

## Research

### Trophic structure alters consequences of environmental warming

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Climate warming can directly affect traits and demographic rates of organisms. However, individuals are embedded in complex networks of ecological interactions with other members of the community, allowing for a range of direct and indirect effects that depend on the trophic structure of the community. Here we show that effects of warming (i.e. increase in mean temperature) on a given species can strongly depend on the community context and trophic complexity of the system. Specifically, we manipulated the presence/absence of two competing tadpole species and their dragonfly predators to simulate different food webs of increasing complexity that were exposed to ambient or warmed conditions. We found that warming dramatically reduced herbivore (tadpole) survival in the absence of strong interspecific competition and predation, but it had no measurable effect on demographic rates on the dominant competitor in more complex communities where it was exposed to interspecific competition and predation. Conversely, our results also indicate that warming reduced the strength of interspecific competition and predation in our system. These results suggest that trophic complexity could potentially buffer climate change effects on populations and emphasize that we often cannot predict the effects of changes in abiotic conditions on a given population without accounting for the community context.

Key words: Climate change, temperature, food web, consumer–resource, predation, competition

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#### Introduction

Climate change is affecting ecosystems worldwide (IPPC 2008, 2013) and mounting evidence indicates that this change can strongly affect natural populations. For instance, changes in temperature regimes can alter demographic rates of populations, their geographic distribution, and extinction risk (Walther et al. 2002, Parmesan and Yohe 2003, Post et al. 2009, Harley 2011, Blois et al. 2013, Ma et al. 2015, Urban 2015). While these studies highlight that changes in climatic conditions can have important ecological consequences, predicting how these changes will affect natural populations and communities across a range of systems and taxa is a major challenge of the 21st century (Walther et al. 2002, Blois et al. 2013, Urban et al. 2016).

The difficulty of making reliable predictions largely arises from the complexity and variability of natural communities (Urban et al. 2016). Early studies only focused on the direct effects of changes in climatic conditions on performance of organisms. While this has helped to outline the boundaries of conditions under which any species could persist, extrapolating these single species studies to natural systems is difficult because species do not exist in isolation. Instead, they interact with other members of the community that can potentially modify the outcome of climatic changes (Davis et al. 1998, Zarnetske et al. 2012, Blois et al. 2013, Post 2013, Urban et al. 2016). Importantly, the structure of communities varies across space and time and changes in climatic conditions can alter community compositions (Thomas et al. 2004, Shurin et al. 2012, Dornelas et al. 2014, Sentis et al. 2014). For instance, species at high trophic levels are often more sensitive and more likely to go extinct at high temperatures (Urban et al. 2017), suggesting a potential reduction in trophic diversity (Petchey et al. 1999). Thus, identifying how variation in community structure interacts with changes in abiotic conditions is essential to understand and predict how climate change will alter the performance and abundance of populations (Tylianakis et al. 2008, Gilman et al. 2010, Blois et al. 2013, Rosenblatt and Schmitz 2016).

Mean temperatures are expected to increase under future climate change scenarios in most ecosystems (IPPC 2013), and it is well established that any changes in ambient temperature can modulate a wide range of life-history traits, including metabolic rates, growth, birth and mortality rates (Kingsolver and Huey 2008, Ohlberger 2013, Ma et al. 2015, Zhang et al. 2015), as well as behaviors, such as foraging rates and habitat use (Barton 2010, Miller et al. 2014, Rosenblatt and Schmitz 2016). However, recent studies indicate that changes in temperature regimes can also indirectly affect a given species by changing its interaction with other community members (Barton and Schmitz 2009, Barton et al. 2009, Harley 2011). As a consequence, the direct effect of increased temperatures on an organism can be modified by concurrent indirect effects on interactions with other community members (Tylianakis et al. 2008, Harmon et al. 2009, Zarnetske et al. 2012, Urban et al. 2017) and modify the net effect of temperature changes on individual species.

The trophic complexity of natural communities likely plays a key role in modulating temperature effects because it determines what direct and indirect interactions are possible. For instance, increased temperature can directly reduce survival of a consumer. However, if higher temperatures also negatively affect survival of a strong interspecific competitor, the reduction in competition may at least partially offset or even compensate for the direct negative effects of higher temperatures on populations. Furthermore, recent empirical studies and metabolic theory suggest that species within and across trophic levels differ in their thermal sensitivities (Dell et al. 2011). Given that primary producers, herbivores, and carnivores typically differ in their metabolic demands and sensitivity (Dell et al. 2011), metabolic theory suggests

that changes in food chain length (e.g. presence or absence of an apex predator) can alter how an organisms' abundance changes with warming (O'Connor et al. 2007, O'Connor 2009, Dell et al. 2014, Gilbert et al. 2014). Furthermore, there is often considerable heterogeneity in thermal responses within trophic levels, even in closely related taxa (Dell et al. 2011, Best et al. 2015). Food web theory suggests that such horizontal (within trophic levels) diversity could buffer natural communities against environmental disturbances, like temperature changes (Duffy et al. 2007, Cardinale et al. 2012). Overall, this suggests that increasing trophic complexity in a community allows for more indirect interactions that are likely to alter and potentially oppose the direct effects of higher temperatures (Jiang and Kulczycki 2004). However, to date most experimental studies on temperature effects have focused on consumer–resource pairs or linear food chains without systematically manipulating trophic complexity. Consequently we still have a limited understanding of how this complexity might alter temperature effects in natural systems.

