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Density constrains cascading consequences of warming and nitrogen from invertebrate growth to litter decomposition

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Abstract. Smaller invertebrate body mass is claimed to be a universal response to climate warming. It has been suggested that body mass could also predict consumer influences on ecosystem processes in a warmer world because generalized rules describe relationships between body mass, temperature, and metabolism. However, the utility of this suggestion remains tenuous because the nutritional and physiological constraints underlying relationships between body mass and consumer-driven processes are highly variable in realistic settings. Here we test, using a generalist invertebrate detritivore, fungi, and leaf litter, the limitations imposed by nutrition on growth and decomposition in response to global change. Strong competition for fungal food resources limited invertebrate growth and reduced body mass plasticity in response to warming and nitrogen pollution scenarios. When competition was relaxed by experimentally reducing invertebrate density, consumption of fungi promoted rapid invertebrate growth and enhanced invertebrate sensitivity to the global change scenarios, especially warming and nitrogen pollution together. Accordingly, fungi promoted invertebrate body mass plasticity and mediated consumer effects on decomposition causing the relative influence of warming and nitrogen pollution to vary across trophic levels. An important implication is that managing nitrogen pollution may alter which trophic level is most sensitive to warming.

Key words: body size; climate warming; density dependence; ecosystem functioning; global change; interaction strength; litter decomposition; nitrogen deposition; phenotypic plasticity; wetlands.

Introduction

Current trends showing warming of the Earth's surfaces are projected to continue in the future (Collins et al. 2013). A critical challenge is, therefore, to identify reliable indicators of the ecological consequences of climate warming (Parmesan and Yohe 2003). One of the most consistent responses to warming comes from syntheses of controlled experiments demonstrating a generalizable relationship between temperature, basal metabolism, and body size (Gillooly et al. 2001, Forster et al. 2012). Invertebrate species grow and develop faster in warmer climates (Forster et al. 2011), and typically their maximum body size is smaller (Atkinson 1994, Kingsolver and Huey 2008). Global declines in body size are consistent with the expected influences of warming (Gardner et al. 2011, Forster et al. 2012, Horne et al. 2015), suggesting that body size could be an important indicator of climate effects on consumer populations (Savage et al. 2004, Parmesan 2006), and consumer effects on ecosystem processes (Brown et al. 2004, Miner et al. 2005).

However, changes in invertebrate life history plasticity and density also result from increased nitrogen supply (Nylin and Gotthard 1998), which influences invertebrate physiology and feeding rates (Camargo and Alonso 2006), and is also one of the leading causes of water pollution world-wide (Galloway et al. 2008, Canfield et al. 2010). Independent of nitrogen pollution, increases in density of competitors can lead to reductions in invertebrate body size and metabolism by limiting food supply

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(Levitan 1989, DeLong et al. 2014). Warming (O'Reilly et al. 2015), nitrogen pollution (Elser et al. 2009), and consumer population densities (Boyero et al. 2011) are distributed heterogeneously in space with strong variation in each factor within and between regions. Whether temperature-size rules governing metabolism can be effectively used to identify effects of warming on consumers and ecosystem processes (Miner et al. 2005, Dillon et al. 2010, Sheridan and Bickford 2011), then, will depend upon the individual and combined consequences of multiple factors of environmental change that confront species in natural environments (Elser et al. 2009, Vörösmarty et al. 2010, Boyero et al. 2011, O'Reilly et al. 2015).

Here we test the cascading consequences of environmental change on body mass and growth of a common freshwater detritivore, *Limnephilus rhombicus* (Trichoptera) feeding on litter and fungi that colonize litter from *Phragmites australis* (Cav.) Trin. ex. Steud, one of the most broadly distributed plants in the world. Constraints on invertebrates imposed by warming, nitrogen pollution, and increased competition for resources can all reduce body mass of invertebrates (Chown 2001). Depending on the global change driver, however, similar reductions in invertebrate body mass may enhance (warming), reduce (density), or have complex effects (nitrogen pollution) on consumer metabolism, resulting in alternative consequences for fungal biomass and subsequently litter decomposition. This range of scenarios allows us to assess, qualitatively and quantitatively, the utility of invertebrate growth and body mass as an indicator of global change impacts on consumers and the ecological processes they drive. Such evidence from field experiments capturing ecological realism is needed to establish reliable connections between syntheses of laboratory experiments (Gillooly et al. 2001) and observations of global trends (Parmesan 2006, Gardner et al. 2011, Forster et al. 2012).

