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Received: 29 March 2022 | Revised: 15 September 2022 | Accepted: 13 October 2022

DOI: 10.1111/fwb.14017

ORIGINAL ARTICLE

Freshwater Biology WILEY

Contrasting short- and long-term outcomes of pairwise interactions between caddisflies at a hydrologically heterogeneous range margin

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Funding information
National Science Foundation; U.S. Department of Agriculture; University of Maine

Abstract

1. Climate change is leading many species to shift their geographical ranges. Species undergoing these range shifts often are moving into areas with heterogeneous abiotic conditions. Additionally, these range-shifting species will encounter resident species with whom they will compete for space and/or resources. However, the ways that these abiotic and biotic factors interact to influence the establishment and persistence of range-shifting species has received little attention.
2. Here, we conduct an *in situ* cage experiment examining how a local wetland hydroperiod gradient (i.e., temporary and semi-permanent ponds) and competition with a resident caddisfly species, *Asynarchus nigriculus*, influences the survival of the range-shifting species *Limnephilus picturatus*. We then use long-term survey data of population densities of these two species to determine whether pairwise interactions observed in the cage experiment translated into long-term dynamics.
3. The cage experiment revealed that *A. nigriculus* had a strong, negative effect on the survival of the range-shifting species *L. picturatus*, regardless of hydroperiod. However, we observed no relationship between the densities or occurrence of *L. picturatus* and *A. nigriculus* in long-term data for either temporary or semi-permanent ponds.
4. Our results suggest that landscape-level abiotic heterogeneity at range margins may not always be important for mediating antagonistic interactions between resident and range-shifting species. However, although an interaction appears ecologically significant in short-term field studies, broader context is needed to understand whether those types of interactions mediate species' distributions and abundance through time.
5. At face-value, our results from the field experiment and long-term data analysis did not align. This suggests that other factors such as additional competitive or trophic interactions may be more important drivers behind the population dynamics of this range-shifting species at its new upper-elevational limit.

KEYWORDS
competition, range-shifts, species interactions, temporal dynamics, Trichoptera

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1 | INTRODUCTION

A common consequence of climate change is for species to shift or expand their geographical ranges across regional gradients into areas that traditionally were considered more abiotically stressful, such as higher-elevation and -latitude habitats (Chen et al., 2011; Parmesan & Yohe, 2003). When species expand their range margins, they will likely encounter competitors and/or predators that are already established at these sites, and these potentially novel interactions may have important consequences for the survival and demography of the shifting and resident species (Cadotte & Tucker, 2017; Shepard et al., 2021; Shepard et al., 2022). However, the strength and outcome of these interactions are unlikely to be uniform across the species' newly expanded range margin. Instead, shifting species often will find heterogenous patchworks of abiotic conditions at their new range margins (Gaston, 2003; Oldfather et al., 2020) which can be as varied as localised gradients in soil compaction for plants (Latimer & Jacobs, 2012) or hydroperiod in clusters of ponds inhabited by aquatic invertebrates (Welborn et al., 1996). This habitat heterogeneity at a range margin may create variation in the survival of range-shifting species through other, larger-scale, abiotic stresses (Oldfather & Ackerly, 2019) and also generate spatial variation in the strength of the new species interactions which they will encounter (Greig et al., 2013). Indeed, because the outcome of species interactions often depend on their abiotic context (Chamberlain et al., 2014), landscape-level habitat heterogeneity at the leading edge of a species range is likely to beget heterogeneity in the strength of these interactions.

The idea that habitat heterogeneity can affect species population dynamics through modifications of species interactions is well-understood (Amarasekare, 2003), particularly in the context of metapopulations (Münkemüller & Johst, 2006) and metacommunities (Kneitel & Chase, 2004). Two hypotheses emerge from this literature for how habitat heterogeneity influences the persistence of range-shifting species at their new range edges. Firstly, landscape-level abiotic heterogeneity may create source populations that can compensate for other sinks in the area (Hanski, 1998). For example, in a study not considering range shifts, heterogeneity in abiotic conditions across habitat patches increased the resistance of a metapopulation of crickets to extinction (Kindvall, 1996). This same mechanism could be important for permitting a range-shifting species to establish and persist in abiotic conditions that may be harsher than those found at the core of their range (e.g., colder temperatures, less precipitation). Secondly, habitat heterogeneity also may promote coexistence between the shifting and resident species by creating refuge habitats that remove or reduce the strength of negative interactions between species. For example, landscape-level heterogeneity in river flow disturbance has promoted the persistence of both invasive and native fish in New Zealand (Boddy et al., 2020). The application of these ideas to understanding population dynamics at the edge of a species' expanding range generally has been overlooked (but see Oldfather et al., 2020, Oldfather & Ackerly, 2019). Filling this knowledge gap is critical if we are to fully understand how shifting species might integrate into resident communities, especially as range shifts continue to be one of the leading responses of organisms to climate change (Pecl et al., 2017).

