Fall 12-2021

Biotic Interactions at Species' Range Limits in a Changing Climate

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BIOTIC INTERACTIONS AT SPECIES' RANGE LIMITS IN A CHANGING CLIMATE

By

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Honors B.S. Oregon State University, 2016

A DISSERTATION

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Ecology and Environmental Sciences)

The Graduate School

The University of Maine

December 2021

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Dissertation Advisor: Dr. Hamish Greig

An Abstract of the Dissertation Presented
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As the global climate changes, many species are shifting their geographic ranges, often towards the poles or upslope in elevation. The ubiquity of these observation has renewed discussions about the mechanisms that determine species' range margins. Leading hypotheses state abiotic variables should be the most important factor for setting range limits in environmentally stressful habitats. However, I propose an alternative hypothesis that biotic interactions may still be critically important for setting range limits, even in abiotically stressful habitats. Using a model system of ponds in the Rocky Mountains of Colorado, I developed several field experiments to empirically test the role of biotic interactions, including competition and predation, for setting range limits at across regional elevational gradients and among local habitats. First, I conducted a field experiment spanning an elevational gradient (2800 – 3400 m a.s.l.) to show that biotic interactions can indeed play important roles in maintaining range limits in abiotically stressful habitats. Second, using a field experiment examining a more localized hydroperiod gradient, I show that predation can facilitate the coexistence of competing resident and range-shifting species further supporting the importance of species interactions for maintaining range limits. Third, I show that long-term patterns in species persistence at their range margins are not always correlated with pair-wise interactions, suggesting the importance of considering the entire suite of interactions a species encounters in the ecological communities at their range margins. Finally, I propose a new

framework for considering species interactions and range margins in a changing climate. This framework takes a whole food-web approach and integrates the effects of abiotic variables like temperature on the population demographics of and interactions between members of ecological communities. Together these studies highlight the importance of considering both abiotic variables and biotic interactions together if we are to truly understand the effects of climate change on species' geographic distribution

DEDICATION

For Scott Wissinger, who taught me about elk wipe, sky hooks, and left-handed smoke shifters.

You are dearly missed.

And,

For my mother, who when I first told her I wanted to be an ecologist, said I should instead try to

get a real job. She was right.

ACKNOWLEDGEMENTS

First, I would like to thank my advisor, Hamish. His endless patience with my shenanigans and many sacrifices of time and effort on my behalf made all this work possible. Scott Wissinger was hugely influential in the development and execution of this dissertation and also in my own personal and professional development. Scott tragically passed away October 5, 2019. His love for life was infectious and his insight into all things, academic or otherwise, was invaluable. I am incredibly fortunate to have counted Scott among my friends and mentors. There is no doubt in my mind I would not be the person I am today without him. Thank you for everything Scott, you are missed by many.

I am also very grateful to the rest of my committee as well. All of them were critical to the development of the ideas in this thesis. Their mentorship in all aspects of ecology have been invaluable and I would not have been able to complete this degree without their help.

The field work for this dissertation was carried out on lands that were traditionally the homelands of Ute tribes including the Parianuche and the Uncomphadre, also known as the Tabeguache. The University of Maine, where this dissertation was written, rests on Marsh Island which is within the traditional homeland of the Penobscot Nation.

In no way could I have completed the field work that supported this dissertation and many wonderful field technicians and assistants were critical to the success of my research. Specifically, I would like to thank Cameron Leitz, Leah Franzlubbers, Kylie Wirebach, Michelle Woods, Karly Studley, Abrianna Sadler, and Mykalya Hagaman among many others for their assistance in the field. I would also like to thank Jared Balik and Amanda DelVecchia for their assistance, guidance, and companionship through long field seasons. I am grateful to the Rocky

My parents have been endlessly supportive of my pursuit of my PhD. From a young age they always pushed me to apply myself at the highest level and I truly would not be where I am today if it were not for their incredible love and encouragement. Thank you for everything and I love you both.

Finally, I would also like to thank my dear friends Zachary S.N. Wood, Cool Joe Mohan, Mitchell Paisker, Kevin Duffy, Brad Erdman, and Jared Balik. Their friendship and support has been critical to my success in graduate school and I am grateful to be surrounded by such wonderful friends.

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PREFACE

Climate change is rearranging communities and causing species to shift their ranges (Parmesan & Yohe, 2003; Chen *et al.*, 2011). This observation has renewed the discussion about the mechanisms that set species range margins (Louthan, Doak & Angert, 2015; Cadotte & Tucker, 2017). This dissertation contributes to that discussion and explores ideas about the role of species interactions for maintaining range limits in abiotically stressful habitats. While each chapter is a unique and independent study, they all seek to bring new understanding to the role of species interactions for maintaining range limits and/or the consequences that species interactions have on resident and range-shifting species.

Chapters 1 - 3 present empirical field studies that explore how species interactions limit range margins at regional and local scales. The experiments are focused on caddisflies (Trichoptera) and some of their invertebrate predators at the Mexican Cut Nature Preserve in the Elk Mountains of Colorado, USA.

In Chapter 1, I explore regional dynamics and how competition varies across the elevational distribution of a range-shifting species. In this chapter I propose a new hypothesis for the role biotic interactions play in maintaining range limits in abiotically stressful areas followed by empirical support for that hypothesis. This chapter has been published in *Global Change Biology* (Shepard *et al.* 2021). In Chapter 2, I shift the focus to local dynamics, exploring how multiple types of interactions work together to set local distributions across gradients of habitat types and how these interactions are likely to affect the consequences of range shifts for both resident and shifting species. This chapter has been published in *Journal of Animal Ecology* (Shepard *et al.* In press). In Chapter 3, I look at the intersection of local and regional gradients by examining how variation in abiotic conditions at range margins impact the interactions between

resident and range-shifting species and what that means for long-term dynamics. Specifically, I compare findings from a field experiment to long-term (18 years) patterns in the density and occupancy of a resident and range-shifting species through time at the upper elevational extent of the shifting species. Finally, in Chapter 4, I take the lessons learned from the previous field experiments and propose a new way of examining the combined effects of abiotic variables and species interactions for setting range limits. This chapter is a synthesis of ideas but does not present new empirical data.

Shepard I.D., Wissinger S.A. & Greig H.S. (2021). Elevation alters outcome of competition between resident and range-shifting species. *Global Change Biology* **27**, 270–281. https://doi.org/10.1111/gcb.15401

Shepard I.D., Wissinger S.A., Wood Z.T. & Greig H.S. (In press). Predators balance consequences of climate-change induced habitat shifts for range-shifting and resident species. *Journal of Animal Ecology*. https://doi.org/10.1111/1365-2656.13631

CHAPTER 1

ELEVATION ALTERS OUTCOME OF COMPETITION BETWEEN RESIDENT AND RANGE-SHIFTING SPECIES

1.1 Abstract

Species' geographic range shifts towards 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 up-slope 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 up-slope 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 up-slope 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.

1.2 Introduction

Shifts in the geographic distribution of species towards higher latitudes and elevations are among the most commonly reported ecological consequences of climate change (Parmesan & Yohe, 2003; Chen *et al.*, 2011; Freeman *et al.*, 2018). 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 (Griggs, 1914; Gaston, 2003; Freeman *et al.*, 2018) there is an ongoing debate about the relative importance of species interactions and abiotic conditions for determining species range margins (Blois *et al.*, 2013; Wisz *et al.*, 2013; Louthan *et al.*, 2015; Alexander *et al.*, 2016; Cadotte & Tucker, 2017; Aguilar-Trigueros, Rillig & Ballhausen, 2017; Westoby *et al.*, 2018).

One hypothesis regarding the relative importance of abiotic and biotic constraints on species' ranges is the Species Interaction-Abiotic Stress Hypothesis (SIASH, Figure 1.1a) (also referred to as the Darwin-MacArthur Hypothesis and the Stress Trade-Off Hypothesis) (Louthan *et al.*, 2015; Freeman *et al.*, 2018). 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 (Darwin, 1859; Dobzhansky, 1950; Connell, 1961; MacArthur, 1972; Menge & Sutherland, 1987; Louthan *et al.*, 2015). Many observed shifts in species ranges have coincided with changes in abiotic conditions in habitats that have traditionally been considered too harsh for their survival, particularly at high latitudes and elevations (Root *et al.*, 2003; Lenoir *et al.*, 2008). 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 (Case *et al.*, 2005; Holt & Barfield, 2009; García-Ramos & Huang, 2013; Svenning *et al.*, 2014; Cadotte & Tucker, 2017). 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 towards 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 1.1b) 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 geographical manifestation of the realized vs. fundamental niche (Hutchinson, 1957; Colwell & Rangel, 2009) 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 1.1). 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 (Fig1; Anderegg & Hille Ris Lambers, 2019)(Anderegg & HilleRisLambers, 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 1.1b.) whereas decreases in the strength of competition towards the edge of a species range, would support SIASH (Figure 1.1a). Importantly, knowing which of these mechanisms are structuring at 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 (Brown & Vellend, 2014; Benning & Moeller, 2019). Yet, these types of experimental tests are rare, especially in animals (but see O'Brien et al., 2017)(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 & Morris (2010) (Doak & 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 (Fjellheim *et al.*, 2009; de Mendoza & Catalan, 2010; 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, Frazier & Dudley, 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 towards 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.
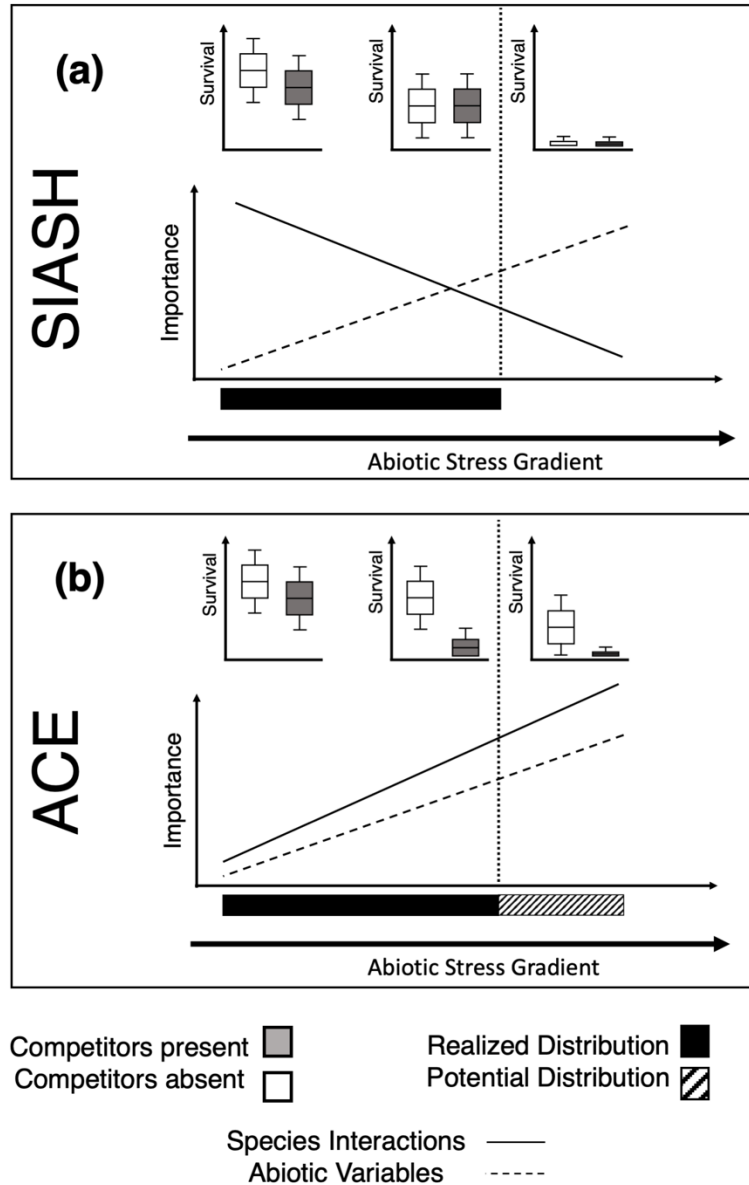
Figure 1.1. Hypotheses on the mechanisms that maintain range limits. A conceptual representation of the Species Interaction-Abiotic Stress Hypothesis (SIASH, Louthan *et al.* 2015), and Apparent Climatic Exclusion (ACE). SIASH (A) predicts that a species may persist along an environmental stress gradient (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.

1.3. Methods

1.3.1. 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)(Wissinger, Perchik & Klemmer, 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)(Wissinger *et al.*, 1999a).

Limnephilid caddisflies (Trichoptera) are the biomass dominant detritivores in our study ponds with 9 species in 5 genera varying regionally along elevational gradients and locally along a hydroperiod gradient from temporary to permanent ponds (Wissinger *et al.*, 1999a; Wissinger,

Brown & Jannot, 2003; Wissinger *et al.*, 2006). We focused our study on competition between two of these caddisfly species: *Limnephilus picturatus* and *Limnephilus externus*. These species co-occur in semi-permanent ponds that dry in the autumn of years with low precipitation (Wissinger *et al.*, 1999b, 2003) 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 et al., 2003; Wissinger, unpublished data). 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) 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.*

1.3.2. 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 4 treatments: (1) a detritus control, (2) *L. picturatus* alone, (3) *L. externus* alone, and (4) *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 (Kiær, Weisbach & Weiner, 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) 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 x 50 x 50cm 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 A1). We added, 100.07 ± 0.06 g (mean $\pm$ 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 ten 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 in 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 m^2 to 820 m^2 (mean $= 295 \pm 137$ 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 (Figure A2), historical data show that the ponds are quite similar in temperature on average (Wissinger, *unpublished data*). However, we accounted for this small variation with a random effect term in our analysis (see *Analysis* below). 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 in order 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 *et al.* 1999b) 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 hours and then weighed them to the nearest 0.001 mg on a Cahn C-31 microbalance (Thermo Scientific, Waltham, Massachusetts USA). 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 sixteen 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 hours and then measured the mass to the nearest 0.001 mg on a Cahn C-31 microbalance (Thermo Scientific, Waltham, Massachusetts USA). 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 (Wissinger *et al.*, 2003; Jannot, Wissinger & Lucas, 2008). Thus, we only analyzed adult data for *L. picturatus*.

1.3.3 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.*, 1999a). 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, Brockhoff & Christensen, 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, 2021) and *coxme* (Therneau, 2020)

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.

1.4 Results

Elevation had a strong, positive effect on *L. picturatus* survival (Table 1.1) and overall, *L. picturatus* showed the highest survival in the absence of competitors at subalpine elevations (Table 1.2; Figure 1.2) 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 x elevation interaction (Figure 1.2; Table 1.1). This negative effect of competition in the subalpine reduced *L. picturatus* to approximately the same level observed in both the montane treatments (Figure 1.2; Table 1.2).

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 1.3). The interaction between elevation and competition was significant (Frailty model $p = 0.005$) 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 1.3).

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 1.4; Table 1.3). Neither competition nor the competition by elevation term were significant (Table 1.3). Unsurprisingly, sex also had a significant impact on adult body mass with males being smaller than females (Table 1.3).

Like *L. picturatus*, *L. externus* had significantly higher survival at subalpine than at montane elevations in the absence of competitors (Figure 1.2; Table 1.2). However, there was no effect of competition on *L. externus* survival at either elevation (Figure 1.2; Table 1.1), nor was there a significant interaction between elevation and competition (Figure 1.2; Table 1.1). 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 1.4; Table 1.3).

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 grams of dry detritus per caddisfly per day (see Figure A3). 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 ($p = 0.812$).

Species	Parameter	χ^2	DF	p-value	Std. Dev.
L. picturatus	Competition	9.732	1	**0.002**	-
	Elevation	6.642	1	**0.010**	-
	Competition*Elevation	6.736	1	**0.010**	-
	Block (Random Effect)	-	-	-	0.498
	Block:Cage (Random Effect)	-	-	-	0.614
L. externus	Competition	0.136	1	0.712	-
	Elevation	11.345	1	**0.001**	-
	Competition*Elevation	0.362	1	0.547	-
	Block (Random Effect)	-	-	-	0.684
	Block:Cage (Random Effect)	-	-	-	0.733

Table 1.1. Elevation and competition effects on caddisfly survival. Likelihood ratio test results for the effects of competition, elevation, and their interaction on survival of *L. picturatus* and *L. externus* caddisflies at montane and subalpine elevations from an in-situ caging experiment in high elevation ponds. Bolded p-values are significant at the 0.05 level.