Methods

We used an outdoor experimental facility designed to parallel the daily and seasonal fluctuations in temperature and nitrate found in natural conditions while simulating four global change scenarios: ambient conditions (control), increased temperature (ambient +2.8°C), increased nitrogen supply (ambient × 5), and increased temperature and nitrogen supply in combination (Hines et al. 2013). Global syntheses show that the mean trend in temperature for lakes has been +0.34°C/decade (95% CI, 0.16–0.52) between 1985 and 2009, although geomorphology of each lake leads to variation in the magnitude of warming (O'Reilly et al. 2015). In addition to mean temperature differences, changes in temperature fluctuations also can influence individual metabolism, community composition, and ecosystem process rates (Dang et al. 2009). Therefore, our experiment, which includes natural variation, allows us to avoid criticisms of experiments that use constant conditions in laboratory settings to make predictions about the influence of climate change on organisms (Schulte et al. 2011). Nitrate concentrations in surface waters of high N-deposition lakes can be up to sevenfold higher than background concentrations in nearby low N-deposition lakes (Elser et al. 2009). These N-deposition rates are higher than projected increases in N deposition for terrestrial surfaces (Reay et al. 2008) because lakes receive mobile ions from broader watersheds they drain, especially in areas with high precipitation (Baron et al. 2012), or reduced vegetation (Elser et al. 2009). Therefore, although considerable spatial variation exists globally, each of our warming and nitrogen treatments reflect scenarios that are highly likely to be realized in the next century (Hines et al. 2013). Each of the four scenarios was replicated four times (16 experimental enclosures total) and assigned a random enclosure located in each of four spatial blocks. The design, functioning, and maintenance of the enclosures are described by Hines et al. (2013) and details are also provided in Appendix S1.

To test the influences of multiple factors of environmental change on invertebrate growth and body mass, we reared *Limnephilus rhombicus* caddisflies in tube cages placed on the sediment surface of each enclosure. Tube cages consisted of PVC tubes (15 cm by 6.5 cm diameter) capped in 250-μm polyester mesh (SEFAR, Heiden, Switzerland) secured with cable ties. Cages were initially stocked with 5.0 ± 0.1 g of fully brown *Phragmites australis* leaf litter and received one of three caddisfly density treatments: (1) caddisflies excluded, (2) low density (one caddisfly per cage corresponding to 300 caddisflies/m^2), (3) high density (six caddisflies per cage corresponding to 1800 caddisflies/m^2). Eggs of *L. rhombicus* are laid in clutches of 150–400 eggs per sac, at densities up to 5–10 egg sacs/m^2. Therefore, early instars of larval *L. rhombicus* often experience densities exceeding 1800 individuals/m^2. Our treatments were chosen to fall within the natural range of densities found in the field and to stay within the carrying capacity of the tube cages. High overall survivorship allowed us to focus on consumer growth plasticity and feeding as causal drivers of changes in decomposition. This focus complements experiments designed to test for effects of warming resulting from simultaneous changes in consumer community composition and metabolism (Yvon-Durocher et al. 2010, Forster et al. 2012). We initially established 288 tube cages (4 global change treatments × 3 caddisfly density treatments × 6 sample dates × 4 replicate enclosures). One replicate of each treatment was removed from each enclosure on six sample dates spanning the duration of caddisfly larval development (day 0, 46, 74, 102, 131, and 158; corresponding to 15 December 2010 and 31 January, 28 February, 28 March, 26 April, and 23 May 2011).

On each sample date, we transported the tube cages to the laboratory where we assessed three types of responses: caddisfly body mass and growth, fungal biomass, and litter mass remaining. To assess caddisfly growth we hand

collected and photographed each caddisfly. Caddisfly length (L) was then measured to the nearest 0.1 mm using ImageJ software (Schneider et al. 2012), which was converted to body mass (B) using the allometric equation $\ln B = 0.002 + 0.169 \ln L$ (J. Hines, *unpublished data*). Caddisfly growth was estimated by fitting a sigmoid three-parameter logistic growth curve ($B = a/[1 + b \times e^{-ct}]$) to the caddisfly biomass data because it was a good fit for all treatments, as indicated by Akaike information criteria (AIC) values (Appendix S1: Table S1). In this equation, B is biomass, a is the asymptote of the growth curve (i.e., maximum body mass), b is the time when body mass is one-half of maximum, c is the scale or the amount of change in body mass, and t is time. Parameters were fit using a Gauss-Newton algorithm in an iterative search process (Pinheiro et al. 2014).