Here we take an experimental approach to test how trophic complexity influences the effects of warming. Specifically, we manipulated the presence/absence of interspecific competitors and predators to simulate different food webs of increasing complexity and exposed these food webs to ambient or raised temperature regimes. This design allowed us to test how changes in the configuration and trophic complexity of simple food webs might influence effects of increased temperatures. Overall, we found that effects of increased temperatures varied significantly across food web configurations and generally decreased with increasing complexity.

## Material and methods

### Study organisms

Here we use fishless pond communities with a focus on two tadpole species, *Hyla versicolor* and *Rana clamitans* as a model system. Amphibians and their aquatic habitats are particularly prone to variation in weather conditions and climate change in general (Root et al. 2003, Heino et al. 2009). These two amphibian species commonly co-occur in a range of natural ponds that can vary considerably in the presence of competitors and predators across space and time, but both species exhibit different suites of behavior and developmental traits. *Hyla versicolor* tadpoles are active foragers utilizing the whole water column and develop quickly, typically reaching metamorphosis in ~17–40 days in our study regions. *Rana clamitans* tadpoles inhabit benthic areas of ponds and spend most of the time hiding in the leaf litter. As a consequence, their larval period is much longer and tadpoles take at least three months to reach metamorphosis and often overwinter in our study sites before metamorphosing in our study region. While both species are affected by high temperatures and reduction in water levels in natural ponds in which they

co-occur, *H. versicolor* can be found in much smaller and more temporary habitats than *R. clamitans* and thus likely more frequently encounters high temperatures. Based on these differences in life-history traits (i.e. foraging, habitat use and development) we suspected that both species would be differentially affected by higher temperatures. Finally, previous studies indicate that *H. versicolor* is a better competitor but more susceptible to predation than *R. clamitans* (Morin 1983, Smith et al. 2004, Rudolf and Rasmussen 2013a, b).

Larvae of the dragonfly *Tramea carolina* are common predators found in fishless ponds and abundant in summer months. These larvae naturally co-occur with the two tadpole species used in this experiment and readily consume tadpoles as a part of their diet. Larvae with an average head width of 5 mm were collected from one fishless pond at Huntsville biological field station in Huntsville, TX on 20 May 2011.

### Experimental design

To test whether and how the effect of warming depends on species interactions and food web complexity, we crossed two temperature levels (ambient and heated) with three food web configurations that simulated an increasing level of food web complexity: both species were either 1) reared without the other tadpole species, or 2) together (interspecific competitor scenario), or 3) with the competing species and the dragonfly predator (competitor + predator scenario). This design is similar to a previous study in protists (Jiang and Kulczycki

2004) and resulted in a total of eight treatments that were randomized in a complete blocked design with four replicates of each treatment (Fig. 1). We collected 80 clutches of *H. versicolor* (10–25 eggs per clutch) and three clutches of *R. clamitans* eggs (1000–7000 eggs per clutch) from five local fishless ponds in Angelina National Forest and Davy Crockett National Forest, TX on 14 May 2011. Tadpoles of both species were introduced at the same time and stage (Gosner stage 25), i.e. when tadpoles first start to actively feed after hatching. Single species treatments received either 250 *H. versicolor* or 270 *R. clamitans* tadpoles, interspecific competition treatments received both species at the same densities as single species treatments (additive design), and predation treatments received both species and 13 similar sized *T. carolina*. Thus, densities of each tadpole species was constant across all treatments, but total tadpole densities summed across both species were higher in competition treatments (270+250). Unlike substitutive designs (which keep total density constant) this additive design does not confounding changes in intra-specific density with inter-specific densities (e.g. like in substitutive designs) (Inouye 2001) and this provides an unbiased, direct measurement of interspecific per-capita strength of competition (Wootton and Emmerson 2005). The differences in density reflected natural differences and egg availability and were not set equal as we expected mortality to be much higher in *R. clamitans* which is competitively inferior. Stocking densities of all species are above densities reported in other field sites (Morin 1983), but equal or lower to densities used in other experiments of both species (Morin

