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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Interspecific interactions are conditional on temperature in an Appalachian stream salamander community

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Abstract

Differences in the rates of responses to climate change have the potential to disrupt well-established ecological interactions among species. In semi-aquatic communities, competitive asymmetry based on body size currently maintains competitive exclusion and coexistence via interference competition. Elevated temperatures are predicted to have the strongest negative effects on large species and aquatic species. Our objectives were to evaluate the interaction between the effects of elevated temperatures and competitor identity on growth and habitat selection behavior of semi-aquatic salamanders in stream mesocosms. We observed interference competition between small and large species. Elevated temperatures had a negative effect on the larger species and a neutral effect on the smaller species. At elevated temperatures, the strength of interference competition declined, and the smaller species co-occupied the same aquatic cover objects as the larger species more frequently. Disruptions in competitive interactions in this community may affect habitat use patterns and decrease selection for character displacement among species. Determining how biotic interactions change along abiotic gradients is necessary to predict the future long-term stability of current communities.

Keywords Climate change · Competition · Interference · Size-structured · Plethodontidae

Introduction

Species may respond to contemporary environmental change by (1) shifting in distribution and latitudinal range, (2) changing life history phenology, and (3) reducing body size (Daufresne et al. 2009; Gardner et al. 2011). Responses to climate change are inconsistent and variable across taxa, trophic levels, and ecosystems (Walther et al. 2002; Blaustein et al. 2010; Sheridan and Bickford 2011). Mismatches in the rates of ecological change within a community could disrupt well-established ecological and evolutionary processes (Van der Putten et al. 2010). Multiple response mechanisms coupled with wide variation in types and rates of responses make it challenging to determine the long-term stability of communities to changing environmental gradients (e.g., temperature or humidity, Narum et al. 2013; Caruso et al. 2014, but see Grant 2014 and Connette et al. 2015). Body size is one trait with generally well-understood connections to species' ecology (e.g., physiology to demography; Ohlberger 2013) and may offer an opportunity to develop predictions about how inter-species interactions will vary with changes in environmental gradients to structure future communities (Jonsson 2014; Peterman et al. 2016).

Global ecological patterns predict that organisms become smaller at warmer temperatures, thus body size reductions are predicted to be a general evolutionary response to elevated temperatures (Bergmann 1847; Gardner et al. 2011; Peterman et al. 2016). For ectothermic organisms, changing thermal regimes directly impact important metabolic relationships and may have more immediate changes on physiology, behavior, and ecology relative to endothermic animals (Angilletta and Dunham 2003; Arendt 2011; Ohlberger 2013). Specifically, ectotherms are expected to have smaller body sizes at warmer temperatures because of (1) increases in metabolism that reduce energy storage in the absence of

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compensatory foraging, (2) shifts in water conserving behaviors as evaporation rates increase, and (3) complete reductions in body size throughout a food web (Vucic-Pestic et al. 2010; Sheridan and Bickford 2011; Li et al. 2013). Others have suggested that body size relationships with thermal regime are primarily a result of temperature influences on competitive interactions (Edeline et al. 2013). Regardless of the mechanism, body size is expected and has been documented to decline within species, communities, and food webs at warmer temperatures (Daufresne et al. 2009).

In size-structured communities, long-term adaptations to current climate regimes have resulted in stable life history traits, species interactions, and community structures that minimize competition allowing coexistence (e.g., character displacement, niche partitioning; Hairston 1980; Werner and Gilliam 1984; Bruce 2008). Rapidly increasing environmental temperatures may, therefore, intensify or weaken the strength of competition potentially reversing the direction of interactions (Price and Secki Shields 2002; Ennen et al. 2016). If smaller species begin to perform better at warmer temperatures, asymmetrical interactions that previously favored larger species may weaken or even reverse direction to favor smaller species (Persson 1985; Daufresne et al. 2009). Species can compete in multiple ways, but theoretical work suggests that size may only be relevant during interference competition (Persson 1985; Price and Secki Shields 2002). Therefore, morphological changes in response to shifting thermal regimes may result in changing community structure when interference competition is present and could accelerate species extinctions (Sinervo et al. 2010; Reuman et al. 2014).