Fungal biomass

We rinsed the litter on a sieve (1-mm mesh), and used subsamples to assess ergosterol concentration as an estimate of fungal biomass (Gessner 2005). We extracted lipids with alkaline methanol, purified the extract by solid phase extraction (SPE), and isolated and quantified the extracted ergosterol using high pressure liquid chromatography (HPLC) with UV detection at 282 nm (Gessner 2005).

Litter decomposition

Rinsed litter was oven dried at 50°C to a constant mass and weighed. Litter decay rate was estimated by fitting the exponential decay model ($m = 100\ e^{-kt}$) to litter mass data, where m is the percent litter mas remaining, k is the decay rate, and t is time.

Statistical analysis

We assessed treatment effects on response variables (caddisfly growth [a], ergosterol concentration, and litter decomposition [k]) using ANOVA with a mixed-model treatment structure. Fixed effects included fully crossed combinations of three levels of caddisfly density (absent, low, high), two levels of warming (ambient, warm), and two levels of nitrogen (ambient, nitrogen addition). Random effects included spatial block and enclosure. As we did not measure caddisfly growth when caddisflies were absent, only two caddisfly density levels were considered for this response. For ergosterol responses, which were not well described by fitting curves through time, we additionally used a compound symmetry repeated-measures error structure to account for covariation of ergosterol concentrations within enclosures through time. All data met assumptions of homogeneity of variance and normality of residuals.

To compare the magnitude of treatment effect sizes among all three response variables, we used the log response ratio $\ln(Y_{\text{treatment}}/Y_{\text{control}}) \pm 95\%$ CI (Hedges et al. 1999). Positive values indicate an increase in the response relative to the control, and negative values indicate a decrease relative to the control. Error bars that overlap with zero indicate no difference between treatments and controls. The subscript "control" in the above formula always indicates the equivalent caddisfly density in ambient conditions (i.e., ln [low $\text{density}_{\text{warming}}$/low $\text{density}_{\text{ambient}}$]). Therefore, significant differences between densities are not due to a numerical effect of increased consumer density, but rather to a change in the effect of warming and/or nitrogen on each response variable for a particular consumer density.

Results

The warming and nitrogen pollution scenarios simulated in our experiment influenced *Limnephilus rhombicus* growth only when the caddisflies developed at low density (Fig. 1A–D; significant W × D and N × D effects, Table 1). In ambient conditions, caddisflies at low density grew rapidly, adding approximately 0.05 mg/d during the period of growth between 31 January and 23 May 2010 (days 46–158 of the experiment), and achieving a maximum body mass of 6.3 ± 0.2 mg (mean ± SE, $n = 4$; Appendix S1: Table S2; Fig. 1A). Warming and nitrogen in concert reduced maximum body mass to 2.0 ± 0.2 mg/individual (Appendix S1: Table S2; Fig. 1D). This 68% decrease in body mass compared to control conditions (Fig. 1A) was greater than the additive effect of reductions in body mass due to warming (17%; Fig. 1B) and increased nitrogen alone (41%; Fig. 1C). At the high population density, caddisfly growth was reduced 40% relative to average growth at low densities (1.75 ± 0.3 vs. 4.35 ± 0.2; Fig. 1A–D), and it became insensitive to climate warming and nitrogen pollution scenarios (no significant high density effect sizes; Fig. 2A; Table 1).