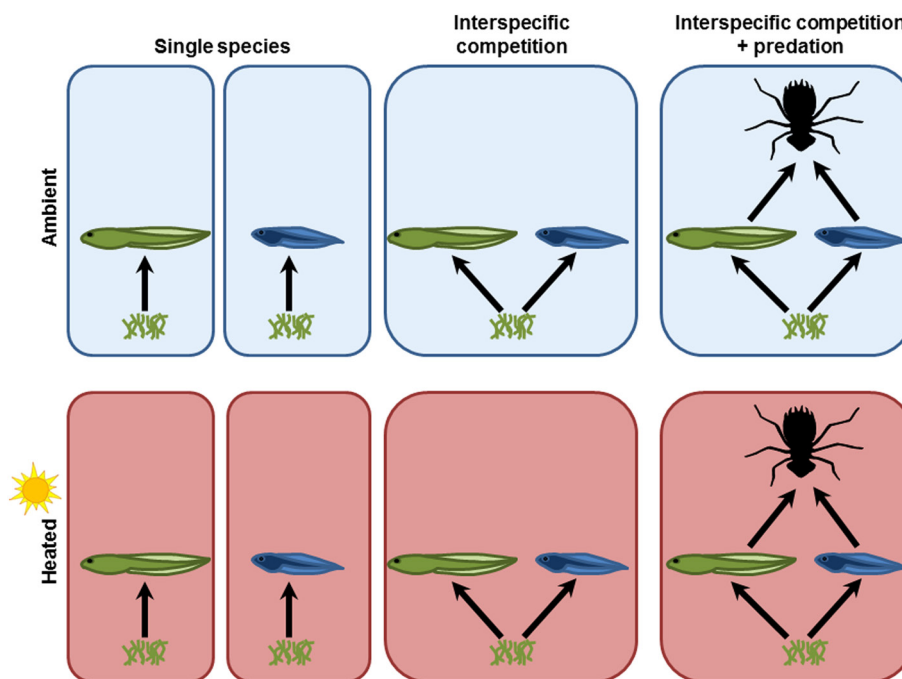


Figure 1. Experimental design. Tadpoles of the two species *Hyla versicolor* or *Rana clamitans* were exposed to three food web configurations of increasing complexity: alone (single species treatments), or together in the absence of predators (interspecific competition) or with predator larvae of the dragonfly *Tramea carolina* (interspecific competition + predation). These food webs were either exposed to ambient conditions or increased temperatures (heated, by  $\sim 2.9^{\circ}\text{C}$ ) resulting in eight total treatments, each replicated four times.

1983, Wilbur 1987, Van Buskirk 1989, Wissinger 1992, Kiesecker and Blaustein 1999, Smith et al. 2004).

### Mesocosm setup

We conducted the experiment in an array of 32 plastic mesocosms, measuring 1.8 m in diameter and 0.7 m in height (1200 liters of water) arranged in a 4 × 8 grid, where each of the four rows represents one block. All mesocosms were set up two months before the start of the experiment (i.e. addition of tadpoles and predators). Each tank was filled with dechlorinated tap water and fitted with a lid composed of 60% shade cloth to mimic the natural forest shaded ponds in eastern Texas. These lids also kept metamorphosing study organisms from escaping before collection and kept unwanted organisms (i.e. amphibians and predators) from invading the mesocosms. Each tank received 0.37 kg of dry mixed leaf litter collected from the margins of natural ponds at the Huntsville biological field station. On 13 May every other tank was heated with a 300-Watt submersible aquarium heater and arranged so that no two heated or unheated mesocosms were side-by-side. Mesocosms were wrapped with insulation which reduced temperature fluctuations and increased heater efficiency. The heater was always on during the experiment. This setup allowed us to maintain a continuous increase of ~2.9°C above the daily and seasonal temperature of ambient (unheated) tanks. We used this temperature difference based on estimated increase in mean temperatures in the next 100–150 years based on future climate change predictions (Jiang and Yang 2012). Importantly, this setup allowed heated mesocosms to follow the same temperature fluctuations within and between days as the unheated mesocosms (Fig. 2). The advantage of this approach is that we have realistic and natural temperature fluctuations and only simulate an increase in mean temperature. Temperatures of the mesocosms were monitored every half hour with ibutton temperature loggers that were submerged in one heated and one unheated tank per block. During the experiment mean temperature within a given tank was 26.9°C (min: 19.1°C, max: 32.2°C) and 29.9°C (min: 22.7°C, max: 35.0°C) in ambient vs. heated treatments respectively. Due to decreasing water levels in the heating mesocosms, the experiment ended when the mesocosms reached water depth between 7–10 cm on 1 August 2011 and well before they dried out. At this point some tadpoles also appeared to show a bit more sluggish movements so we terminated the experiment to avoid unusual heat stress. Note that all dragonflies and >80% of *Hyla* had metamorphosed > 30 days prior to the end of the experiment and before water levels started to be noticeable lower in heated tanks. From the addition of newly-hatched tadpoles (19 May), the experiment ran for 75 days.

### Response variables

Metamorphosing amphibians and predators were collected daily and taken back to the laboratory and weighed once tails were fully absorbed. We determined number and dry

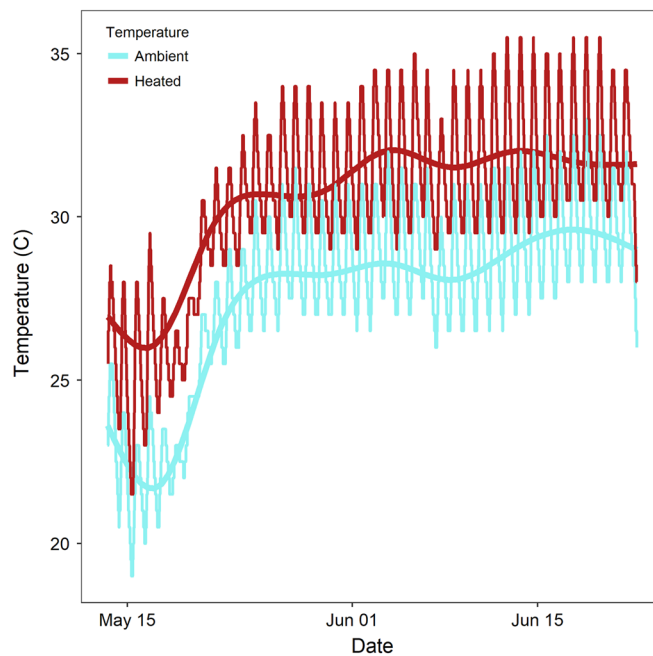


Figure 2. Temperature patterns in ambient and experimentally heated mesocosms. Thick lines indicate daily mean temperatures across all mesocosms within a treatment and thin lines show representative daily temperature fluctuations in two individual mesocosms in both treatments. Standard errors of the smooth means are generally smaller or equal to the lines and thus not shown here.