There are two ways that we can investigate the effects of habitat heterogeneity and biotic interaction on range-shifting species. One approach is to conduct experiments to isolate abiotic and biotic variables to understand mechanisms behind establishment and survival of range-shifting species (e.g., Shepard et al., 2021). Empirical studies of isolated pairwise interactions are appealing since they are tractable and are useful for identifying and quantifying interactions that have the potential to shape long-term population dynamics. However, it is necessary also to examine pairwise interactions within the context of greater spatiotemporal and ecological scales (e.g., ecological communities) since interaction strength often is modified by other abiotic (Chamberlain et al., 2014) or biotic (Chase et al., 2002; Jones et al., 2020) factors. Using observational data to assess correlations between the densities of interacting species through time is a useful approach with which to assess the community and temporal context for pairwise interactions (Berlow et al., 2004). An advantage of this approach is that observational data on species densities provide us with the cumulative effect of all interactions that a species engages in with other species and with the abiotic environment. Therefore, long-term patterns in species densities should show an inverse relationship if one species has strong, negative impacts on another as demonstrated in short-term empirical experiments (Ives et al., 1999) despite the potential for other factors to modify species densities. However, results from short-term experiments do not always manifest themselves in long-term data making it critical that we pair them to get a more complete understanding of the systems thaty we are seeking to understand (Marcarelli et al., 2020).

We conducted a cage experiment and analysed long-term data on larval caddisflies to understand the combined effects of biotic interactions and habitat heterogeneity, in the form of pond hydroperiod, on the establishment and persistence of a range-shifting species. We hypothesised that habitat heterogeneity would lead to differences in survival for the range-shifting species. Specifically, we hypothesise that the range-shifting caddisfly *Limnephilus picturatus* MacLachlan would have lower survival and growth in temporary ponds than in semi-permanent ponds. Temporary ponds can have lower quality food resources than other, more permanent waterbodies (Inkley et al., 2008), while simultaneously requiring faster development times for organisms to escape desiccation (Wissinger et al., 2003). Additionally, the lower water volume of temporary ponds typically means larger diurnal temperature fluctuations than larger more permanent ponds (Mitsch & Gosselink, 2000; Wissinger, 1999). *Limnephilus picturatus* is likely to find these conditions stressful as it may not be able to develop quickly enough to pupate before the ponds dry (Wissinger et al., 2003). We do not anticipate this to be the case for the resident caddisfly, *Asynarchus nigriculus* Banks, which has a suite of fast life-history traits consistent with adaptation to temporary pond habitats (Wissinger et al., 2003).

We also hypothesise that this habitat heterogeneity will beget differences in interaction strengths between the range-shifting and resident species. Indeed, in general we expect that *A. nigriculus* will

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negatively affect the survival of the range-shifting *L. picturatus* because *A. nigriculus* is known to be an aggressive competitor and intraguild predator of other caddisfly species (Wissinger et al., 1996; Wissinger et al., 2004). However, we hypothesise that this negative effect will be stronger in ponds with shorter hydroperiods because *A. nigriculus* is more aggressive in temporary ponds (Lund et al., 2016) and antagonistic interactions often are greater in temporary ponds since their shallower depths and shrinking benthic habitat area as they dry can increase encounter rates (Greig et al., 2013). Moreover, *L. picturatus* already has been shown to be more vulnerable to antagonistic interactions in abiotically stressful habitats (Shepard et al., 2021). Given the potential for *A. nigriculus* to strongly impact *L. picturatus*, we expect inverse correlations between the densities of these two species to be evident in the long-term data, especially in temporary ponds.

2 | METHODS

2.1 | Field site and natural history

We conducted our experiment at the Mexican Cut Nature Preserve (MCNP) located at 3400 m a.s.l. in the Elk Mountains of Colorado, U.S.A. (39.030, −107.064) near the Rocky Mountain Biological Laboratory. The MCNP has a high degree of among-pond habitat heterogeneity with a collection of over 60 ponds that together span three hydroperiod categories: temporary ponds that dry completely every year, semi-permanent ponds that dry in the autumn of years with low precipitation, and permanent ponds that never dry (Wissinger, Bohonak, et al., 1999, Wissinger et al., 2003). Caddisflies (Trichoptera) are among the most biomass-dominant macroinvertebrates in these ponds, and the distribution of six species across five genera varies across the hydroperiod gradient (Wissinger et al., 2003, 2006; Wissinger, Bohonak, et al., 1999). For this study, we focused on the resident species *A. nigriculus* and the range-shifting species *L. picturatus*. *A. nigriculus* is one of the most abundant species at the MCNP whereas *L. picturatus* tends to be rarer and was first recorded at the MCNP in 1996 but did not fully establish until 1998 (see results). Both species can be found throughout the East River Valley of the Elk Mountains in Colorado. The elevational extent of *A. nigriculus* historically has been constrained to subalpine elevations (3,000–3,500 m a.s.l.) whereas, before its range shift, *L. picturatus* was found only at montane elevations (2,500–3,000 m a.s.l.) and lower (Wissinger et al., 2003; Wissinger & Greig, unpublished data 1989–2021). At the MCNP, these two species currently co-occur in 95% of the ponds that *L. picturatus* has been recorded in, suggesting that any negative consequences that stem from interactions with *A. nigriculus* are likely to be an important driver of *L. picturatus* population dynamics through time at its upper range margin. Both species inhabit temporary and semi-permanent ponds but often are excluded from permanent ponds by salamander predation (Wissinger et al., 2003, 2004, 2006). At this field site, both species are univoltine with eggs that overwinter and then hatch during spring snow-melt (Wissinger et al., 2003).