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

Table 1.2. Estimates of effect sizes. Logit and transformed estimates from binomial mixed effects models of survival for *L. externus* and *L. picturatus* caddisflies at montane and subalpine elevations in the presence and absence of competition in an in-situ caging experiment.
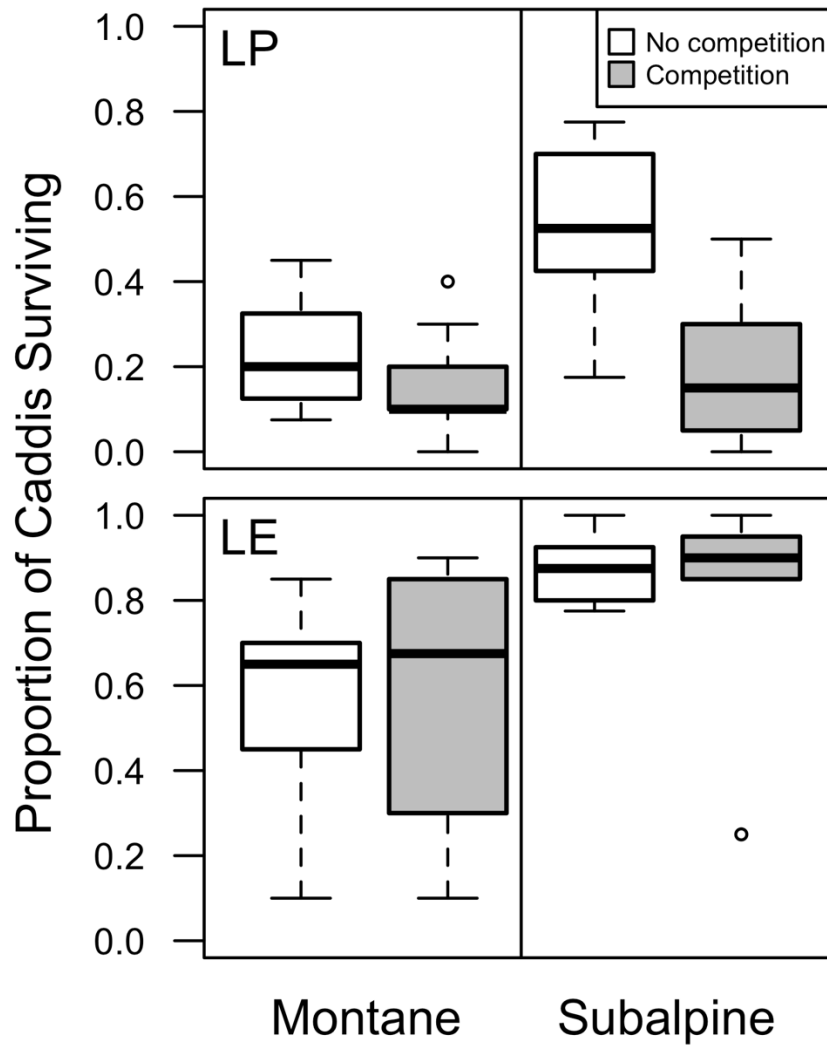
Figure 1.2. Caddisfly survival across elevations. Proportions of (top) *Limnephilus picturatus* (LP) and (bottom) *Limnephilus externus* (LE) that survived when they were and were not competing with each other for detritus resources in cages at montane (2,800 m a.s.l.) and subalpine (3,400 m a.s.l) elevations in the Elk Mountains, CO. Points represent outliers. The middle bar of the boxes represents the median, the edges of the box represent the 25% quantiles and the whiskers represent the 75% quantiles.
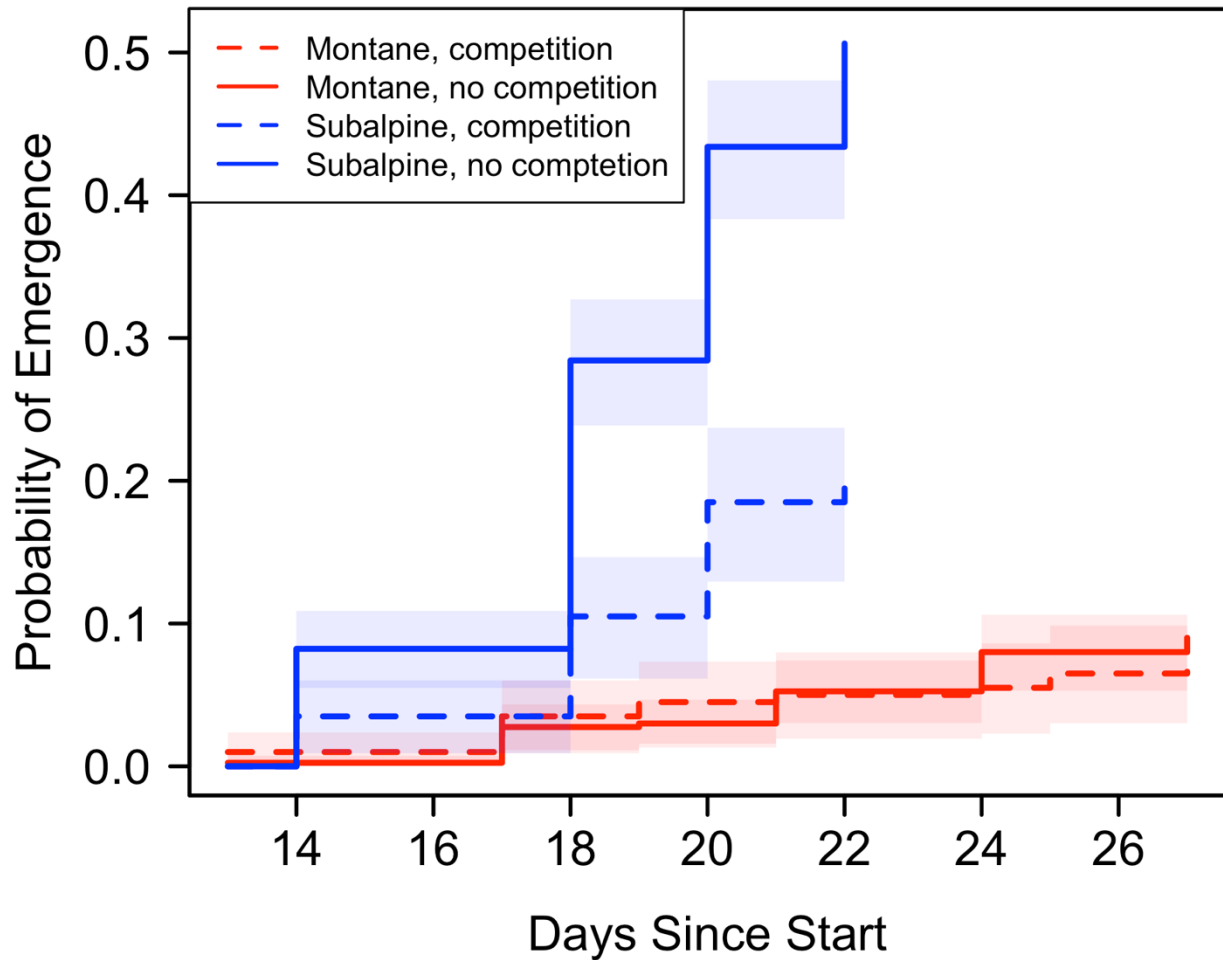
Figure 1.3. Caddisfly emergence through time. Probability of *Limnephilus picturatus* emergence in cages in the Elk Mountains, CO, at subalpine elevations (blue) in the absence (solid) and presence (dashed) of competitors and at montane elevations (red) in the absence (solid) and presence (dashed) of competitors. Dashed lines represent 95% confidence intervals. Probabilities were calculated from a Kaplan-Meier estimate (see text).
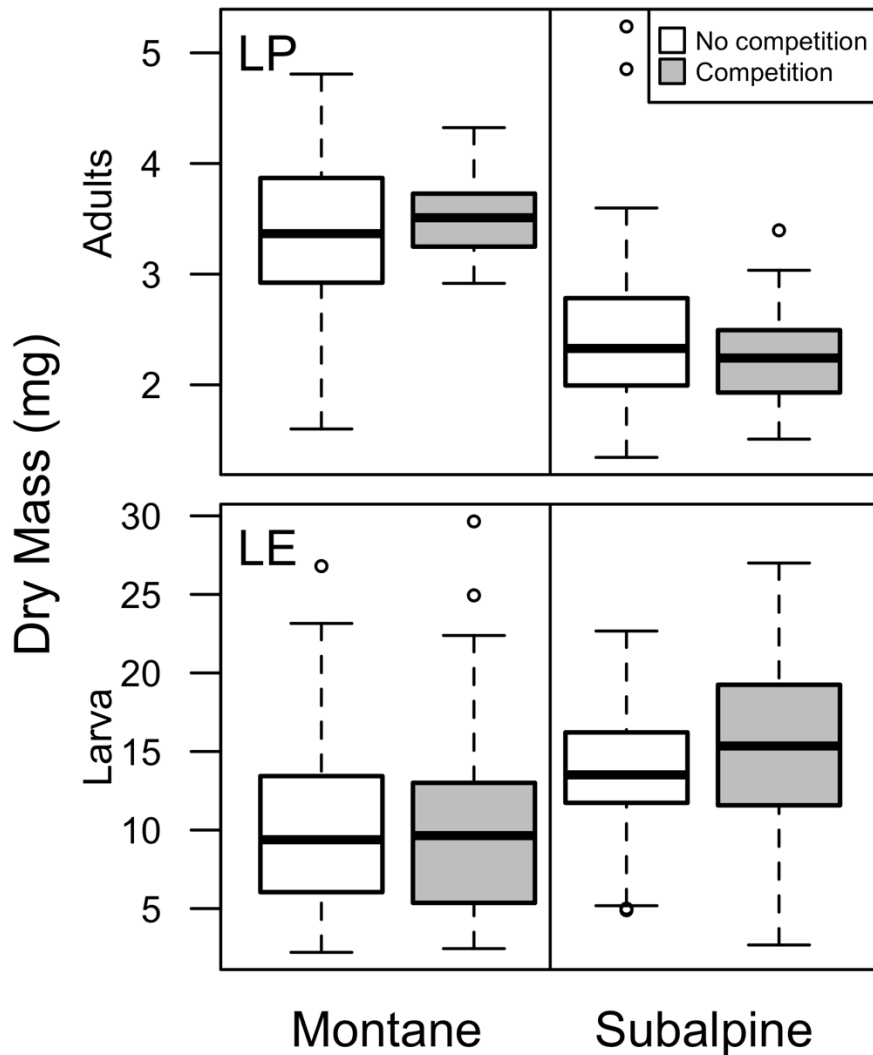
Figure 1.4. Caddisfly mass across elevations. Dry mass in milligrams of (top) *Limnephilus picturatus* (LP) adults and (bottom) *Limnephilus externus* (LE) larva in the presence (grey bars) and absence (white bars) of competitors at montane (2,800 m a.s.l) and subalpine (3,400 m a.s.l.) in ponds in the 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. The middle bar of the boxes represents the

median, the edges of the box represent the 25% quantiles and the whiskers represent the 75%

quantiles.

| Response Variables | Explanatory Variables | | | | Random Effects | | |
	Subalpine Elevation	Competitor Present	Subalpine Elevation* Competitor Present	Male Sex	Block	Block: Cage	D.F.
L. externus larval mass	**3.440**	-0.039	1.804	N/A	2.420	1.043	1/363
L. picturatus adult mass	**-1.038**	0.290	-0.436	**-0.520**	0.119	0.141	2/263

Table 1.3. Effects of elevation and competition on caddisfly mass. Model coefficients from

linear mixed effects models examining the effect of competition, elevation, and their interaction

on larval *L. externus* mass and adult *L. picturatus* mass. Bolded values indicate significance at

the $p < 0.05$ level and random effects values are standard deviations.

1.5 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, in order 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 range-shifting species *Limnephilus 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. 1.1). 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. 1.1). 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 (Honěk, 1993; Jannot, Bruneau & Wissinger, 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, Eldermire & Whissel, 2004b). 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 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, Downes & Lancaster, 2019), we don't 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 modelling 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 it's 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 (Fjellheim *et al.*, 2009; de Mendoza & Catalan, 2010), 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 was 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 (Hering *et al.*, 2009; Hampe & Jump, 2011; Brivio *et al.*, 2019). 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.*, 2013). 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), 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, Wissinger & Peckarsky, 2016), and intraguild predation (Wissinger *et al.*, 1999b, 2004b, 200; Greig & Wissinger, 2010). 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 1.1). 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).

1.6 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 1.1). 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 1.1). 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 the environmental context-dependent species interactions (Chamberlain, Bronstein & Rudgers, 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.

CHAPTER 2

PREDATORS BALANCE CONSEQUENCES OF CLIMATE-CHANGE INDUCED HABITAT SHIFTS FOR RANGE-SHIFTING AND RESIDENT SPECIES

2.1 Abstract

While many species distributions are shifting poleward or up in elevation in response to a changing climate, others are shifting their habitats along localized gradients in environmental conditions as abiotic conditions become more stressful. Whether species are moving across regional or local environmental gradients in response to climate change, range-shifting species become embedded in established communities of competitors and predators. The consequences of these shifts for both resident and shifting species are often unknown, as it can be difficult to isolate the effects of multiple species interactions. Using a model system of insects in high-elevation ponds in the Rocky Mountains of Colorado, we sought to disentangle the effects of predation and intraguild interactions on the survival and development of a semi-permanent pond resident caddisfly *Limnephilus externus* and the habitat-shifting caddis *Asynarchus nigriculus* that is being forced into semi-permanent ponds as temporary ponds dry too quickly to complete development. We conducted a manipulative in-situ pond cage experiment in which *L. externus* and *A. nigriculus* caddisfly larvae in single-species treatments and together were exposed to the presence/absence of predatory *Dytiscus* diving beetle larvae. This approach allowed us to isolate the effects of intraguild interactions and predation on the survival and development of both the resident and habitat-shifting species. We found that intraguild interactions had strong negative effects on the resident and habitat-shifting species. Intraguild interactions reduced the survival of the resident *L. externus* and increased the variation in survival of the shifting *A. nigriculus*.

However, *Dytiscus* predators reduced these negative effects, stabilizing the community by increasing *L. externus* survival and reducing variation in *A. nigriculus* survival. We also found that intraguild interactions reduced *L. externus* biomass but resulted in increased *A. nigriculus* development. *A. nigriculus* development was also increased by predation. Our results show that strong intraguild interactions between resident and shifting species are likely to have negative consequences for both species. However, the presence of predators reduces these negative consequences of the habitat shift on both the resident and the shifting species.

2.2 Introduction

Localized environmental gradients play important roles in maintaining biodiversity and structuring ecological communities. Often times, this occurs as a consequence of evolutionary trade-offs where adaptations to conditions (both abiotic and biotic) at one end of the gradient decrease performance at the other (Lubchenco, 1980; Welborn, Skelly & Werner, 1996; Kneitel & Chase, 2004). A classic example is in the rocky intertidal where competition in the abiotically comfortable low tide zone forces some species to adapt to the desiccation stress of the high tide zone (Connell, 1961). However, climate change is altering environmental gradients which is likely to have significant consequences for the processes structuring ecological communities (Martin, 2001; Parmesan, 2006). Moreover, while species range shifts across elevational and latitudinal gradients are a well-documented response to increased abiotic pressures induced by climate change (Parmesan & Yohe, 2003; Chen *et al.*, 2011), species may also alter their habitat use along localized environmental gradients and seek refuge in areas they may have traditionally been rare in or excluded from by abiotic stress, biotic interactions, or both (Davies *et al.*, 2006; Harley, 2011; Kordas *et al.*, 2015).

Studies of range or habitat shifts in response to climate change have largely focused on relationships between the shifting species and abiotic variables or pair-wise interactions with competitors, but the community consequences of habitat shifts are less understood (e.g. Lenoir & Svenning, 2015; Shepard, Wissinger & Greig, 2021). When a species moves into a habitat it was previously absent from or rare in, it becomes embedded within a suite of new, or previously rare, interspecific interactions including competition and predation. The outcome of any such shift will depend on the balance of these interactions (Lurgi, López & Montoya, 2012). For example, resident predators may play important roles in altering competitive or other intraguild interactions between resident and shifting species of lower trophic levels (Chase *et al.*, 2002; Chesson & Kuang, 2008; Jones *et al.*, 2020). Disentangling the roles that these various, simultaneous, interactions play in the outcomes of shifts in habitat use should be one of the primary objectives of studies seeking to understand the outcomes of species responses to climate change. Here we experimentally investigate the consequences of predation and intraguild interactions for resident and habitat-shifting species.

Understanding the impact of species interactions on the outcomes of habitat shifts also requires examining multiple life history variables. Demographic compensation, where decreases in fitness due to changes in one demographic variable are offset by increases in another is common population response to changing environments (Villellas *et al.*, 2015). For example, increased growth rates have been shown to offset survival rates in tundra plants (Doak & Morris, 2010). Indeed, examining multiple life history parameters can be critical in disentangling the relative importance of abiotic and biotic variables for determining the outcomes of habitat shifts (Shepard *et al.*, 2021).

One habitat where climate-change induced alterations to localized abiotic gradients is likely to be particularly important is high elevation ponds and wetlands. These habitats are generally considered to have low diversity (Füreder *et al.*, 2006; Fjellheim *et al.*, 2009; de Mendoza & Catalan, 2010) so even modest changes in community structure may have outsized impacts on diversity, stability, and function (Rooney & McCann, 2012; Tilman, 1999, Wissinger et al. 2016). Hydroperiod—the duration for which a pond holds surface water—is a critical environmental gradient in alpine habitats (Welborn *et al.*, 1996; Wissinger *et al.*, 1999b, 2003, 2006) and climate change is expected to shorten hydroperiod as spring snowmelt timing advances, summer temperatures increase, and precipitation becomes less predictable (Barnett, Adam & Lettenmaier, 2005; Tuytens *et al.*, 2014). As a result, species that inhabit temporary ponds may be forced to use ponds with longer hydroperiods if temporary ponds dry faster than species' development rates can tolerate (Sim *et al.*, 2013; Lund *et al.*, 2016). These shifting organisms will then be interacting with a different, and potentially more diverse, assemblage of competitors and predators than what is typical of more temporary habitats (Welborn et al., 1996; Wissinger et al., 2009).

To understand the potential biotic consequences of this predicted change in habitat use, we conducted an *in-situ* cage experiment in semi-permanent ponds at the Mexican Cut Nature Preserve in Colorado, USA in which we examined the interaction between *Asynarchus. nigriculus* (Banks, 1908)*, Limnephilus externus* (Hagan, 1861) and a top predator, *Dytiscus* diving beetle larva. *A. nigriculus* is common in temporary ponds (those that dry every year) and occasionally is found in semi-permanent basins as well (Wissinger *et al.*, 2003, 2006). We anticipate, however, that as hydroperiods shorten with climate change *A. nigriculus* will be forced to shift its habitat and rely on semi-permanent ponds (those that only occasionally dry) to

sustain its population, thus shifting its habitat. *L. externus* is commonly found in semi-permanent ponds, as are *Dytiscus* beetle larvae (Wissinger *et al.*, 1999a).

Previous studies of this system have shown that the aggressive foraging traits of *A. nigriculus* that underlie its success in temporary ponds reduces the survival of *L. externus* when the two compete for resources (Wissinger *et al.*, 1999b). Indeed, both species consume detritus as their primary food source (Wissinger *et al.*, 2018) but *A. nigriculus* is also known to engage in intraguild predation on confamilial species including *L. externus* (Wissinger *et al.*, 1996). Therefore, we would expect *A. nigriculus* reduce the survival of *L. externus* when the two species are together. However, we anticipate that higher order predators would modify this interaction by removing the more aggressive species, in this case *A. nigriculus*, and allow for a more stable coexistence (Paine, 1966; Leibold, 1996; Chase *et al.*, 2002). Indeed, *Dytiscus* predators in microcosms select *A. nigriculus* larvae over *L. externus* larvae because they are more active and poorly defended (Wissinger *et al.*, 2006). Thus, in the more biologically realistic scenario with both competitors and predators present, we hypothesize that *A. nigriculus* may have reduced survival while *L. externus* maintains a relatively high population. To ensure we did not miss any effects of demographic compensation we also quantified the responses of development and body mass in these caddisflies in response to predation and intraguild interactions. We hypothesized that these variables would follow similar patterns to survival because behaviors that promote development and growth in these caddisflies also make them more vulnerable to adverse effects of competitors and predators(Wissinger *et al.*, 1999b, 2006).

2.3. Methods

2.3.1. Study System

Our research was conducted at the Mexican Cut Nature Preserve (MCNP) in the Rocky Mountains of Colorado, USA (39.030, -107.064). This site contains a collection of more than 60 subalpine ponds and wetlands of varying hydroperiod (Wissinger *et al.*, 1999a). Limnephilid caddisflies are the biomass-dominant macrodetritivores in the ponds at the MCNP with 5 species distributed across permanently inundated ponds, semi-permanent ponds that dry in autumn of years with low precipitation, and temporary ponds that dry in summer every year (Wissinger *et al.*, 1999b, 2003). One species, *A. nigriculus* is the dominant temporary pond species but may also be found, in semi-permanent ponds, though typically in lower abundances (Wissinger et al., 2003). This very aggressive and active species develops rapidly (first instar to adult in < 45 days) but is vulnerable to predators found in permanent and semi-permanent ponds (Wissinger *et al.*, 1999b, 2003, 2006). In contrast, *L. externus*, which is dominant in permanent and semi-permanent ponds, is well defended against predators but its slow development excludes it from temporary habitats (Wissinger et al., 2003; 2006). Additionally, *L. externus* has a Holarctic distribution (Rasmussen & Morse 2020; Morse, 2021) and is broadly distributed across the regional elevation gradient (2200 – 3400 m a.s.l.) while *A. nigriculus* is largely restricted to subalpine elevations (3200 – 3500 m a.s.l.) and is only found in a small subset of the United States (Rasmussen & Morse 2020; Morse, 2021).

