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Elevation alters outcome of competition between resident and range-shifting species

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Abstract

Species' geographic range shifts toward higher latitudes and elevations are among the most frequently reported consequences of climate change. However, the role of species interactions in setting range margins remains poorly understood. We used cage experiments in ponds to test competing hypotheses about the role of abiotic and biotic mechanisms for structuring range boundaries of an upslope range-shifting caddisfly *Limnephilus picturatus*. We found that competition with a ubiquitous species *Limnephilus externus* significantly decreased *L. picturatus* survival and emergence at subalpine elevations supporting the notion that species interactions play a critical role in determining upslope range limits. However, without competitors, *L. picturatus* survival was greater at high-elevation than low-elevation sites. This was contrary to decreases in body mass (a proxy for fecundity) with elevation regardless of the presence of competitors. We ultimately show that species interactions can be important for setting upslope range margins. Yet, our results also highlight the complications in defining what may be abiotically stressful for this species and the importance of considering multiple demographic variables. Understanding how species ranges will respond in a changing climate will require quantifying species interactions and how they are influenced by the abiotic context in which they play out.

KEYWORDS

apparent climatic exclusion, context dependence, range margins, range shift, species' interactions, Trichoptera

1 | INTRODUCTION

Shifts in the geographic distributions of species toward higher latitudes and elevations are among the most commonly reported ecological consequences of climate change (Chen et al., 2011; Freeman et al., 2018; Parmesan & Yohe, 2003). As a result, there has been increased interest in understanding the mechanisms that constrain species geographic ranges in the first place. While ecologists have long sought to understand mechanisms that create the boundaries of species geographic distributions (Freeman et al., 2018; Gaston, 2003; Griggs, 1914), there is an ongoing debate about the relative importance of species interactions and abiotic conditions for determining species range margins (Aguilar-Trigueros et al., 2017; Alexander et al., 2016; Blois et al., 2013; Cadotte & Tucker, 2017; Louthan et al., 2015; Westoby et al., 2017; Wisz et al., 2012).

One hypothesis regarding the relative importance of abiotic and biotic constraints on species' ranges is the Species Interaction–Abiotic Stress Hypothesis (SIASH; Figure 1a; also referred to as the Darwin–MacArthur Hypothesis and the Stress Trade-Off Hypothesis; Freeman et al., 2018; Louthan et al., 2015). SIASH proposes that abiotic conditions should set range boundaries at the stressful end of environmental gradients while species interactions such as competition and predation should be the primary structuring force at the less physically harsh end of an environmental gradient (Connell, 1961; Darwin, 1859; Dobzhansky, 1950; Louthan et al., 2015; MacArthur, 1972; Menge & Sutherland, 1987). Many observed shifts in species ranges have

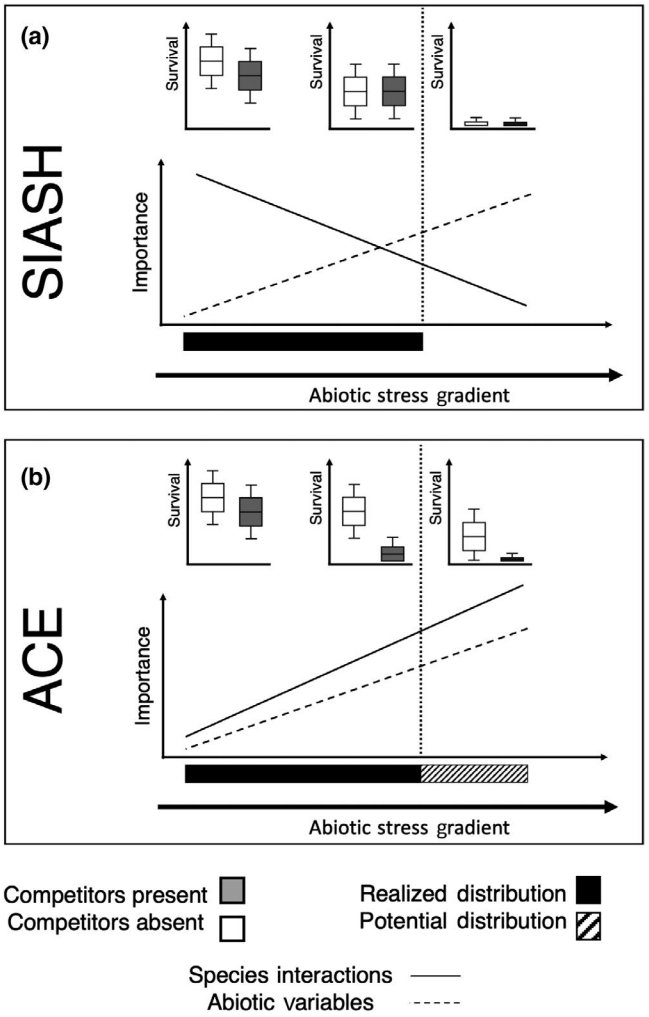

FIGURE 1 A conceptual representation of the Species Interaction–Abiotic Stress Hypothesis (SIASH, Louthan et al., 2015), and Apparent Climatic Exclusion (ACE). SIASH (a) predicts that a species may persist along an environmental stress gradient (black box) until some threshold of environmental conditions are reached (dotted vertical line) that constrain the species' range. As abiotic conditions become more stressful, we would expect the negative consequences of species interactions to disappear and survival to be approximately equal in both the presence and absence of species interactions (box plots). Thus, as abiotic stress increases, species interactions (solid line) become less important for structuring the population while abiotic conditions (dashed line) become more important. Alternatively, ACE (b) predicts that a species can persist along a stress gradient (black box) until some threshold is reached (dotted line) beyond which stress from abiotic conditions increases vulnerability to antagonistic interactions such that the species can no longer persist. However, in the absence of antagonistic interactions, we may find this species present beyond the threshold (hatched box). As abiotic conditions become more stressful, antagonistic interactions like competition continue to drive survival lower than would be expected based on the abiotic conditions alone (boxplots) In ACE, both abiotic (dashed line) and biotic (solid line) interactions increase in importance along an abiotic stress gradient but species interactions should have a steeper slope

coincided with changes in abiotic conditions in habitats that have traditionally been considered too harsh for their survival, particularly at high latitudes and elevations (Lenoir et al., 2008; Root et al., 2003). Thus, many researchers suggest that SIASH dynamics are what tend to constrain the harsh edge of species ranges. However, a recent review of studies on species undergoing elevational range shifts observed that patterns in upslope range shifts are not adequately explained by changes in abiotic variables alone, especially in temperate regions (Freeman et al., 2018).

