Warming alters community size structure and ecosystem functioning

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Global warming can affect all levels of biological complexity, though we currently understand least about its potential impact on communities and ecosystems. At the ecosystem level, warming has the capacity to alter the structure of communities and the rates of key ecosystem processes they mediate. Here we assessed the effects of a 4°C rise in temperature on the size structure and taxonomic composition of benthic communities in aquatic mesocosms, and the rates of detrital decomposition they mediated. Warming had no effect on biodiversity, but altered community size structure in two ways. In spring, warmer systems exhibited steeper size spectra driven by declines in total community biomass and the proportion of large organisms. By contrast, in autumn, warmer systems had shallower size spectra driven by elevated total community biomass and a greater proportion of large organisms. Community-level shifts were mirrored by changes in decomposition rates. Temperature-corrected microbial and macrofaunal decomposition rates reflected the shifts in community structure and were strongly correlated with biomass across mesocosms. Our study demonstrates that the 4°C rise in temperature expected by the end of the century has the potential to alter the structure and functioning of aquatic ecosystems profoundly, as well as the intimate linkages between these levels of ecological organization.

Keywords: community structure; ecosystem functioning; global warming; body mass; size spectrum

1. INTRODUCTION

The ecological implications of global warming have been documented across many levels of biological organization (e.g. species-level range shifts, changes in individual body mass), and across many different types of ecosystems [1–3]. While abundant evidence exists on the consequences of environmental warming at the species and population level [1,2], the manifestation of these responses within complex communities [4–6] are only just beginning to be uncovered [2]. Recent work has demonstrated that warming has the potential to alter both the structure of communities [3,7–9] and the rates of the key ecosystem processes they mediate (e.g. nutrient cycling, decomposition and carbon sequestration) [7,10–13]. However, the mechanisms that reciprocally bind community structure and ecosystem functioning, and which will determine how the effects of warming propagate through ecosystems, are poorly understood. This is partly because they frequently involve indirect effects that are difficult to predict, but also because they are logistically difficult to examine [14]. We attempted to bridge this gap by simultaneously analysing the effects of warming at both the community and ecosystem level in an aquatic mesocosm experiment.

Few studies have attempted to explore the consequences of warming on benthic invertebrate communities [15,16] (but see [3,17]), and most of our current understanding of the effects of warming on aquatic ecosystems is drawn from studies that focus on planktonic communities [7,10,18,19]. The observed shifts in community structure and composition reported by these studies have been interpreted in the light of the biophysical and physiological constraints that limit the amount of energy and nutrients fixed by photosynthetic organisms [20,21]. However, these constraints may not necessarily apply directly to benthic food webs for several reasons. First, in contrast with pelagic zones, benthic communities typically have multiple energy pathways based on either living (e.g. benthic algae) and/or non-living (e.g. detritus) organic matter [22]. The presence of multiple energy pathways can enhance community stability [23] and thus may modulate the response of benthic communities to environmental stressors (e.g. warming). Second, size-dependent (e.g. predation) and size-independent (e.g. consumption of amorphous detritus) interactions co-occur in benthic communities, suggesting that the energy available to the individuals belonging to a particular size is not solely derived from smaller individuals in the food web [24,25]. Donor-controlled interactions (e.g. detritivory) can therefore result in a breakdown of the classical body mass–trophic level relationships that characterize planktonic food webs [26,27]. Third, many freshwater benthic communities are dominated by insects, which typically have both aquatic (larval) and terrestrial (adult) life stages. The peaks of adult insect emergence from early spring to late summer can have dramatic effects on the size and biomass structure of benthic communities [22].

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Recent work has demonstrated that experimental warming can hasten the emergence of aquatic invertebrates, as well as increasing the total flux of organisms from the aquatic to the terrestrial realm [17]. The effects of warming on benthic community size structure and ecosystem functioning are therefore expected to be complex, and driven by both the direct physiological constraints of increased temperature on metabolism and the indirect effects of altered phenology and temporal decoupling of species interactions [2,17,28].