2.2 | Cage experiment

In order to determine the effect of *A. nigriuclus* on *L. picturatus* in a heterogenous landscape, we conducted an *in situ* caging experiment in five temporary and five semi-permanent ponds at the MCNP. Cages were 50 × 50 × 50 cm wood-framed cubes with 1-mm mesh walls and floors. Each pond received an array of three cages with the following treatments: *L. picturatus* only, *A. nigriculus* only, and both species together. Densities were held constant at 160 individuals/m^2 across all cages. These densities fall within the range of natural densities found at this site for both species (3–183/m^2 for *L. picturatus*, 1–193/m^2 for *A. nigriculus*) and approximates the density where strong competition is known to occur for caddisflies at the MCNP (Klemmer et al., 2012; Shepard et al., 2021). Our experiment thus was a substitutive experimental design where only 20 *L. picturatus* and 20 *A. nigirculus* were present in the cages where both species were together. Substitutive designs may be less likely to detect the effects of interspecific competition because they simultaneously weaken intraspecific interactions, thus making our design a more conservative approach than additive designs (Kiær et al., 2013; Shepard et al., 2021).

Individuals for the caging experiment were sourced from ponds where they were found in high abundances to reduce the impact of the removal of individuals from the overall population. Species' identities were confirmed identifying voucher specimens in the laboratory with a stereomicroscope. We added 50 g of air-dried, senesced sedge *Carex aquatillis* detritus to each cage which is the major food resource for both species (Wissinger et al., 2018). Sedge was collected from ponds at the MCNP and inoculated in the cages for 7 days before the beginning of the experiment to permit the colonisation and growth of natural algal and microbial communities. In one instance during the experiment, cages in one of the ponds were moved 1–2 m towards the pond center to prevent desiccation and subsequent loss of a replicate. Otherwise, cages were left to experience dry-down naturally.

The experiment was terminated after 19 days when the majority of the larvae had begun pupation. We then removed the cages from the ponds and removed and enumerated the remaining caddisflies. The remainder of the cage contents, including any unconsumed sedge, was taken back to the laboratory and inspected for any remaining caddisflies that were missed in the field. We combined the counts from the laboratory and the field to quantify the total remaining number of individuals of each species in each cage.

We used binomial generalised mixed-effects (GME) models to assess the effects of competition, hydroperiod, and their interaction on individual-level survival of both *L. picturatus* and *A. nigiriculus* in the cage experiment. We ran separate models for each species. To account for variation across space we used a nested random effect for the intercept of cage within pond, treating each individual caddisfly as a replicate. Competition and hydroperiod were included as categorical, binary variables. We used Type II Wald χ^2 tests to determine the significance of the model terms. We performed

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this analysis in R v4.1.0 (R Core Team, 2021) using the *lme4* (Bates et al., 2015) and *car* (Fox & Weisburg, 2019) packages.

2.3 | Annual surveys

Annual censuses of caddisfly densities at the MCNP began in 1989 but we focused our analysis on 1998–2021 because that is the time period that *L. picturatus* was established at the MCNP. Each year, a single 1/3 m^2 sample was taken at each of the four cardinal points of various ponds at the MCNP using a D-net with 1-mm mesh. We used these four replicate samples to calculate average densities (abundance per m^2) of each species in each pond. Although we were unable to sample every pond every year, most ponds were sampled multiple times over the 24-year record. Three years were missing from the dataset: 2000, 2001 and 2020. We analysed the data using two methods: an autoregressive generalised least squares (GLS) model, and a zero-inflated model.

We used the GLS model with an autoregressive error term to examine the effect of *A. nigriculus* on *L. picturatus* while accounting for the temporal autocorrelation in the data. This analysis was performed in R v4.1.0 (R Core Team, 2021) using the *nlme* package (Pinheiro et al., 2021). For this analysis we looked at the total average densities of both *A. nigriculus* and *L. picturatus* across all temporary and semi-permanent ponds at the MCNP. We did this because not every pond was sampled every year, violating a key assumption of autocorrelative analyses. Likewise, because there were no data for 2000, 2001 and 2020, we only examined the data for the years 2002–2019. Ultimately, these continuity limitations in the data made it impossible for us to assess the role of hydroperiod in this specific analysis. Significance of the model terms and the correlation structure was assessed using likelihood ratio testing.