Despite the differences in the breadths of their distributions, both of these species can co-occur in semi-permanent habitats (Wissinger et al., 2003). However, as hydroperiod shortens with climate change (Tuytens *et al.*, 2014), we expect *A. nigriculus* may not be able to rely on temporary ponds (Lund *et al.*, 2016) and habitat use in semi-permanent ponds may play a larger

role in the maintenance of the meta-population, especially in particularly dry years. Indeed, drying events resulting in cohort failures of *A. nigriculus* in temporary ponds have been becoming more frequent at this site in recent years (Lund *et al.*, 2016) and semi-permanent ponds provide refuge habitats from which recolonization of temporary ponds can occur.

2.3.2. Cage Experiment

We investigated whether the interaction between *A. nigriculus* and *L. externus* is modified by *Dytiscus* predatory diving beetle larva by conducting a field experiment with cages set within ponds at the MCNP (39.030, -107.064). Cages (50 x 50 x 50cm , 1-mm mesh walls) were set within in the shallow littoral zone of 5 semi-permanent ponds that dry in the late summer of warm years with little precipitation but remain inundated during wetter years (Wissinger *et al.*, 1999a). Each pond received 6 cages, each with a different treatment: *L. externus* on its own, *A. nigriculus* on its own, *L. externus* and *A. nigriculus* together, with those three treatments crossed by the presence and absence of predation pressure by *Dytiscus* diving beetle predators. Thus, the treatments that had both species of caddisfly included intraguild predation and competition which we describe hereafter as intraguild interactions.

To avoid artificially inflating predation rates by enclosing a mobile predator in a confined arena with high densities of prey (Englund, 1997; Bergström & Englund, 2002; Petersen & Englund, 2005) we only exposed caddisflies to predators for 1 hour every other day. Furthermore, we did not begin putting predators into the appropriate cages until one week after the experiment began to mimic the phenological lag between the *Dytiscus* predators and the caddisflies (Wissinger *et al.*, 2006; Greig & Wissinger, 2010). Each cage received 99.90 ± 0.24 grams of *Carex* sedge detritus as a basal resource for the caddisflies and densities were held constant at 160 individuals m^{-2} resulting in 40 individuals per cage. Thus, in the intraguild

interaction treatments, we used a substitutive design with 20 individuals of each species (Shepard *et al.*, 2021). The densities we used in this experiment fall within the natural observed range in semi-permanent ponds for *L. externus* (3-393 m^2) and temporary ponds for *A. nigriculus* (1 – 193 m^2). Our use of a substitutive design matches patterns of replacement we have observed in these ponds previously (S. A. Wissinger, unpublished data). Furthermore, substitutive designs tend to make it more difficult to detect effects of intraguild interactions thus making our approach to a more conservative one in this regard (Kiær *et al.*, 2013). Initial instar ratios were kept consistent across the treatments. *A. nigriculus* was kept at 15% 4th instars and 85% 5th instars and *L. externus* was started at 15% 2nd instars and 85% 3rd instars. These ratios reflect what was observed in natural surveys of the ponds taken at the beginning of the experiment and reflect the developmental advantage of *A. nigriculus* over *L. externus* that facilitates intraguild predation (Greig & Wissinger, 2010). Cages were fitted with emergence traps on the lids to capture any adult caddis that emerged during the experiment. Emergence traps were checked every other day during the course of the experiment.

The cage experiment ended after 19 days (August 1, 2019 – August 19, 2019) when a majority of *A. nigriculus* had begun to pupate. At this point, we removed the cages from the ponds and collected remaining caddisfly larvae and pupae from each cage. We also collected and froze the remaining detritus in each cage which was subsequently inspected in the lab to detect any caddisflies that may have been missed in the field. The total number of caddisflies from each cage were enumerated and their development stage identified. Pupae were divided into two groups: early and late based on whether developing wings were visible. No special ethical approvals were required for this research.

2.3.3. Analysis

2.3.3.1. Individual survival

We used binomial general linear mixed models to determine whether intraguild interactions, predation, or the interaction of both influenced the survival of both *L. externus* and *A. nigriculus*. The interaction term was included to test whether there were any non-additive effects of having both intraguild interactions and predation occurring at the same time. We ran separate models for each species. In both models we included random effects for pond and cage within to account for variation across space. We used Type II Wald chi-squared tests to determine the significance of the intraguild interactions, predation, and intraguild interactions by predation interaction terms in both models. Finally, we used Tukey *post-hoc* tests to examine pairwise differences in the four treatment survival estimates (intraguild interactions present/absent × predation present/absent) for both models. Mixed-effects models were created using the *lme4* package (Bates *et al.*, 2015), the Wald chi-square tests were performed using the *car* package (Fox & Weisburg, 2019), and the Tukey tests were performed using the *multcomp* package (Hothorn, Bretz & Westfall, 2008) in R version 3.6.1 (R Core Team, 2019).

We also examined the effects of predation, intraguild interactions, and their interaction on the variation in individual survival for both *L. externus* and *A. nigriculus.* To do this, we examined the ratio of observed variation in individual survival to the expected variation therein for each treatment in the above two models. If observed variation is higher than expected variation, then survival rates are highly variable or stochastic within a given treatment. If observed variation is lower than expected variation, then survival rates are largely consistent within a given treatment. Expected variation for a binomial variable with rate p is equal to $p(1-p)$. We therefore calculated the expected variation in individual survival by multiplying the

treatment-specific survival estimates by one minus themselves. We calculated actual variation using the residuals from each treatment, then calculated the ratio of observed to expected variation. We used bootstrapping (n=1000) to generate standard errors around these ratios. We then conducted Tukey *post-hoc* tests to examine pairwise differences in the four-treatment observed/expected variation ratios for both models, using the actual residual data degrees of freedom (594).

2.3.3.2. Development

We also examined the effect of intraguild interactions, predation, and their interaction on the development of the caddisflies. To do this, we used ordinal regression to estimate the probability that an individual *A. nigriculus* would be in a given development stage for a given treatment. In other words, we used this model to predict how development would be influenced by the presence of intraguild interactions and/or predators. This model also had an interaction term to determine whether there were any non-additive effects on development when both predation and intraguild interactions were present. To account for variation across space, we also included a term for cage in the model. Our model and predictions were generated using the *ordinal* package (Christensen, 2019) in R version 3.6.1 (R Core Team, 2019). We assessed the parallel lines assumption using a Brant test using the *brant* package (Schlegel & Steenbergen, 2020) in R version 3.6.1 (R Core Team, 2019) which indicated that the assumption was met. We did not conduct development stage analysis on *L. externus* because all All *L. externus* individuals at the same developmental stage (5th instars) at the end of the experiment. Term significance was determined using a Wald test from the car package (Fox & Weisburg, 2019).

2.3.3.3. Mass

Lastly, we examined the final mass of the individual larvae in the cages. Mass data was collected by removing caddisfly larvae from their cases and then drying the bodies in an oven at 60°C for 48 hours. We then measured the individual dry mass of up to 10 individuals from each cage to the nearest 0.001mg with a Cahn C-31 microbalance (Thermo Scientific, Waltham, Massachusetts USA). We only analyzed larval mass for *L. externus* because most of the *A. nigriculus* had pupated or emerged as adults resulting in too small a sample size for analysis on late instar body mass. The anatomical and physiological changes that occur between pupation and adulthood mean that late instar larva, pupal, and adult body masses are not comparable. Examination of *L. externus* body mass data showed that it had a strong right skew, which we reduced with a square root transformation. We used general linear mixed-effects models to determine the effect of intraguild interactions, predation, and their interaction on *L. externus* larval mass. As in the other two models, the interaction term was used to test for non-additive effects of the combination of predation and intraguild interactions. These models also had a nested random effect of cage within pond to account for variation across space. We conducted a Type II Wald F test to determine the significance of each term in the model. Models were created using the lme4 package (Bates *et al.*, 2015) and Wald tests were done using the car package (Fox & Weisburg, 2019) in R version 3.6.1 (R Core Team, 2019).

2.4. Results

2.4.1. Survival

Broadly, our analyses indicate that predation reduces the effects of intraguild interactions on either the mean or variation in survival. Whether these effects of intraguild interactions and predation affect the mean, or the variation, depends on species identity. The resident species, *L.*

externus, showed changes in its mean survival based on treatment (Figure 2.1a) while the shifting species, *A. nigriculus*, showed changes in the variation around survival based on treatment (Figure 2.1d).

L. externus had the highest survival in the absence of both intraguild interactions and predators (Figure 2.1a). Intraguild interactions with *A. nigriculus* reduced *L. externus* survival to 45% compared to 80% survival in single species *L. externus* treatments (Figure 2.1a; Table 2.1). However, the effect of these interactions was only significantly different from all other treatments when predators were absent. When predators and intraguild interactions were present, *L. externus* survival was 53% which was not significantly different from treatments with only *L. externus* or *L. externus* and intraguild interactions (significant intraguild interaction x predation interaction, Table 2.1, Figure 2.1a), (Figure 2.1a). Predation on its own had similar effects on *L. externus* survival whether intraguild interactions were present or not and, on its own was not significant (Table 2.1, Figure 2.1a). Together these results indicate intraguild interactions have a stronger influence on *L externus* survival than predation.

In contrast, our models indicated that *A. nigiriculus* had consistently low survival (19-30%) across all treatments (Figure 2.1b) and there were no significant effects of intraguild interactions, predation, or their interaction on their survival (Table 2.1). While seemingly low, the overall observed rate of mortality for *A. nigriculus* in our experiment matched that seen in natural ponds both with and without predators (Figure B1).

The variation in survival within treatments for both species showed a much different pattern than mean survival. *L. externus* had relatively consistent variation across all treatments, and observed variation was largely in line with expected variation with no significant differences between treatments (Figure 2.1c). However, we did see significant effects of intraguild

interactions and predation on the variation in *A. nigriculus* survival. Specifically, in the absence of both intraguild interactions and predators *A. nigriculus* survival showed lower variation than expected (Figure 2.1d). However, the presence of intraguild interactions increased the variation in survival, with a ratio of expected to observed variation greater than one. When predators were added to this interaction, the observed variation decreased back below zero with the treatment where *A. nigriculus* was on its own being the only one with lower variation. However, due to large amounts of variation in the estimate for the intraguild interaction only treatment, the difference between intraguild interaction treatments with and without intraguild interactions was not significant. On their own, predators reduced variation in *A. nigriculus* survival but not as much as the combination of predators and intraguild interactions (Figure 2.1d).
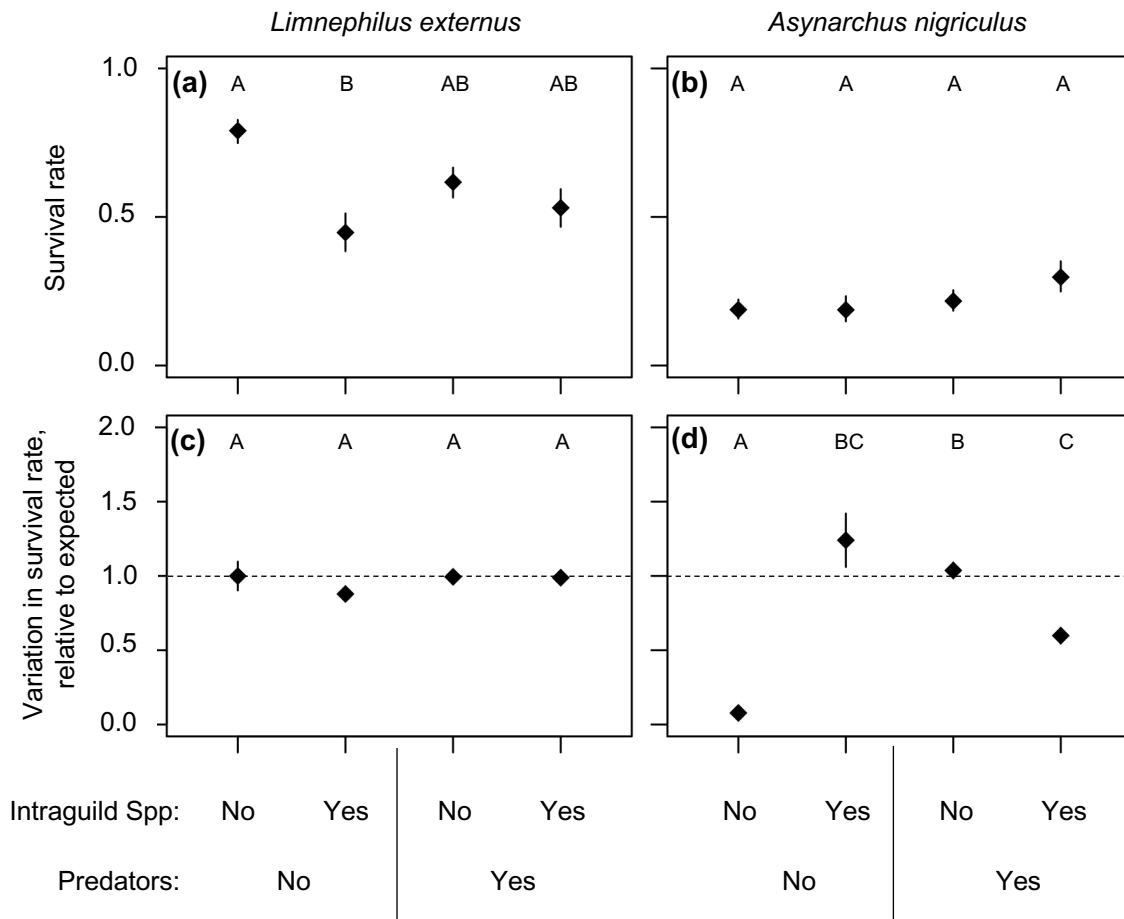
Figure 2.1. Rate and variation in caddisfly survival. Survival rate of (a) *L. externus* and (b) *A. nigriculus* in the presence and absence of intraguild interactions and predators in high alpine ponds in Colorado, USA. The lower panels show the observed versus expected variation in survival (see methods) for (c) *L. externus* and (d) *A. nigriculus* in the presence and absence of intraguild interactions and/or predators in high alpine ponds in the Elk Mountains, Colorado, USA. Points above the dashed line show greater than expected variation while points below show less variation than expected. Error bars show standard errors. Letters indicate results of Tukey Honest Significant Difference Tests (see methods).

Species	Term	χ^2	DF	p	SD
L. externus	Intraguild Ints.	14.652	1	< 0.001	
	Predation	2.048	1	0.152	
	Intraguild Ints. × Predation	6.090	1	0.014	
	Pond				0.080
	Pond:Cage				0.342
A. nigriculus	Intraguild Ints.	0.966	1	0.326	
	Predation	2.271	1	0.132	
	Intraguild Ints. × Predation	0.829	1	0.363	
	Pond				9.53×10^{-7}
	Pond:Cage				0.237

Table 2.1. Effects of species interactions on caddisfly survival. Type II Wald Chi^2 Tests on two binomial mixed effects models estimating individual survival of two species of caddisfly under different intraguild interaction and predation treatments in high alpine ponds. *L: Limnephilus; A: Asynarchus*.

2.4.2. Development

Estimates of the probabilities that *A. nigriculus* would develop to a given stage within the timeframe of our experiment showed that reaching the late pupal stage (i.e., wings developing) was the most common outcome in all treatments (Figure 2.2). Development was the fastest in treatments with both intraguild interactions and predators (Figure 2.2). The intraguild interaction by predation interaction term was not significant indicating no non-additive effects of the two treatments together (Table 2.2). However, in the absence of intraguild interactions or predators, individual *A. nigriculus* were more likely to be found in earlier instars than in any other treatment after the same amount of time (Figure 2.2). Moreover, the probability of a surviving individual developing to adulthood was the highest when both predators and intraguild interactions were present. Intraguild interactions and predation, but not their interaction, had significant effects on the development of *A. nigriculus* (Table 2.2). In other words, development

was slowest when *A. nigriculus* was on its own, intermediate when either predators or intraguild interactions were present, and fastest when both intraguild interactions and predators were present (Figure 2.2). No development analysis was conducted for *L. externus* because all individuals recovered at the end of the experiment were in the same development stage.
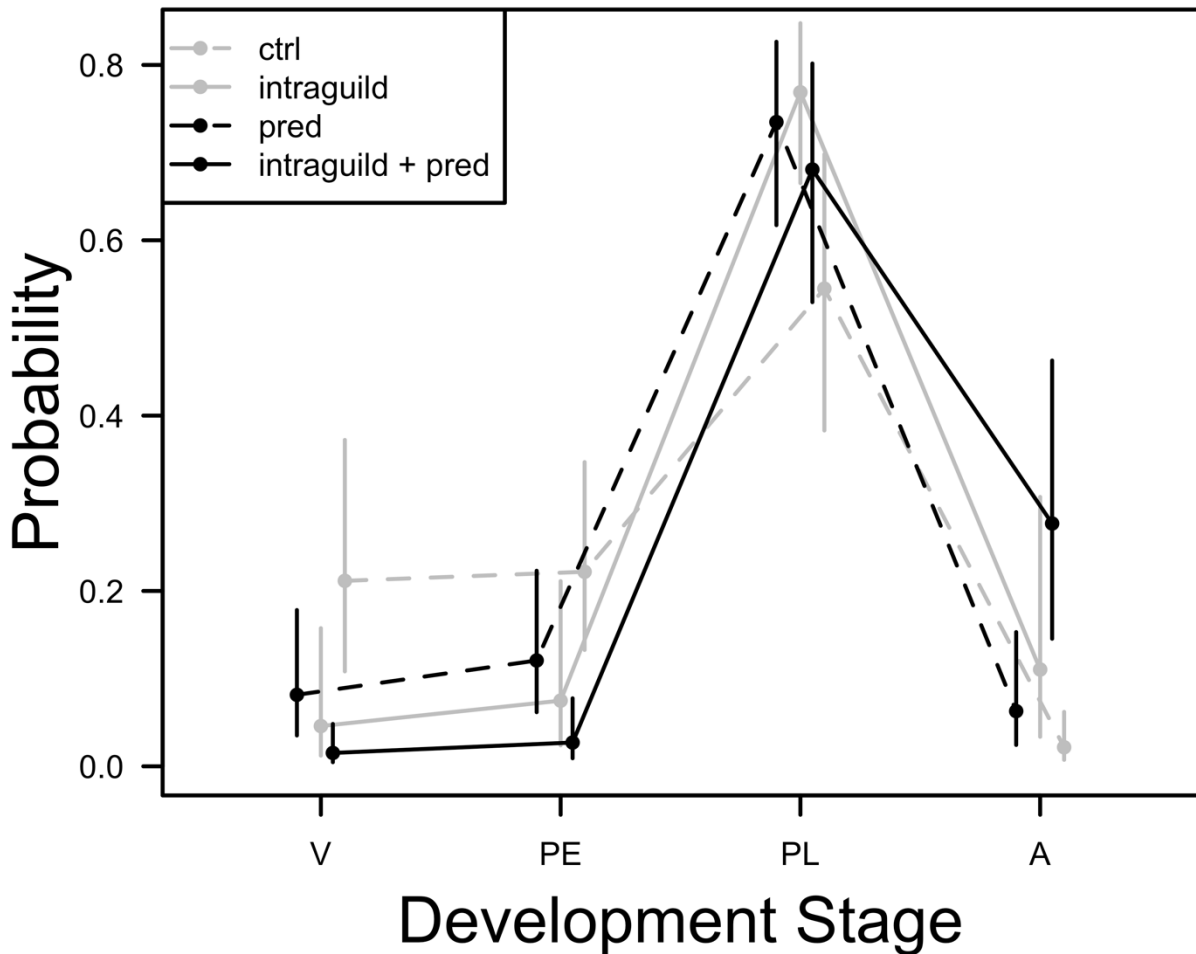
Figure 2.2. Caddisfly development stages. Probability of a surviving individual *A. nigriculus* being either fifth instar larva, early pupa, late pupa, or adult after 19 days of exposure to intraguild interactions (intraguild), predators (pred), both (intraguild + pred), or neither (ctrl) in high elevation ponds in the Elk Mountains of Colorado, USA. Error bars represent 95% confidence intervals.