One size-structured community used to develop the theoretical framework of species coexistence is the stream salamander guild of desmognathan salamanders (Hairston 1987). Extreme size differences and variability in cutaneous resistance to desiccation among species appear to be a result of strong character displacement with large individuals occupying streams where they exclude smaller individuals to semi-terrestrial and terrestrial habitats (Hairston 1980). Furthermore, even interspecific interactions between similarly sized individuals are asymmetrical in favor of the larger plethodontid species (Price and Secki Shields 2002; Bruce 2008; Adams 2010). While aggressive interactions may be rare, they are presumed to maintain interference competition and competitive exclusion of smaller members of the community from aquatic habitats (Persson 1985). Though competition governs interactions between similarly sized individuals, large size differences can result in intra- and inter-species predation (Southerland 1986; Hairston et al. 1987). Both processes reinforce spatial niche partitioning and morphological and physiological variation among species (Rissler et al. 2004). Should morphological and physiological traits become more similar in the future, disruption of these well-adapted community structures is likely to occur, negatively impacting community stability and maintenance of biodiversity (Sheridan and Bickford 2011).

Salamanders in the family Plethodontidae are small lungless ectotherms that require cutaneous respiration for gas exchange (Feder 1983; Riddell and Sears 2015). Because moisture is necessary for oxygen to diffuse across their skin, plethodontids are especially sensitive to changes in moisture and temperature that increase desiccation rates (Blaustein et al. 2010; Connette et al. 2015). Precipitation patterns in the region are predicted to become more extreme making drought conditions more likely, and warmer temperatures are likely to exacerbate low humidity conditions (Dore 2005; Alexander et al. 2006). Large aquatic salamander species may respond more quickly to changes in humidity because of small surface area to volume ratios relative to small species and lower cutaneous resistance to desiccation (Houck and Bellis 1972; Riddell and Sears 2015). These changes are particularly important because adult semi-aquatic salamanders primarily forage terrestrially (Petranka 1998; Grover and Wilbur 2002; Peterman et al. 2008). Consequently, large species may become increasingly resistant to leaving streams to forage as a water conserving behavior, and in the absence of interference competition in near-stream terrestrial habitats, smaller salamander species may move closer to streams (Hairston 1980; Feder and Londos 1984). Ultimately, when moisture conserving behaviors of larger species restrict terrestrial foraging behaviors necessary to compensate for increased metabolic rates at elevated temperatures, their performance and size may decrease increasing their metabolic needs (Reading 2007; Rollinson and Rowe 2018; Caruso et al. 2014, but see Grant 2014; Connette et al. 2015). For smaller species with higher resistances to desiccation, having a broader climatic niche and the ability to access high moisture habitat may allow their performance to increase resulting in positive changes in frequency and abundance relative to larger species (Daufresne et al. 2009; Sheridan and Bickford 2011).

Phylogeographic studies suggest that much of the Appalachian salamander diversity evolved in specific climatic regimes and that adaptations to these regimes may prevent high performance in others (Pörtner and Farrell 2008; Angilletta 2009; Kozak and Wiens 2010; Ohlberger 2013). Shifts in processes that have historically constrained species's life histories and ecological roles could have strong negative effects on community stability and future function (Rissler et al. 2004; Sinervo et al. 2010; Edeline et al. 2013). Evaluating short-term responses to elevated temperatures is necessary to assess the long-term stability of organisms in the context of their communities, which has been a key limiting factor in predicting species extinctions using abiotic variables alone (Adams 2010; Brose 2010). We expect that the stability of size-structured communities is based on interference competition that will be reduced in strength at elevated temperatures (Persson 1985). We performed an experiment to evaluate if increased temperatures would decrease size asymmetry between pairs of competing *Desmognathus* salamander species. Competitive interactions may be altered as a result of (1) declining performance of the larger species at warmer temperatures, (2) increasing performance of the smaller species at warmer temperatures, and (3) increased aquatic habitat use by both species at warmer temperatures.