We also examined whether *A. nigriculus* density had any effects on *L. picturatus* density across all ponds, ignoring the autocorrelative aspect of year. This was justified by the previous model in which the autoregressive term was not statistically significant (see results). To do this, we conducted a zero-inflated mixed-effects model to account for the large number of samples where no *L. picturatus* was detected. This model had two parts, a zero-inflated model and a conditional model. The zero-inflated model was used to determine the effects that *A. nigriculus* density had on the presence or absence of *L. picturatus* in a pond. We also included hydroperiod as a categorical variable, in line with the field experiment, and an interaction term between *A. nigriculus* density and hydroperiod. Additionally, we included year and pond as random effects in this portion of the model to account for similarities between ponds and years. It should be noted that while accounting for individual years, this approach does not account for autocorrelation between years. The second portion of the model estimated the effect that *A. nigiriculus* density had on *L. picturatus* density after removing the effects of the other variables determined to influence the presence or absence of *L. picturatus* in all of the ponds sampled at all time points. This conditional model had *A. nigiriculus* density, hydroperiod, and their interaction as the explanatory variables. The *p*-values for this analysis were estimated using Wald tests (Brooks et al., 2017). This analysis was conducted in R v4.1.0 (R Core Team, 2021) using the *glmmTMB* package (Brooks et al., 2017).

3 | RESULTS

3.1 | Cage experiment

The proportional survival of the range-shifting species, *L. picturatus*, in cages was lower when *A. nigriculus* was present (Figure 1), decreasing from an average survival rate of 70% across pond types when *L. picturatus* was alone, to 57% survival in cages with *A. nigriculus*. The GME model provided evidence for a significant reduction in proportional survival imposed by *A. nigriculus* on *L. picturatus* but there was no significant effect of hydroperiod or a hydroperiod × competition interaction on *L. picturatus* survival (Table 1). Neither competition with *L. picturatus*, hydroperiod, nor their interaction had significant effects on *A. nigriculus* survival (Table 1).

The temporary ponds were shallower than the semi-permanent ponds throughout the experiment (Figure S1) and, at the end of the experiment were, on average, 15.8 ± 8.5 cm deep (mean ± *SD*) whereas the semi-permanent ponds were 23.9 ± 7.6 cm deep. However, linear regression revealed that the rate of drying between pond types was not significantly different. Indeed, the ponds got deeper for the first half of the experiment from heavy summer monsoon rains

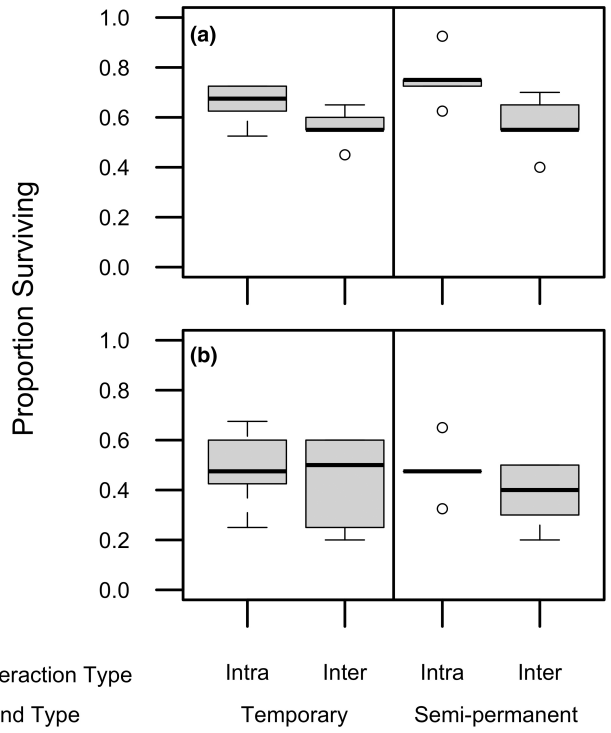

FIGURE 1 Proportional survival of *Limnephilus picturatus* (a) and *Asynarchus nigriculus* (b) in temporary and semi-permanent ponds both with intra- and interspecific interactions at the Mexican Cut Nature Preserve, Elk Mountains, Colorado, U.S.A. Open circles represent outliers