Variable	Estimate	St. Error	z	p
Cage	0.009	0.016	0.609	0.543
Intraguild Ints.	1.706	0.688	2.478	0.013
Predation	1.101	0.465	2.468	0.018
Intraguild Ints.×Predation	0.030	0.838	0.035	0.972

Table 2.2. Effects of species interactions on caddisfly development. Model output from ordinal regression on the effects of intraguild interactions, predation, and their interaction on the development of *Asynarchus nigriculus* in semi-permanent ponds in the Elk Mountains of Colorado, USA. P-values obtained from Wald tests.

2.4.3. Mass

Our linear mixed effects model showed a strong, negative effect of intraguild interactions on *L. externus* larval mass. *L. externus* individuals from treatments with *A. nigriculus* were, on average, 40% smaller than those in treatments without intraguild interactions (Table 2.3, Figure 2.3). However, there was no significant effect of predation on body mass, or a intraguild interaction x predation interaction term (Table 3, Figure 2.3).

Term	F	DF	p	SD
Intraguild Ints.	45.994	1/11.73	<0.001	
Predation	0.162	1/11.63	0.695	
Intraguild Ints. ×Predation	0.419	1/11.67	0.530	
Pond				0.243
Pond:Cage				0.094

Table 2.3. Effects of species interactions on caddisfly mass. Type II Wald F test on a linear mixed effects model, plus random effect standard deviations, examining the effects of predation and intraguild interactions on *L. externus* mass in high elevation ponds. DF is the numerator over denominator degrees of freedom.
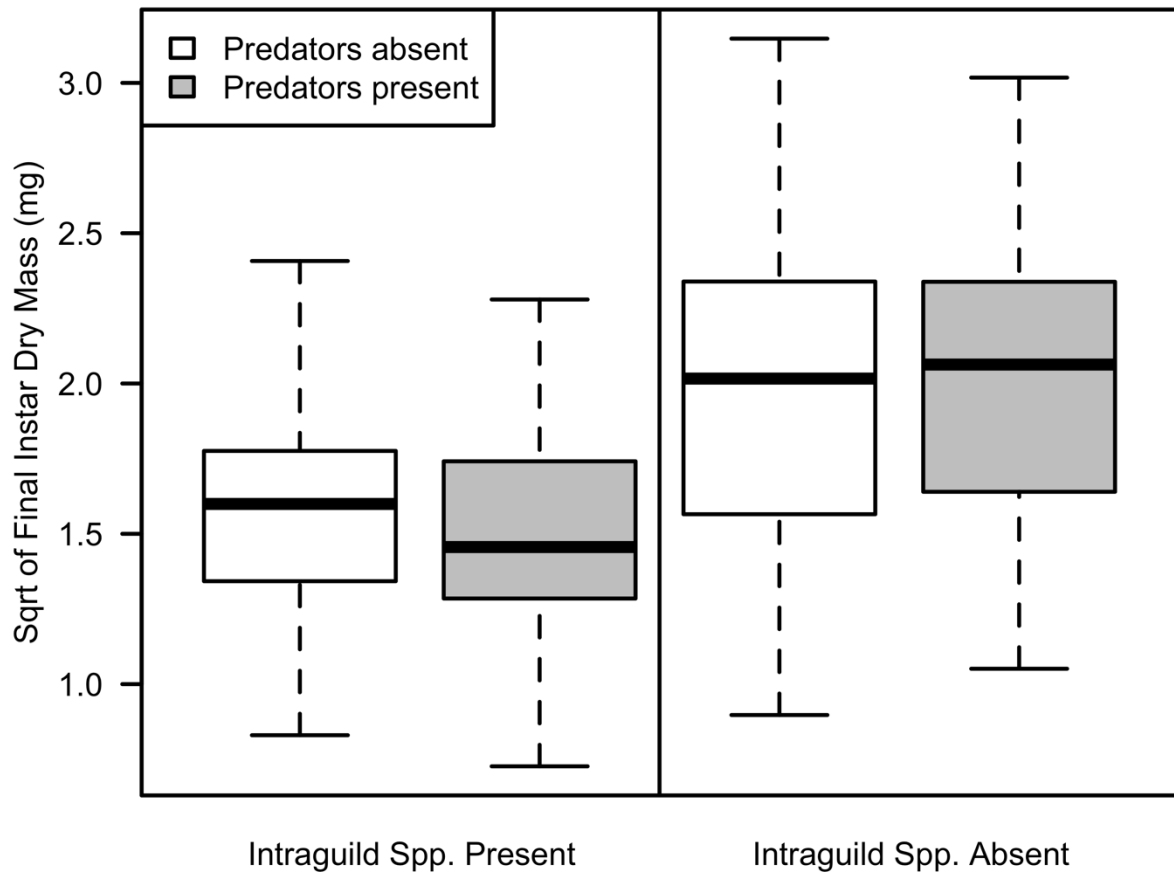
Figure 2.3. Caddisfly masses and species interactions. The square root of the dry mass of fifth instar *L. externus* alone and in the presence of an intraguild species, predators, and both in high alpine ponds in the Elk Mountains of Colorado, USA. The middle bar of the boxes represents the median, the edges of the box represent the 25% quantiles and the whiskers represent the 75% quantiles.

2.5. Discussion

Our study provides strong empirical evidence that the outcome of climate-induced shifts in habitat use along environmental gradients are shaped by interspecific interactions with

resident intraguild species and predators in the recipient community. *L. externus*, the resident species in this experiment, largely responded in ways we predicted, with intraguild interactions reducing survival and predators weakening that effect. This was not the case for *A. nigriculus*, the shifting species in our study, which showed no differences in survival between treatments. By exploring the mechanisms driving these observed responses we can hypothesize the broader consequences for the future of these high alpine pond systems. Moreover, we may be able to develop a generalizable understanding of how communities may respond to future environmental changes and what is necessary to predict the outcomes of such changes.

Proportional survival was highest for *L. externus* when individuals interacted only with conspecifics and the lowest in the presence of the aggressive competitor/intraguild predator, *A. nigriculus*. These results indicate that reductions in *L. externus* survival from intraguild predation and other aggressive behaviors by *A. nigriculus* (e.g. Wissinger *et al.*, 2004a) likely exceed the density-dependent declines in survival and performance observed in single species *L. externus* assemblages (Klemmer *et al.*, 2012). Predation on its own did not have a significant effect on *L. externus* survival which is not surprising given the robust case and risk sensitive behavior of *L. externus* substantially reduces its vulnerability to predators (Wissinger *et al.*, 2006). However, the combination of predation and intraguild interactions significantly decreased the proportional *L. externus* survival, albeit less than when predators were not included in the intraguild interaction treatment. This outcome could be because predators reduce *A. nigriculus* survival, thereby releasing *L. externus* from intraguild predation and other antagonistic interactions (as in Chase *et al.*, 2002). However, we observed consistently low *A. nigriculus* survival across all treatments and no significant effects of *Dytiscus* predation on *A. nigriculus* survival. This would indicate that the role of predation in this regard is likely more indirect.

We can better understand the mechanism through which predation reduces the effect of *A. nigriculus* on *L. externus* survival by examining other demographic data. In the presence of predators, we saw increased development of *A. nigiriculus*. Given that *A. nigriculus* individuals don't accelerate their development in response to predators (Greig & Wissinger, 2010), we hypothesize that predators may remove smaller, more slowly developing *A. nigriculus* individuals from the population generating a demographic structure that would appear to show an increased development rate. Moreover, if slower-to-develop individuals are selectively removed from the population early by predation, *L. externus* will be exposed to fewer intraguild predators as the remaining, later instar, *A. nigriculus* individuals quickly begin to pupate and cease being intraguild predators. Nevertheless, *L. externus* at the beginning of the experiment is still probably experiencing some antagonistic interactions from the larger *A. nigriculus* before they pupated, as evidenced by the observed decrease in *L. externus* survival in the presence of both predators and intraguild interactions compared to *L. externus* on its own. Indeed, this intraguild predation likely was a mechanism behind the more advanced development in *A. nigriculus* we observed in the presence of the intraguild species as *A. nigriculus* develops more quickly if it has a protein rich diet consistent with intraguild prey (Wissinger *et al.*, 2004a). Thus, the advanced development of *A. nigriculus* we observed in the presence of predators and intraguild species is likely an additive response of predators removing the more slowly developing individuals and intraguild predation allowing those that survived to develop more quickly.

While *A. nigriculus* had a markedly negative effect on *L. externus* survival, the overall fitness ramifications of a potential shift by *A. nigriculus* to semi-permanent ponds don't stop there. Intraguild interactions with *A. nigriculus* significantly decreased the 5th instar body mass

of *L. externus* regardless of the presence of predators. *L. externus* is risk sensitive in the

presence of predators and aggressive competitors, often retreating into its case and remain still

when threatened (Wissinger *et al.*, 2006). This behavior decreases foraging time and resource

acquisition (Wissinger *et al.*, 2004b). Thus, the constant pressure of *A. nigriculus* in the

treatments with intraguild interactions might have reduced the amount of time *L. externus* spent

foraging, with costs to larval mass. Larval body mass has a well-known predictor of adult body

mass (Day, Rowe & Miles, 2002) and fecundity in insects, especially non-feeding females

(Honěk, 1993; Jannot *et al.*, 2007). Thus, should *A. nigriculus* shift its habitat to interact with *L.*

externus more frequently, we may see an overall decrease in the fecundity of the *L. externus*

population at the MCNP. Indeed, assuming that the relationship between body mass and

fecundity is the same for both of these confamilial species, a 40% decrease in body mass such as

we observed would decrease individual fecundity by 33% (Wissinger *et al.*, 2004a). However,

knowing for certain whether these decreases in mass would ultimately impact *L. externus*

population size, even in the presence of predators, would require quantifying differences in total

egg production (e.g. Jannot *et al.*, 2008) and whether egg production influences recruitment and

subsequent population size (Hildrew *et al.*, 2004).

Regardless, it is clear *L. externus* is likely to suffer some negative consequences if *A.*

nigriculus abundance increases in semi-permanent ponds in response to climate change. This

may have important ramifications on the rest of the community as *L. externus* is the most

common and biomass-dominant caddisfly species in the system (Wissinger *et al.*, 1999a).

Decreases in its local abundance may allow other range-shifting species, such as those from

lower elevations, to establish a greater foothold in the region (Shepard *et al.*, 2021). There may

also be important consequences for ecosystem level processes such as detritus breakdown and

nutrient dynamics in these ponds as *L. externus* is the single greatest detritus processer in the oligotrophic system where we conducted our study (Klemmer *et al.*, 2012; Wissinger *et al.*, 2018).

In contrast to the resident species, the shifting species, *A. nigriculus* did not respond as we predicted. Proportional survival was low and nearly uniform across all treatments with no significant effects of predation or intraguild interactions. This suggests that *A. nigriculus* shows strong density-dependent morality driven by space and resource availability. It would be easy to assume that these results are the product of a context-independent, internally driven process and that densities are regulated by intraspecific interactions such as cannibalism (Wissinger, Steinmetz et al., 2004). Yet, our data showing treatment effects on both development stage and the variation around proportional survival indicate that there are likely different mechanisms removing individuals from the population in different scenarios. Indeed, mortality rates of *A. nigriculus* in cages with and without *Dytiscus* predators are nearly the same as those in ponds with and without *Dytiscus* (Figure B1). As discussed above, *Dytiscus* predators were likely important for removing slow to develop individuals from the population. Further support for this notion is seen in the amount of variation in the estimates of proportional survival which were nearly equal to lower than model estimates when predators were present, indicating consistent, predictable removal of individuals from the population.

A. nigriculus populations in the presence of *L. externus* without predators showed much higher variation in survival than expected by the model. Incidental cannibalism may be responsible for this outcome. As described by Wissinger *et al*. (1996) and Wissinger *et al*. (2004b), *A. nigriculus* exhibit a mob-like 'feeding frenzy' behavior in instances of intraguild predation, or cannibalism, in which individuals are attracted to an *A. nigriculus* that is consuming

prey. The aggressive encounters that ensue result in injury of conspecifics and the subsequent expulsion of body fluids into the water by the wounded individual triggers further cannibalism (Wissinger *et al.*, 2004b). Thus, it is possible that intraguild predation events may be associated with instances of secondary cannibalism that increases variability in *A. nigriculus* survival among replicates. Moreover, individuals that gain a protein boost from cannibalism may become larger than their conspecifics (Wissinger *et al.*, 2004a) which could further promote cannibalism as it has been shown to be size-structured (Wissinger *et al.*, 1996). In sum, we hypothesize that low frequency events that trigger a positive feedback loop may generate the irregularities in survival seen across replicates with intraguild interactions.

Together, our observations of the response of *A. nigriculus* to the intraguild interactions and predators of semi-permanent ponds show that this species has the potential to exploit and thrive in these habitats should the need arise. Indeed, the increased development shows that *A. nigriculus* will likely develop in time to emerge from semi-permanent ponds, even as future climate scenarios predict these ponds may dry more often or more quickly (Tuytens *et al.*, 2014). However, the overall low observed survival rate would indicate that additional perturbations to the system might cause this species to lose its foothold in these habitats since smaller populations are more susceptible to localized extinctions (O'Grady *et al.*, 2004). The performance of *A. nigriculus* in semi-permanent habitats may be critically important since semi-permanent ponds may become source populations and their preferred, temporary ponds, may become sink populations under future climate predictions (Sim *et al.*, 2013; Lund *et al.*, 2016). Under this scenario, continued persistence of this species will depend on whether population density and recruitment in semi-permanent habitats can compensate for losses in the regional metapopulation as temporary ponds become uninhabitable. Indeed, local scale metapopulation dynamics can play

important roles in determining species persistence as climate change drives shifts in habitat use (Wilson, Davies & Thomas, 2010; Fordham *et al.*, 2013). Future work examining whether population dynamics in these semi-permanent ponds can offset losses in temporary ponds will be fruitful in this regard.

On a broader level, our study reveals that climate-change-induced localized habitat shifts may result in the destabilization of ecological communities. The interaction between *L. externus* and *A. nigriculus* had significant consequences for *L. externus* survival and growth, which can be a hallmark of strong interactions (Berlow *et al.*, 2004). Strong interactions in ecological communities tend to be destabilizing (Gellner & McCann, 2016). The increasing regularity of such a strong interaction, especially one that involves a foundational species in the system may have broad consequences for community persistence (Landi *et al.*, 2018). Furthermore, this intraguild interaction resulted in high variation in *A. nigriculus* survival, which at the population level is also an important indicator of instability, particularly in a changing climate (Halley, Houtan & Mantua, 2018). Instability in the potentially shifting species can decrease establishment success in new refuge habitats if currently preferred habitat becomes inhospitable due to climate change as unstable populations are less likely to persist through time (Lande, 1993). However, our results indicate *Dytiscus* predators reduce this instability by weakening the interaction between *A. nigriculus* and *L. externus* while simultaneously reducing the amount of variation in *A. nigriculus* survival. This reinforces the importance of maintaining, intact ecological communities with high order predators when promoting the resilience of ecological systems to habitat shifts in response to climate change (Wang, Liu & Wang, 2020).

Indeed, the beneficial role of the *Dytiscus* predation we observed is perhaps unsurprising given the keystone role of predators for maintaining biodiversity (Chase *et al.*, 2002) and

stabilizing ecological communities (Rooney & McCann, 2012) is well understood. However, the role of predation in determining the outcomes of climate-induced habitat shifts has largely been overlooked. While there has been some consideration of the role that shifting predators may play on community structure and stability (Bartley *et al.*, 2019), little evidence exists demonstrating how resident consumers alter the outcomes of shifts involving organisms from lower trophic levels. Our findings demonstrate that the members of resident communities and their interactions with each other and with shifting species can be critically important for determining how communities will respond to shifts in habitat use as the climate changes.

2.6 Conclusions

Here we have shown that some species may respond in predictable ways to localized habitat shifts while others might not. However, using a deep knowledge of the organisms' life histories we can readily explain the mechanisms likely responsible for the observed patterns even if they were beyond what we predicted initially, especially when multiple life-history variables were considered. Predators were particularly important in reducing the strength of intraguild interactions between these species and reducing variation in the survival of the potentially shifting species which, together, has important implications for the stability of this community in the future. Ultimately, this kind of information is important for predicting how communities will respond to current and future climate change by helping us identify which species may need special protections to ensure their survival in the new communities that emerge. Future studies examining larger components of the food web will be fruitful in this regard.

CHAPTER 3

CONSEQUENTIAL PAIRWISE INTERACTION AT A HETEROGENEOUS RANGE MARGIN DOESN'T AFFECT LONG-TERM DYNAMICS OF A RANGE-SHIFTING SPECIES

3.1. Abstract

Species undergoing geographic range shifts are often moving into areas that have variation in the types and qualities of habitat available. 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. Here, we conduct an *in-situ* cage experiment examining how a local wetland hydroperiod gradient and competition with a resident species, *Asynarchus nigriculus* influences the survival of the range-shifting caddisfly *Limnephilus picturatus*. We then use long-term survey data of population densities of the resident and shifting species to determine whether pairwise interactions observed in cage experiment translated into long-term dynamics. The cage experiment revealed that *A. nigriculus* had a strong, negative effect on the survival of range-shifting *L. picturatus*, regardless of hydroperiod. However, we observed no relationship between the densities or occurrence of *L. picturatus* and *A. nigriculus* the long-term data regardless of hydroperiod. This inconsistency suggests that factors such as other competitive or trophic interactions are likely more important drivers behind the population dynamics of this range-shifting species at its new upper-elevational limit.

3.2. Introduction

A common consequence of climate change is for species to shift or expand their geographic ranges across regional gradients into areas that were traditionally considered more abiotically stressful, such as higher elevations and latitude habitats (Parmesan & Yohe, 2003; Chen *et al.*, 2011). 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 (Cadotte & Tucker, 2017; Shepard *et al.*, 2021) and resident species (Shepard *et al.* In press). However, the strength and outcome of these interactions are unlikely to be uniform across the species' newly expanded range margin. Shifting species will often find heterogenous patchworks of abiotic conditions at their new range margins (Gaston, 2003; Oldfather *et al.*, 2020) which can could be as varied as localized gradients in soil compaction for plants (Latimer & Jacobs, 2012) or hydroperiod in clusters of ponds inhabited by aquatic invertebrates (Welborn *et al.*, 1996). This localized habitat heterogeneity may create variation in the ability of range-shifting species to survive through abiotic stresses (Oldfather & Ackerly, 2019) and also generate spatial variation in the strength of the new species interactions they will encounter. Indeed, because the outcome of species interactions often depend on their abiotic context (Chamberlain *et al.*, 2014), localized 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, particularly in the context of metapopulations (Münkemüller & Johst, 2006) and metacommunities (Kneitel & Chase, 2004). From this literature we can hypothesize at least two ways in which habitat heterogeneity might

be important for influencing the persistence of range shifting species at their new range edges. First, 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 crickets to extinction (Kindvall, 1996). This same mechanism could be important for permitting a range-shifting species establish and persist in abiotic conditions that may be harsher than those found at the core of their range. Second, habitat heterogeneity may also 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, heterogeneity in river flow disturbance has promoted the persistence of both invasive and native fish in New Zealand (Boddy, Booker & McIntosh, 2020). Similarly, variation in water clarity allows for the coexistence of native and invasive aquatic macrophytes (Salgado *et al.*, 2021). The application of these ideas to understanding population dynamics at the leading edge of a species' expanding range has generally been overlooked (but see Oldfather & Ackerly, 2019; Oldfather *et al.*, 2020). 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).