Similar to the results for caddisfly biomass, fungal biomass was most sensitive to global change scenarios when low densities of caddisflies were present (Fig. 1E–H; significant W × D and density effects, Table 1). However, the effects were variable through time (Fig. 1E–H), and the direction and magnitude of effects depended upon whether caddisfly absence, or equivalent caddisfly densities in control conditions, were considered as the baseline. That is, fungal biomass was consistently suppressed by caddisflies at low density compared to when caddisflies were absent; fungal biomass decreased by 27% ± 4% in control, 34.4% ± 3% in warming, 32.3% ± 6% in nitrogen addition, and 13.3% ± 4% in warming and nitrogen addition (Fig. 1E–H). Both fungal growth and caddisfly consumption contributed to variation in magnitude of these effects. For example, warming limited the positive effect of nitrogen on fungal biomass when both factors were applied in combination (significant W × N and N effect, Table 1). Further, relative to equivalent consumer density in control conditions, fungal biomass was suppressed (warming), and had no influence (nitrogen addition) or was enhanced (warming and nitrogen

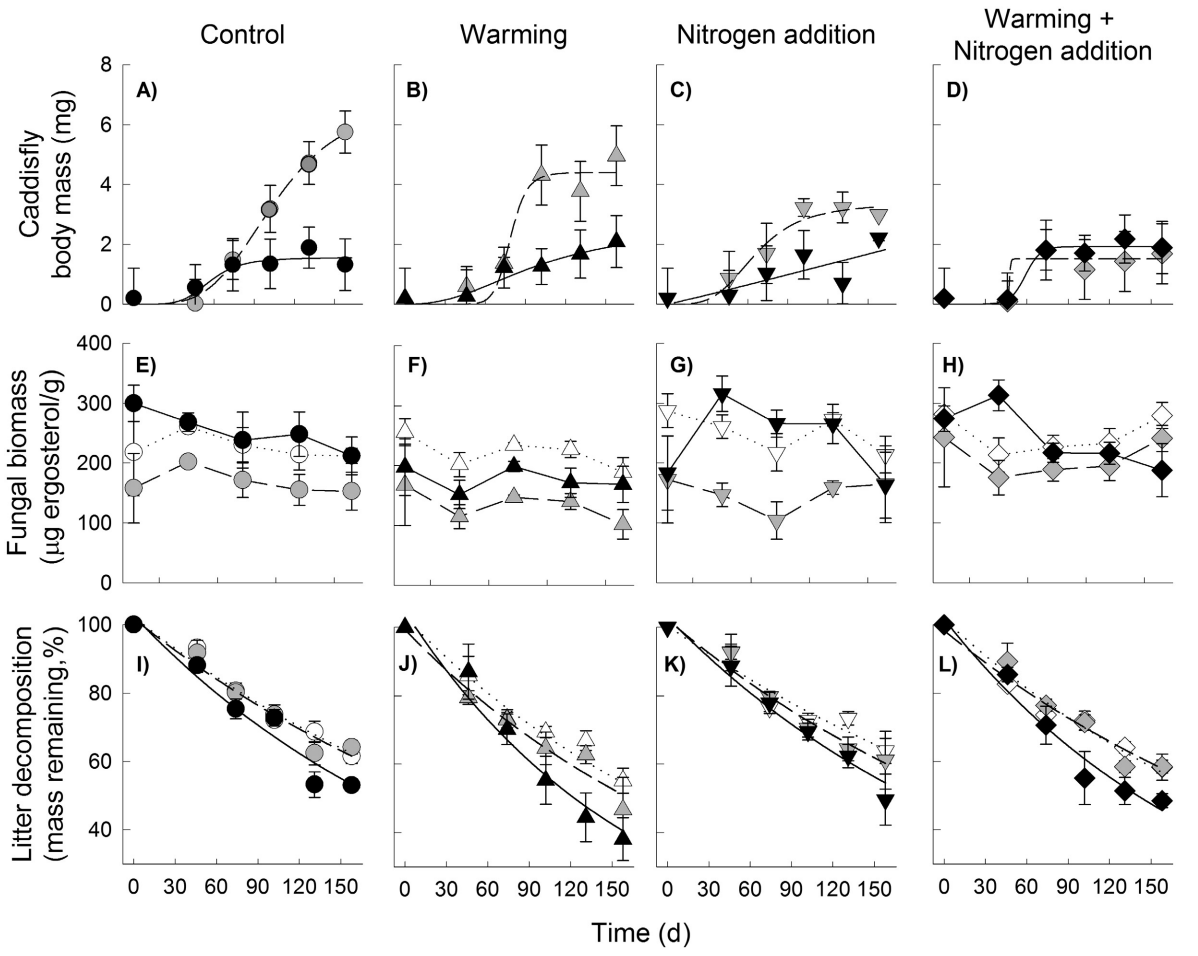

FIG. 1. The influence of four global change scenarios (control [circles], warming [up-pointing triangles], nitrogen addition [down-pointing triangles], and warming + nitrogen addition [diamonds]) on three response variables: (A–D) *Limnephilus rhombicus* body mass, (E–H) fungal biomass, and (I–L) *Phragmites* leaf litter mass remaining on six sample dates. Each symbol shows mean ± SE ($n = 4$). Shading of symbols in each panel refers to *L. rhombicus* density (open, excluded; gray, low density; black, high density).