It is possible that species range margins in abiotically stressful areas could instead be a product of biotic interactions. Theory predicts that harsh abiotic conditions can make species more susceptible to predation and competition, constraining ranges to be smaller than would be predicted based on physiological tolerances and abiotic variables alone (Cadotte & Tucker, 2017; Case et al., 2005; García-Ramos & Huang, 2012; Holt & Barfield, 2009; Svenning et al., 2014). For example, if population growth rates are low in abiotically stressful environments, even modest effects of antagonistic interactions on individual survival and fecundity could lead to localized extirpation (Baer & Maron, 2018). In this way, deteriorating abiotic conditions toward the edge of a species range create scenarios where the negative consequences of antagonistic interactions have an outsized effect that results in the creation of range margins. We refer to this scenario as Apparent Climatic Exclusion (ACE, Figure 1b) because, without experimental manipulations, it is unclear that range margins in abiotically or climatically stressful areas are determined by species interactions rather than abiotic constraints. In essence, ACE may be thought of as a geographic manifestation of the realized versus fundamental niche (Colwell & Rangel, 2009; Hutchinson, 1957) where the abiotically stressful end of the realized niche is actually determined by species interactions.

Testing these hypotheses requires examining the isolated and combined effects of abiotic and biotic variables on a species survival within, at, and/or beyond their observed range (Figure 1). For example, data on the relative strength of species interactions at the center and edge of a species range can provide strong evidence for the underlying mechanisms determining their range limits prior to an observed shift. This is because, specific, observable patterns in the relative strength of competition across a species range should emerge depending on whether SIASH or ACE dynamics sets the boundary of a species range in abiotically stressful habitats (Figure 1; Anderegg & Hille Ris Lambers, 2019). Stronger effects of competition closer to the edge of a species range would support ACE dynamics as mechanism determining a species observed distribution (Figure 1b), whereas decreases in the strength of competition toward the edge of a species range would support SIASH (Figure 1a). Importantly, knowing which of these mechanisms are structuring a species range margins requires knowledge of which end of the abiotic gradient of interest is most stressful for the focal species.

Patterns in the relative impact of species interactions and abiotic variables on fitness and survival across a species range following a range shift can likewise be useful for determining the mechanisms

that were important for setting the range prior to an observed shift. If ACE was important before, antagonistic interactions should be strongest at the new edge of the range but less so at the center. Alternatively, if SIASH was important, antagonistic interactions should not be consequential to overall fitness at the new edge of the range. Again, we must assume that the new range expansion has been into habitats that have typically been abiotically stressful for the focal species.

Empirical studies examining how the strength of competition varies across a species range remain uncommon despite numerous transplant experiments related to range shifts and range boundaries (Hargreaves et al., 2014; Lenoir & Svenning, 2015) as many of these studies rarely seek to isolate the effects of abiotic and biotic conditions (Gaston, 2009). However, at least two studies on plants have shown that biotic interactions can play outsized roles in determining survival of species beyond their geographic ranges (Benning & Moeller, 2019; Brown & Vellend, 2014). Yet, these types of experimental tests are rare, especially in animals (but see O'Brien et al., 2017).

Evaluating these ACE and SIASH hypotheses requires examining multiple life-history variables. This is because measures of survival, individual growth rate, fecundity, or any other vital rate in isolation may not be sufficient to determine the complex constraints on a species range. Species interactions and abiotic variables may not act equally on all life-history parameters leading to demographic compensation, a process where decreases in one vital rate are offset by increases in another (Villellas et al., 2015). For example, Doak and Morris (2010) showed that decreases in survival and recruitment may be offset by increases in growth rate for some tundra plants at the southern end of their range, though they did not consider the role of species interactions. Building species interactions into these assessments of multiple life-history variables is likely to provide a deeper understanding of the mechanisms determining species' ranges.

We conducted a cage experiment in ponds at two elevations to directly test whether SIASH or ACE dynamics contributed to the geographic distribution of a range-shifting species. Specifically, we examined whether the strength of competition between our focal species, an upslope range-shifting caddisfly (Trichoptera) *Limnephilus picturatus* Hagen, and a ubiquitous competitor, *Limnephilus externus* McLachlan, varied between montane (2,500–3,000 m a.s.l.) and subalpine (3,000–3,500 m a.s.l.) elevations. Quantifying the effects of species interactions and abiotic variables on the ability for populations to persist across their ranges offers powerful tests of the mechanisms that determine range margins.

In general, elevation and its associated abiotic variables seem to play a role in limiting the upward distributions of many species of lentic invertebrates including caddisflies (de Mendoza & Catalan, 2010; Fjellheim et al., 2009; Wissinger et al., 2016). Indeed, subalpine lentic habitats may be considered more stressful than those at montane elevations as they tend to have low nutrient availability, short growing seasons, cold winter temperatures, and extreme summertime diurnal temperature fluctuations which can be stressful abiotic conditions for ectothermic organisms such as caddisflies (Dillon et al., 2006; Wissinger et al., 2016). Therefore, assuming that higher elevations are more abiotically stressful for our focal species, if SIASH was important for structuring the elevational range of *L. picturatus* prior to or during its range shift we would anticipate that the relative strength of competition would decrease toward the upper elevational limit of the species' range. Conversely, if ACE dynamics structured the prior or current elevational extent of *L. picturatus*, we would expect that the relative strength of competition would increase with elevation.

