultimately what shapes the structure of communities (Kraft et al., 2015; McPeek, 2017).

Our motivation for developing this unifying framework was the notion that ideas such as "intra-relative to interspecific competitive effects" are often divorced from the underlying ecological mechanisms governing these phenomenological responses. When wrapped up in demographic responses alone, the insights gained from experimental manipulations provide only a partial answer to the deeper mystery of not only if, but how species might coexist. The benefit of adopting the framework we outlined is that it allows for the development of this mechanistic insight. From this framework, it should also be apparent that it is impossible to determine whether or not species can coexist based on results from a single location. Species may or may not coexist in any one location, but there is simply no reason to suspect that the abilities for species to coexist are somehow fixed at the species level (Bried & Siepielski, 2019). Rather, the demographic responses to competition and other interspecific interactions that species exhibit likely vary in response to their ecological differences and how local adaptation or plasticity might affect species performances along environmental gradients (Lankau, 2011; Turcotte & Levine, 2016). A research programme focused on combining results from phenomenological studies with mechanistic insight should help develop a much broader perspective towards understanding what ecological differences among species shape the rich diversity of life found in communities.

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AUTHORS' CONTRIBUTIONS

A.M.S. conceived of the study and drafted the manuscript; B.H.O. analysed the data, set up and ran the experiments; M.S. ran experiments and laboratory processing, J.T.B. set up the experiments; all authors edited the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1sn2352 (Ousterhout, Serrano, Bried, & Siepielski, 2019).

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SUPPORTING INFORMATION

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