Understanding how benthic communities will respond to changes in environmental temperature is important because they are key components of aquatic ecosystems (see [29] for a review), and are often responsible for a significant proportion of total ecosystem metabolism [30]. By incorporating detrital energy into food webs, benthic communities help to support secondary production of the whole system [31] and, furthermore, they facilitate the microbially mediated remineralization of carbon and nutrients from detritus [22,32,33]. Studies that have investigated the relationship between ecosystem processes (e.g. decomposition rates) and community structure [34] have, however, rarely considered the potential synergies with warming. Those that have, have focused solely on the horizontal structure of detritivore assemblages (e.g. the diversity of organisms within a single trophic level [35]). Very few also accounted for the combined effects of temperature and vertical food web structure (e.g. changes in more than one trophic level [11,36]) on decomposition rates, despite the fact that in natural systems, the overall rates of ecosystem processes occur within the 'cradle' of the food web (i.e. they are biotically driven) and may be dependent on structure in complex nonlinear ways (e.g. via indirect effects [9]).

In this study, we analysed a set of replicated benthic communities within a well-established mesocosm experiment that simulated the level of warming expected by the end of the century on shallow freshwater ecosystems (see [12] for details). We addressed three aims. First, we determined the effects of temperature on the community body mass (μg C) distribution. The distribution of abundance with body mass is a fundamental property of ecological communities, and describes how energy and nutrients are partitioned among the biomass of an ecosystem [27,37]. The log-transformed scaling relationship between mass, M, and abundance, N, is often referred to as the community size spectrum (CSS) [38,39], and changes in its slope can be used to assess the effects of changes in environmental conditions (i.e. perturbations) at the community level [39,40]. In particular, larger organisms, which are usually towards the top of food chains, tend to be more susceptible to anthropogenic perturbations (e.g. overfishing, habitat loss and modification, warming), owing to their lower population densities and greater energetic demands [27,41]. Therefore, if resource supply rates remain constant, warmer systems should: (i) support lower population densities of larger organisms, thereby increasing the steepness of the CSS; and (ii) support a lower overall standing biomass (μg C m^{-2}) [5].

Second, we aimed to determine the effects of warming on the compositional diversity of the benthic communities. Whether warming alters community structure via shifts in the taxonomic composition, via alterations in the body mass distribution or via a combination of these will be key to managing and predicting the future consequences of warming in aquatic ecosystems. Previous

work on microbial food webs showed that warming alters trophic structure and consequently the rate of ecosystem functioning [9,42]. However, to the best of our knowledge, comparable research has not been carried out for benthic communities.

Finally, we attempted to unravel the mechanisms that link community structure to ecosystem functioning, and assess whether changes in temperature have the potential to disrupt these linkages as the climate warms in the coming decades. Decomposition rates in aquatic ecosystems are driven both by the direct effects of temperature on metabolism and resource consumption rates, but also by the total biomass of detritivores [33]. Thus, we may expect decomposition rates to increase with temperature as organisms should exploit their resources at a faster rate. However, if the structure of the communities is also affected by changes in temperature, we may expect to observe significant interactions between warming, community structure and decomposition rates.

2. MATERIAL AND METHODS

(a) *Experimental design*

The mesocosm experiment was carried out at the Freshwater Biological Association River Laboratory (50°11′30″ N, 2°11′00″ W) in southern England. Detailed information regarding the experimental set-up is provided in the study of Yvon-Durocher *et al.* [12]. The experiment comprised 20 outdoor freshwater mesocosms (approx. 1 m^3, 0.5 m water depth): 10 replicates were left at ambient temperature as controls, while the other 10 were warmed to 3−5°C (mean 4°C) above ambient. After the mesocosms were seeded with organic substrates and invertebrates in December 2005, experimental warming commenced in September 2006. Further time was left for natural colonization before the beginning of the study in April 2007.

(b) *Invertebrate sampling*

The benthic invertebrate communities from each of the mesocosms were sampled twice (once in April and once in October 2007). On each sampling occasion, one sample was collected in every mesocosm ($n = 40$) using a Hess sampler (mesh size 250 μm, sampler area 78.5 cm^2) and preserved in 4 per cent formaldehyde. The collected samples were sieved at 250 μm to remove detritus, and organisms were counted, measured and identified to the lowest possible taxonomic level (electronic supplementary material, S1).