2 | MATERIALS AND METHODS

2.1 | Study system and natural history

We conducted our experiments in two wetland complexes in the Elk Mountains of western Colorado, USA. The montane experiment was conducted in a large wetland at 2,800 m a.s.l. that is part of a cluster of mid-valley kettle ponds (detailed habitat descriptions in Wissinger et al., 2018) adjacent to the Rocky Mountain Biological Laboratory (RMBL). The subalpine experiment was conducted in a subset of ponds at the Mexican Cut Nature Preserve (MCNP) at an elevation of 3,400 m a.s.l. (detailed habitat description in Wissinger, Bohonak, et al., 1999).

Limnephilid caddisflies (Trichoptera) are the biomass dominant detritivores in our study ponds with nine species in five genera varying regionally along elevational gradients and locally along a hydroperiod gradient from temporary to permanent ponds (Wissinger, Bohonak, et al., 1999; Wissinger et al., 2003, 2006). We focused our study on competition between two of these caddisfly species: *L. picturatus* and *L. externus*. These species co-occur in semi-permanent ponds that dry in the autumn of years with low precipitation (Wissinger et al., 2003; Wissinger, Whiteman, et al., 1999) and therefore we elected to conduct our experiments in semi-permanent habitats at both montane and subalpine elevations.

L. externus has occurred at both the montane and subalpine elevations sites over the 30 years in which we have been observing these caddisflies (Wissinger et al., 2003; Wissinger, unpublished data, 1989–2019). Elevations at the MCNP are consistent with *L. externus*'s upper range margin in adjacent mountain valleys, whereas *L. externus*'s lower elevational range extends at least as low as 2,200 m a.s.l. in our study region. In contrast, from at least 1988 to 1996 *L. picturatus* only completed its life cycle at upper montane elevations (2,400–3,100 m a.s.l.; Wissinger, unpublished data, 1989–2019) near the RMBL. However, in 1997, it was recorded as having expanded its elevational range to include subalpine habitats at the MCNP which constitutes the upper documented limit of its elevational range (Wissinger et al., 2003, 2016). These distributional shifts are concomitant with an increase in the growing season length and higher minimum and average summer temperatures in this region over the past 30 years (Anderson et al., 2012).

The recent *L. picturatus* range expansion provides a unique opportunity to examine how abiotic conditions and biotic interactions vary from the center to edge of a species range and test whether SIASH or ACE dynamics can explain the previously observed patterns in range margins for *L. picturatus* and whether they contribute to current distributions. *L. externus* is abundant in the majority of semi-permanent ponds at both elevations while *L. picturatus* is found in a lower proportion of semi-permanent ponds at subalpine than montane elevations (Wissinger et al., 2003). Thus, this pairwise interaction is common for the range-shifting species, *L. picturatus*, but less common for the ubiquitous elevational generalist, *L. externus*.

2.2 | Caging experiments and data collection

We conducted two replicated caging experiments, one each in montane and subalpine ponds, to test how the strength of interspecific competition varies between elevations. Each experiment consisted of 10 replicates of four treatments: (a) a detritus control, (b) *L. picturatus* alone, (c) *L. externus* alone, and (d) *L. picturatus* and *L. externus* together. Density was held constant at 160 individuals/m^2, or 40 total individuals per cage, across all treatments in a substitutive design in which competition treatments had 20 individuals of each species. Substitutive experimental designs may be less likely to detect interspecific competition effects (Kiaer et al., 2013) making our study a more conservative approach to testing our hypothesis that the strength of interspecific competition should increase along a stress gradient. Furthermore, field observations in our system have shown that range-shifting species tend to replace resident taxa rather than add to the overall abundance of caddisflies (Wissinger, unpublished data, 1989–2019) making this substitutive design the most appropriate choice for our study. The overall densities of caddisflies (160 individuals/m^2) was chosen to match those where competition for food resources occurs (Klemmer et al., 2012) and falls within the range of naturally occurring densities of these species in both the montane (3–183 m^{-2} for *L. picturatus* and 27–231 m^{-2} for *L. externus*) and the subalpine (3–333 m^{-2} for *L. picturatus* and 3–393 m^{-2} for *L. externus*). The cages were 50 × 50 × 50 cm cubes consisting of 1.2 mm fiberglass insect screen affixed on all sides of a wooden frame. Cage lids were outfitted with an inverted cone emergence trap to capture adults as they emerged (Figure S1). We added 100.07 ± 0.06 g (mean ± *SE*) of wet *Carex aquatilis* sedge detritus as a basal resource to each cage.

In the montane experiment, all cages were scattered across a large (~18,500 m^2), heterogeneous semi-permanent pond near the RMBL (38.944, −106.975). Cages were divided into 10 blocks (50–100 m apart) with each block containing cages assigned to each treatment. To account for only having a single pond at our disposal for the experiment, blocks were placed in different microhabitats within the pond (e.g., variation in the density and composition of macrophytes) to encompass the abiotic heterogeneity typical of ponds at montane elevations in our study region. Our focal species of caddisfly co-occur this pond, but the individual larvae used for this experiment were collected from a nearby wetland where collection was logistically more feasible. The experiment began on June 8, 2018 and it ran for 27 days.

The subalpine experiment was conducted at the MCNP (39.030, −107.064). Cages were spread across five different semi-permanent ponds, with each pond receiving two blocks of cages with one replicate of each treatment per block. Similar to the montane experiment, blocks of cages were placed within the ponds so as to encompass the abiotic variation typical of semi-permanent habitats at subalpine elevations in our study region (detailed site description in Wissinger, Bohonak, et al., 1999). All ponds were within 150 m of each other and ranged in size from roughly 21 to 820 m^2 (mean = 295 ± 137 m^2). Though some of the ponds at the MCNP varied in their temperature profiles relative to the others over the course of our experiment (see Figure S2), historical data show that the ponds are quite similar in temperature on average (Wissinger, unpublished data, 1989–2019). However, we accounted for this small variation with a random effect term in our analysis (see Section 2.3). While both species occur within the ponds we used in the experiment, caddisflies for this experiment were collected from other ponds at the MCNP where higher densities made collection more logistically feasible and were then transferred to the experimental cages. We started this experiment July 8, 2018 and it ran for 22 days. This later start date reflects the phenological lags in caddisflies associated with later snowmelt at subalpine compared to montane elevations (Wissinger et al., 2003). The starting stage of *L. picturatus* larvae for both experiments was 30% fourth instars and 70% fifth instars. There was variation between *L. externus* instars at the beginning of each experiment with them being 30% fourth and 70% fifth instars in the montane experiment and 70% fourth and 30% third instars in the subalpine experiment. However, both species progress rapidly through the first four instars, accruing the majority (~75%) of larval biomass in the fifth instar, especially *L. externus* which has an extended period (35%–45% of its larval duration) of final instar development (Wissinger et al., 2003).