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Species	Parameter	χ^2	*df*	*p*-value	*SD*
L. picturatus	Interspecific interactions	11.649	1	>0.001	–
	Hydroperiod	1.961	1	0.161	–
	Interspecific interactions*Hydroperiod	1.547	1	0.214	–
	Pond (random effect)	–	–	–	>0.001
	Pond:Cage (random effect)	–	–	–	0.237
A. nigriculus	Interspecific interactions	1.599	1	0.206	–
	Hydroperiod	0.147	1	0.702	–
	Interspecific interactions*Hydroperiod	0.138	1	0.710	–
	Pond (random effect)	–	–	–	0.420
	Pond:Cage (random effect)	–	–	–	>0.001

TABLE 1 Results from Type II Wald χ^2 tests for the effects of interspecific interactions, pond hydroperiod, and their interaction on the survival of *Limnephilus picturatus* and *Asynarchus nigriculus* larva in an *in situ* cage experiment at the Mexican Cut Nature Preserve, Colorado, U.S.A.

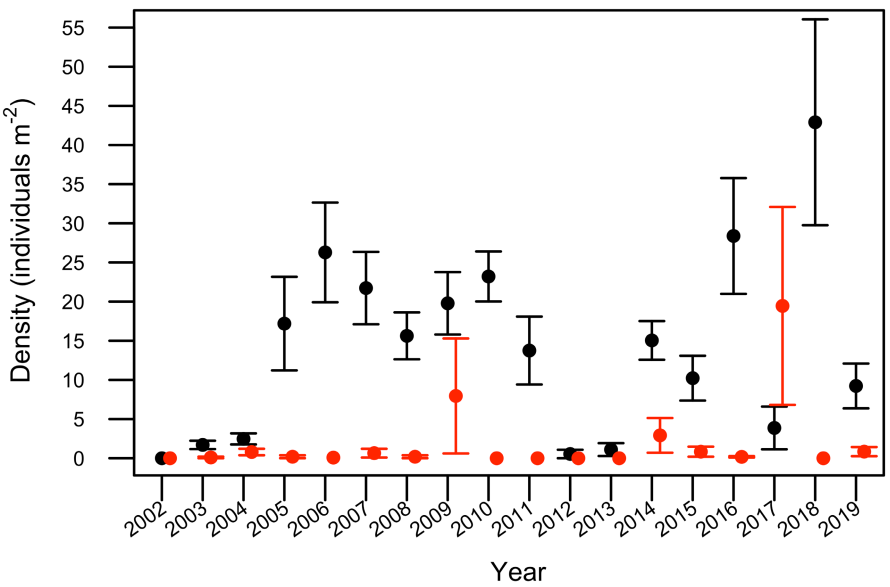

FIGURE 2 The average densities of *Asynarchus nigriculus* (black) and *Limnephilus picturatus* (red) from 2002 to 2019 in temporary and semi-permanent ponds at the Mexican Cut Nature Preserve, Colorado, U.S.A. Error bars represent one *SEM*

before drying down during the second half (Figure S1). Despite this, the shallower depths of the temporary ponds meant that the total volume of water and thereby total space in which the species could interact, was smaller in the cages in those ponds than in the semi-permanent ponds.

3.2 | Annual surveys

Across nearly all years, *A. nigriculus* densities were an order of magnitude higher than those of *L. picturatus* (Figure 2) with an average density of approximately 13±18 individuals/m^2 (mean±*SD*) compared to 2±12 individuals/m^2, respectively. The GLS analysis showed no relationship between *A. nigriculus* and *L. picturatus* densities through time (Table 2). Moreover, the autoregressive coefficient was not significant in this model (Table 2) meaning that densities in one year were not predicted by densities in the year prior.

At the coarsest level, a plot of the relationship between *L. picturatus* density and *A. nigriculus* density in all ponds across all years provide suggestive evidence that higher *L. picturatus* densities typically occurred when *A. nigriculus* densities are lower (Figure 3). Additionally, when *A. nigriculus* densities are very high, *L. picturatus* appeared to be very rarely present (Figure 3). In a statistical test of this observation, our zero-inflated GME model generated negative coefficients for the effects of *A. nigriculus* density on *L. picturatus* density in both the zero-inflated and conditional portions of the model (Table 3). However, these effects were not statistically significant (Table 3). In addition, the effects of hydroperiod, and the interaction between hydroperiod

TABLE 2 Output from a Generalised least squares and likelihood ratio tests on an autoregression examining the effects of *Asynarchus nigriculus* density on *Limnephilus picturatus* density in subalpine ponds between 2002 and 2019 at the Mexican Cut Nature Preserve, Colorado, U.S.A. Phi is a measure of association between each year in the data

Parameter	Estimate	*SE*	Likelihood ratio	*p*-value
A. nigriculus density	−0.167	0.097	2.178	0.14
Year - AR(1)	Phi = 0.280	–	0.308	0.580