(c) *Body mass measurement*

Body mass measurements (electronic supplementary material, S1) were achieved with an image analysis system (camera: DS-L1, Nikon, Derby, UK; software: ImageJ, U.S. National Institutes of Health, Bethesda, MD). Body mass (dry weight μg) was estimated for macroinvertebrates using published length−weight regression equations for the identified organisms (electronic supplementary material, S1). For microcrustaceans (e.g. Cladocera, Copepoda and Ostracoda), body mass was derived from biovolumes by assigning organisms to a geometric figure that most closely represented their shape; biovolumes were then converted to wet weight by applying a conversion factor of 1.1, and then dry weight by applying a dry/wet weight ratio of 0.25 [43]. For both groups, body mass was expressed in units of carbon (μg C) by assuming that 40 per cent of total dry weight is C [43].

(d) Community size spectra

The CSS was constructed for each mesocosm in April and October 2007 ($n = 40$; see electronic supplementary material, S2). Size spectra were constructed by dividing the total range of $\log_{10}(M)$ values, where M is body mass in µg C, into n logarithmic bins of equal width, and the logarithm of the total abundance of all organisms ($\log_{10} N$) in each bin was regressed against the centre of the bin (after White *et al.* [38]). The number of bins ($n = 6$), which was fixed across all replicates, was chosen to maximize the linearity of the size spectrum and reduce the occurrence of empty bins. The lower boundary of the size distribution used for CSS analysis was set in correspondence with the peak of the size distribution of the organisms that were small enough to be washed through the 250 µm sieve, and thus were most likely to be affected by under-sampling (electronic supplementary material, S3).

(e) Leaf litter decomposition rate

Leaf litter decomposition experiments were performed by adding to each mesocosm a fixed amount (4 ± 0.001 g) of air-dried litter (*Populus nigra* L.). For each combination of treatment and date, one coarse (total decomposition; mesh aperture: 10 mm) and one fine (microbial decomposition; mesh aperture: 500 µm) mesh bag, containing the leaf litter, were placed in each mesocosm for 30 days, after which they were removed and immediately frozen. In the laboratory, the remaining leaf litter at the end of the experiment was separated from invertebrates, and oven-dried (60°C) to a constant weight. The dry weight loss over the duration of the experiment was calculated, and total and microbial decomposition rates were determined using the exponential decay coefficient $kd = \ln (M_f/M_i)/d$, where M_i is the initial weight in the litter bag, M_f is the weight remaining after exposure in the mesocosms and d is the cumulative number of days of exposure. To remove the effect of temperature on the rate of decomposition and isolate the effects of community composition on the rate of leaf litter decomposition, we temperature-corrected the exponential decay coefficients using $kdd = \ln (M_f/M_i)/dd$, where dd is the cumulative number of degree days of exposure (after Petersen & Cummins [44]).

(f) Statistical analysis

We carried out a linear mixed effects analysis using the *lme* function in the nlme package in R v. 2.12.2 [45] to determine both the slope of the CSS and to test for differences between treatments and seasons in the following variables: (i) total standing biomass (µg C m^{-2}), expressed as the sum of the individual body masses (µg C) per mesocosm multiplied by the density (no. m^{-2}; estimates of standing biomass were $\log_{10}$-transformed prior analysis to achieve normality); (ii) taxonomic diversity, measured using the Shannon index $H' = -\sum p_i \ln p_i$, where p_i is the proportion of the individuals found for the *i*th species, and evenness, measured using the Shannon evenness index: $\mathcal{J}' = H'/\ln S$, where S is the number of species; and (iii) leaf litter decomposition rates.