We conducted a cage experiment in alpine ponds to understand the consequences of local habitat heterogeneity on species interactions at the leading range margin of a species undergoing shifts. We examined how competition between the range-shifting caddisfly *Limnephilus picturatus* MacLachlan and the resident species *Asynarchus nigriculus* Banks varied between temporary ponds that dry every summer and semi-permanent ponds that dry only in years with low precipitation. We hypothesize that the shifting *L. picturatus* 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, Wissinger & Baros, 2008), while simultaneously requiring faster development times 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 (Wissinger, 1999; Mitsch & Gosselink, 2000). *L. 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 *A. nigriculus* which has a suite of fast life-history traits consistent with adaptation to temporary pond habitats (Wissinger *et al.*, 2003).

We also hypothesize that *A. nigriculus* will negatively affect the survival of the range-shifting *L. picturatus* because *A. nigriculus* is known to be aggressive competitors and intraguild predators of other species of caddisfly (Wissinger *et al.*, 1996, 2004b). However, we anticipate that this negative effect would be stronger in ponds with shorter hydroperiods because *A. nigriculus* is more aggressive in temporary ponds (Lund *et al.*, 2016) and antagonistic interactions often increase as ponds dry due to increased encounter rates as water volume shrinks (Greig, Wissinger & McIntosh, 2013). Moreover, *L. picturatus* has already been shown to be more vulnerable to antagonistic interactions in abiotically stressful habitats (Shepard *et al.*, 2021).

Empirical studies of isolated pairwise interactions, such as those between *L. picturatus* and *A. nigriculus,* are tractable for experiments, and are useful for identifying and quantifying interactions that have the potential to shape long-term population dynamics. However, it is necessary to also examine pair-wise interactions in the context of the broader community since interaction strength is often 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 useful approach 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 total effect of all interactions a species engages in, that is, with other species and with the abiotic environment. Therefore, if a strong pair-wise interaction in simplified empirical studies is important to the broader demography of a species of interest, there should be an inverse relationship between the densities of these two species through time (Ives, Carpenter & Dennis, 1999). Thus, in addition to pairwise cage experiments, we also examined long-term (1998-2020) survey data of population densities for *L. picturatus* and *A. nigriculus* at our field site to test whether there was negative covariance between the two species.

3.3. Methods

3.3.1. 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, USA (39.030, -107.064) near the Rocky Mountain Biologcal Laboratory. The MCNP is a collection of over 60 ponds that each fall into one of 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 *et al.*, 1999b, 2003). Caddisflies (Trichoptera) are among the most biomass-dominant macroinvertebrates in these ponds, and the distribution of nine species across five genera varies across the hydroperiod gradient (Wissinger *et al.*, 1999a, 2003, 2006). For this study, we focused on the resident species *Asynarchus nigriculus* Banks and the range-shifting species *Limnephilus picturatus* MacLachlan. *A. nigriculus* is one of the most abundant species at

the MCNP while *L. picturatus* tends to be rarer and was first recorded at the MCNP in 1996 but did not fully establish until 1998 (see results). These two species co-occur in 95% of the ponds that *L. picturatus* has been recorded in at the MCNP, 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 are often excluded from permanent ponds by salamander predation (Wissinger *et al.*, 2003, 2004b, 2006).

3.3.2. Cage experiment

To determine the effect of *A. nigriuclus* on *L. picturatus* across the hydroperiod gradient, we conducted an *in-situ* caging experiment in five temporary and five semi-permanent ponds at the MCNP. Cages were 50 x 50 x 50 cm cubes with 1mm mesh walls and floors. Each pond received an array of three cages with the following treatments: *L. picturatus* on its own, *A. nigriculus* on its own, 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* and 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 was thus a substitutive experimental design where only twenty *L. picturatus* and twenty *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 (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.

We added 50g of air-dried, senesced *Carex aquatillis* detritus to each cage which is the primary food resource for both species (Wissinger *et al.*, 2018). Sedge collected from ponds at the MCNP and was inoculated in the cages for seven days prior to the beginning of the experiment to permit the colonization 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 caddis. The remainder of the cage contents, including any unconsumed sedge, was taken back to the lab and inspected for any remaining caddisflies that we missed in the field. We combined the counts from the lab and the field to quantify the total remaining number of individuals of each species in each cage.

We used binomial generalized mixed-effects 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 Chi^2 tests to determine the significance of the model terms. We performed this analysis in R version 4.1.0 (R Core Team, 2021) using the *lme4* (Bates *et al.*, 2015) and car (Fox & Weisburg, 2019) packages.

3.3.3. 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* has been 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. We were unable to sample every pond every year, though most ponds were sampled multiple times over the twenty-four-year record. Three years were missing from the dataset: 2000, 2001, and 2020.

We used a generalized least squares 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 version 4.1.0 (R Core Team, 2021) using the *nlme* package (Pinheiro *et al.*, 2021). For this analysis we looked at the total average density 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. Because there was no data for 2000, 2001, and 2020, we only examined the data for the years 2002-2019. Significance of the model terms and the correlation structure was assessed using likelihood ratio testing.

We examined whether *A. nigriculus* density had any effects on whether *L. picturatus* was able to be present in a pond at all. We explored this with a binomial mixed-effects model with *L. picturatus* presence and absence as the response variable and *A. nigriculus* density as the explanatory variable. We ignored the effects of time in this analysis and treated each sample, regardless year, as independent because the autocorrelation error structure we used in the generalized least squares model did not explain a significant component of variation in the

dataset (see results). We included hydroperiod as a binomial term (either temporary or semi-permanent) in this model to assess the importance of abiotic context and included pond identity as a random effect. A Wald Type II Chi^2 test was used to assess the statistical significance of effects. This analysis was conducted in R version 4.1.0 (R Core Team, 2021) using the *lme4* package (Bates *et al.*, 2015) and the *car* package (Fox & Weisburg, 2019).

3.4. Results

3.4.1. Cage experiment

The proportional survival of *L. picturatus* in cages was lower when *A. nigriculus* was present (Figure 3.1), 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 generalized mixed-effects 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 by competition interaction on *L. picturatus* survival (Table 3.1). Neither competition with *L. picturatus*, hydroperiod, nor their interaction had significant effects *A. nigriculus* survival (Table 3.1)

The temporary ponds were shallower than the semi-permanent ponds throughout the experiment (Figure C1) and, at the end of the experiment were, on average, 15.8 ± 8.5 cm deep (mean ± sd) while the semi-permanent ponds were 23.9 ± 7.6 cm deep (mean ± sd). 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 before drying down during the second half (Figure C1).
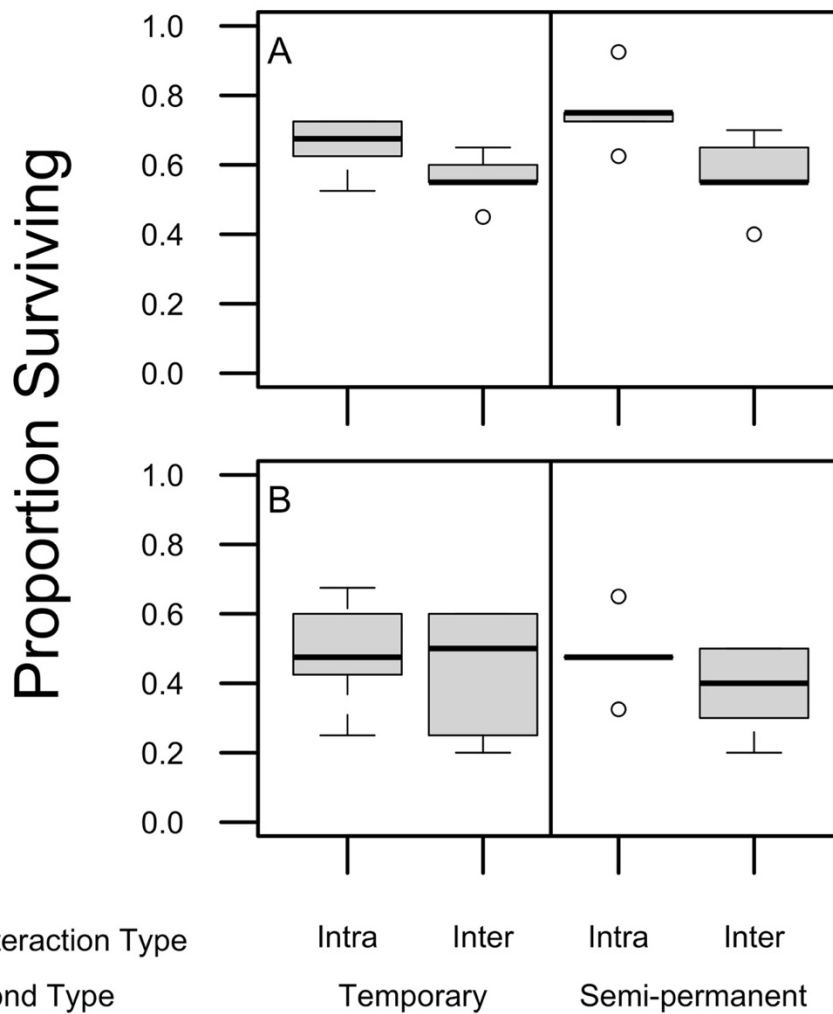
Figure 3.1. Caddisfly survival in relation to hydroperiod and species interactions.

Proportional survival of *L. picturatus* (A) and *A. nigriculus* (B) in temporary and semi-permanent ponds both with intra and interspecific interactions the Mexican Cut Nature Preserve in the Elk Mountains of Colorado, USA. Points represent outliers. The middle bar of the boxes represents the median, the edges of the box represent the 25% quantiles and the whiskers represent the 75% quantiles.

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 3.1. Effects of intraguild interactions and hydroperiod on caddisfly survival. Results from Type II Wald Chi[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 in Colorado, USA.

3.4.2. Annual surveys

Across nearly all years, *A. nigriculus* densities were an order of magnitude higher than those of *L. picturatus* (Figure 3.2) with an average density of approximately 13 ± 18 individuals

m^{-2} compared to 2 ± 12 individuals m^2 (mean $\pm$ SD), respectively. The generalized least squares analysis showed no relationship between *A. nigriculus* and *L. picturatus* densities through time (Table 3.2). Moreover, the autoregressive coefficient was not significant in this model either (Table 3.2) meaning that densities in one year were not predicted by densities in the year prior.

At the coarsest level, plots of the relationship between *L. picturatus* density and *A. nirgiculus* density in all ponds across all years provide suggestive evidence that *L. picturatus* densities typically occurred when *A. nirgiculus* densities are lower (Figure 3.3a). Additionally, when *A. nigriculus* densities are very high, *L. picturatus* appeared to be very rarely present (Figure 3.3a). However, there was ultimately no pattern in *L. picturatus* presence in relation to *A. nigriculus* density (Figure 3.3b). Additionally, the hypothesis that *A. nigriculus* density affects occupancy of habitats by *L. picturatus* was not supported by our binomial mixed effect model: *A. nigriculus* density did not have a significant effect in *L. picturatus* presence/absence in the ponds (Table 3.3). Together, the generalized least squares analysis on the temporal data and the mixed-effects model on the presence/absence data show that *L. picturatus* does not appear to be affected by *A. nigriculus* in the natural ponds regardless of whether temporal trends are accounted for in the models.
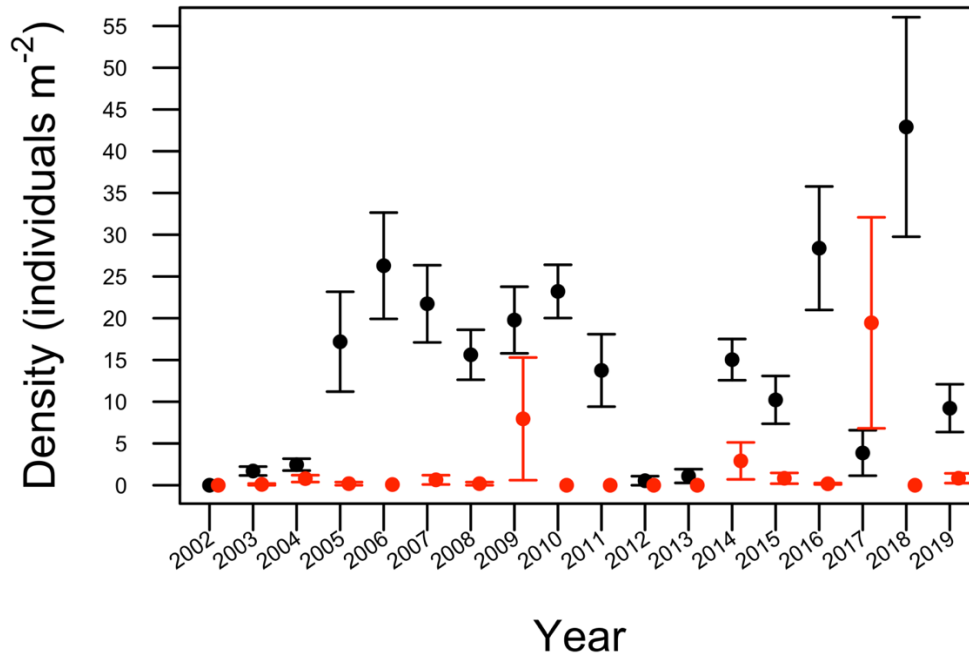
Figure 3.2. Caddisfly densities through time. The average densities of *Asynarchus nigriculus* (black) and *Limnephilus picturatus* (red) from 2002 to 2019 in temporary and semi-permanent ponds at the Mexican Cut Nature Preserve in Colorado, USA. Error bars represent standard errors.

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

Table 3.2 Effects of competitors on *L. picturatus* through time. General Least Squares and likelihood ratio test output examining the effects of *Asynarchus nigriculus* density on *L. picturatus* density in subalpine ponds between 2002 and 2019 at the Mexican Cut Nature Preserve in Colorado, USA. Phi is the measure of association between each year in the data.
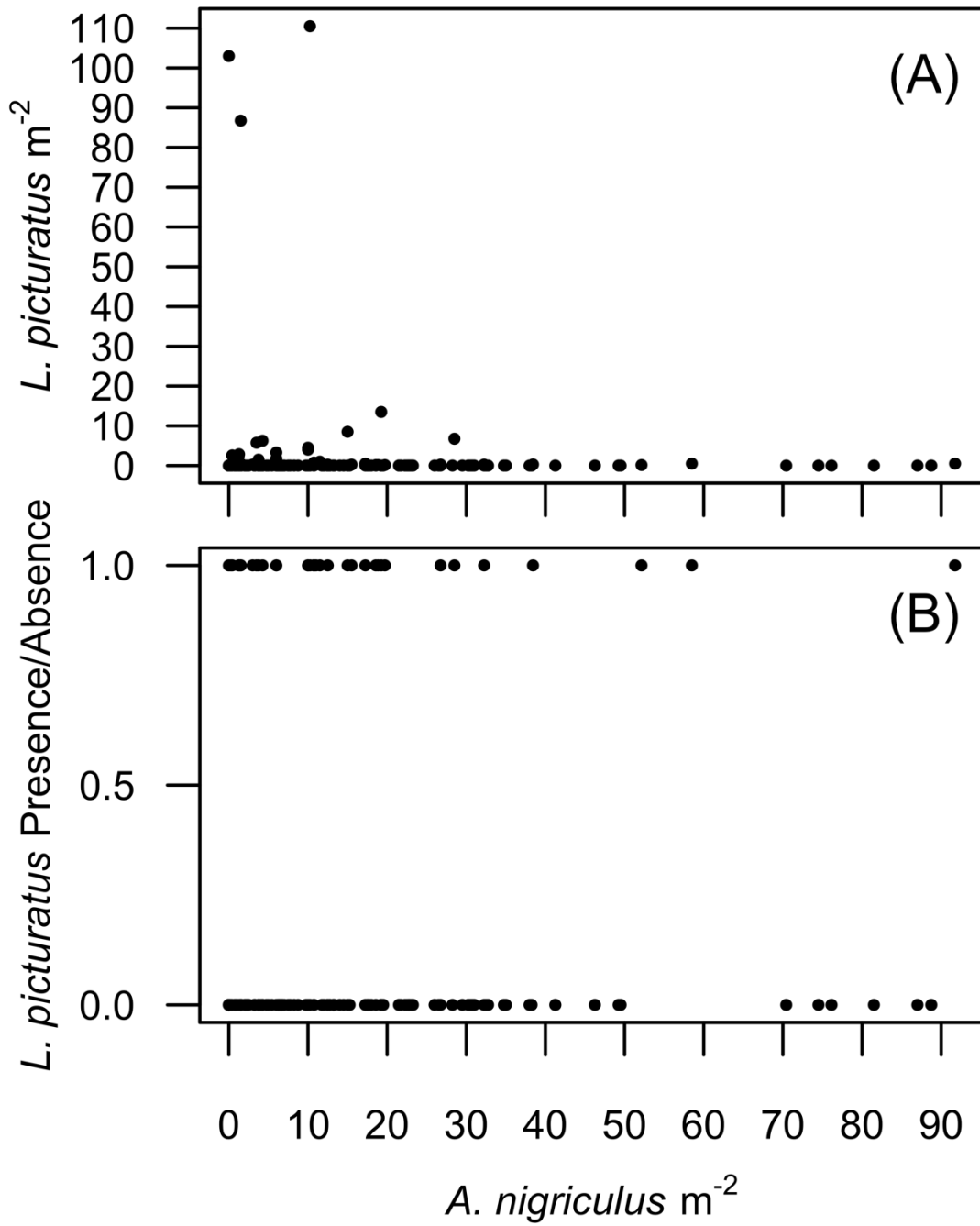
Figure 3.3. Relationship between *L. picturatus* and *A. nigriculus*. Plots of *Limnephilus picturatus* (a) density and (b) presence/absence in relation to the density of *Asynarchus*

nigriculus in both temporary and semi-permanent ponds at the Mexican Cut Nature Preserve in the Rocky Mountains of Colorado between 2002 and 2019.

Parameter	χ^2	DF	p-value	SD
A. nigriculus density	1.061	1	0.303	-
Hydroperiod	0.135	1	0.714	
Pond (Random Effect)	-	-	-	1.008

Table 3.3. Effects of competitor density on *L. picturatus* presence. Output from Type II Wald Chi^2 Tests for the effect of *Asynarchus nigriculus* density and hydroperiod on the presence of *Limnephilus picturatus* in temporary and semi-permanent ponds at the Mexican Cut Nature Preserve in Colorado USA between 2002 and 2019.