Cages were checked for emerged adults once every other day for the duration of each experiment to estimate the rate of caddisfly emergence among treatments. At the end of each experiment, we took the cages from the water and removed remaining caddisfly larvae and detritus from each cage. Larval and adult caddisflies and detritus were frozen until analysis.

In the laboratory, we picked through the detritus a second time to collect any caddisflies that were missed in the field. Total survival for each cage was quantified as the number of larvae and pupae recovered at the end of the experiment (following Klemmer et al., 2012; Wissinger, Whiteman, et al., 1999) plus the number of adults that had emerged over the course of the experiment. To measure the final dry mass of caddisflies, we removed up to 10 individual larvae of each species from each cage from their cases and dried them at 60°C in an oven for 24 hr and then weighed them to the nearest 0.001 mg on a Cahn C-31 microbalance (Thermo Scientific). We used these dry masses to quantify the mean and variance of body mass of larvae from each cage. Insufficient *L. picturatus* larva were remaining at the end of either experiment to provide enough statistical power for analysis (n = 61 for montane

experiment, $n = 11$ for subalpine experiment) and 16 cages had no *L. picturatus* remaining. Therefore, we only analyzed larval mass for *L. externus*.

Adults were processed in the same way for both the montane and subalpine experiments. After determining the sex of each individual, we placed them in the drying oven at 60°C for 24 hr and then measured the mass to the nearest 0.001 mg on a Cahn C-31 microbalance (Thermo Scientific). No *L. externus* individuals emerged during the course of either experiment, which was not surprising because of the extended time they spend in the final instar (Jannot et al., 2008; Wissinger et al., 2003). Thus, we only analyzed adult data for *L. picturatus*.

2.3 | Analysis

We used binomial generalized linear mixed-effects models with logit link functions to determine whether elevation, competition, and the elevation by competition interaction explained individual-level survival rate for *L. picturatus* and *L. externus*. To account for variation across space, we included a nested random effect for the intercept with Cage ID nested within Block. Elevation and competition were included as categorical, binary variables. We ran separate models for each of the two species and for both models we used Type II Likelihood Ratio Testing to determine the significance of each term in the model. Then, using these models, we estimated the survival of the two species in logit space, which, when exponentiated, gives the odds ratio of survival for each species in a given treatment. The generalized linear, mixed-effects models were created with the lme4 package (Bates et al., 2015) in R version 3.6.1 (R Core Team, 2019).

In addition to the binomial mixed-effects models of individual survival rate, we also created linear mixed-effects models to determine the effects of competition and elevation on the body mass of *L. picturatus* and *L. externus*. We inspected these models for normality and heteroscedasticity of residuals and determined that transformation was not necessary. As with the individual-level survival rate models, we ran separate models for each species. For *L. picturatus*, we examined adult body mass with competition, elevation, and their interaction included as fixed effects. We also included sex as a fixed effect in these models as males are consistently smaller than females (Wissinger et al., 2003). We again included a nested random effect for the intercept with Cage ID nested within Block to account for any variation across space. For *L. externus*, we examined larval rather than adult body mass due to the lack of sufficient numbers of emerged adults. Model terms were the same as in the *L. picturatus* model except sex was not included for *L. externus* as males and females are indistinguishable in their larval stage. Models were built using restricted likelihood estimates with the lme4 package (Bates et al., 2015) and the significance of terms was assessed using Satterthwaite approximation with the lmerTest package (Kuznetsova et al., 2017).

We tested the effects of competition, elevation, and their interaction on *L. picturatus* emergence with survival analysis using a Kaplan–Meier estimate and a frailty model (random effects model for time) based on a Cox regression of censored survival data (Muenchow, 1986). This frailty model included elevation and competition as fixed effects and block as a random effect for the intercept. Our frailty model did not assume a set distribution for the data, but it did assume a Gaussian distribution for the random block effect. Effect sizes were calculated as the Hazard Ratio by taking the exponent of the coefficients of the frailty model, which when multiplied by 100 gives the percent difference in the probability of emergence happening compared to the control group (i.e., low elevation *L. picturatus* in the absence of competitors). We conducted our analysis using the survival (Therneau, 2015) and coxme (Therneau, 2018) package in R version 3.6.1 (R Core Team, 2019).

While there are many different mechanisms through which these two species could compete, we focused on the potential for exploitation competition for detritus resources which has been observed in prior experiments with these caddisflies (Klemmer et al., 2012). Thus, we quantified the per-capita rates of detritus consumption of each species on its own and tested whether these values could explain the amount of detritus consumed in the treatments that had both species together. Discrepancies between predicted and observed detritus consumption in the competition treatments would indicate that the interaction between these two species either increased or decreased the per-capita rates of one of the species present. However, because we are unable to determine exactly how much detritus was consumed by each species in the interspecific competition treatments, we cannot be certain which species influenced the per-capita rate of the other.

Per-capita rates were calculated as detritus dry mass (g) consumed per caddisfly per day. We used the geometric mean for caddisfly density to account for decreasing densities as the experiment proceeded. Detritus mass in each cage was corrected for losses due to leaching and microbial respiration using the amount lost in the control treatments. We estimated cage-specific per-capita rates of detritus consumption for *L. picturatus* and *L. externus* in the absence of competitors. Then, using the estimated per-capita rates for each species on its own we calculated the total amount detritus we expected to be consumed in the competition treatments by both *L. picturatus* and *L. externus* together if the interaction between the species did not alter their per-capita rates. We then compared this calculated value to the actual dry mass of detritus consumed in the competition treatment cages using a *t* test paired by block.