Materials and methods

Multiple species within the genus *Desmognathus* coexist in streams as a result of spatial niche partitioning and contribute to the high biodiversity of the southern Appalachian Mountains (Carr and Taylor 1985; Hairston 1987). We focused on two large congeners of the genus for which previous research has described spatial exclusion of the smaller species (*D. monticola;* seal salamander) by the larger species (*D. quadramaculatus;* black-bellied salamander; Hairston 1980; Rissler et al. 2004). *Desmognathus monticola* occupies a range of habitats where it co-occurs with *D. quadramaculatus* in the southern Appalachian Mountains, but it has an expanded range north into the central Appalachian Mountains, west to the Cumberland Plateau, and south to the lower coastal plain of Alabama (Petranka 1998). *Desmognathus quadramaculatus* is found exclusively within the southern Appalachian Mountains (Petranka 1998; Camp et al. 2002). Typically found within first and second order streams, *D. quadramaculatus* is a larger, more aquatic competitor that prefers to avoid high temperatures (Cecala et al. 2017). All salamanders for this experiment were collected by hand from a single population at Mill Creek in Murray County, Georgia. We collected adult salamanders without evidence of previous tail autotomy.

We designed two, two-factor experiments investigating how intra- versus interspecific competition affected body condition at current and elevated temperatures. Each of these experiments used a different species in intraspecific treatments because of limitations in mesocosm availability ($N = 16$). We first evaluated *D. monticola* in intraspecific treatments followed by *D. quadramaculatus* in intraspecific treatments. Interspecific treatments were repeated with different individuals in both experiments. The experiment with *D. monticola* as the focal species was carried out from 8-Feb to 25-Mar-2016 for a total of 45 days in a greenhouse at the Tennessee Aquarium Animal Care Facility. Experiments with *D. quadramaculatus* as the focal species were carried out from 13-Feb to 27-Mar-2017 for a total of 42 days in a covered and fenced outdoor facility at the new Tennessee Aquarium Conservation Institute. The location of experiments differed due to the unavailability of the greenhouse in the spring of 2017. Elevated temperatures were warmed 2 °C to match predictions for stream temperature increases by 2100 (Isaak and Rieman 2013; Van Vliet et al. 2013).

Salamanders were captured less than 1 week prior to initiation of each study. They were transported to the University of the South where they were held at 12 °C in native stream water in complete darkness to minimize stress associated with capture and temporary housing because salamanders rarely select well-lit locations during daylight hours (Cecala and Maerz 2016). Salamanders were measured [snout–vent length (SVL) and total length (TL)], weighed and anesthetized to implant PIT (passive integrated transponder) tags (Mitchell et al. 2017). We used a stratified random approach to randomly assign intraspecific and interspecific pairs to avoid large size differences between individuals (< 5 mm SVL) resulting in densities of 2 salamanders per mesocosm to approximate densities of adult salamanders in situ (2.1 m^{-2}; Jaeger 1979; Peterman et al. 2008). Similar sizes were used to minimize the risk of predation between treatment individuals and to maintain observations of competitive interactions. Each pair (intra- or interspecific) was randomly assigned to either a current or elevated temperature mesocosm resulting in 4 replicates of each competition-temperature treatment.