Linear mixed effects models were used to assess the effects of treatment and date (fixed effects) on our measures of community structure and ecosystem functioning, while accounting for the temporal pseudoreplication in our data (e.g. repeated measurements in each mesocosm on two dates) [46]. We fitted all models, including mesocosm as a random effect on the intercept: in doing so, we corrected for the inflation of the residual degrees of freedom that would have occurred if we were using repeated measurements as true replicates. We assessed the significance of the fixed effect terms by starting with the most complex

model and then simplifying by removing non-significant terms identified using likelihood ratio tests. Models used in the likelihood ratio test were fitted using maximum likelihood, because they had different fixed effects structures (i.e. different degrees of freedom) [47]. The final model was then refitted using restricted maximum likelihood to determine the parameter estimates. If the model validation plots showed heteroscedasticity, we implemented a variance function of the form varIdent (form = ~1|treatment × date), to estimate the within-group variance and account for unequal variances among the strata of treatment and date. The likelihood ratio test was used to assess whether the implemented models significantly improved the fit to the data. Finally, differences among the levels of the fixed effects in the final model were determined using multiple comparison post-hoc analyses (general linear hypothesis test, hereafter glht).

Pearson correlation coefficients were also used to further investigate the role of macroinvertebrates in the decomposition of leaf litter. Total decomposition rates (kd_{tot} and kdd_{tot}) were tested for correlation against total community biomass (µg C m^{-2}), density (no. m^{-2}), diversity measures and water temperature.

3. RESULTS

(a) Effect of warming on community size structure

In total, 19 410 individual organisms were counted and measured. Body mass spanned five orders of magnitude ranging from 0.12 to 17 820 µg C in the ambient systems, whereas a truncated range, 0.04–10 920 µg C, was detected in the heated systems. The slope of the CSS was always negative (i.e. log abundance declined with increasing log body mass; figure 1a,c) and was significantly affected by the interaction between date and treatment (table 1a; electronic supplementary material, S3). In April, warming significantly increased the steepness of the CSS slope (table 1a; figure 1a,b), whereas in October, CSS slopes were shallower in the warmed mesocosms (table 1a; figure 1c,d). In the ambient mesocosms, the CSS slope remained constant between April and October.

Standing community biomass was not significantly affected by warming on average, though the interaction between treatment and date was significant (table 1b; electronic supplementary material, S3). Heated mesocosms supported less standing community biomass in April (table 1b; figure 2). By contrast, in October, standing community biomass increased in the warmed mesocosms (table 1b; figure 2).

(b) Effects of warming on biodiversity

Our metrics of diversity (H') and evenness ($\mathcal{J}'$) were not significantly affected by warming; H' decreased between April and October in the ambient mesocosms only, while $\mathcal{J}'$ decreased across seasons in both treatments (table 1c,d; figure 3a,b).