mass of all surviving *T. carolina* metamorphs from the experiment. Note that all surviving predators reached metamorphosis. Surviving *H. versicolor* did not always reach metamorphosis. Therefore we analyzed the number of survivors (tadpoles + metamorphs) and proportion of survivors that achieved metamorphosis. At the end of the experiment we collected all surviving tadpoles and euthanized them with MS222. Tadpoles were then photographed to measure snout vent length (SVL), and oven-dried for 48 h at 60°C to determine total tadpole dry mass (= biomass) per tank and species. No *R. clamitans* tadpoles reached metamorphosis because of their much longer developmental period so we analyzed the number and dry mass of the surviving tadpoles. For *H. versicolor* we calculated total biomass (tadpoles + metamorphs) at the end of the experiment by converting metamorph wet mass into dry mass using established scaling relationships (Rudolf and Rasmussen 2013a, b). To estimate food (resource) availability for tadpoles we quantified biomass of benthic algae (periphyton) from chlorophyll-a extractions of algae collected weekly on microscope slides. In addition we also collected phytoplankton (pelagic algae) samples at the same time intervals as a reference. Standing biomass of periphyton was estimated from three glass microscope slides per tank (0.74 × 0.25 cm) that were floated separately in the tank for seven days. After seven days, glass slides were removed for processing and replaced with a set of new slides. We combined periphyton from both sides of all

three slides from the respective sample period for the analysis. Biomass of Phytoplankton was quantified from 250-ml water samples collected at mid water level weekly from each tank. Periphyton and phytoplankton concentrations were then determined fluorometrically through chlorophyll-a extraction in MeOH. All extractions and sampling procedures followed standard protocols (Rudolf and Rasmussen 2013a, b).

### Statistical analysis

To examine the effects of warming across different species interactions and food web complexity, we used generalized linear mixed models (GLMM) with proportional survival and total biomass of either of *H. versicolor* or *R. clamitans* per tank as a response variable and heating and food web configuration treatment (species alone, with competitor, with competitor+predator) and their interaction as categorical fixed effects and observation nested within block as random effect. We use binomial error structure for survival with observational level random effect to account for overdispersion, and log-normal error for total biomass. This analysis allowed us to determine 1) how competition and predation alter the effect of increase temperature on a focal species and 2) whether the effect varied between both species. In addition, we repeated the analyses with the proportion of *H. versicolor* that completed metamorphosis as response variable to determine how heating, competition, and predation affected the development rate of this species. Note that *R. clamitans* never reached metamorphosis so we could not conduct this analysis for both species. Finally, we determined treatment effects on mean periphyton (the major food source of tadpoles) and phytoplankton abundances (averaged across weekly samples) with food web configuration and heating as fixed effect with log-normal errors. All data were analyzed with the 'lme4' package in R (<[www.r-project.org](http://www.r-project.org)>) and p-values were obtained from 'car' package based on type II Wald  $\chi^2$ -tests.

### Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.jf45095>> (Rudolf and Roman 2018).

Table 1. Effect of increased temperature and trophic complexity treatments on survival and total biomass of two competing tadpole species *Hyla versicolor* and *Rana clamitans*. Species were introduced to mesocosms that were either heated or experienced ambient conditions. Trophic complexity reflects three treatments in Fig. 1 that manipulated food web configuration, i.e. species was alone, with competitor, or with competitor +predator.

Treatment	Hyla				Rana			
	Survival		Total biomass		Survival		Total biomass	
	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p
Heated	16.5	<0.0001	0.1	0.7404	17.0	<0.0001	6.5	0.0110
Trophic complexity (TC)	27.5	<0.0001	9.3	0.0098	31.6	<0.0001	27.1	<0.0001
Heated $\times$ TC	10.7	0.0051	0.9	0.6497	1.1	0.5894	1.7	0.4267

## Results

### Effects on consumers

The food web configurations significantly affected all demographic parameters of the two tadpole species (Table 1, Fig. 3). Survival and biomass of *Hyla versicolor* were highest in single species treatment, followed by competition–no predator treatments and lowest in competition–predator treatments. In contrast, survival and biomass of *Rana clamitans* was highest in single species treatments but lowest in competition–no predator treatments (Fig. 3). Thus, interspecific competition negatively affected both species, but the effects were much stronger for *R. clamitans*. For instance, at ambient temperatures, *R. clamitans* survival was nine fold (54% versus 6%) in competition–no predator treatments while *H. versicolor* survival was only 1.7 times lower (76% versus 44.1%). (Fig. 3). Interestingly, this also indicates that predator had a net positive effect on *R. clamitans* but a negative effect on *H. versicolor*. The proportion of *H. versicolor* survivors that reached metamorphosis differed significantly across food web configurations ( $\chi^2 = 32.1$ ,  $p < 0.0001$ ) and was highest with predators (98.6%  $\pm$  0.8%) and lowest with only the interspecific competitor present (54.3%  $\pm$  9.7%) (Fig. 4).