We used 16 independent stream mesocosms (Ennen et al. 2016: Liles et al. 2017). Mesocosms were $1.20\ \mathrm{m} \times 0.60\ \mathrm{m} \times 0.53\ \mathrm{m}$ and each had a circulation system that drained to a plastic sump with a pump that returned water to the tank. Water circulated at a rate of 0.6 Ls^{-1} representative of sampled streams (Liles et al. 2017; Ennen et al. 2016). The water depth was maintained using a standpipe set at 10 cm. Streams were initially filled with 176 L of dechlorinated water with additional water added as needed to compensate for evaporation. To prevent salamanders from escaping, enclosures were covered with window screen and secured tightly with binder clips. In each mesocosm, we randomly assigned a coarse mix of sand and gravel as stream substrate and gathered a portion to form a small (~ 5 cm) terrestrial strip. We also randomly assigned two rocks (0.09 m^2) with one placed halfway out of the water and halfway in the water and the other was fully submerged. These rocks served as cover objects for the salamanders. The temperatures of the elevated mesocosms were maintained using aquarium heaters (175 L Aqueon aquarium heater, Franklin, WI) placed in the sump. Heaters were on a diel cycle, turned on in the morning and off at night to mimic diel fluctuations of natural streams. HOBO data loggers (Onset, Bourne, MA) were used to assess temperature of the land and water within the enclosures at 15 min intervals for the length of the study.

Salamanders were fed 1.27 cm crickets weekly for the length of the study. We fed 10 crickets weekly in the *D.*

monticola focused experiment and 5 crickets weekly in the *D. quadramaculatus* focused experiment because results of the *D. monticola* focused experiment resulted in salamanders that grew up to 8.77 times faster than observed in situ minimizing competition among individuals (Bruce 2016). To prevent overfeeding, we reduced the number of available prey items. To evaluate differences in habitat use, we recorded the location of each salamander using a PIT tag reader that allowed regular observations without disturbing the mesocosm (Mitchell et al. 2017). Enclosures were checked daily when possible for a total of 34 observations of the *D. monticola* focused experiment and 28 observations of the *D. quadramaculatus* focused experiment, and no more than 1 day passed without an observation. We noted where each individual was in the enclosure and totaled the number of times we found individuals in aquatic or terrestrial habitat or under the same cover object as the other salamander in their enclosure. At the completion of the study, salamanders were removed from the enclosure, identified, measured, and weighed to assess outcomes of competition.

To evaluate individual success, we used differences in individual scaled mass index between pre-and post-experiment measurements divided by the individual's beginning scaled mass index (Peig and Green 2009) hereafter referred to as body condition. Briefly, the scaled mass index compares ratios of length and mass measurements relative to predicted values developed from the group of individuals in this study. It has been established to be the best practice for estimating body condition of small vertebrates in the absence of direct measurements of fat storage (Peig and Green 2009). The fixed effects of competitive and temperature treatments on all individual body condition differences were evaluated using a linear mixed model using mesocosm identity as a random factor (lme4; Bates et al. 2015). All individuals were used to evaluate differences in body condition by treatment, and Satterthwaite approximations were used to estimate F-values using type three sums of squares in package lmerTest (Kuznetsova et al. 2016). Habitat use data (frequency of aquatic habitat use and frequency of cohabitation) were evaluated using two linear mixed models assuming an underlying Poisson distribution (MASS; Venables and Ripley 2002) to evaluate their response to fixed factors of competitive and temperature treatments. Overdispersion was evaluated for each variable for each species by comparing the residual deviance to the degrees of freedom. To maintain a balanced experiment, we randomly selected an individual in intraspecific treatments in the *D. monticola* focused experiment for habitat use evaluations. For the *D. quadramaculatus* experiment, we used both individuals in the mesocosms due to limited numbers of replicates (see "Results" below). All data analysis procedures were run in program R (R CoreTeam 2016) and were repeated for each experiment.