TABLE 1. Results of ANOVA testing the effects of warming (W), increased nitrogen supply (N), and caddisfly density (D) on asymptote of *L. rhombicus* growth, fungal biomass, and litter decomposition.

Source of variation	Caddisfly growth			Fungal biomass			Litter decomposition^k		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Warming (W)	1, 9	**6.98**	**0.03**	1, 12	**7.72**	**0.01**	1, 9	**6.47**	**0.03**
Nitrogen (N)	1, 9	**48.7**	**0.0001**	1, 12	**13.5**	**0.003**	1, 9	0.75	0.40
Density (D)	1, 12	**272.3**	**<0.0001**	2, 216	**43.8**	**<0.0001**	2, 24	**21.9**	**<0.0001**
W × N	1, 9	0.49	0.50	1, 12	**13.3**	**0.003**	1, 9	0.41	0.53
W × D	1, 12	**32.82**	**0.0001**	2, 216	**7.1**	**0.001**	2, 24	2.38	0.11
N × D	1, 12	**94.9**	**<0.0001**	2, 216	0.8	0.4	2, 24	0.30	0.74
W × N × D	1, 12	1.84	0.20	2, 216	1.8	0.2	2, 24	1.01	0.38

Note: Significant effects ($p < 0.05$) are indicated in boldface type for clarity.

addition) by caddisflies at low densities, an effect that results from consideration of caddisfly consumption and fungal growth together (Fig. 2B). At high densities, caddisflies had weak and inconsistent effects, suppressing fungal biomass only when warming was applied alone (19.8% ± 5.0% decrease; Fig. 1F), and having no

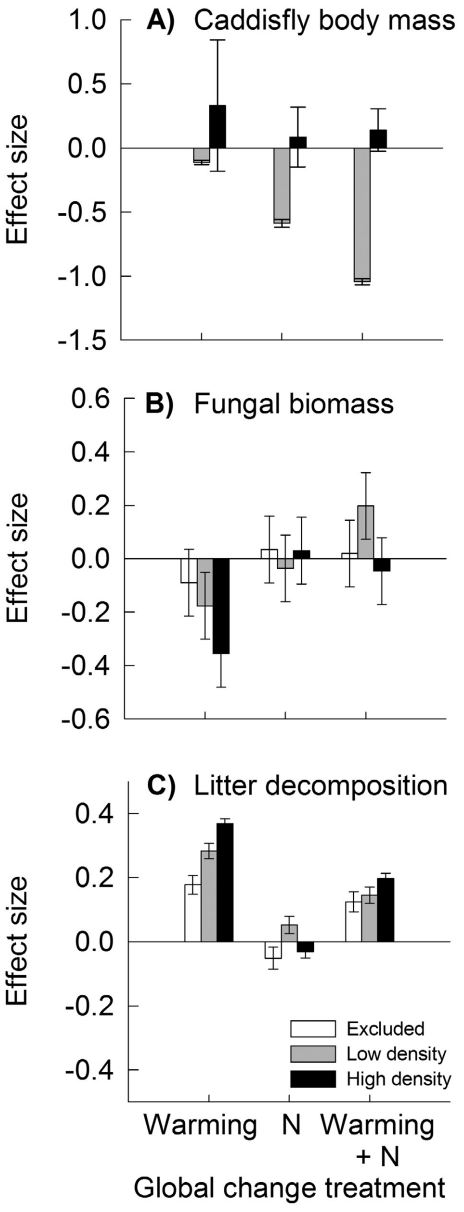

FIG. 2. The influence of warming, increased nitrogen supply, and warming + increased nitrogen supply on (A) caddisfly body mass, (B) fungal biomass, and (C) litter mass loss. Bars show the effect sizes (log response ratio ± 95% CI, $n = 4$) for three caddisflies densities. Effect sizes were measured as ln(treatment/control).

consistent effect over time in the other scenarios independent of whether the effects were compared across environmental scenarios (Fig. 1E,G,H) or relative to equivalent caddisfly densities in control conditions (Fig. 2B).