3 | RESULTS

Elevation had a strong, positive effect on *L. picturatus* survival (Table 1) and overall, *L. picturatus* showed the highest survival in the absence of competitors at subalpine elevations (Table 2; Figure 2). There was a strong, negative effect of competition on *L. picturatus* survival at subalpine habitats but not at montane habitats, as indicated by the significant competition × elevation interaction (Figure 2; Table 1). This negative effect of

TABLE 1 Likelihood ratio test results for the effects of competition, elevation, and their interaction on survival of *Limnephilus picturatus* and *Limnephilus externus* caddisflies at montane and subalpine elevations from an in situ caging experiment in high-elevation ponds

Species	Parameter	χ^2	*df*	*p* value	*SD*
L. picturatus	Competition	9.732	1	**.002**	–
	Elevation	6.642	1	**.010**	–
	Competition*Elevation	6.736	1	**.010**	–
	Block (Random Effect)	–	–	–	0.498
	Block:Cage (Random Effect)	–	–	–	0.614
L. externus	Competition	0.136	1	.712	–
	Elevation	11.345	1	**.001**	–
	Competition*Elevation	0.362	1	.547	–
	Block (Random Effect)	–	–	–	0.684
	Block:Cage (Random Effect)	–	–	–	0.733

Note: Bolded *p* values are significant at the .05 level.

TABLE 2 Logit and transformed estimates from binomial mixed effects models of survival for *Limnephilus externus* and *Limnephilus picturatus* caddisflies at montane and subalpine elevations in the presence and absence of competition in an in-situ caging experiment

Species	Group	Logit estimate	*SE*	Odds ratio	Odds ratio – *SE*	Odds ratio + *SE*
L. picturatus	Montane	−1.439	0.297	0.237	0.176	0.319
	Montane + Competition	−1.79	0.328	0.167	0.120	0.231
	Subalpine	0.148	0.272	1.160	0.884	1.523
	Subalpine + Competition	−1.594	0.320	0.203	0.150	0.280
L. externus	Montane	0.308	0.336	1.361	0.972	1.905
	Montane + Competition	0.570	0.360	1.769	1.234	2.535
	Subalpine	2.091	0.357	8.091	5.662	11.564
	Subalpine + Competition	2.000	0.398	7.356	4.939	10.956

competition in the subalpine reduced *L. picturatus* survival to approximately the same level observed in both the montane treatments (Figure 2; Table 2).

Similarly, our Kaplan–Meier estimate showed that *L. picturatus* was most likely to emerge at subalpine elevations in the absence of competitors and that competition reduced the probability of emergence only at subalpine elevations (Figure 3). The interaction between elevation and competition was significant (Frailty model $p = .005$) with a reduction in the probability of emergence by 36.6% in the subalpine competition treatments compared to subalpine cages that did not have competition. Competition had no statistically significant effect on the probability of *L. picturatus* emergence at montane elevations, but overall emergence was low (Figure 3).

Our models examining how body mass was influenced by interspecific competition and elevation showed that *L. picturatus* adults emerging from subalpine elevation cages were significantly smaller (34% reduction) than those from the montane elevation cages (Figure 4; Table 3). Neither competition nor the competition by elevation term was significant (Table 3). Unsurprisingly, sex also had a significant impact on adult body mass with males being smaller than females (Table 3).

Like *L. picturatus*, *L. externus* had significantly higher survival at subalpine than at montane elevations in the absence of competitors (Figure 2; Table 2). However, there was no effect of competition on *L. externus* survival at either elevation (Figure 2; Table 1), nor was there a significant interaction between elevation and competition (Figure 2; Table 1). The mass of individual *L. externus* larvae was significantly greater at subalpine elevations compared to montane elevations but no effects of competition were detected (Figure 4; Table 3).

Per-capita rates of detritus consumption in the absence of interspecific competition were not significantly different between species or elevations and overall averaged 0.0106 ± 0.002 g of dry detritus per caddisfly per day (see Figure S3). The predicted amount of detritus consumed by *L. picturatus* and *L. externus* together in the competition treatments based on species-specific per-capita rates was not significantly different from the measured amount of dry detritus consumed in the cages where both species were together ($p = .812$).

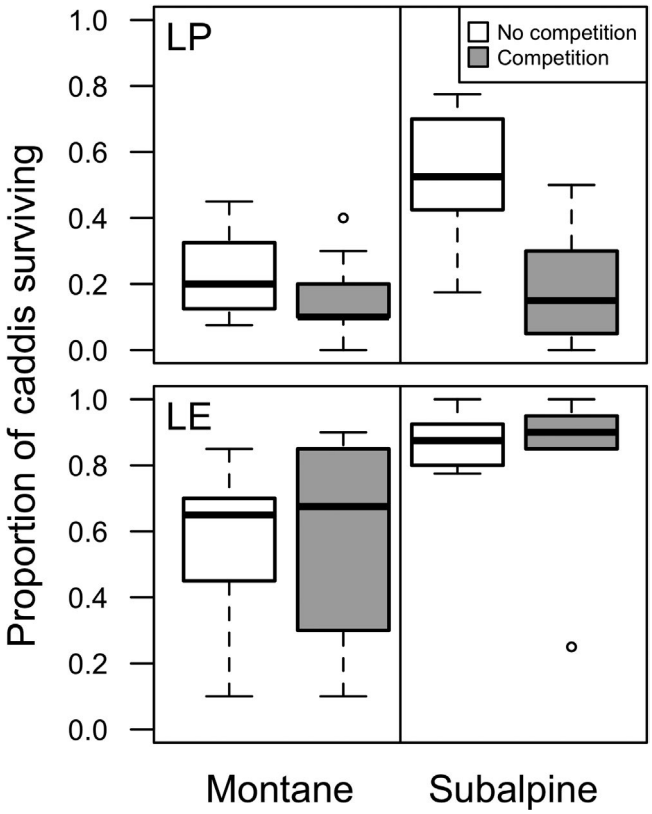

FIGURE 2 Proportions of (top) *Limnephilus picturatus* (LP) and (bottom) *Limnephilus externus* (LE) that survived when they were and were not competing with each other for detritus resources in cages at montane (2,800 m a.s.l.) and subalpine (3,400 m a.s.l.) elevations in the Elk Mountains, CO. Points represent outliers