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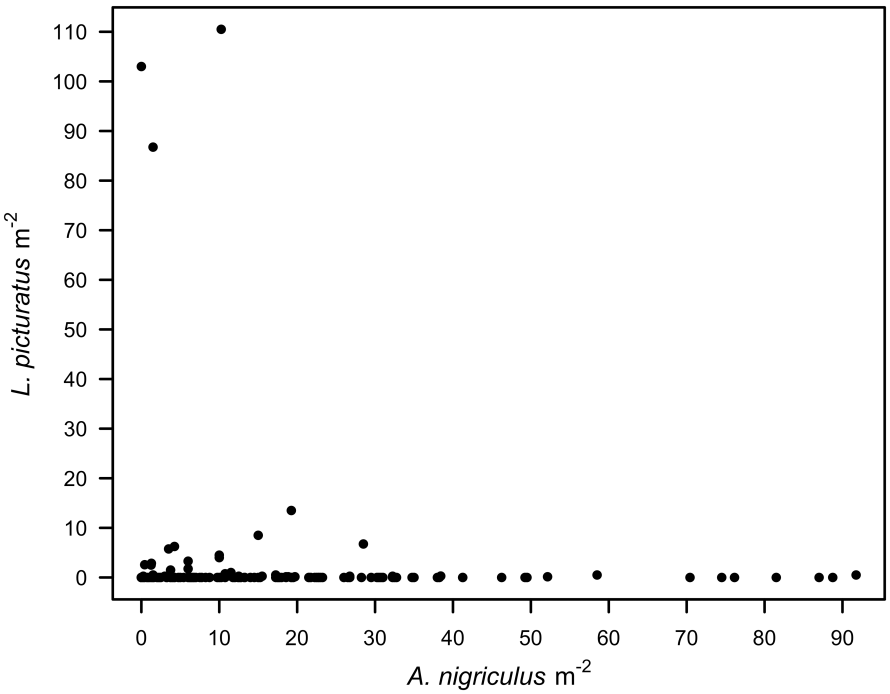

FIGURE 3 *Limnephilus picturatus* density in relation to the density of *Asynarchus nigriculus* in both temporary and semi-permanent ponds at the Mexican Cut Nature Preserve, Elk Mountains, Colorado, U.S.A., between 2002 and 2019. Each point represents the average density in each pond sampled during every year of the sampling

TABLE 3 Results from a zero-inflated, mixed-effects model examining the effects of *Asynarchus nigriculus* density on *Limnephilus picturatus* density in all ponds between 2002 and 2019 at the Mexican Cut Nature Preserve, Colorado, U.S.A. Each sample taken in each pond across all years was treated as independent (see methods for details)

Model	Parameter	Estimate	*SE/SD*	*p*-value	Variance[a]
Conditional model	*Asynarchus* Density	−0.220	0.266	0.408	–
	Hydroperiod (Temporary)	8.393	13.676	0.539	–
	Asynarchus Density * Hydroperiod	−0.397	0.587	0.498	
Zero-inflation model	*Asynarchus* Density	−0.002	0.015	0.899	–
	Hydroperiod (Temporary)	−0.481	1.012	0.635	
	Asynarchus Density * Hydroperiod	0.004	0.029	0.889	
	Pond	–	1.450	–	2.102
	Year	–	0.437	–	0.191

Note: *SE*, for fixed effects; *SD*, for random effects.
[a]Random effects only.

and *A. nigriculus* density were not statistically significant. Thus, the GLS analysis on the temporal data and the zero-inflated GME models together show that *L. picturatus* does not appear to be affected by *A. nigriculus* in the natural ponds, irrespective of landscape level-heterogeneity (i.e., hydroperiod) and regardless of whether temporal trends are accounted for in the models.

4 | DISCUSSION

4.1 | Pairwise interaction between *L. picturatus* and *A. nigriculus*

Pairwise interactions can be important controls of species populations at their range margins (Price & Kirkpatrick, 2009). Our cage experiment showed that the resident *A. nigriculus* can negatively impact the survival of the range-shifting *L. picturatus* at the upper limit of its geographical range. This outcome was in line with our initial predictions: *L. picturatus* is a poor competitor with other species at sub-alpine elevations (Shepard et al., 2021) whereas *A. nigriculus* is very aggressive towards other caddisflies, especially in drying habitats (Lund et al., 2016; Wissinger et al., 1996, 2004). However, this interaction was not affected by landscape-level habitat heterogeneity, as the negative effect of *A. nigriculus* on *L. picturatus* survival was not significantly different between temporary and semi-permanent ponds. This is a surprising result because the temporary ponds were shallower than the semi-permanent ponds at the end of the experiment. Since both species, especially *L. picturatus* make use of the vertical structure offered by the cage walls (Shepard, Greig, personal observation), we would expect that having shallower water would generate more frequent encounters between *L. picturatus* and *A. nigriculus* in the temporary ponds. Yet, although unexpected in this

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context, other studies have shown that interactions between *A. nigriculus* and another caddisfly species, *Limnephilus externus*, also were not impacted by hydroperiod, in that case, among permanent and semi-permanent ponds (Wissinger et al., 1996). The lack in variation in the biotic interaction across the abiotic gradient may suggest that the abiotic differences between the temporary and semi-permanent ponds were not sufficient to alter the pairwise interaction that we studied.