(c) Effects of warming on leaf litter decomposition rate

Total (kd_{tot}) leaf litter decomposition rates were significantly affected by the interaction between treatment and date, while microbial (kd_{micr}) decomposition rates were positively affected by treatment in both months, and declined significantly between April and October in both treatments (table 1e,f; figure 4a). Post-hoc analysis revealed that warming increased kd_{tot} both in April and October, and that kd_{tot}
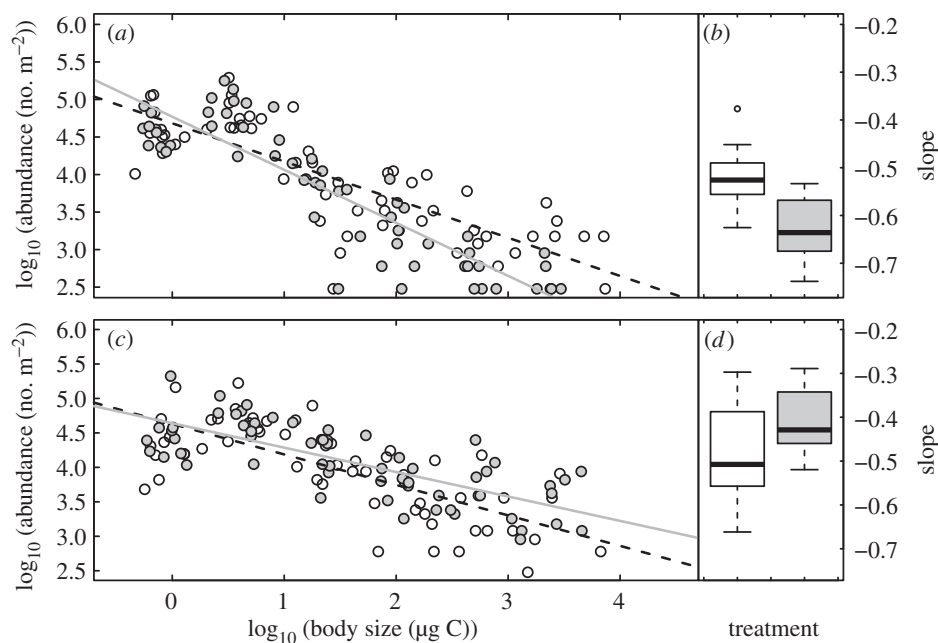
Figure 1. Benthic community size spectra of the mesocosms in (a,b) April and (c,d) October. Open circles and dashed lines refer to ambient treatments, filled circles and solid lines refer to heated treatments. Regression lines represent the fixed effects of the fitted linear mixed effects model: (a) ambient: $y = 3.91 - 0.51x$; heated: $y = 3.75 - 0.73x$; (b) ambient: $y = 3.96 - 0.48x$; heated: $y = 4.07 - 0.41x$. In the ambient mesocosms, the slopes remained approximately constant in the two sampling occasions, while in the heated mesocosms, the effect of warming on the slope acted in opposite directions in spring and autumn (table 1a).

decreased with date in both heated and unheated meso-cosms (table 1e; figure 4a). kd_{micr} increased with warming and decreased with date, although their interaction was not significant (table 1f; figure 4a). Pearson correlation tests revealed that both kd_{tot} and kd_{micr} were positively cor-related with water temperature ($r = 0.6$, $p < 0.001$; $r = 0.68$, $p < 0.001$, respectively).

After dividing the decomposition rates by the number of degree days (kdd), total (kdd_{tot}) decomposition rate was significantly affected by the interaction between warming and date (table 1g; figure 4b). Post-hoc analysis revealed that in April kdd_{tot} decreased with warming, while in October it was considerably higher in the heated mesocosms compared with the ambient (table 1g; figure 4b). In the heated mesocosms only, April kdd_{tot} was higher in October compared with April (table 1g; figure 4b), whereas microbial (kdd_{micr}) temperature-corrected decomposition rates were negatively affected by warming in both months (table 1h; figure 4b). Pearson correlation tests revealed a significant positive correlation between April kdd_{tot} and total community bio-mass ($r = 0.37$, $p = 0.018$), whereas April kdd_{tot} was not significantly correlated with H' ($r = -0.02$, $p = 0.891$) and $\mathcal{J}'$ ($r = 0.13$, $p = 0.396$).

4. DISCUSSION

Our study adds to the mounting body of recent evidence which suggests that the 4°C rise in mean annual tempera-ture predicted for the end of the century has the potential to alter the structure and functioning of aquatic commu-nities [7–9,11–13]. Warming shifted the size structure of the benthic communities in our mesocosm experiments, though it had no detectable effect on their diversity or evenness. The effects of warming on the steepness of

the CSS, and the biomass of the different trophic groups within the communities, acted in opposite direc-tions in spring and autumn. This suggested that warming may disrupt the phenological succession of benthic macroinvertebrate communities, in line with another recent experimental study in freshwater meso-cosms [17]. Shifts in benthic size structure were also mirrored by marked changes in the decomposition rate of organic material, demonstrating that in freshwater ecosystems these community and ecosystem properties are fundamentally linked by size, rather than taxono-mic composition (e.g. diversity or evenness). Moreover, our findings suggest that changes in environmental temperature could disrupt the intimate links between community size structure and ecosystem process rates (e.g. decomposition).