Results

Experiment 1—*Desmognathus monticola* focused experiment

In the current temperature mesocosm, water temperatures were 14.15 ± 0.10 °C, which matched terrestrial temperatures (14.14 ± 0.10 °C). Elevated temperature mesocosms had water temperatures 2.7 °C higher (17.21 ± 0.16 °C) with terrestrial temperatures approximately 1.5 °C warmer (15.69 ± 0.10 °C). Minimum temperatures were equivalent across the two temperature treatments, but maximum temperatures were 2.96 ± 0.65 °C higher in elevated temperature treatments. Salamanders of both species grew in length, mass, and body condition over the course of this study though we note that body condition improved 1.08–1.36 times more at current temperatures than at elevated temperatures (Table 1). Variance associated with mesocosm identity was small at 0.03 ± 0.18. Though the main effects of competition and temperature treatments were not statistically significant ($F_{df=3,19}=0.329$, $p=0.576$; $F_{df=3,19}=1.61$, $p=0.228$ respectively), the interaction between temperature and competition treatment significantly affected changes in *D. monticola* body condition ($F_{df=3,19}=4.93$, $p=0.038$; Fig. 1). At current temperatures, *D. monticola* increased their body condition 30.4 ± 0.09% more in intraspecific than interspecific pairs (Table 1). At elevated temperatures, *D. monticola* body condition differences were minimized between intra- and interspecific treatments. *Desmognathus quadramaculatus* body condition at elevated temperatures achieved 74.7% of body condition increases at current temperatures ($t_{df=1,6}=-1.77$, $p=0.134$).

Desmognathus monticola did not exhibit differences in aquatic habitat use among temperature ($z_{df=1,12}=0.47$, $p=0.64$) or competitive ($z_{df=1,12}=0.93$, $p=0.35$) treatments nor their interaction ($z_{df=1,12}=-0.84$, $p=0.40$; Fig. 2a). Cohabitation was not influenced by competitive treatment ($z_{df=1,12}=0.28$, $p=0.78$) but was higher at elevated temperatures ($z_{df=1,12}=2.644$, $p=0.008$). Cohabitation was most likely in interspecific treatments at higher temperatures ($z_{df=1,12}=-2.62$, $p=0.009$; Fig. 2b). The ratio of residual deviance to the degrees of freedom for the habitat use data ranged from 0.93–1.34 indicating that the data were not generally overdispersed.

Experiment 2—*Desmognathus quadramaculatus* focused experiment

In this experiment, 18 salamanders escaped from the mesocosms leaving only 8 replicates remaining with both

Table 1 Growth in snout–vent length (mm), mass (g), and change in body condition relative to initial body condition (scaled mass index) for each species and treatment

	Current	Elevated
Experiment 1 *Desmognathus monticola*		
Snout–vent length		
Intraspecific	3.38 ± 1.15	3.25 ± 0.65
Interspecific	4.75 ± 1.44	3.75 ± 1.18
Mass		
Intraspecific	2.17 ± 0.18	1.65 ± 0.23
Interspecific	2.14 ± 0.07	1.85 ± 0.30
Body condition		
Intraspecific	0.042 ± 0.005	0.034 ± 0.007
Interspecific	0.037 ± 0.004	0.033 ± 0.004
Experiment 1 *Desmognathus quadramaculatus*		
Snout–vent length		
Interspecific	3.52 ± 0.87	3.54 ± 0.50
Mass		
Interspecific	2.12 ± 0.23	1.45 ± 0.20
Body condition		
Interspecific	0.036 ± 0.004	0.016 ± 0.010
Experiment 2 *Desmognathus quadramaculatus*		
Snout–vent length		
Intraspecific	0.51 ± 0.50	0.00 ± 0.86
Mass		
Intraspecific	− 0.23 ± 0.09	− 0.84 ± 0.15
Body condition		
Intraspecific	0.027 ± 0.011	− 0.020 ± 0.005

Note that these data were obtained from two different experiments. All intraspecific values for *D. quadramaculatus* came from the second experiment focused on *D. quadramaculatus* whereas all values for *D. monticola* and interspecific treatments for *D. quadramaculatus* came from the first experiment focused on *D. monticola*