3.5. Discussion

3.5.1. Pair-wise interaction between *L. picturatus* and *A. nigriculus*

Pair-wise 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 geographic range. This outcome was in line with our initial predictions: *L. picturatus* is a poor competitor with other species at subalpine elevations (Shepard *et al.*, 2021) while *A. nigriculus* is very aggressive towards other caddisfly species, especially in drying habitats (Wissinger *et al.*, 1996, 2004b; Lund *et al.*, 2016). However, this interaction was not affected by the abiotic context, as the negative effect of *A. nigriculus* on *L. picturatus* survival was not significantly different between temporary and semi-permanent ponds. While unexpected in this context, other

studies have shown that interactions between *A. nigriculus* and another caddisfly species, *Limnephilus externus,* were also 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 pair-wise interaction we studied.

It is possible that the abiotic gradient along which we ran this experiment was not steep enough to alter the outcome of the interaction between *L. picturatus* and *A. nigriculus*. Indeed, we did not observe any effect of hydroperiod on the survival of *L. picturatus* or *A. nigriculus* when there were no intraguild interactions present. Previous studies with *A. nigriculus* showed increased frequency of aggressive interactions in drying vs. non-drying ponds (Lund *et al.*, 2016). However, in our experiment, the ponds did not dry down much below their initial levels due to heavy rainfall during the first half of the experiment. The low rate of drying the summer of our experiment could have meant that *A. nigriculus* was not pressed enough to increase its aggressiveness. However, even if the hydroperiod gradient had been steeper during our experiment, the contrast between temporary and semi-permeant 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 (Wissinger, 1999; Mitsch & Gosselink, 2000).

Clearly, these differences were not sufficient to elicit an effect on the interaction between these two species either.

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

Variation in the strength of antagonistic interactions, often mediated by heterogeneous abiotic conditions, can be important for facilitating the persistence and coexistence of species in patchy habitats (Amarasekare, 2003). Instead of variation, we observed uniformly negative consequences of *A. nigriculus* on *L. picturatus* across different habitat types at the upper range limit of *L. picturatus.* This means that *A. nigriculus* has potential to strongly regulate *L. picturatus* populations in this habitat (Tilman, 1994). However, whether this antagonistic interaction is strong enough to result in long-term impacts on *L. picturatus* depends on the milieu of other interactions within the rest of the community. Our analysis of the long-term data was a broad-stroke attempt at this contextualization and revealed no relationship between the annual densities of *A. nigriculus* and *L. picturatus.* This outcome suggests that this interaction is not important for long-term dynamics of *L. picturatus* at its range margin relative to other drivers of population density. There are several reasons 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 organization 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.

First, *L. 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, are also critically important and declines in one demographic variable may be offset by increases in others in a process termed demographic

compensation (Doak & Morris, 2010). While our experimental design did not allow us to collect the data needed to test for demographic compensation, 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).

Second, the nature of the pair-wise interaction between *L. picturatus* and *A. nigriculus* may also contribute to the lack relationship between the two species' densities through time. From example, field observations indicate that these two species may partition micro-habitats within a given pond that reduce in their interaction frequency or intensity outside of the cage environment. *A. nigriculus* typically utilizes the open pond basins and benthic substrate (Wissinger *et al.*, 1999b) while *L. picturatus* often inhabits the stalks of sedge higher up in the water column (Shepard, Greig, *personal observation*). While the cage walls likely permitted some three-dimensional 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 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 three-dimensional 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 due to reductions in three-dimensional space are not consistent enough to result in long-term effects, as discussed above.

Lastly, 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 pair-wise interaction could be relatively weak compared to interactions *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 those observed in the present study. Additionally, direct 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.*, 1999b, 2006). 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 predators like diving beetle larva or salamanders can weaken the strength of competition between caddisflies at the MCNP (Wissinger *et al.*, 1999b; Shepard *et al.*, In press). 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 pair-wise interactions or the interaction between a species and its abiotic environment. Here, we showed that even when these pair-wise interactions are significant on their own, 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.*, In press) but entire ecological

communities into their studies.

CHAPTER 4

A FOOD-WEB PERSPECTIVE ON RANGE SHIFTS

4.1. Abstract

As the global climate changes, many species are shifting their geographic distributions. Typically, species have been observed moving up in elevation and/or latitude. As a result, there has been renewed discussions about the mechanisms that generate species range margins and the consequences of range shifts. Much of this discussion has centered around the range-shifting species themselves and the relative importance of abiotic variables and biotic interactions in their population dynamics. However, less consideration has been given to the communities that range-shifting species are moving into. Here, we propose a new framework that focuses on food webs to understand the causes and consequences of range shifts. Specifically, we propose that climate change will alter the structure and stability of ecological communities which will determine whether range-shifting species are able to establish. Moreover, the traits of a range-shifting species, such as trophic position, will influence how its establishment influences the structure and stability of recipient communities. We provide three hypothetical examples to demonstrate the utility of this approach as well as guidelines for ways to empirically test the causes and consequences of range shifts within this framework.

4.2. Introduction

Climate change is causing many species to shift or expand their geographic ranges, typically up in latitude or elevation as the climate warms (Parmesan & Yohe, 2003; Chen *et al.*, 2011). This observation has catalyzed important discussions around the causes and consequences

of these observed changes to the distributions of species. Central to this discussion has been a debate on when and where abiotic conditions or biotic interactions are more important for setting species ranges or facilitating range shifts (Blois *et al.*, 2013; Wisz *et al.*, 2013; Louthan *et al.*, 2015; Alexander *et al.*, 2016; Cadotte & Tucker, 2017; Aguilar-Trigueros *et al.*, 2017; Westoby *et al.*, 2018). Though this topic has been discussed and studied for decades (Darwin, 1859; MacArthur, 1972), recent empirical findings offer little in the way of consensus e.g. (Lynn *et al.*, 2019; Shepard *et al.*, 2021).

The role of abiotic conditions for setting species range margins cannot be denied. All species have physiological limits; places where abiotic conditions that approach or exceed these limits will create boundaries to species ranges. However, in some locations, changes to species range margins may not directly track changes in abiotic conditions (Freeman *et al.*, 2018, 2021) and be determined by biotic variables in a phenomenon akin to the geographical manifestation of the realized versus fundamental niche (Hutchinson, 1957; Colwell & Rangel, 2009). This disconnect in distributions created by species' interactions has been one of the primary critiques of species distribution models that rely solely upon temperature data and species physiological tolerances (Wisz *et al.*, 2013).

To address this issue, scientists have looked for patterns in when and where either species interactions or abiotic conditions are the primary determinants of range margins. A leading hypothesis is the Stress Gradient Hypothesis (SGH, also known as the Species interaction-abiotic stress hypothesis and the Darwin-MacArthur Hypothesis) (Freeman *et al.*, 2018). The SGH posits that most species are distributed across an abiotic gradient where one end is more stressful than the other and that species interactions are the dominant driver of range margins at the less abiotically stressful end (Figure 4.1a). This hypothesis also states that range margins at the

abiotically stressful end of the gradient are determined by the stress gradient itself and species physiological tolerances for the conditions along that gradient (Dobzhansky, 1950; Connell, 1961; MacArthur, 1972; Menge & Sutherland, 1987; Louthan *et al.*, 2015). The observation that many species have responded to climate warming by shifting their ranges up in elevation and/or latitude to areas that are typically considered abiotically harsh anecdotally supports this hypothesis (Root *et al.*, 2003; Lenoir *et al.*, 2008). Moreover, there is some empirical support for this hypothesis from studies that have examined the mechanisms behind range margins (Paquette & Hargreaves, 2021), especially among plants along elevational gradients (e.g. (Anderegg & HilleRisLambers, 2019; Lynn *et al.*, 2019)). However, other, conflicting evidence suggests that many warm/abiotically less stressful range edges are still constrained by abiotic factors (Cahill *et al.*, 2014).

Counter to SIASH predications, a growing body of literature supports an alternative hypothesis termed Apparent Climate Exclusion (ACE) (Shepard *et al.*, 2021). ACE predicts that even in abiotically stressful habitats, species interactions may still limit species ranges as deteriorating abiotic conditions make populations more vulnerable to the negative consequences of antagonistic interactions (Case *et al.*, 2005; Holt & Barfield, 2009; García-Ramos & Huang, 2013; Svenning *et al.*, 2014; Cadotte & Tucker, 2017; Shepard *et al.*, 2021). In this way, species ranges may appear to be determined by abiotic variables since the strength of biotic interactions increases with abiotic stress (Figure 4.1b). Thus, the effects of abiotic and biotic controls of range limits cannot be distinguished by observational studies alone. Manipulative experiments are needed to show that biotic interactions are the mechanism behind the range limit and that changing temperatures (or other climatic variables) modify or weaken the interaction sufficiently to allow range shifts to occur (Shepard *et al.*, 2021). For example, herbivore exclusion

experiments showed that the upper elevational range of sugar maples *(Acer* saccharum) in Canada are determined by seed predation as opposed to the originally hypothesized colder climatic conditions (Brown & Vellend, 2014). Another example is seen a species of forb in North America where seed predation and pollen suppression on top of abiotically stressful conditions set the northern range limit of this species (Baer & Maron, 2018).

The reality is that both abiotic and biotic variables are inextricably linked and will together have important consequences for the distributions of species and the facilitation of range shifts in a changing climate (Gaston, 1998; Cadotte & Tucker, 2017). Species interactions depend on their abiotic context (Chamberlain *et al.*, 2014) and the ability for species to persist in hash abiotic environments can be improved (Godsoe *et al.*, 2017; LaManna *et al.*, 2021) and hampered (Baer & Maron, 2018; Shepard *et al.*, 2021) by species interactions. Moreover, the outcomes of pairwise interactions can be affected by interactions with additional species (Chase *et al.*, 2002; Jones *et al.*, 2020) which also depend on the abiotic context. All of these forces can have conflicting outcomes on different demographic variables resulting in unexpected outcomes for species persistence (Doak & Morris, 2010). Moreover, when species shift their ranges, they enter established communities of potential predators, competitors, and mutualists. When we conduct studies that isolate the various roles that species interactions and abiotic variables play in the persistence of species at their range margins in a changing climate, we lose the context that makes them biologically meaningful. Therefore, any future approaches should encompass the interconnected nature of biotic interactions and abiotic variables. Thus, we propose a new framework centered on the effects of abiotic variables on food webs to understand the mechanisms that generate range margins and how climate change can facilitate range shifts.
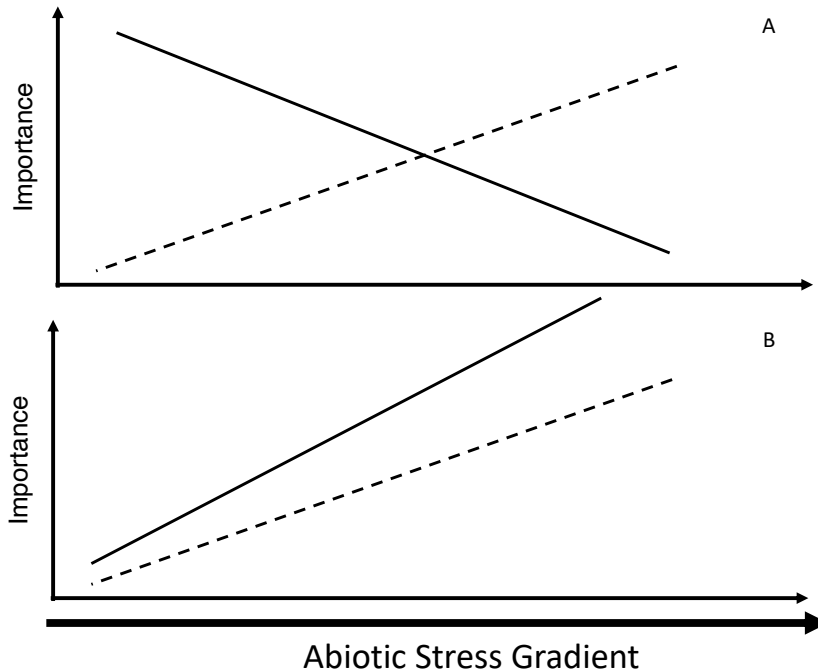
Figure 4.1. Abiotic stress and species interactions. The relationship between abiotic stress gradients and the importance of species interactions (solid lines) and abiotic variables (dashed lines) for controlling a species' population in the (A) stress-gradient hypothesis and (B) apparent climate exclusion hypothesis. Adapted from Shepard *et al.* 2021.

4.3. A food-web perspective to species range shifts

A key aspect of this new approach to understanding the causes and consequences of range shifts is to take the emphasis off the shifting species and place it onto the recipient community and the interactions that comprise their food webs. Food webs that are stable are often resistant to the establishment of invasive species (Romanuk *et al.*, 2009; Frost *et al.*, 2019). In many ways, the introduction of range-shifting species to recipient communities is akin to the introduction of invasive species. However, one of the major differences here is that invasive species are usually considered exotic to the community of interest and may be introduced by

humans from geographically distant locations (Simberloff, 2013). Range-shifting species, on the other hand, are likely to be entering adjacent communities and may already interact with some of the members of the recipient communities in other parts of their range. Alternatively, they could have interacted with these species in the past when nonanalog climates arranged their distributions differently (Williams & Jackson, 2007; Veloz *et al.*, 2012). The introduction of invasive or range-shifting species typically occur when a perturbation or disturbance alters the recipient community in some way, often towards instability (Hui & Richardson, 2019). Indeed, the introduction of these species can be a source of further perturbation that further facilitates the success of the introduction. Therefore, it behooves us to briefly explore what makes communities stable and how climate change might destabilize them to promote range shifts.

Stable food webs (Box 4.1) are comprised of non-random arrangements of interactions between species (Pimm, 1980). Specifically, most stable food webs have many weak and a few strong species interactions (de Ruiter, Neutel & Moore, 1995; Wootton & Stouffer, 2016). However, these many weak and few strong interactions must be organized in specific ways to promote stability in food webs. One arrangement that promotes stability is to have asynchronous channels of energy flow coupled by higher order consumers (Rooney *et al.*, 2006; Rooney & McCann, 2012). This asynchrony is often established by having a 'fast' and a 'slow' energy channel. In the 'fast' channel, there is typically low taxonomic diversity and strong interaction strengths (either measured as per-capita impacts of consumers on resources or via energy flux) while the 'slow' channel has higher diversity and weak interaction strengths (Rooney & McCann, 2012). These two channels are usually linked by the feeding of high-trophic-level, mobile consumers. Indeed, this pattern of slow and fast channels within food webs may be common (Wolkovich *et al.*, 2014). For example, in a marine community (Sánchez & Olaso,

2004), portions of the food web that originate from detritus-based resources tend to be more

diverse and have slower energy movements while portions originating from algal resources are

less diverse and faster (Rooney & McCann, 2012). These two channels are then linked by higher

order consumers such as large fish (Rooney & McCann, 2012). This arrangement of interactions

promotes stability by, dampening oscillations in predator-prey cycles, and allowing for

compensation by higher consumers following perturbations via compartmentalization of food

webs (McCann, Hastings & Huxel, 1998; Rooney & McCann, 2012), a process that has

independently been shown to promote stability in whole food webs (Stouffer, Bascompte &

May, 2011).

Processes that synchronize the channels or change their connectance to each other will

lead to destabilization, including increasing the diversity or decreasing interaction strengths in

the fast channel, decreasing the diversity or increasing interaction strengths in the slow channel,

or changing the diversity or strength of interactions in the higher-order consumers linking these

channels (Rooney & McCann, 2012). To summarize, changes to the asymmetry in the strengths

of species interactions (Emmerson & Raffaelli, 2004; Emmerson & Yearsley, 2004) or diversity

in food webs (de Mazancourt *et al.*, 2013) can lead to their destabilization. Extinction risk is

expected to increase which will alter the diversity within food webs and the subsequent

composition and frequency of modules (Maclean & Wilson, 2011). The strength of species

interactions are highly dependent on their abiotic context (Chamberlain *et al.*, 2014) so increases

in temperature are likely to have significant effects on the strength of species interactions (Rall *et

al.*, 2010; Gilbert *et al.*, 2014) which will translate to changes in food-web structure (Sentis,

Hemptinne & Brodeur, 2014; Sentis *et al.*, 2017). These predicted changes are likely to result in

destabilized food webs which are more susceptible to invasive species (Sentis, Montoya & Lurgi,

2021) and thus, likely the introduction of range-shifting species as well. However, in some instances, climate change might stabilize food webs by reducing the strength of top-down control (Vucic-Pestic *et al.*, 2011). The conflicting ways in which climate change may affect ecological communities reinforces the notion that we need to take approaches that integrate abiotic and biotic variables while considering whole food webs.

Using the above observations about the mechanisms that generate stability in food webs and how they might be affected by climate change, we can create a framework to explore the causes and consequences of species range shifts. The general approach is to determine: 1) if and how climate change alters the structure of the recipient community, 2) whether those changes facilitate or inhibit the introduction of a range-shifting species, and 3) how the food web in the recipient community continues to change in the presence of that shifting species under climate change. This approach is flexible to allow researchers to investigate the role of any abiotic variable on species interactions and energy flows. However, we will focus our attention in this paper on temperature, which is one of the core drivers of species range shifts in response to climate change. Temperature is easy to measure and is known to have significant impacts on species interactions and demography (Kordas, Harley & O'Connor, 2011; Matías & Jump, 2012; Villellas *et al.*, 2015) making it the easiest abiotic consequence of climate change to integrate into this framework. Moreover, there is already theoretical and empirical infrastructure in place to investigate the impacts of temperature on consumer-resource interactions that are the foundation of food webs (e.g. Gilbert et al. 2014, Rall 2010). Therefore, the emphasis of the rest of this paper will be on the role of temperature, although other abiotic variables could readily be applied to this framework also.

This proposed approach allows us to determine the mechanisms through which range-shifting species enter recipient communities by comparing warmed and non-warmed networks. Specifically, we can identify what aspects of communities are affected by warming and determine how that either facilitates range shifts or makes communities more resilient to them (See *Theoretical predictions* below). Additionally, it may be possible to examine the consequences of range shifts by continuing to examine the warmed and non-warmed communities following the introduction of the range shifting species. This will allow us to determine the continued effects of warming, and range-shifting species have on the diversity and interactions in their recipient communities. Given the strong links between diversity, community structure, and ecosystem function (Hooper *et al.*, 2005; LaRue *et al.*, 2019), we can further extrapolate how these changes will translate into broader, ecosystem-level consequences.

Box 4.1. Stability in food webs. There are many metrics to quantify stability that are useful to ecologists and many of them are correlated with each other (Donohue *et al.*, 2013). However, one metric that is easy to measure in both empirical and theoretical studies is variation over time or space. High variation, specifically in biomass, is associated with decreased stability since higher variation means that systems are less likely to persist through time (Ives & Carpenter, 2007; Donohue *et al.*, 2013). To measure variation, ecologists often use the coefficient of variation to quantitatively measure stability. This approach has precedent in both theoretical and empirical studies and is among the most commonly used metrics for stability (Donohue *et al.*, 2016). The fact that this metric can be quantified in both theoretical and empirical studies is important because it allows us to directly compare outcomes of these two approaches.