Slopes of the CSS were significantly steeper in the warmed mesocosms in April. This effect appeared to be driven by systematic declines in the abundance of large organisms, and reflected reductions in whole community biomass and in the abundance of the top predator, the dragonfly *Orthetrum cancellatum* L. (see electronic sup-plementary material, S5 for community composition analysis). For many of the large insect taxa, April effec-tively represents the start of the main emergence period, which peaks over the summer in temperate regions [48,49]. Therefore, we expect that the patterns in invert-ebrate community structure in April are the consequence of constraints imposed during the overwintering period after the summer recruitment period. In this respect, stee-per CSS slopes and reduced biomass of large organisms at this time might be a consequence of elevated energetic constraints, which tend to be magnified towards the top of food chains [9]. Because basal metabolic rate is posi-tively correlated with body mass and temperature, if

Table 1. Results from the linear mixed effect model analyses. For each variable, listed from (*a*) to (*h*), the most parsimonious fixed effects structures, number of parameters, Akaike information criterion (AIC) score, log-likelihood, χ^2 and *p*-values are presented in the main table. Every model was fitted with mesocosm as random effect on the intercept. Nested sub-tables present the output of the *glht* multiple comparison tests for each variable. Estimates of the average difference (est.) among the levels of the fixed effect terms are presented along with their standard error, *z*- and *p*-values. Significant differences are reported in bold. kd_{tot} and kdd_{tot} were fitted using a weighted model, to account for unequal variances among levels of the fixed effects (see electronic supplementary material, S3 for the variance structure specifications).

| model	no. parameters	AIC	log-lik	χ^2	*p*
(*a*) CSS					
log ab ~ mass × treatment × date	10	265.771	−122.88	40.182	**<0.001**
		est.	s.e.	*z*	*p*
slope Apr A versus slope Apr H		−0.207	0.064	−3.235	**0.004**
slope Oct A versus slope Oct H		−0.142	0.074	−1.814	0.240
slope Apr A versus slope Oct A		0.065	0.065	1.000	0.677
slope Apr H versus slope Oct H		−0.349	0.045	−7.705	**<0.001**
(*b*) whole community biomass					
log biomass ~ treatment × date	3	42.118	−15.059	8.512	**0.003**
		est.	s.e.	*z*	*p*
Apr A versus Apr H		0.345	0.143	2.406	**0.034**
Oct A versus Oct H		−0.627	0.110	−5.675	**<0.001**
Apr A versus Oct A		0.023	0.152	0.155	0.998
Apr H versus Oct H		−0.972	0.192	−5.059	**<0.001**
(*c*) diversity (H′)					
H′ ~ treatment × date	6	13.312	−0.656	4.141	**0.041**
		est.	s.e.	*z*	*p*
Apr A versus Apr H		0.191	0.119	1.618	0.273
Oct A versus Oct H		−0.003	0.101	−0.034	1.000
Apr A versus Oct A		0.288	0.101	2.844	**0.013**
Apr H versus Oct H		−0.194	0.185	−1.047	0.062
(*d*) evenness (J′)					
J′ ~ treatment + date	5	−55.123	32.5616	6.24465	**0.012**
		est.	s.e.	*z*	*p*
A versus H		0.032	0.035	0.902	0.599
Apr versus Oct		0.088	0.035	2.500	**0.025**
(*e*) total decomposition rate					
kd_{tot} ~ treatment × date	9	−307.19	162.598	4.80254	**0.028**
var. structure = 1 | treatment × date					
		est.	s.e.	*z*	*p*
Apr A versus Apr H		−0.003	0.002	−2.177	**0.029**
Oct A versus Oct H		−0.006	0.002	−2.295	**0.022**
Apr A versus Oct A		0.013	0.002	7.657	**<0.001**
Apr H versus Oct H		0.009	0.004	2.760	**0.007**
(*f*) microbial decomposition rate					
kd_{micr} ~ treatment + date	5	−375.50	192.752	51.7435	**<0.001**
		est.	s.e.	*z*	*p*
A versus H		−0.002	6.2×10^{-4}	3.968	**<0.001**
Apr versus Oct		0.006	6.1×10^{-4}	10.425	**<0.001**
(*g*) total temperature-corrected decomposition rate					
kdd_{tot} ~ treatment × date	9	−416.48	217.242	14.2552	**<0.001**
var. structure = 1 | treatment × date					
		est.	s.e.	*z*	*p*
Apr A versus Apr H		0.001	3.4×10^{-4}	−3.174	**0.040**
Oct A versus Oct H		−0.006	1.1×10^{-3}	−4.988	**<0.001**
Apr A versus Oct A		0.001	4.4×10^{-4}	1.041	0.910
Apr H versus Oct H		−0.007	1.2×10^{-3}	−5.612	**<0.001**
(*h*) microbial temperature-corrected decomposition rate					
kdd_{micr} ~ treatment + date	5	−567.10	288.552	4.23397	**0.039**
		est.	s.e.	*z*	*p*
A versus H		1.8×10^{-4}	5.8×10^{-5}	3.084	**0.004**
Apr versus Oct		1.1×10^{-4}	5.8×10^{-5}	2.033	0.082
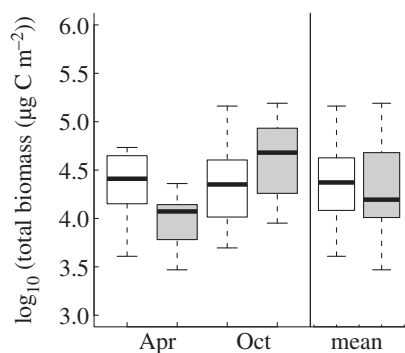
Figure 2. Effects of warming on total community biomass. Dark bars represent the median of the $\log_{10}$ total biomass across the mesocosms for each treatment and sampling occasion ($n = 20$ per treatment for the overall mean; $n = 10$ per treatment for each sampling occasion), while the boxes denote the interquartile range. Filled boxes denote heated treatments, while open boxes denote the ambient treatments.