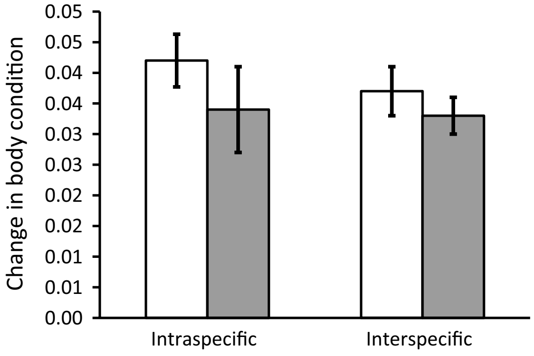

Fig. 1 Change in body condition (scaled mass index ± 1 SE) scaled to initial body condition of *Desmognathus monticola* from the *D. monticola* focused intraspecific interactions and interspecific interactions with *D. quadramaculatus* in current (open bar) and elevated temperatures (shaded bar). Elevated temperatures minimized differences in body condition between intraspecific and interspecific treatments ($F_{df=3,19}=4.93$, $P=0.038$, $N=24$)

individuals at 42 days. Six replicates remained of *D. quadramaculatus* intraspecific competition treatments. Therefore, we only considered data from *D. quadramaculatus* intraspecific competition treatments at current and elevated temperatures for which we had 3 replicates of each treatment. Water temperatures were 11.21 ± 0.04 °C and 13.97 ± 0.04 °C in current and elevated mesocosms respectively with terrestrial temperatures 0.78 ± 0.12 °C higher in elevated mesocosms. The diel cycle was accomplished with low temperatures at night and higher temperatures during the day where lows among both temperature treatments were equivalent, but maximum temperatures were 5.3 ± 0.63 °C higher in elevated temperature treatments. Body condition of *D. quadramaculatus* declined at elevated temperatures ($F_{df=2,9}=7.83$, $p=0.049$), but we note that the effect of temperature was larger in experiment 2 than in experiment 1 with a 189% decline in body condition in elevated temperature treatments relative to current temperature treatments. Mesocosm identity had neutral residuals of 0.066 ± 0.082. Temperature did not impact use of aquatic habitat ($z_{df=1,8}=0.496$, $p=0.62$) but did result in more frequent cohabitation of refugia ($z_{df=1,8}=2.88$, $p=0.004$). Data were not over dispersed with ratios of residual deviance to degrees of freedom of 0.94 and 1.11 for aquatic habitat use and cohabitation data respectively.

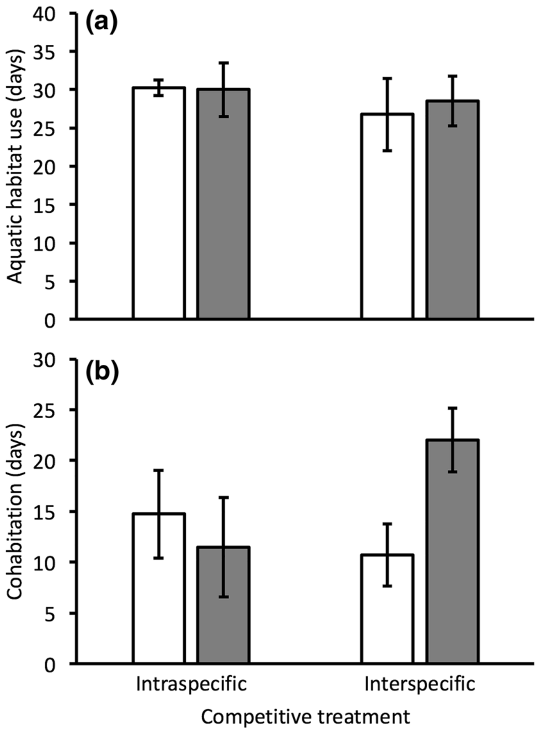

Fig. 2 Days (±1 SE) spent by *D. monticola* in **a** aquatic habitat or **b** cohabitating the same location as their competitor among competitive treatments at current (open bars) and elevated (shaded bars) temperatures in the first experiment focused on *D. monticola* intraspecific interactions and interspecific interactions with *D. quadramaculatus*. Aquatic habitat use was not influenced by competition or temperature treatments ($z_{df=1,12}=-0.84$, $P=0.40$, $N=24$), but cohabitation was higher at elevated temperatures and was most likely in interspecific treatments at higher temperatures ($z_{df=1,12}=-2.62$, $P=0.009$, $N=24$)