The consequences of warming were context dependent and varied with the configuration of the food web (i.e. presence of competitors and predators) and species identity (Table 1, Fig. 3). On average, warming reduced survival and biomass of *R. clamitans*, and the effect size (i.e. proportional change) was comparable across food web treatments (Fig. 3 right panels). In contrast, the effects of warming on survival of *H. versicolor* dramatically decreased with increasing food web complexity: warming treatments reduced survival by 2.1 times (Ambient: 76% versus Heated: 35.8%) in the absence of competition and predation, 1.7 times (A: 44.1% versus H: 25.9%) when the interspecific tadpole competitor was present, and had no effect when both predators and competitors were present (A: 25.4% versus H: 24.9%). Furthermore, adding a predator to the competition treatment did not alter *H. versicolor* survival in mesocosms with increased temperatures but reduced survival under ambient temperature regimes (Fig. 3). Finally, heating had no effect on the total biomass of *H. versicolor* across food web treatments (Table 1). Given that survival declined at higher temperatures, this indicates an increase in

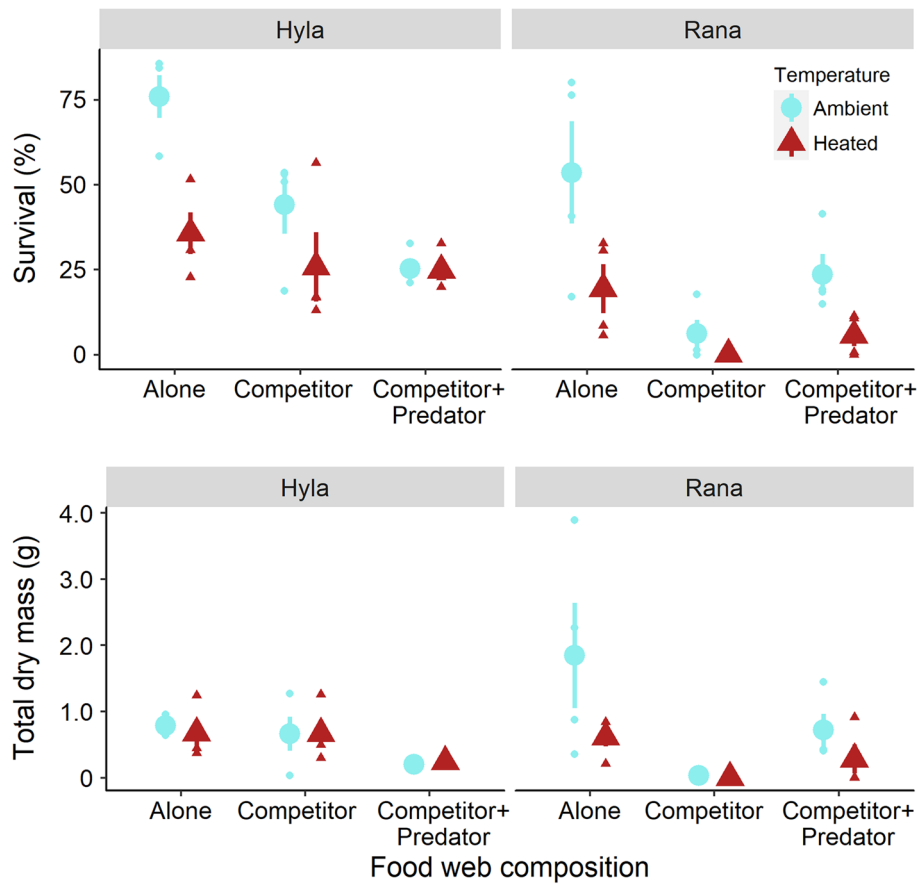


Figure 3. Effect of increased temperature on survival and total biomass of two competing tadpole species *Hyla versicolor* and *Rana clamitans* across different food web configurations. Tadpole species were either raised separately ('alone'), or together resulting in interspecific competition ('competitor') with or without dragonfly predators in mesocosms experiencing ambient temperature (N = normal, blue), or increased temperature (H = heated, red) regimes (Fig. 1). Small symbols indicate individual replicates and large symbols treatment means  $\pm 1$  SE.

the per capita biomass (and thus growth rates) of tadpoles and thus biomass compensation at the population level. A smaller proportion of surviving individuals reached metamorphosis in heated mesocosms ( $\chi^2 = 3.69$ ,  $p = 0.0545$ , heated:  $72.6\% \pm 9.1\%$ , ambient:  $82.2\% \pm 7.0\%$ ), indicating a slower average developmental rate at higher temperatures, independent of food web treatment (Heated  $\times$  Trophic complexity:  $\chi^2 = 1.9$ ,  $p = 0.356$ ) (Fig. 4).

### Effects on primary producers

Periphyton, the primary food source of both tadpole species peaked at the second sample and then declined over time for all treatments but this pattern was consistent across treatments (i.e. no significant time  $\times$  treatment interactions). On average, periphyton was highest in treatments with only *R. clamitans* followed by treatments with both tadpole species and the predator, and lowest with only *H. versicolor* only or both species without predator leading to a marginal effect of trophic complexity treatment (Trophic complexity:  $\chi^2 = 7.63$ ,  $p = 0.0542$ ) (Fig. 5). There was no overall effect of warming

on periphyton density (Heated:  $\chi^2 = 0.42$ ,  $p = 0.519$ , Heated  $\times$  Trophic complexity:  $\chi^2 = 1.24$ ,  $p = 0.743$ ).