It is possible that the heterogeneity in the landscape where we ran this experiment was not sufficient to alter the outcome of the interaction between *L. picturatus* and *A. nigriculus*. Indeed, there was no effect of habitat heterogeneity, in this instance hydroperiod, on the survival of *L. picturatus* or *A. nigriculus* when each species was isolated from competitors. Previous studies with *A. nigriculus* showed increased frequency of aggressive interactions in drying versus non-drying ponds which may have been driven by cues such as increasing conductivity, reduced habitat area and temperature extremes as ponds dry (Lund et al., 2016). However, in our experiment, the ponds did not dry down much below their initial levels as a consequence of heavy rainfall during the first half of the experiment, which may have limited the presence of cues that trigger *A. nigriculus* to become more aggressive as ponds dry. However, even if the hydroperiod gradient had been steeper during our experiment, the contrast between temporary and semi-permanent varies across years. Indeed, the rate at which temporary ponds dry each summer at the MCNP is variable (Wissinger and Greig, unpublished data 1989–2021). As in many high-elevation areas, the hydroperiod of ponds at the MCNP depends on snowpack (Barnett et al., 2005) and summer precipitation (Lee et al., 2015). Thus, even if a more rapid dry-down than what we observed in our experiment increases the strength of the interaction between *A. nigriculus* and *L. picturatus* in temporary ponds, this effect is likely not consistent from year-to-year. However, other abiotic differences remain between temporary and semi-permanent ponds including decreased nutrient availability and greater diurnal temperature swings in temporary ponds (Mitsch & Gosselink, 2000; Wissinger, 1999). Even so, it is understood that these intense diurnal temperature swings can constrain development rates (Jannot et al., 2008; Lund et al., 2016) preventing *A. nigriculus* from developing faster and growing larger in temporary ponds. Thus, it is unlikely that the size difference between *L. picturatus* and *A. nigriculus* is greater in temporary ponds, leading to no change in interaction strengths between these habitats.

4.2 | Long-term relationship between *L. picturatus* and *A. nigriculus*

Surprisingly, our analysis of the long-term data revealed no significant relationship between the annual densities of *A. nigriculus* and *L. picturatus*. Indeed, the observed, uniformly negative consequences of *A. nigriculus* on *L. picturatus* across different habitat types in our field experiment would suggest that *A. nigriculus* has the potential to strongly regulate *L. picturatus* populations at the upper edge of its distribution over long time periods, regardless of habitat heterogeneity (*sensu* Tilman, 1994). Ultimately, this lack of concordance between long-term densities and short-term experiments suggests that other factors may be important at broader time scales. Some of these differences may be related to artifacts of the sampling effort. For example, it is possible that we did not detect an effect of *A. nigriculus* densities on long-term *L. picturatus* densities because of inconsistent sampling of ponds across years at the MCNP that obscured patterns within given ponds. While our aim was to sample every pond every year, this was not always logistically possible, and these data gaps may have led to a false negative in our assessments. Nevertheless, there also are numerous biological explanations for the different outcomes in the long-term data analysis and short-term experiment. Specifically, we have identified three ecological hypotheses for why the negative effects *A. nigriculus* had on *L. picturatus* survival in our cage experiment may not translate to long-term population impacts. These potential mechanisms span scales of biological organisation ranging from intrapopulation effects of *L. picturatus* on itself, the interaction between *L. picturatus* and *A. nigriculus*, and the interaction of these two caddisflies with the broader ecological community.

Limnephilus picturatus may, itself, be able to compensate for reductions in survival imposed by *A. nigriculus*. Survival is just one variable that can control a species' demography. Other variables, such as reproductive output, also are critically important and declines in one demographic variable may be offset by increases in others (i.e., demographic compensation; Doak & Morris, 2010). Our experimental design did not allow us to collect the data needed to test for demographic compensation, yet its impact should not be ignored when determining the effects of species interactions at the margins of species ranges. However, in this instance, we do not believe that demographic compensation would be sufficient to overwhelm the negative effects of competition by *A. nigriculus*. Previous studies have shown that *L. picturatus* body mass, a parameter closely related to fecundity (Honěk, 1993), is smaller at the upper extent of its elevational range making it harder for this species to overcome significant negative effects of competition via compensation through increases in individual fecundity (Shepard et al., 2021).