resource supply rates remain constant, while temperatures rise, the biomass of larger organisms high in the food web should decline owing to greater resource limitation [5]. This is in line with our previous findings, and other experimental work on the effects of temperature on predator–prey interactions [50–53].

Classical size spectrum theory predicts that the steepness of the slope of the CSS is the product of the efficiency of energy transfer from small, abundant organisms at the base of the food web to large, scarce predators at the top [54–57]. Inefficient energy transfer gives rise to steeper size spectra slopes, because the abundance of larger organisms is constrained to a greater extent by a lack of available energy [23,37,54–57]. The steeper slopes, and reduced biomass in the larger size classes at the end of the post-recruitment growth period might be a product of greater constraints on the efficiency of energy transfer along food chains at higher temperatures. Indeed, the trophic transfer efficiency reflects the fraction of available energy lost at each step along the food chain, owing to the constraints imposed by the second law of thermodynamics (i.e. the continual production of 'negentropy' by organisms [58]) on maintenance and growth [57]. Thus, at higher temperatures, if a greater proportion of energy is lost to maintenance and growth, the successive decline in the proportion of available energy at each trophic level may be amplified in warmer environments.

In stark contrast to April, CSS slopes in October were significantly shallower in the warmed treatments. This result appeared to be driven by dramatic increases in total standing community biomass. The dominant detritivore taxon in our experiment was the isopod *Asellus aquaticus* L., which exhibited a marked increase in abundance in the warmed mesocosms (electronic supplementary material, S5). *Asellus aquaticus* has multiple generations per year [48]; thus, the shallower size spectrum slopes and increased biomass in October might be the result of greater recruitment success and more rapid population growth rates in the warmed treatments throughout the summer. Both growth and development rates are correlated with temperature in ectotherms [59,60]; therefore, newly recruited populations in the warmed treatments may actually benefit from elevated
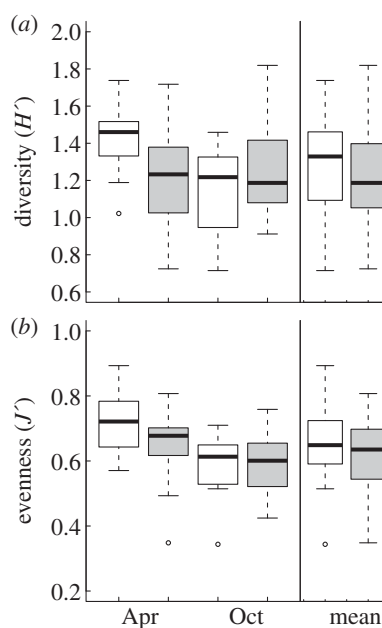