Phytoplankton, the pelagic primary producer, did not vary systematically over time but was on average 1.85 times higher in heated treatments ( $\chi^2 = 13.67$ ,  $p = 0.0002$ , Fig. 5), and varied across trophic complexity ( $\chi^2 = 17.56$ ,  $p = 0.0005$ ) and these effects were independent (Heated  $\times$  Trophic complexity:  $\chi^2 = 1.9$ ,  $p = 0.59$ ). Phytoplankton densities were opposite to periphyton densities and highest in treatments that included *H. versicolor* (*H. versicolor* alone and *H. versicolor* + *R. clamitans*) but no predators (Fig. 5).

### Effects on predators

Predators emerged on average five days earlier in heated mesocosms (heated: 23 days, ambient: 28.2 days,  $\chi^2 = 10.86$ ,  $p = 0.001$ ) but neither the number ( $\chi^2 = 0.18$ ,  $p = 0.691$ ) or the average mass ( $\chi^2 = 0.33$ ,  $p = 0.564$ ) of dragonfly predators that emerged during the experiment differed between ambient (5.25 ind., 54.0 mg) or heated mesocosms (5.5 ind., 54.1 mg).

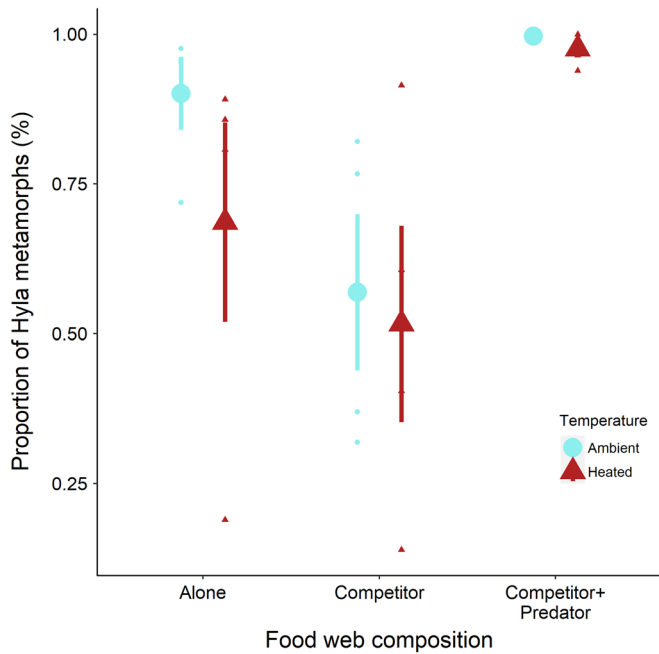


Figure 4. Proportion of surviving *Hyla versicolor* tadpoles that reached metamorphosis across different food web configurations. Tadpole species were either raised separately ('alone'), or together resulting in interspecific competition ('competitor') with or without dragonfly predators in mesocosms experiencing ambient temperature (N = normal, blue), or increased temperature (H = heated, red) regimes (Fig. 1). Small symbols indicate individual replicates and large symbols treatment means  $\pm 1$  SE.

## Discussion

Our results indicate that the effects of warming (i.e. increase in mean temperature) on a given species can strongly depend on the community context and trophic complexity of the system. Warming dramatically reduced herbivore survival in the absence of strong interspecific competition and predation. However, warming had no measureable effect on demographic rates on the dominant competitor in more complex communities where it was exposed to interspecific competition and predation. Conversely, changes in food web configuration had less of an effect at high temperatures. Thus, our results also indicate that warming can reduce the strength of interspecific competition and predation in our system. Overall, our results emphasize that we cannot always predict the effects of changes in abiotic conditions (e.g. due to climate change) on a given population without accounting for the community context. They also suggest that trophic complexity could potentially buffer climate change effects on populations.

### Effects of warming on top-down control

Increased temperatures are expected to alter trophic interactions within food chains but predicting the net effect on communities and organisms has remained challenging. For instance, theory often suggest that asymmetries in metabolic demands of consumer and resources should strengthen top down control, especially in primary