Alternatively, the nature of the pairwise interaction between *L. picturatus* and *A. nigriculus* also may contribute to the lack of relationship between the densities of these two species through time. For example, field observations indicate that these two species may partition microhabitats within a given pond that reduce in their interaction frequency or intensity outside of the cage environment. *Asynarchus nigriculus* typically utilises the open pond basins and benthic substrate (Wissinger, Whiteman, et al., 1999) whereas *L. picturatus* often forage on sedge fronds higher up in the water column (Shepard, Greig, personal observation). Although the cage walls likely permitted some 3D microhabitat partitioning in our experiment, it likely does not match the same level of microhabitat heterogeneity in the surrounding ponds. This lack of microhabitat diversity

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may have caused an increase in interactions between *L. picturatus* and *A. nigriculus* leading to the significant negative effects we observed. However, even with microhabitat partitioning, we would still expect to see a relationship between *L. picturatus* and *A. nigriculus* in the temporary ponds because as they dry down, the 3D space in the ponds decreases which can lead to an increase in antagonistic interactions (Greig et al., 2013; Lund et al., 2016). Even so, interannual variation in drying rate may mean that potential increases in the strength of this interaction resulting from reductions in 3D space are not sufficiently consistent to produce long-term effects, as discussed above.

Finally, the lack of evidence for long-term consequences of *A. nigiriculus* on *L. picturatus* could be due to the broader community context of the interaction. It is possible that this pairwise interaction could be relatively weak compared to interactions that *L. picturatus* has with other community members. For example, previous work has shown that competition with *Limnephilus externus* can have important consequences for *L. picturatus* survival and development in semi-permanent ponds (Shepard et al., 2021), which may outweigh the interactions observed in the present study. Additionally, predation by tiger salamanders (*Ambystoma tigrinum nebulosm*) and *Dytiscus* diving beetle larva can have strong, negative impacts on the survival of *L. picturatus* (Wissinger et al., 2006; Wissinger, Whiteman, et al., 1999). Moreover, these diving beetle and salamander predators may modify the outcomes of competition between *L. picturatus* and *A. nigriculus*. Other work in this system has shown that diving beetle larva or salamanders can weaken the strength of competition between caddisflies at the MCNP (Shepard et al., 2022; Wissinger, Whiteman, et al., 1999). Indeed, it is very common for the outcome of competitive interactions to be modified by the presence of other competitors or predators (Chase et al., 2002; Chesson & Kuang, 2008; Jones et al., 2020), and this is likely to be an important mechanism determining species range margins.

Most studies seeking to understand the controls of species range margins and the consequences of range shifts have focused on pairwise interactions or the interaction between a species and its abiotic environment. Here, we showed that even when these pairwise interactions are significant on their own, other factors such as broader community effects may override them and generate unexpected long-term population dynamics at species' expanding range margins. Future studies seeking to understand the causes and consequences of range shifts should incorporate not just additional trophic levels (Jones et al., 2020; Shepard et al., 2022), but entire ecological communities into their studies.

AUTHOR CONTRIBUTIONS

Conceptualisation: IDS, HSG, SAW. Developing Methods: IDS, SAW, HSG. Conducting Research: IDS, SAW, HSG. Data Analysis: IDS. Data Interpretation: IDS, HSG. Preparation of figures & tables: IDS. Writing: IDS, HSG. Note: posthumous authorship given to SAW for significant contributions to all aspects of the research before manuscript development.

ACKNOWLEDGMENTS

We would like to thank Abrianna Sadler, Leah Franzlubbers and Michelle Woods for their invaluable help with field work. Moreover, we would like to thank Wendy Brown and the countless numbers of undergraduate field technicians, largely from Allegheny College, who have helped over the past 30 years to collect the long-term caddisfly data used in this paper. We are also grateful to Susan Wissinger for providing access to these data and Jared Balik for digitising countless datasheets. Mike Kinnison, Brad Taylor, Jacquelyn Gill, Amanda Klemmer and two anonymous reviewers provided valuable comments that helped improve this manuscript. This research was supported by a Chase Distinguished Research Fellowship to IDS from the University of Maine in addition to NSF DEB 1556788 to HSG and NSF DEB 1557015 to SAW. This research also was supported by the USDA National Institute of Food and Agriculture, Hatch Project no. ME0-21607 through the Maine Agricultural and Forest Experiment Station.

FUNDING INFORMATION

Funding for this research was provided by a Chase Distinguished Research Fellowship to IDS from the University of Maine in addition to NSF DEB 1556788 to HSG and NSF DEB 1557015 to SAW. This research also was supported by the USDA National Institute of Food and Agriculture, Hatch Project number ME0-21607 through the Maine Agricultural and Forest Experiment Station.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Upon publication, data used in this paper will be available from the authors upon reasonable request.

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How to cite this article: Shepard, I. D., Wissinger, S. A., & Greig, H. S. (2023). Contrasting short- and long-term outcomes of pairwise interactions between caddisflies at a hydrologically heterogeneous range margin. *Freshwater Biology*, *68*, 202–211. https://doi.org/10.1111/fwb.14017

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