Discussion

Future communities will be the product of a complex set of responses to shifting abiotic and biotic drivers with disruption of evolutionarily stable relationships between community members (Walther et al. 2002; Daufresne et al. 2009). Studies seeking to develop predictions about community composition are typically confounded by interactions between abiotic and biotic factors (Van der Putten et al. 2010), but this study isolates these effects to evaluate the interplay between temperature and competitive interactions. We hypothesize that increased cohabitation rates were due to reductions in performance and competitive ability of the larger species though we were unable to test this hypothesis directly. This study demonstrated that elevated temperatures disrupted the strength of competitive interactions and may weaken selection promoting character displacement.

The smaller and larger species responded differently to warming. The larger species, *D. quadramaculatus,* demonstrated sensitivity to warming through smaller increases or reductions in body condition and increased cohabitation at elevated temperatures in both experiments despite changes in feeding rates, thermal variation, and experiment location. *Desmognathus monticola* did not experience body condition declines associated with temperature, whereas *D. quadramaculatus* responded negatively to elevated temperature in both experiments. Furthermore, *D. quadramaculatus* negatively responded to elevated temperatures in both intra- and interspecific treatments though these outcomes are not directly comparable. Reduced feeding rates in the *D. quadramaculatus* focused experiment may have prevented feeding compensation, which is one potential mechanism for maintenance of ecothermic body mass at warmer temperatures (Vucic-Pestic et al. 2010; Sheridan and Bickford 2011; Li et al. 2013). Furthermore, we achieved higher diurnal warming than anticipated in the second experiment. High temperature variation observed in this experiment is within diurnal temperature ranges observed in streams with deforested riparian zones in the geographical ranges of these two species (e.g., Long and Jackson 2013; Cecala et al. 2017), but high temperature variability can contribute to stress associated with chronic high temperatures and create challenges for making predictions about thermal reaction norms in other contexts (Raffel et al. 2006; Niehaus et al. 2012; Paaijmans et al. 2013). Regardless of experimental differences between the *D. monticola* and *D. quadramaculatus* focused experiments, elevated temperatures consistently had a negative influence on body condition of *D. quadramaculatus* and yielded more frequent cohabitation between individuals.

Though body size reduction is predicted to be a common response to climate change (Daufresne et al. 2009), our study corroborates others that suggest that rates of change may be species-specific and those rates of change could be dependent on body size (Sheridan and Bickford 2011; Naya et al. 2017; Rollinson and Rowe 2018). Larger sizes could be maladaptive at warmer temperatures due to increased metabolic needs and concomitant declines in foraging activity and prey body size (Pörtner and Farrell 2008; Forster et al. 2012; Edeline et al. 2013). Many Appalachian salamanders evolved at specific climatic regimes meaning they may have reduced performance at higher or lower temperatures (Pörtner and Farrell 2008; Angilletta 2009; Ohlberger 2013). In fact, salamanders in this community exhibit declines in metabolic rates when exposed to water temperatures predicted for the future that could minimize caloric deficits associated with elevated temperatures, but most likely is a physiological indicator of thermal stress (Bernardo and Spotila 2006). Consumer-resource models suggest that maximum growth occurs at higher temperatures for smaller species allowing them to perform better at elevated temperatures while larger species perform suboptimally (Ohlberger et al. 2011). Regardless of the physiological mechanism contributing to morphological changes, determining whether observed change in body size is an evolutionary shift, a plastic physiological response, or a statistical or methodological artifact should be a priority for future studies (Caruso et al. 2014; Grant 2014; Connette et al. 2015; Peterman et al. 2016). Though researchers have suggested that a broader climatic niche may confer higher adaptability or resistance to climate change (Bernardo et al. 2007), an evolutionary change in body size could simultaneously reduce genetic diversity and species' long-term stability (Daufresne et al. 2009).