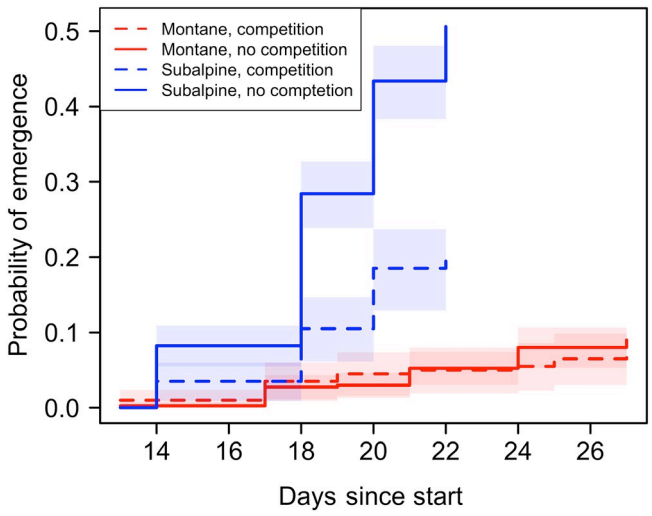

FIGURE 3 Probability of *Limnephilus picturatus* emergence in cages in the Elk Mountains, CO, at subalpine elevations (blue) in the absence (solid) and presence (dashed) of competitors and at montane elevations (red) in the absence (solid) and presence (dashed) of competitors. Dashed lines represent 95% confidence intervals. Probabilities were calculated from a Kaplan–Meier estimate (see text) [Colour figure can be viewed at wileyonlinelibrary.com]

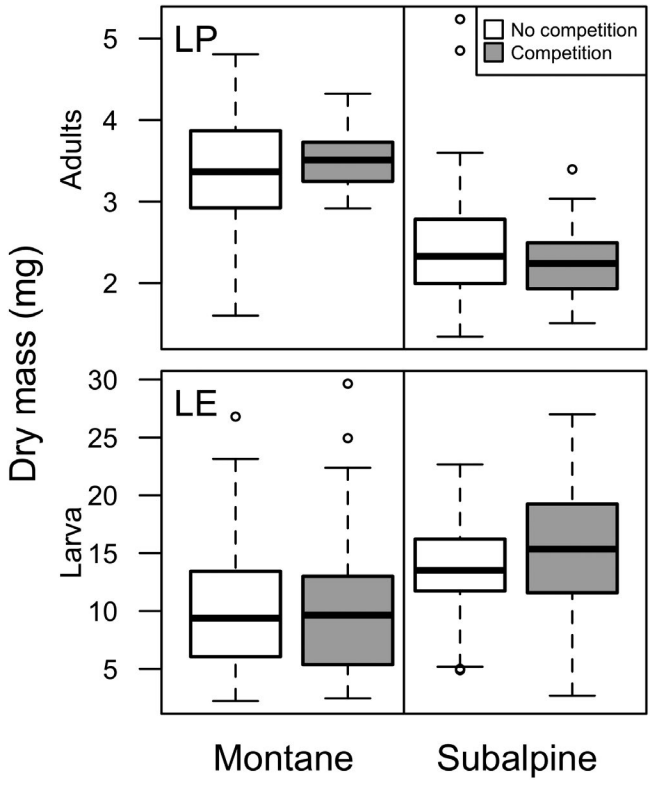

FIGURE 4 Dry mass in milligrams of (top) *Limnephilus picturatus* (LP) adults and (bottom) *Limnephilus externus* (LE) larva in the presence (grey bars) and absence (white bars) of competitors at montane (2,800 m a.s.l.) and subalpine (3,400 m a.s.l.) in ponds in the Elk Mountains, CO, USA. Points indicate outliers. For *L. picturatus* sample sizes were 33 for montane without competition, 11 for montane with competition, 198 for subalpine without competition, and 29 for subalpine with competition. For *L. externus* sample sizes were 94 for montane without competition, 82 for montane with competition, 100 for subalpine without competition, and 94 for subalpine with competition

4 | DISCUSSION

Our experiments enabled us to evaluate whether biotic interactions are relatively more important (ACE) or less important (SIASH) for individual-level survival and body mass at the recently expanded, abiotically stressful margin of a species range. The population growth rate of marginal populations can be affected by multiple vital rates which, in turn, may be differentially affected by abiotic and biotic variables. Therefore, to make conclusions about the relative importance of abiotic and biotic variables in controlling a species geographic distribution, we must consider the response of multiple life-history variables. Demographic compensation by one life-history variable may overcome the negative impacts of any abiotic or biotic factor on any one life-history parameter (Villellas et al., 2015). In our study, it takes examining both survival and body mass data for a clear picture to emerge as to whether this system appears to follow ACE or SIASH dynamics.