4.3. Theoretical Predictions

Undoubtably, the consequences of climate change on the structure and diversity of a recipient community will be strongly influenced by the initial structure and composition of that community (Calizza *et al.*, 2019). This makes it difficult to develop broad, generalized predictions (Gibert, 2019). However, the advantage of this proposed approach is that, rather than creating generalizable predictions, it creates a generalizable framework that it allows us to use our knowledge of communities of interest to generate specific, testable hypotheses about the causes and consequences of range shifts within those communities. Specifically, we can use food-web models to develop hypotheses that can be tested empirically to understand system-specific dynamics. Critically, these models will need to incorporate growth rates and interactions between species that are dependent on the abiotic variables a researcher is interested in. For example, Gilbert et al. (2014) presents an approach to integrate temperature dependence into biomass-specific, consumer-resource models which can be further scaled up by integrating the

temperature-dependence to multi-species interaction models (Yodzis & Innes, 1992; McCann *et al.*, 1998; Stouffer & Bascompte, 2010; McLeod & Leroux, 2020). Starting small with models of food-web modules will help us better understand the interactions between temperature and food-web stability, however it is important to note that while some of the conclusions may scale up the whole food webs (Box 2) others will require the use of additional types of models like niche models (Williams & Martinez, 2000; McLeod & Leroux, 2020) among others (Ulanowicz, 2004). The purpose of these theoretical tests is to determine what changes may be necessary in food webs to allow for the establishment of a range-shifting species. The outcomes generated from such models should be considered hypotheses which can be tested empirically. Critically, this modeling step will help narrow down the broad range of potential responses of a community of interest and help researchers craft targeted empirical studies. Additionally, the best models for this will be parameterized by experimental or observational data from natural systems to increase their utility for generating testable hypotheses.

As a thought exercise, we examine hypothetical mechanisms that would allow for the establishment of three different range-shifting species: a basal species, an intermediate consumer, and a top predator. We focus this exercise on a multi-resource omnivory module (Kratina *et al.*, 2012; McLeod & Leroux, 2020) (Figure 4.2). Multi-resource omnivory is characterized as having a top consumer that feeds on two different resources, one of which is an intermediate consumer that feeds on an entirely different resource than the top consumer (Figure 4.2).We selected this module because omnivory in general has been shown to be important for food-web stability (Thompson *et al.*, 2007; Rip *et al.*, 2010; Gellner & McCann, 2012) and multi-resource omnivory in particular appears to be critically important for the stability of food webs (Kratina *et al.*, 2012; McLeod & Leroux, 2020). Additionally, multi-resource omnivory is a

small-scale representation of the slow and fast channels of energy flow that often underlies stability at the level of an entire food web (Rooney *et al.*, 2006; Rooney & McCann, 2012; McLeod & Leroux, 2020). While the outcomes of each scenario will be highly dependent on the initial conditions of the community and the effects of temperature on interactions and growth rates, we opt to discuss specific possible outcomes to demonstrate the integrated nature of the effects of temperature on the species of interest, the interactions in the community, and the consequences of the introduction of a range-shifting species for community stability.

Box 4.2. Food-web modules. Repeated patterns of connections, known as modules or motifs, have been observed across a wide range of network types (Milo *et al.*, 2002). In food webs, these modules include well-known types of interactions such as tri-trophic food chains, omnivory, intraguild predation, and apparent competition among others and can be found in all types of ecosystem (McCann *et al.*, 1998; Bascompte & Melián, 2005; Stouffer *et al.*, 2007). The role that these modules play in promoting whole food-web stability has been open for debate (Brose, Berlow & Martinez, 2005). However, the hierarchical nature of many of these modules (Clauset, Moore & Newman, 2008), the ways that they arrange and balance strong and weak interactions (Stouffer *et al.*, 2011), and other tests (Kondoh, 2008; Borrelli, 2015) suggest that they could be critical for stability of food-webs as a whole. Moreover, the to their smaller size of modules makes them less computationally cumbersome than whole food webs (McCann *et al.*, 1998). Indeed, large food webs can be computationally difficult to model on their own even without considering the role of temperature (Montoya, Pimm & Solé, 2006). Data useful for modeling entire food webs can also be difficult to come by (Martinez, 1991). However, the best models will be parameterized by empirical data. Thus, working with smaller portions of food webs, which will be easier to parameterize, is probably the best approach at this time.
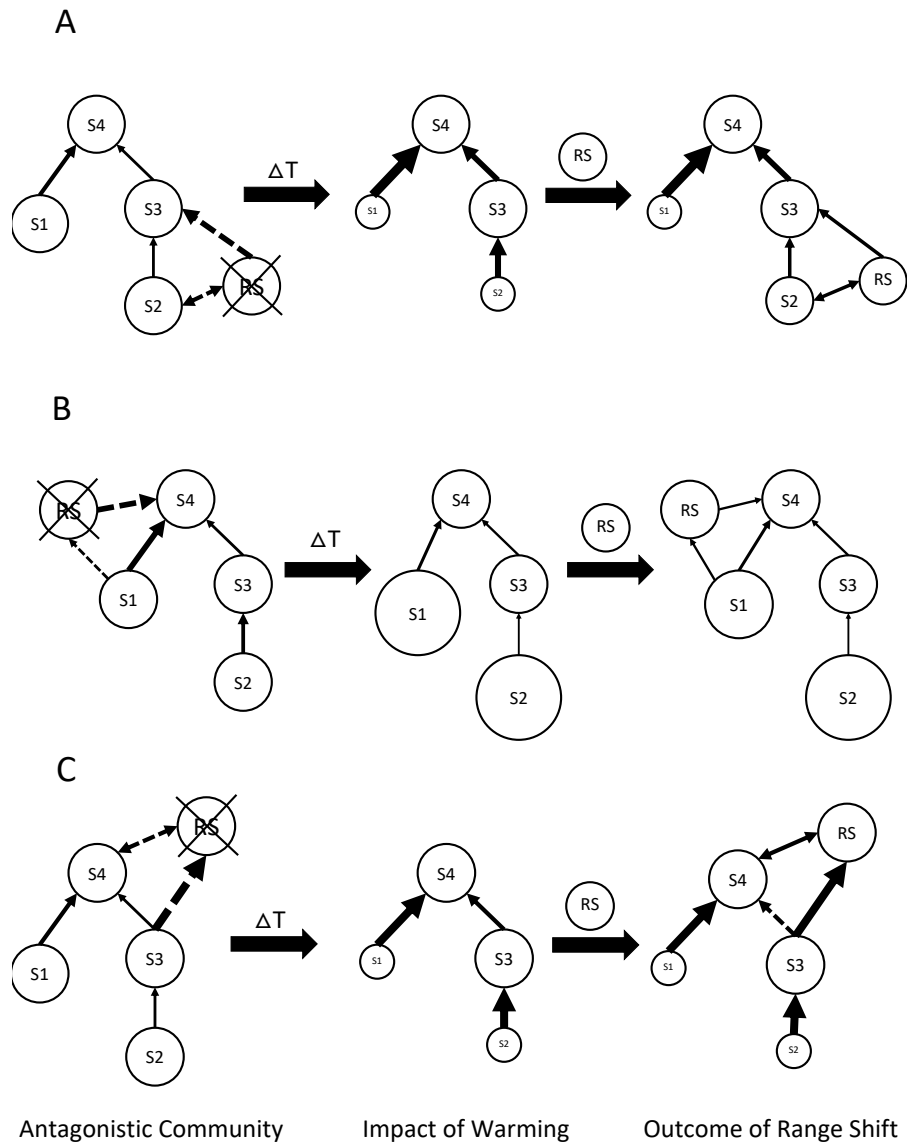
Figure 4.2. Effects of warming and range shifts on ecological communities. Examples of how warming may alter food-web structure and allow the introduction of a range-shifting (a) basal species, (b) intermediate consumer, or (c) top consumer. Circle sizes correlate to standing-stock biomass and line width correlates to interaction strength. Dashed lines represent interactions that could be or were present but are not due to a change in the community. Single-headed arrows indicate predation and double-headed arrows indicate competition. See text for further details.

4.3.1. Basal resource

For the first scenario (Figure 2a), let us consider a range-shifting basal resource (RS) that could potentially enter the recipient community as a competitor with the basal species (S2) in the long chain and a potential prey item of the intermediate consumer (S3). We might hypothesize that this species (RS) is unable to enter this food-web for several reasons. First, competition (Price & Kirkpatrick, 2009) and predation (Holt & Barfield, 2009) from the resident species may preclude the shifting one from establishing. Second, the individual and/or population growth rate of the species might be low at cooler temperatures compounding the issue (Finstad *et al.*, 2011; Shepard *et al.*, 2021). These abiotic and biotic effects do not operate independently from each other, and warming will likely affect them both (Kaur & Dutta, 2020).

While there are many ways that warming could affect this food-web module, one way is that warming could lead to destabilization through changes to interaction strengths. Specifically, warming may increase the strength of top-down control by S3 and S4 (Figure 2a) leading to reductions in the biomass of the basal species S1 and S2 in the food-web module (Vasseur & McCann, 2005; O'Connor *et al.*, 2009; Rall *et al.*, 2012; Garzke *et al.*, 2019; O'Gorman *et al.*, 2019). An increase in interaction strength in this manner potentially synchronizes the rate of energy flow through the long and short channels (Figure 2a). In other words, increasing the interaction strengths in the long channel will increases the synchrony between the fast and slow channel, which could lead to a decrease in stability of the module (Rooney *et al.*, 2006; Rooney & McCann, 2012). However, this very instability may allow the range-shifting species to successfully establish (Figure 2a). With its competitor's (S2) density reduced and its predator's (S3) density kept relatively consistent via increased consumption from the top predator (Figure

2a), the range-shifting species may experience reductions in antagonistic interactions and successfully integrate into the community (Hui & Richardson, 2019). Additionally, increases in temperature may increase the growth rate and/or the carrying capacity of the range-shifting species (DeLong & Hanson, 2011) if they are better adapted to warmer climates (Buizer *et al.*, 2012). This higher growth rate or carrying capacity may increase their resilience to antagonistic interactions further promoting their establishment.

The introduction of this range-shifting species may help restore stability to this community. In this scenario, instability was created by increasing the rate of energy flow through the long channel, synchronizing dynamics with the short channel. The introduction of the range-shifting species to the long chain may help restore asynchrony and increase stability. By establishing as an alternative prey item for the intermediate consumer (S3), the range-shifting species may weaken the effects of the intermediate consumer (S3) on its basal resource (S2) (Figure 2a) since higher connectance is often associated with decreased interaction strengths (Montoya & Solé, 2003; O'Gorman *et al.*, 2010). This decrease in interaction strengths/rate of energy flow should move the long chain out of synchrony with the short chain creating conditions consistent with what is observed in many stable food webs (Rooney *et al.*, 2006; Rooney & McCann, 2012).

4.3.2. Intermediate consumer

For the second scenario (Figure 2b), let us consider a situation where that the range-shifting species (RS) is an intermediate consumer that feeds on the basal resource of the short chain (S1) but is also consumed by the top consumer (S4). Prior to warming, the range-shifting species may be excluded from the resident community because the top consumer both outcompetes and actively consumes the range-shifting species, it making it difficult for it to

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establish (Holt & Barfield, 2009; Price & Kirkpatrick, 2009). Additionally, the initial abiotic conditions of the recipient community may affect the temperature-dependent population growth rate of the range shifting species such that it has difficulty maintaining a sufficiently high population size for persistence (Bernhardt, Sunday & O'Connor, 2018).

Again, while warming may have many consequences on the food-web module, one outcome could be that warming increases the biomass for the resources at the base of the module through reduced interactions with higher consumers and increases in productivity (Petchey *et al.*, 1999; Binzer *et al.*, 2012, 2016) (Figure 2b). Specifically, the increases in consumer metabolic rate associated with increases in temperature may not be met by increases in consumption rates (Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011). This decrease in interaction strength and resulting increase in lower trophic-level biomass may be stabilizing in some instances as it weakens top-down control (Binzer *et al.*, 2012, 2016). However, the presence of some strong interactions are still important for stability since it creates asynchrony in the food web (Wootton & Stouffer, 2016). Therefore, reducing all consumptive interactions may lead to synchronization and destabilization of the food web module (Rooney & McCann, 2012). The changes to the food web in this scenario may allow the range-shifting intermediate consumer to enter the food web (Figure 1b) as competition and predation risk with the top consumer (S4) will have decreased with temperature while biomass of its food resource simultaneously increases (Binzer *et al.*, 2012). This benefit may be increased if warming creates abiotic conditions that also increase the growth rate of the range-shifting species.

Establishment of the range-shifting species may allter the stability of the food-web module by changing synchrony in the community (Figure 2b). In this scenario, the range-shifting species integrates into the short channel where it interacts with S1 and S4. Similar to the

previous scenario, the introduction of the range-shifting species will increase the connectance of the half of the module it enters leading to a decrease in interaction strengths (Montoya & Solé, 2003; O'Gorman *et al.*, 2010). However, in this instance, instead of creating asynchrony between the two channels of the module, this introduction will increase synchrony between them by slowing down the shorter, quicker channel (Figure 1b). Indeed, increasing the diversity of the shorter, faster channel may slow down the flow of biomass (Rooney & McCann, 2012). By slowing the rate of biomass flow, the short channel may become synchronized with the longer channel that already has high diversity and slow biomass flow rates. This synchronization is associated with decreased stability (Rooney *et al.*, 2006; Rooney & McCann, 2012).

4.3.3. Top consumer

Finally, for the scenario considering a range-shifting top consumer (Figure 2c). This species may be excluded from the recipient community by temperature alone and the structure of the recipient community may have no impact on its survival and persistence. Indeed, in this scenario the range-shifting species (RS) may be able to outcompete the resident species (S4) for the intermediate consumer (S3) in the long channel, but temperature alone prevents this shifting species (RS) from successfully establishing. Thus, any changes to the recipient community resulting from warming may be inconsequential for the establishment of this range-shifting species. However, changes to the recipient community caused by warming may have important impacts for the long-term stability of the community, especially following the introduction of the range-shifting species.

For this example, warming may increase the strength of consumptive interactions and top-down control in a similar fashion to the first example (Figure 2a, 2c). In this scenario, the

standing biomass of the basal species (S1) and (S2) would be decreased as a result of the increased interaction strengths in the module (Figure 2c).

Once warming allows the range-shifting species to integrate, it is possible that the new predator will outcompete and exclude the resident top-consumer from feeding on the intermediate consumer (Figure 2c). While these changes in consumption patterns by the top-consumer may not directly impact prey populations (Mofu *et al.*, 2019), the two channels of the multi-resource omnivory module would become decoupled (Figure 2c). This would create two independent food-web modules that are likely to be unstable due to the overwhelming abundance of strong interactions (Rooney & McCann, 2012; Wootton & Stouffer, 2016) resulting from warming increasing the strength of top-down control (Vasseur & McCann, 2005; O'Connor *et al.*, 2009; Garzke *et al.*, 2019).

4.4. Empirical tests

Developing empirical approaches to understand the food-web context of range shifts presents a number of logistical hurdles. However, by using mathematical models we can generate specific hypotheses around which we can test our theories. As discussed above (see *Theoretical predictions*), using food web models that integrate abiotic context dependence (i.e. Gilbert *et al.* 2014) we can determine if and how food webs of interest might be altered by climate and which links might be most affected by abiotic changes. While most easily accomplished at the scale of food-web modules, larger scale models may be used as well (e.g. niche models) (William & Martinez, 2000).

Once models of ecological communities (e.g. food web module vs entire community) have been used to generate specific hypotheses, our proposed framework allows for straightforward empirical tests of these hypothesis. We propose six key steps in conduct

experiments under the proposed framework: 1) establishing a community of interest, 2) assessing the community, 3) warming the community, 4) assessing the impacts of warming, 5) introducing a range shifting species, and 6) assessing the combined effects of warming and range-shifting species. Establishing a community of interest can be done artificially through, for example, the establishment of pond communities in outdoor mesocosms (e.g. (Jones *et al.*, 2020)), or naturally through, for example, the fencing of vegetation plots. The next step is to assess the current community state. Assessing the community state is critically important because the outcomes are likely to depend on whether the community has reached an equilibrium or is still in a transient state (as observed in Gilbert et al 2014). While it may not be logistically practical to ensure the community has reached an equilibrium at the beginning of the experiment, simply quantifying its state after it has been established will provide the context required to interpret the outcomes of the experiment. This quantification will require surveys to determine the identities and relative abundances of the various community members in either the artificially established or naturally occurring plots. It is also necessary to quantify the interactions between species at this step. This will require integrating the relative species densities with information on biomass flow or relative consumption rates of the species in the food web (Berlow *et al.*, 2004). Multiple approaches can generate this information, including gut content analysis (Novak *et al.*, 2017; Preston *et al.*, 2018), stable isotope/fatty acid analysis (Nielsen *et al.*, 2018), or prior knowledge of the community based on previous experiments or surveys among other methods (Berlow *et al.*, 2004). Small-scale assays examining consumption rates or interaction strengths nested within the experimental setup may also be helpful in this regard. For example, in a terrestrial experiment, herbivory could be quantified by placing mesh coverings over individual leaves of some of the plants in each replicate across all treatments. This step is likely to be a logistically

difficult task further supporting the idea that focusing on food-web modules might be a good place to start.

Once the initial members of the community and their interactions are quantified, the next step is to add a warming treatment. Half of the established or selected community plots should be warmed in accordance with projected temperature increases for the region in which the study is being conducted. This warming can be accomplished in a variety of ways ranging from aquarium heaters for pond mesocosm experiments e.g. (Shurin *et al.*, 2012) to plastic enclosures for plots of vegetation e.g. (Jónsdóttir *et al.*, 2005). After the warming has been applied for an amount of time appropriate for the community being studied, subsamples should be taken to determine the relative abundances of the community members and the strengths of their interactions in both the warmed and non-warmed treatments. This will allow for comparisons between warmed and non-warmed communities to determine how climate change will alter the arrangement and strengths of interactions, if at all. This also allows researchers to determine the state of the communities prior to the introduction of the range-shifting species.

Following the subsampling, half of the warmed and half of the non-warmed treatments should receive a range-shifting species of interest. Following an appropriate amount of time, all established communities should be destructively sampled to get precise estimates of the final relative densities of each of the community members and their interactions which can, again be assessed using methods described above. Like the theoretical approach, this empirical method will result in 4 groups to compare: a non-warmed control, a non-warmed treatment with a range-shifting species, a warmed control, and a warmed treatment with a range-shifting species. This final group of replicates is the one of primary interest as most closely mimics the scenarios many communities and species experience as climate change continues to facilitate range shifts. The

expected outcomes of such an experiment are varied and will depend on the communities and range-shifting species of interest (see above).

4.5. Identifying recipient communities of interest

Shifting the focus away from the range-shifting species themselves and towards the communities that these species are likely to be moving into begs the question as to which communities are most likely to experience the introduction of range-shifting taxa and should be the focus of this work. We believe, based on the current literature, that communities at high latitudes and altitudes are high priority habitats for understanding the causes and consequences of range shifts.

The bulk of evidence suggests that, under current climate change conditions, most range shifts are occurring either up in latitude or elevation (Parmesan & Yohe, 2003; Chen *et al.*, 2011; Pecl *et al.*, 2017). While this is not entirely universal (Freeman *et al.*, 2018) the fact that so many species are moving in those directions means that communities at higher latitudes and elevations are more likely to be subject to the introduction of range-shifting species. Climate change is also occurring at a much faster rate in high latitude and elevation habitats their low latitude and elevation counterparts (Post *et al.*, 2009; Pepin *et al.*, 2015; Koenigk, Key & Vihma, 2020) meaning that food webs in high latitude and elevation habitats are more likely to experience changes in structure and/or stability due to shifts in abiotic conditions.