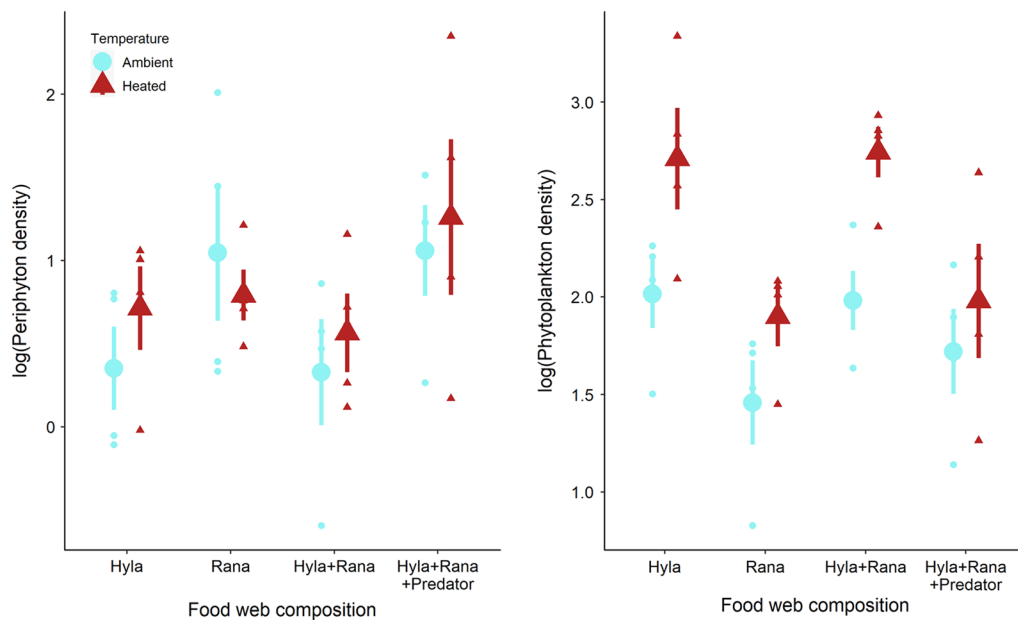


Figure 5. Effects of increased temperature on density of two primary producers, periphyton (benthic algae), and phytoplankton (pelagic algae), across different food web configurations. All labeling as described in Fig. 2. Density of both primary producers are based on chlorophyll a concentration. Small symbols indicate individual replicates and large symbols treatment means  $\pm 1$  SE.

producer–herbivore systems (Vasseur and McCann 2005, O’Connor 2009, O’Connor et al. 2009, Hoekman 2010, Rall et al. 2010, Kratina et al. 2012, Shurin et al. 2012, Dell et al. 2014, Lang et al. 2014, Miller et al. 2014). While this prediction is consistent with many empirical studies (O’Connor 2009, O’Connor et al. 2011, Kratina et al. 2012, Svensson et al. 2017), we found the opposite: adding a predator decreased survival of its tadpole prey at ambient temperatures (relative to predator free competition control) but had no effect at elevated temperatures. Furthermore, the biomass of primary producers (periphyton) that serves as the main resource for herbivores was not affected by temperature treatments while herbivore survival decreased and biomass either remained constant or decreased. This pattern indicates that warming either did not affect or actually reduced top down control which is opposite to most empirical studies in similar systems (Jiang and Kulczycki 2004, O’Connor 2009, O’Connor et al. 2009, Hoekman 2010, Kratina et al. 2012, Shurin et al. 2012, Lang et al. 2014, Miller et al. 2014).

The discrepancy between our results and previous work could arise from several mechanisms. Theory predicting an increase in top–down control and foraging rates assumes moderate changes in average temperatures that largely act on metabolic rates but do not directly and negatively affect survival of organisms and their foraging rates, or alter the behavior or traits of organisms (Vasseur and McCann 2005, Rall et al. 2010). Our experimental system was exposed to natural temperature regimes that could reach high temperatures during the day (Fig. 2). Increasing mean temperature also increases frequency of extreme temperature events, suggesting that organisms in warmed mesocosms were potentially exposed to extreme temperatures more frequently. This is consistent with increased mortality of tadpoles in heated tanks. Increased mortality also reduces the density of tadpoles, which should reduce predator–prey encounter and thus total predation rates. Extreme temperatures can also reduce consumption rates either via physiological constraints (Uszko et al. 2017) or behavioral changes to mitigate heat stress (e.g. reduced activity or switching of micro-habitats) (Barton 2010, Miller et al. 2014). Such a decrease in per capita predation rates could weaken mortality due to predation and thereby compensate for the direct negative effect of warming on consumers.

In our and many other system, predation rates decline as absolute and relative prey/predator size increases (Caldwell et al. 1980, Travis et al. 1985, Richards and Bull 1990, Babbitt and Tanner 1998, Gunzburger and Travis 2004). If tadpoles grow faster in warmed mesocosms this would result in a concordant reduction in the per capita predation rate over the course of the experiment. Consistent with this prediction, tadpoles in warmed mesocosms indeed reached larger per capita mass. Thus, warming also likely reduced per capita predation rates via changes in the growth rates of tadpoles which could further help explain deviations from model predictions.

Finally, it is theoretically possible that the decline in water level in heated tanks towards the end of the experiment altered species interactions and resulted in resource limitation for tadpoles or reduced water quality (e.g. increased ammonia levels). However, most (>85%) of *Hyla* tadpoles and all dragonflies reached metamorphosis and left the ponds more than a month before the differences were noticeable. Furthermore, the reduction in water level should have 1) increased encounter rates and thereby increasing predation rates, and 2) increased resource limitation (i.e. less periphyton for tadpoles) and thus strengthen interspecific competition in heated tanks. Instead, we found the opposite pattern, i.e. predation and competitive effects were significantly reduced in heated tanks. Overall, this suggests that the decline in water level or resource availability was unlikely to be a major driving factor of the observed patterns, but it could play an important role in other systems. Temperature changes are always likely to modify more than one aspect of natural systems, and disentangling the individual components is a major challenge for future studies.

Together, our results indicate that warming can weaken the top–down control given through two non-exclusive mechanisms: changes in per capita interaction strength and prey density. These mechanisms are likely to occur in the majority of natural systems with growing predator and prey, emphasizing the need integrate them into current theory.