Warming and caddisflies at high densities both accelerated litter decomposition (Fig. 1J,L; Table 1). High densities of caddisflies accelerated litter mass loss rate (k) 1.50 ± 0.03-fold in ambient conditions, and 2.3 ± 0.4-fold in warming conditions compared to when they were absent (Fig. 1I,J). Therefore, the observed acceleration of litter decomposition was not strictly a numerical effect of increased consumer density. That is, compared to equivalent densities in ambient conditions, high densities of caddisflies accelerated litter mass loss 1.8 ± 0.2-fold in warming scenarios (Fig. 2C). Increased nitrogen supply alone had no influence on decomposition (Fig. 1K,L), although nitrogen addition limited the acceleration of decomposition caused by warming when both treatments were applied in combination (Fig. 2C).

DISCUSSION

Correlative studies have shown that long-term trends in invertebrate development time and growth are consistent with expected influences of climate warming (i.e., faster development, smaller body size; Parmesan 2006, Gardner et al. 2011, Van Asch et al. 2013). Our finding that the influence of global change on caddisfly growth is density dependent supports an important qualification preventing use of invertebrate body mass or phenology as an unambiguous indicator of climate warming. Specifically, at high densities, individual caddisfly growth was not sensitive to environmental conditions, but at low densities when caddisflies would normally benefit from relaxed competition and grow larger, they showed enhanced susceptibility to the three global change drivers tested here: warming, nitrogen addition, and most severely from both factors together. Reductions in larval body mass are generally associated with reduced fecundity (Honek 1993, but see Kingsolver and Huey 2008). Therefore, one implication of this study is that global environmental change might accelerate invertebrate species declines by limiting fitness of individuals in low-density populations.

A second important result is that reductions in caddisfly growth were not consistently associated with reductions in litter decomposition. Although equations relating temperature and body mass are used to make projections of ectotherm metabolism globally (Dillon et al. 2010), our findings emphasize the importance of identifying causal mechanisms underlying changes in metabolism and growth before extrapolating to global ecosystem process rates. Our data on fungal biomass in decomposing litter provides mechanistic links between caddisfly nutrition, plasticity of caddisfly growth, and the influence of caddisflies on decomposition. In particular, the consistent reduction of fungal biomass concentration we observed when consumer densities were low suggests that caddisflies selectively feed on fungi, effectively suppressing fungal biomass in leaf litter when invertebrate competitors are rare. It appears that by selectively removing fungi and ingesting higher-quality food than litter, caddisflies at low densities enhanced their own growth, but at the same time limited the influence of fungi on litter decomposition. Therefore, consumer influences on decomposition, a key ecosystem function, likely were buffered by the influence of fungi as an intermediate resource.

The outcome can be different, however, when consumers face strong intraspecific competition. Our results indicate that high caddisfly densities inhibited selective feeding on fungi, and resulted in poor consumer growth. Caddisflies reared at high density apparently spent energy on other activities such as warding off aggressive conspecifics or repairing cases that they use for defense, rather than on foraging or accruing biomass. Such changes in behavior according to perceived threats are common (Boyero et al. 2006). Further, *L. rhombicus* larvae can utilize up to 35% of their protein budget on case construction in ambient conditions (Mondy et al. 2011), highlighting the importance of energy and nutrient expenditure for consumer activities beyond basal metabolism and growth. Caddisfly shredding of litter material for case construction and repair coupled with fungal activity can explain why decomposition was fastest when caddisflies were reared in high density, despite lower caddisfly body mass and no effect of caddisfly density on fungal biomass. The combined influence of fungi and caddisflies on decomposition then becomes more important as caddisfly densities increase, whereas a classic trophic cascade from caddisflies feeding on fungi, which would otherwise accelerate decomposition, appears to operate when caddisfly densities are low. Considered together, the density dependent response of invertebrate growth, consumption, and decomposition demonstrate the challenges imposed by using static variables like body mass to infer the outcome of coupled dynamic processes in global change scenarios.