High latitude and elevation communities typically have low diversity (Hillebrand, 2004; Sergio & Pedrini, 2007; Wissinger *et al.*, 2016). This makes high elevation and latitude habitats relatively tractable for quantifying the relative abundances and interactions between all the members of a community. Moreover, the increase in diversity that results from a range shift is likely to have outsized consequences in these depauperate communities as the addition of a

single species constitutes a greater percentage increase in total diversity and may also introduce novel functional traits (Dubuis *et al.*, 2013). Thus, potential effects of climate change and range shifts on community structure and stability should not only be easier to detect but understanding these consequences is likely to have significant conservation implications

Once a recipient community of interest has been identified, it is up to the researcher to determine what the potential range-shifting species might be. As with any meaningful ecology, this will require scientists to have a deep knowledge of the natural history of the system they are working in (Dayton & Sala, 2001; Anderson, 2017). One way this can be done is through the development of long-term datasets in ecosystems of interest (Lindenmayer *et al.*, 2012) including natural history observations (e.g. Wissinger, *unpublished data*, others)(Alward, Detling & Milchunas, 1999; Holmes & Sherry, 2001; Willis *et al.*, 2008). Despite this, there are some generalizations we can make to narrow down the possibilities of potential range-shifting species. Species that are generalists both in terms of diet or abiotic preferences may be more prone to shifting their ranges as the climate changes (Angert *et al.*, 2011; Yang *et al.*, 2020). Additionally, species with high dispersal capabilities may also be more likely to shift their ranges (Pöyry *et al.*, 2009; Fitt *et al.*, 2019). Thus, higher order consumers that link various trophic pathways may be more likely to shift their ranges due to their increased mobility and generalist tendencies (Bartley *et al.*, 2019). In contrast, specialized consumers are unlikely candidates for range shifters as their ability to move into a new habitat is predicated on the presence of their preferred resource (Angert *et al.*, 2011). Exceptions are bound to exist but that only reinforces the importance of ensuring researchers have a strong understanding of the natural history of the systems they are working in.

4.6. Conclusions

Approaches that integrate abiotic variables and biotic interactions are critical to furthering our understanding of the mechanisms behind range shifts, especially in a changing climate. Our food-web approach moves the focus of these efforts away from the shifting species and onto the recipient community. Moreover, our approach is generalizable in that it creates a framework which can be applied to any type of ecological community and any type of abiotic variable to generate hypotheses specific to the community of interest. By emphasizing the role ecological communities in range-shift dynamics, it also becomes easier to translate findings into information for meaningful conservation or management practices that emphasize ecosystems and their functions rather than individual species (Sinclair & Byrom, 2006; Cadotte, Carscadden & Mirotchnick, 2011; Harvey *et al.*, 2017).

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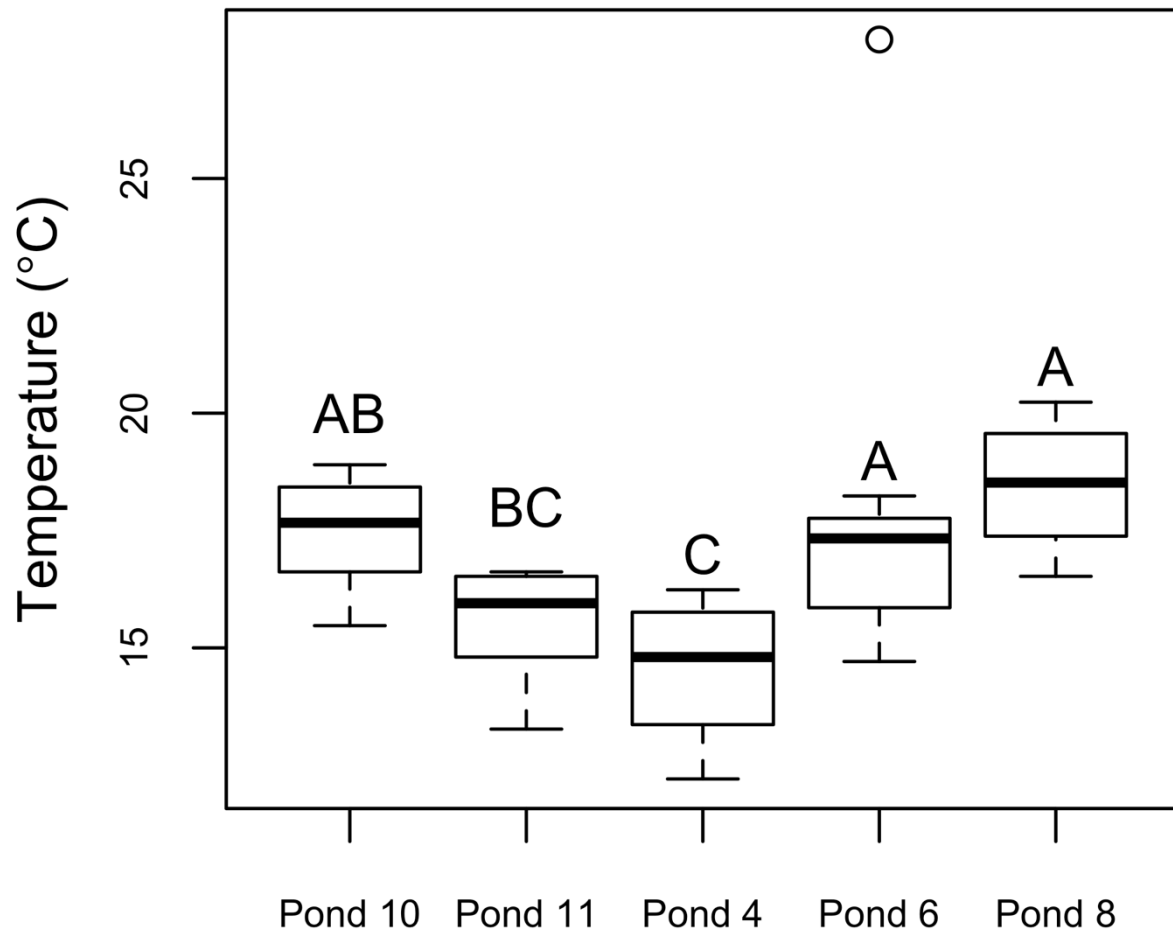
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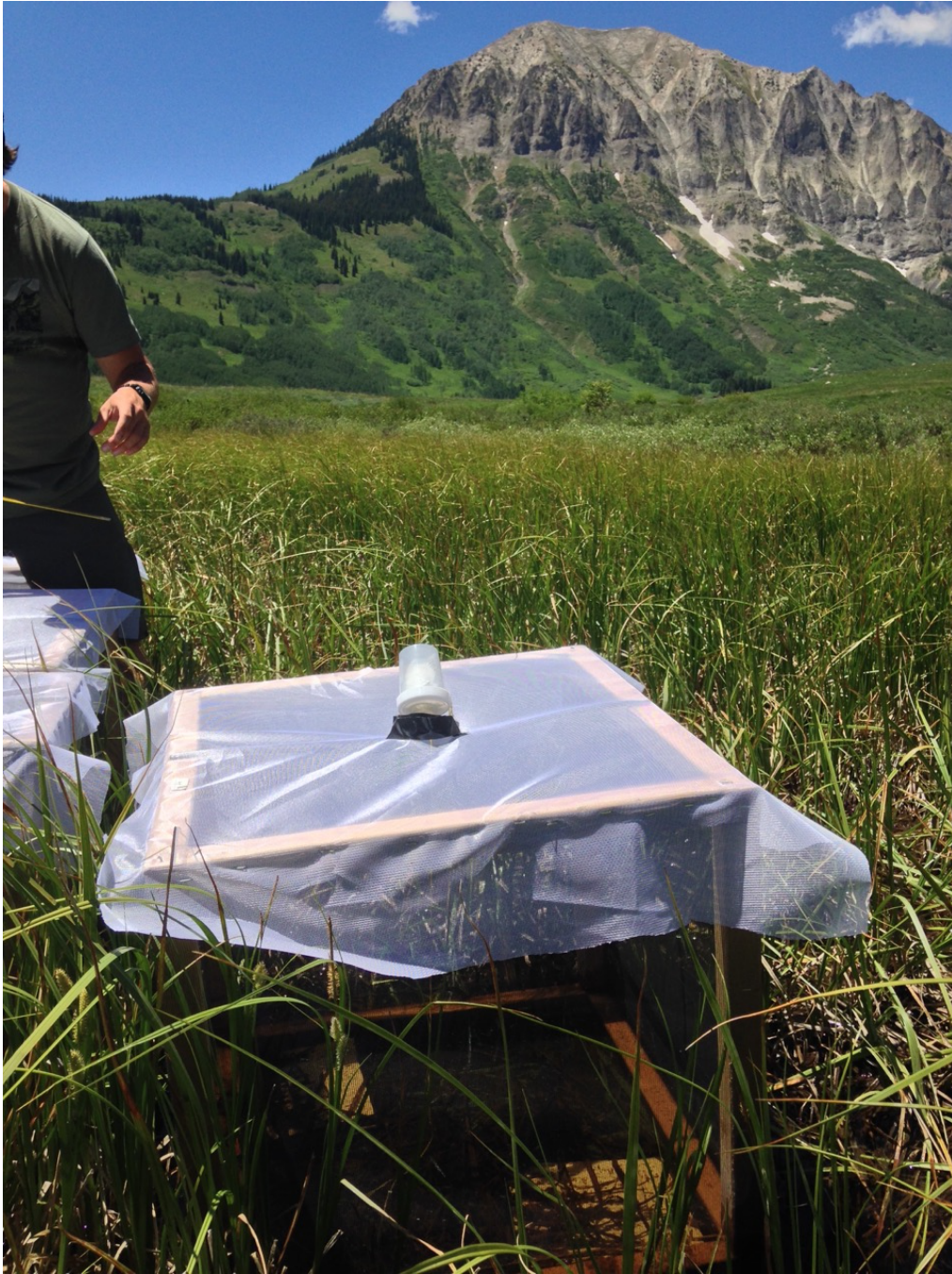
Figure A1. Example of cage with lid. An image of one of the cages used in the montane field experiment showing the lid and emergence trap. Photo credit: Hamish Greig.

Figure A2. Pond Temperatures. Average noon-time temperature of the 5 ponds used at the Mexican Cut Nature Preserve for the subalpine experiment taken from the final 14 days of the experiment. Letters indicate significantly different groups ($p < 0.05$) from a Tukey Honest Differences post hoc analysis. Points indicate outliers.
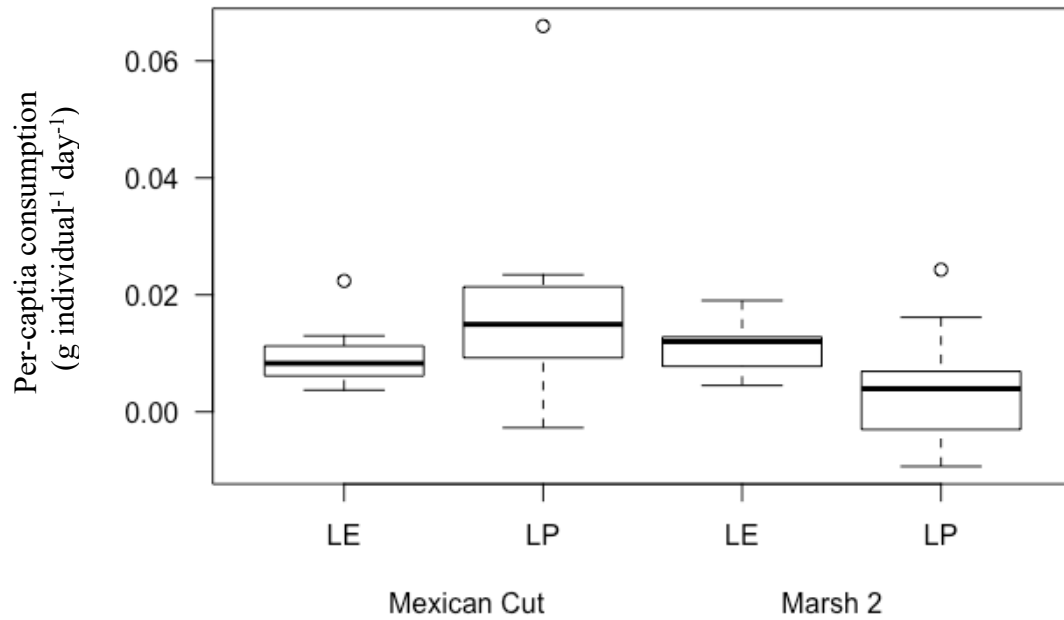
Figure A3. Per-capita detritus consumption. Per-capita rates of detritus consumption of

Limnephilus externus (LE) and *Limnephuilus picturatus* (LP) in cages at subalpine (Mexican cut)

and montane (Marsh 2) elevations in the Elk Mountains CO. Points indicate outliers.
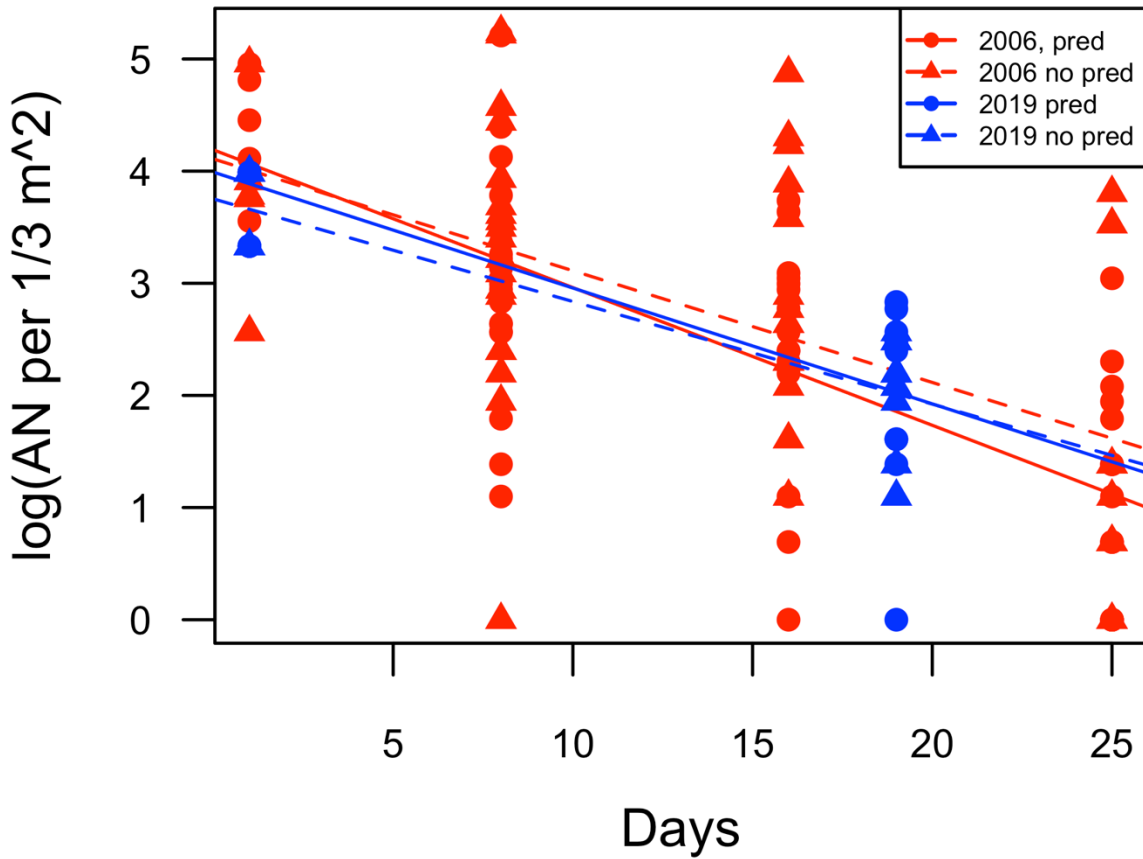
Figure B1. Caddisfly density declines through time. Natural log density of *Asynarchus nigriculus* (AN) in ponds (red) and cages (blue) with (circles) and without (triangles) beetle larva predators (pred) over the course of August in the Elk Mountains of Colorado, USA. Pond data were collected from surveys taken multiple days throughout the August of 2006. Lines show best line of fit for the absence (solid) and presence (dashed) of beetle larva predators. Linear regression shows that none of the slopes of these lines were significantly different from each other.
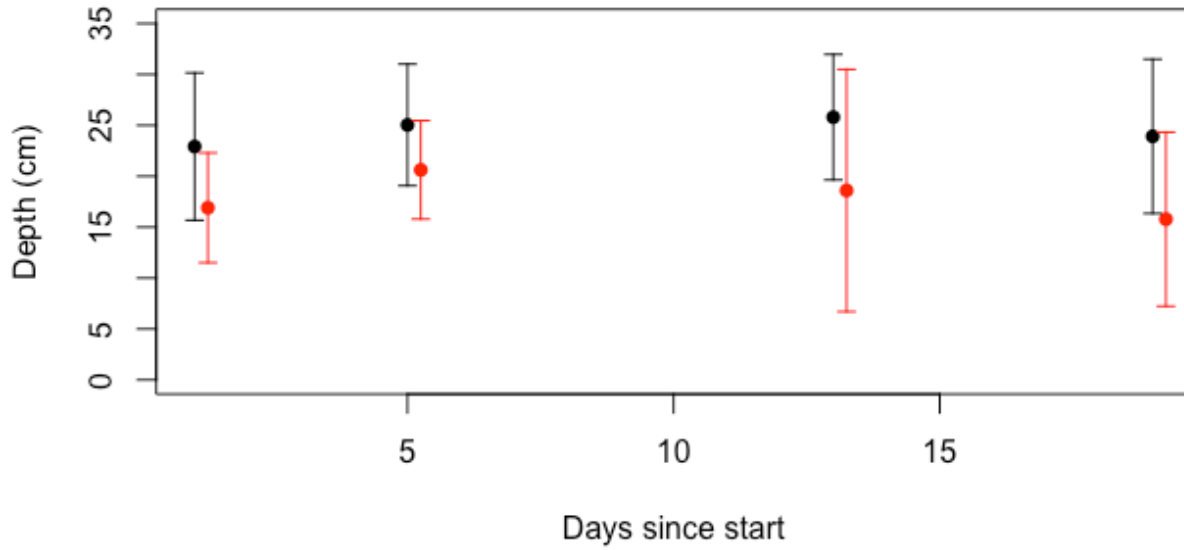
Figure C1. Cage depths. Average depth of the temporary (red) and semi-permanent (black) ponds during the caging experiment at the Mexican Cut Nature Preserve in the Elk Mountains of Colorado, USA. Error bars represent 1 standard deviation. Points are offset to improve clarity of visual.

BIOGRAPHY OF THE AUTHOR

Isaac D. Shepard was born in Corvallis, Oregon in March of 1994. While developing a love for the outdoors and the natural world, Isaac attended Corvallis High School where he graduated as Valedictorian in 2012. He then went on to earn an Honors Bachelor of Science in Biology with a Marine Biology Option in 2016 at Oregon State University where he graduated *summa cum laude*. He is a candidate for the Doctor of Philosophy degree in Ecology and Environmental Sciences at the University of Maine in December 2021.