### Warming and trophic complexity

Predictions concerning how changes in temperature regimes affect species are often based on environmental tolerances of species (Hannah et al. 2014, Ma et al. 2015), but this approach has been criticized because it neglects species interactions and the evolutionary potential of species (Angert et al. 2011, Mouquet et al. 2015, Urban et al. 2016). Warming can have direct effects on demographic rates of organisms, but it can also indirectly affect them by modifying their interactions with other community members. If direct and indirect effects have the same ‘sign’ (e.g. both have negative effects on fitness), warming effects could not be affected or strengthened in presence of strong interspecific interactions in more complex communities. On the other hand, if warming has opposing effects on direct and indirect interactions, more complex communities could buffer negative effects of warming on a given populations. Our results support the latter complexity-buffering hypothesis. In simple communities without strong competitors or predators, tadpole survival dramatically declined in heated mesocosms indicating a clear direct negative effect of warming on demographic rates. However, for one species (*H. versicolor*), this warming effect was diminished and even disappeared in more complex communities with strong interspecific competition and predation. Consistent with previous studies (Barton and Schmitz 2009, Barton et al. 2009, Kratina et al. 2012, Shurin et al. 2012) these results emphasize that species interactions can play a key role in modulating the response of populations to warming.



Experiments always have to strike a balance between control and natural conditions. While mesocosm experiments play a key role in identifying and testing mechanisms driving dynamics of natural communities, they still have to strike a compromise between complexity of natural systems and experimental control. Densities of focal species in our study are similar to many previous experiments and set up to increase our statistical power to identify patterns and mechanisms. However, natural densities reported in the literature are lower and future studies are needed to determine whether and how the observed interactions might be influenced by relative densities of the interacting species (e.g. surface response design). For instance, lower tadpole densities will reduce inter-specific competition and predation rates. Reduction in the total interaction strength (effect of species A on species B) should also weaken the effect of trophic complexity and indirect interactions, and effects of warming would approach single species treatments the weaker the interactions become. Future studies that test this hypothesis will be an important next step to predict warming effects across a range of conditions and systems.

### Species specific responses and asymmetric interactions

Species that vary in traits are also likely to vary in their response to temperature changes. In our system, we found that insect (dragonfly) predators were little affected by warming, while both tadpole species were strongly negatively affected. This is consistent with previous studies indicating that amphibians can have low critical thermal limits and low warming tolerance (Duarte et al. 2012). Furthermore, we found that the importance of community structure for modifying warming effects varied across species. The dominant competitor (*H. versicolor*) was strongly affected by the interaction of warming and food web structure, while both factors had simple additive effect on the inferior competitor (*R. clamitans*). This difference likely arises because *H. versicolor* is the much more vulnerable to predation and a faster growing species, so temperature effects on growth rates are more likely to affect predation. This contrasts with previous studies on protists that also showed an asymmetric response but the weaker competitor was more affected by competition under a warming scenario (Jiang and Kulczycki 2004). While it is difficult to compare a multi-generational microcosm experiment with potential evolutionary changes to a natural mesocosm experiment within a single generation, the discrepancy likely arises from biomass strength of intra- versus interspecific competition. In our experiment, the single species treatment clearly indicate that warming reduced survival of the dominant competitor but it increased growth rates and thus biomass of surviving individuals. As a consequence, total biomass of this species did not change at the population level (biomass ‘compensation’) in heated and ambient mesocosms. Thus, warming shifted higher survival and low survival and high growth rates. If

competition is largely driven by total biomass, this could explain why the context dependent effects of warming on survival of the dominant competitor did not translate to changes in the inferior competitor, assuming that per unit biomass competition effect remain unchanged. Interestingly, this would also suggest that warming altered the strength of intra-specific competition, but not interspecific competition because the reduction in intra-specific competition led to biomass compensation in the dominant competitor. Such differences in the relative strength of intra- versus interspecific competition could have interesting effects on long-term dynamics, including eco-evolutionary feedbacks, and coexistence (Chesson 2000), especially under predicted changes in abiotic conditions.

### Negative feedbacks and long-term consequences

Climate change has emerged as a new factor threatening the persistence of species around the globe (Thomas et al. 2004, Urban 2015). Experimental studies indicate that extinction rates increase with warming, especially at higher trophic levels (Petchey et al. 1999, Jiang and Kulczycki 2004). In addition, active harvesting and habitat fragmentation have led to human mediated decline in top predators (trophic downgrading) in both terrestrial and aquatic systems worldwide (Baum and Worm 2009, Estes et al. 2011). Our results suggest that such a reduction in trophic complexity can increase the effect of warming on individual populations. Warming could therefore result in a vicious cycle: warming reduces trophic complexity which in turn strengthens the negative effects of warming on the persisting species, and this could lead to an accelerated decline in the abundance and persistence of species and ultimately biodiversity. It also supports recent evidence indicating that human mediated exploitation of ecosystems could accelerate the negative effects of climate warming and emphasizes the potential importance of biological interactions in buffering climate change effects (Bates et al. 2017). However, our study is clearly too short (and was not intended) to test this prediction, and we need to be careful when extrapolating the observed patterns. For instance, it is possible that while survival decreased for a species, density-dependent regulation and compensatory mechanisms during later stages could compensate for the reduction in survival. In addition, effects might change depending on the relative and absolute densities of competitors and predators. Finally, evolutionary changes could further modify long-term dynamics, especially given the potential of eco-evolutionary feedbacks in this and many other systems. Thus, an important next step in research on effect of temperature changes and climate change in general is to link the short-term dynamics to long-term patterns. Connecting a series of short term experiments like ours that focus on mechanisms to long-term observations and models to identify long-term effects will be a fruitful venue to help predict long-term consequences of climate change on natural ecosystems.

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