Our experiments provided strong evidence that competition has negative consequences on survival and emergence of the

TABLE 3 Model coefficients from linear mixed-effects models examining the effect of competition, elevation, and their interaction on larval *Limnephilus externus* mass and adult *Limnephilus picturatus* mass

	Explanatory variables				Random effects		
Response variables	Subalpine elevation	Competitor present	Subalpine elevation* Competitor present	Male sex	Block	Block:Cage	*df*
L. externus larval mass	**3.440**	−0.039	1.804	N/A	2.420	1.043	363
L. picturatus adult mass	**−1.038**	0.290	−0.436	**−0.520**	0.119	0.141	263

Note: Bolded values indicate significance at the $p < .05$ level and random effects values are standard deviations.

range-shifting species *L. picturatus* in higher-elevation subalpine habitats but not in lower-elevation montane habitats. This increase in the importance of competition counter to the hypothesized stress gradient of elevation is consistent with ACE being important prior to the observed shift; that is, competitive interactions at the stressful end of a species range may have constrained their realized distribution to a subset of what is physiologically possible (Figure 1). However, this experimental support for ACE is complicated by our finding that, in the absence of competitors, *L. picturatus* showed the greater survival in subalpine habitats than montane, and that competition merely reduced overall survival to levels equivalent to those observed in montane habitats. In a system governed strictly by ACE dynamics, we would expect to see a reduction in individual performance with an increase in the stress gradient regardless of the presence or absence of competitors (Figure 1). However, by examining other life-history parameters, namely body mass, the body of support for ACE becomes more evident.

We found evidence that adult body mass for *L. picturatus* decreased at subalpine elevations compared to montane elevations regardless of the presence of competitors. Adult body size is closely correlated with fecundity in many aquatic invertebrates, including caddisflies (Honek, 1993; Jannot et al., 2007). For example, a 30% reduction in the body mass of a confamilial species *Asynarchus nigriculus* results in a 25% decrease in the number of eggs (Wissinger et al., 2004). Thus, we expect the smaller subalpine *L. picturatus* adults to lay fewer eggs than their montane counterparts which could lead to a situation where reduced reproductive output limits its population viability and increases extinction risk (Hutchings et al., 2012). This decrease in a fitness proxy along the elevational gradient, independent of species interactions, indicates that higher elevations are likely more stressful for *L. picturatus* than lower elevations. The low nutrient availability, short growing season, cold winter temperatures, and extreme summertime diurnal temperature fluctuations of high-elevation ponds (Wissinger et al., 2016) support the hypothesis that the higher subalpine ponds constitute a more stressful environment for *L. picturatus* than the lower montane ponds. Moreover, decreases in population-level fecundity may have outsized consequences at the subalpine as *L. picturatus* eggs and early instar larva, which often hatch while there is still ice on the ponds, do not tolerate freezing well (Wissinger et al., 2003) which is more likely to occur later into the summer in the subalpine compared to the montane.

Higher larval survival and emergence rates in subalpine *L. picturatus* could result in demographic compensation, overcoming the effects of reduced individual *L. picturatus* fecundity (Villellas et al., 2015). However, the presence of competitors reduced subalpine *L. picturatus* survival to the low levels seen in the montane population. Thus, when we consider multiple life-history variables, it would appear as though mechanisms controlling the elevational distribution of *L. picturatus*, particularly prior to its range expansion, follow expectations of the ACE hypothesis, whereby competition may constrain the ability for increased survival and emergence to demographically compensate for what appears to be abiotically driven declines in mean individual fecundity.

Yet, demographic compensation may still play a role in allowing *L. picturatus* to continue to persist in the subalpine habitats following their recent range expansion. Caddisflies at our study sites show strong density-dependent mortality among early larval stages (Klemmer et al., 2012). Thus, fewer eggs may not result in significant changes to long-term population dynamics at subalpine elevations compared to montane habitats. Indeed, strong density dependence has been observed to offset relationships between recruitment and late instar density in aquatic insect populations (Hildrew et al., 2004). If this were the case in our system, then any negative consequences of environmental constraints on reproductive output at higher elevations likely will not alter the long-term population dynamics, and ACE dynamics would not be at play.

Additionally, individuals from other, down-valley populations may be contributing to the pool of adults in subalpine ponds, generating demographic compensation through immigration. While we suspect that these organisms are generally not limited from reaching higher-elevation sites through their dispersal abilities (Bovill et al., 2019), we do not have evidence to quantify the exchange of adults among populations at different elevations. Determining whether the differences in adult body size and survival influence *L. picturatus* population persistence at subalpine and montane habitats requires examining long-term demographic data or modeling populations based on body mass–fecundity relationships, survival rates, and estimates of immigration and emigration of adults across elevation (e.g., Kissel et al., 2019). More broadly, research that determines the sensitivity of population dynamics to changes in the suite

of demographic parameters among elevations should be a fruitful in understanding species ranges and range shifts, especially for animals with complex life histories where different developmental stages and life-history parameters are often affected differently by environmental variables (Kingsolver et al., 2011).

While our data provide strong evidence for ACE, as opposed to SIASH, as the mechanism influencing *L. picturatus*'s elevational extent prior to its observed range shift, it relies on the biologically realistic assumption that the subalpine habitats are more abiotically stressful than the montane ones for this species. However, it is possible that this assumption is incorrect and that the lower-elevation habitats of *L. picturatus*' range are more abiotically stressful than the higher-elevation habitats and thus that SIASH rather than ACE dynamics have controlled its elevational distribution. Like many elevational distributions, we assumed from the outset that the higher-elevation subalpine ponds historically constituted a more abiotically stressful habitat than lower-elevation ponds for *L. picturatus*. This assumption is based on the fact that aquatic insect diversity generally decreases with elevation (de Mendoza & Catalan, 2010; Fjellheim et al., 2009), indicating few taxa have adapted to the low nutrient levels, short growing season, and extreme diurnal temperature fluctuations common in these habitats. However, physiological and biogeographic evidence suggests limnephilid caddisflies evolved in cool, boreal waters (Ross, 1967; Ward & Stanford, 1982) and, in general, more often occur in cold water habitats (Wiggins, 1996). This habitat preference is evident in the restriction of limnephilids to higher elevations throughout their southern ranges (Hering et al., 2009). Thus, the higher temperatures and lower oxygen concentration found in montane ponds may be more stressful for *L. picturatus* than the cooler, oligotrophic conditions found in subalpine habitats. Further support for lower-elevation habitats being more stressful for limnephilid caddisflies may be seen in the survival data for *L. externus*. Survival and body mass were significantly lower for *L. externus* in the montane cages than in the subalpine ones indicating that the abiotic conditions of these habitats may be less suitable, especially since competition had no significant effect on *L. externus* survival at either site.