Physiological constraints imposed by our global change scenarios also influenced the relationship between invertebrate growth and litter decomposition. Metabolic theory predicts that warmer conditions accelerate metabolism resulting in smaller animals that consume more food per unit body mass (Sheridan and Bickford 2011). Our data suggest that the smaller caddisflies developing at elevated temperature were more effective than their larger conspecifics at suppressing fungal biomass in both low and high-density caddisfly treatments. This and the fact that warming accelerated decomposition for all caddisfly densities relative to comparable densities in ambient conditions lends support to the conclusion that trophic interactions are intensified and ecosystem processes accelerated in warmer climates (O'Connor 2009, Dell et al. 2011, Burnside et al. 2014).

Nitrogen addition also influenced consumer-resource interactions. Our results showing strongest effects of nitrogen on caddisflies at low densities and diminished effects on lower trophic levels, such as fungi and litter, could be driven by at least two non-exclusive mechanisms. One explanation is that increased N supply altered the resource ratio (i.e., C:N:P) of caddisfly diets, resulting in nutritional deficiencies of elements besides N, such as C or P, which can also limit invertebrate growth (Franier et al., 2016). Fungi can assimilate nutrients from the water, resulting in enhanced fungal nitrogen concentrations when nitrogen supply increases (Danger and Chauvet 2013, Danger et al. 2016). That caddisflies at low density suppressed fungal biomass throughout much of the experiment, suggests that although caddisflies were feeding, their assimilation efficiency was reduced and/or respiration increased due to changes in diet quality. Alternatively, nitrogen pollution could have imposed a physiological rather than a nutritional constraint. Nitrate can convert hemocyanin, the oxygen-carrying protein in arthropods, into methemoglobin, a pigment that is incapable of carrying oxygen; therefore, nitrate can severely constrain invertebrate metabolism, especially for sensitive benthic species (Camargo and Alonso 2006). The nitrate concentrations in our experiment (<10.0 mg NO_3^--N/L; Hines et al. 2013) were well below those considered toxic during short term exposure (LD_{50} of 66–184 mg NO_3-N/L in 72–120 h; Camargo et al. 2005), but nitrogen toxicity increases with duration of exposure. This suggests that long-term exposure even to moderate levels of nitrate pollution, although not leading to immediate mortality, could curb invertebrate growth.

Regardless of whether observed nitrogen effects were due to nutritional or physiological mechanisms, increased metabolic demand in warmer waters should exacerbate growth inhibition due to nitrogen pollution. That is exactly what we observed–caddisfly growth was reduced most strongly when warming and nitrogen were applied in combination. In this scenario, caddisflies had limited effects on fungal biomass and the combined influence of fungi and caddisflies on litter decomposition, was reduced compared to the warming alone scenario. These results suggest that nitrogen pollution will become a greater problem for aquatic invertebrates in areas that are experiencing warming, and that attempts to attribute changes in body size to environmental change should consider variation in both drivers (Elser et al. 2009, Vörösmarty et al. 2010, Boyero et al. 2011, O'Reilly et al. 2015).

In conclusion, benthic macroinvertebrates, such as caddisflies, are often used as biological indicators in water quality assessments (Jacobsen et al. 2012). Our results are consistent with a recent meta-analysis showing that growth of invertebrate consumers is sensitive to climate warming, one of the most prevalent factors of environmental change worldwide (Horne et al. 2015). However, an important caveat is that consumer growth is also sensitive to constraints imposed by nitrogen pollution, and limitations resulting from an inability to acquire food (high quantity and/or quality of fungal patches in leaf litter) as consumer densities increase. This caveat limits the utility of body mass as an independent indicator of climate influences on invertebrate populations. Further, although nitrogen reduces acceleration of decomposition due to warming, its detrimental effects on caddisfly growth suggest that nitrogen pollution will restrict the ability of invertebrates to cope with climate warming. Buffering against influences of global environmental change on aquatic ecosystems will then depend not only on curbing global warming, but also on reducing

nitrogen pollution to levels that allow invertebrate populations to persist.

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