Body size of individuals in size-structured communities is predicted to be most important in interactions that result from interference competition (Persson 1985; Price and Secki Shields 2002). Though our study was not designed to explicitly test if interactions between these species are a result of exploitative or interference competition, we infer that it is more likely that these interactions are due to interference competition for aquatic refugia (Keen 1982). First, in intraspecific treatments, we observed a smaller increase in body condition by the smaller species at elevated temperatures that is likely due to an increase in metabolism and the limits on compensatory feeding. We did not observe the same decline in interspecific treatments suggesting that exploitative competition is stronger in intra-species relative to inter-species interactions. Secondly, cohabitation was significantly higher in interspecific treatments at elevated temperatures. At elevated temperatures, we observed decreased performance by the larger species that is consistent with decreased aggression towards the smaller species in short-term experiments (Bissell, K. unpublished data) and higher aquatic cohabitation frequencies in the present experiment. Because aquatic species are more likely to experience body size reductions at elevated temperatures relative to terrestrial species (Forster et al. 2012), communities that exhibit interference competition across this ecotone are most likely to become unbalanced as species respond differentially to thermal regimes.

Asymmetrical competition that maintains character displacement is one process that supports coexistence of closely related species by minimizing overlap in resource use (Werner and Gilliam 1984; Price and Secki Shields 2002). Morphological responses of the larger, more aquatic species to increasing temperature and changes in habitat use by both species suggests reduced strength of asymmetrical competition between the two species. Should this interaction change direction with smaller individuals being competitively superior, large aquatic species may experience accelerated, climate-induced declines (Sinervo et al. 2010). Furthermore, reduced selection for maintenance of traits in the smaller species that facilitate terrestrial habitat use such as small size and high cutaneous resistance to evaporative water losses could result in changing ecological roles or a redistribution of headwater vertebrates (Ennen et al. 2016). More research on interactions of species pairs within a community context is essential for determining whether short-term, ex situ responses are indicative of long-term, in situ responses to environmental gradients. Salamander escapes and simplified spatial and temporal thermal regimes prevented evaluation of spatial or temporal shifts in behaviors or long-term and evolutionary responses to warming (Connette et al. 2015). Similarly, it could be that different skull morphology may favor one species over the other in feeding on crickets rather than the diverse prey base available in situ, but no comparative study of cranial morphology (as with terrestrial *Plethodon* spp.) has been conducted of these two species (Adams et al. 2007). Furthermore, individual responses to climatic gradients can vary widely across the range of a species making complementary in situ surveys particularly vital to broader inference (Blaustein et al. 2010; Urban et al. 2012; Riddell and Sears 2015).

More research is necessary to understand how changes in competitive outcomes within the salamander community will propagate through headwater ecosystems or how changes in alpha selection among species will change the stability or resilience of the community to synergistic or additive threats. Disruption of well-maintained ecological roles could make the community more susceptible to establishment of invasive species (Shea and Chesson 2002), or novel interactions with fish could transform community assembly in southeastern headwater systems (Ennen et al. 2016). Likewise, amphibians are recognized as one taxon important for transporting energy and nutrients across ecosystem boundaries (Vanni et al. 2002; Davic and Welsh 2004), which could be disrupted if terrestrial foraging is minimized. Differences in body size impose important constraints on how organisms interact with their environment and it can affect the strength, type, and symmetry of interactions within an entire community (Schoener 1974; Wilson 1975; Werner and Gilliam 1984). This study supports conclusions that aquatic species will be most immediately affected by elevated temperatures (Forster et al. 2012). Reductions in interference competition that minimize competitive exclusion may result in changes in behavior that could have larger spatiotemporal effects. Outcomes of biotic interactions are clearly tied to environmental gradients (Sinervo et al. 2010), and untangling these interacting effects should be a priority to improve predictions of community assembly, stability, and change with shifting climatic gradients.

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Author contribution statement MH, KC, JE and JD designed the experiments; MH, KC, JE, SM and JD performed the research and

collected the data; MH and KC analyzed the data and wrote the first draft with contributions from all.

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