The possibility that higher elevations may constitute less stressful habitats for *L. picturatus* and *L. externus* is consistent with some broader trends in elevational dynamics of species distributions. It is understood that mountain-top habitats serve as refugia for many cold adapted species (Brivio et al., 2019; Hampe & Jump, 2011; Hering et al., 2009). Species that have evolved to conditions found at high elevations will require cooler temperatures (or other abiotic variables associated with high-elevation habitats) while hot environments associated with lower elevations will likely be stressful, resulting in lower elevation boundaries that are controlled by abiotic variables. Evidence that climate can play an important role in constraining the warm edge of the elevational distributions for a broad range of species in temperate mountains suggests that this may be a common phenomenon (Cahill et al., 2014; Freeman et al., 2018). Moreover, increased local and regional extinctions of mountain-top species are anticipated as climate change continues to create warm, potentially stressful abiotic conditions at higher and higher elevations (Urban, 2018). Therefore, understanding the context and evolutionary history of a species on geologic time scales can help us make better predictions about not only the mechanisms that might determine current ranges but also where they might move to as the current global climate continues to change (Jackson et al., 2009; Lavergne et al., 2012). Yet, the fact the *L. picturatus* was previously excluded from the higher-elevation habitats and mean body mass decreases with elevation is curious as such observations would not be predicted if SIASH were at play and the lower-elevation habitats were more stressful. Indeed, these observations are more consistent with higher-subalpine elevations being more stressful regardless of whether ACE or SIASH is important for structuring the prior and current range of *L. picturatus*.

Much of the challenge in determining the processes governing the spatial distribution of species comes down to understanding what conditions might be considered stressful for the species of interest. Complicating this assessment is that abiotic conditions may exert conflicting responses in different life-history parameters whereby conditions considered abiotically stressful in one context may not be deemed so if different life-history parameters are measured (Doak & Morris, 2010). For example, in our study, *L. picturatus* showed opposite patterns in body mass and individual survival across the elevational gradient in the absence of competitors. Similarly, as we have shown, species interactions may be stressful in some abiotic contexts when some life-history variables (e.g., survival) are measured but not others (e.g., body mass). Clearly, defining certain sets of conditions, whether abiotic or biotic, as stressful requires careful consideration of multiple parameters. Moreover, this complex process is necessary if we are to make meaningful headway in determining how changes to species interactions and abiotic conditions will influence species distributions as the climate continues to change.

Species interact through a diverse array of mechanisms. Linking these mechanisms to effects on life-history parameters within the context of the abiotic environment is important for understanding the structuring forces behind species range margins. Our examination of just one mechanism, effects of interspecific competition on per-captia consumption rates of detritus between larval *L. externus* and *L. picturatus*, was inconclusive in this regard. This may be explained by the fact that *L. externus* populations appear regulated by intraspecific competition (Klemmer et al., 2012) rather than competition with other caddisflies. Furthermore, the substitutive nature of our experiment, mimicking observed patterns in species co-occurrence (Wissinger, unpublished data, 1989–2019), made it difficult for us to disentangle how changes in intraspecific density might have impacted the mechanism and outcome of the interactions between *L. externus* and *L. picturatus*. Other mechanisms that could explain the pattern we observed in the data include exploitation competition for resources other than detritus (Wissinger et al., 2018), case and silk grazing (Klemmer et al., 2012; Lund et al., 2016), and intraguild predation (Greig & Wissinger, 2010; Wissinger et al., 2004; Wissinger, Whiteman, et al., 1999). Future studies that connect the mechanisms of interactions between species to specific, limiting demographic variables across a species range will improve models of how range-shifting populations might persist into the future.

Our study focused on how species interactions varied within the observed range of our focal species to elucidate the roles of species interactions and abiotic variables for determining fitness at the center and edge of the range (Figure 1). While we were unable to expand our study to include tests beyond the range of *L. picturatus*, future tests that examine the relative importance of these two factors beyond the species observed range as well will be instrumental in helping ecologists make informed predictions about how future range shifts may play out (Gaston, 2009).

5 | CONCLUSIONS

Here, we have found empirical support for ACE as the likely mechanism setting a species range margin prior to an observed shift. However, this hinges on the sensitivity of our focal species to different demographic parameters and the extent to which higher-elevation sites are actually more stressful for *L. picturatus*. If we assume lower montane elevations to be more stressful for *L. picturatus* than the higher-subalpine elevations, the observed decrease in survival at lower elevations and a strong effect of competition at higher-elevations matches with predictions made by SIASH (Figure 1). Alternatively, when we take a more holistic view of the life history of *L. picturatus* and consider how elevation appears to negatively impact reproductive potential through decreased adult body mass, we see that, when combined with the effects of competition, the population-level fitness of *L. picturatus* may be reduced at higher elevations in a manner consistent with ACE predictions (Figure 1). However, regardless of which end of the elevational gradient exerts stronger abiotic stress on our focal species, our experiments provided evidence that competition may play a significantly larger role in the marginal populations at higher elevations than it does in the central populations at lower ones. This motivates the need to consider environmentally context-dependent species interactions (Chamberlain et al., 2014) as potential mechanisms generating species range margins and their expansion. Moreover, these pairwise interactions do not occur in isolation from the remainder of the food web, and interactions such as predation are likely to modify the outcome of competitive interactions at range margins (Abrams, 2001; Chase et al., 2002). Quantifying the role of multiple community interactions in limiting (or facilitating) the geographic distributions of species is a major challenge but may hold the key to understanding and anticipating species range shifts and their community and ecosystem outcomes.

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AUTHOR CONTRIBUTION

I.D.S. and H.S.G. designed the experiment. I.D.S., H.S.G. and S.A.W. conducted the field experiment. I.D.S. analyzed the data and led the writing of the manuscript and H.S.G. and S.A.W. contributed to writing and editing.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository at https://doi.org/10.5061/dryad.31zcrjdjc.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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