Figure 3. Effects of warming on (*a*) diversity (H') and (*b*) evenness (J'). Dark bars represent the median across the mesocosms for each treatment and sampling occasion ($n = 20$ per treatment for the overall mean; $n = 10$ per treatment for each sampling occasion), while the boxes denote the interquartile range. Filled boxes denote heated treatments, while open boxes denote the ambient treatments.

growth and development rates, leading to greater biomass production, while resources are plentiful. While consistent with our previous experimental findings and the wider literature [17], these hypotheses clearly require rigorous verification with more highly resolved seasonal measurements of community structure. Nevertheless, our experimental findings provide a hint that phenological shifts in invertebrate community size structure may occur in response to warming.

Both total and microbially mediated decomposition rates unsurprisingly increased with experimental warming, reflecting the direct influence of temperature on metabolism and resource consumption rates [61]. However, once this 'metabolic' effect had been controlled for, the treatment effect on rates of total decomposition closely reflected the patterns observed in community biomass, but were independent of diversity or evenness. For instance, in April, total temperature-corrected decomposition rates were lower in the warmed treatments, in line with the reductions observed in the whole community standing biomass and the steeper size spectra. By contrast, in October total temperature-corrected decomposition rates were significantly enhanced in the warmed treatments, matching the elevated biomass and the shallower size spectra. Because biodiversity was unaffected by warming, we observed no correlation between either diversity or evenness with decomposition rates. This finding is in line with recent evidence from freshwater ecosystems [11,62], highlighting the apparent prevalence of taxonomic redundancy within functional groups in aquatic communities. Our results therefore suggest that community size structure may have a stronger effect on ecosystem functioning than taxonomic diversity *per se* in aquatic ecosystems. Moreover, they demonstrate that these linkages might be disrupted by warming, potentially leading to increased
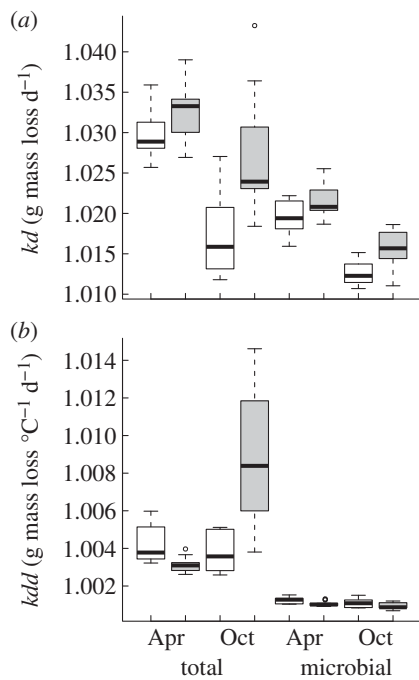
Figure 4. Effect of warming on (*a*) total and (*b*) microbial decomposition rate per day (kd), and per degree day (kdd). Dark bars represent the median across the mesocosms for each treatment and sampling occasion ($n = 10$ per treatment for each sampling occasion), while the boxes denote the interquartile range. Filled boxes denote heated treatments, while open boxes denote the ambient treatments.

mineralization of allochthonous material, resulting in greater CO_2 and/or CH_4 emission from aquatic ecosystems, effects that have been previously documented in our experimental system [12,13].

In conclusion, our experiment revealed that warming of $4°C$ has the potential to alter the size structure of aquatic communities. Our findings also highlight that the linkages between community structure and ecosystem functioning are fundamental for determining the response of ecosystem process rates to temperature change. Although there is clearly a great deal of further experimental and theoretical work yet to be done, the next steps will involve developing a deeper mechanistic understanding of these phenomena needed to predict the future consequences of climate change on biota and the ecosystem services they provide.

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