

LETTER

Experimental climate change weakens the insurance effect of biodiversity

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Abstract

Ecosystems are simultaneously affected by biodiversity loss and climate change, but we know little about how these factors interact. We predicted that climate warming and CO₂-enrichment should strengthen trophic cascades by reducing the relative efficiency of predation-resistant herbivores, if herbivore consumption rate trades off with predation resistance. This weakens the insurance effect of herbivore diversity. We tested this prediction using experimental ocean warming and acidification in seagrass mesocosms. Meta-analyses of published experiments first indicated that consumption rate trades off with predation resistance. The experiment then showed that three common herbivores together controlled macroalgae and facilitated seagrass dominance, regardless of climate change. When the predation-vulnerable herbivore was excluded in normal conditions, the two resistant herbivores maintained top-down control. Under warming, however, increased algal growth outstripped control by herbivores and the system became algal-dominated. Consequently, climate change can reduce the relative efficiency of resistant herbivores and weaken the insurance effect of biodiversity.

Keywords

Food web, *Gammarus locusta*, *Littorina littorea*, marine, mesograzer, metabolic theory of ecology, realistic biodiversity loss, response-effect traits, temperature, *Zostera marina*.

Ecology Letters (2012) 15: 864–872

INTRODUCTION

Biodiversity can provide insurance against disturbance and environmental change by increasing the chance that at least some resistant species can maintain ecosystem functioning when others fail (McNaughton 1977; Naeem & Li 1997; Elmqvist *et al.* 2003). Even though rarely stated, this ‘insurance hypothesis’ hinges on the assumption that the traits that determine how species respond to factors or changes in their environment (‘response traits’, e.g. the degree of physical and/or behavioural protection against predation) are *uncorrelated* with the traits that determine how species affect their environment (‘effect traits’, e.g. consumption rate, see Fig. 1a). For the insurance effect to operate, the traits should be distributed in such a way that at least some efficient species are also resistant enough to maintain functioning (Suding *et al.* 2008). In systems with such trait distributions, loss of vulnerable species (i.e. ‘realistic’ or ‘non-random’ loss) has weak effects, because most species are functionally redundant (Chapin *et al.* 1996; Walker *et al.* 1999). Theoretically, biodiversity loss can also have negligible, or even positive, effects if response and effect traits are *positively* correlated (Fig. 1b). However, loss of vulnerable species will have stronger effects than those expected from random loss of species, when response and effects traits are *negatively* correlated (Fig. 1c) (e.g. Solan *et al.* 2004; Zavaleta & Hulvey 2004; Larsen *et al.* 2005; Bracken *et al.* 2008). In such circumstances high diversity provides weak insurance. It is a well-known fact that negative correlations between response and effect traits can be caused by evolutionary trade-offs, e.g. between

competitive ability and resistance (Kneitel & Chase 2004). However, our understanding about which trait correlations dominate in different systems or contexts is limited (Suding *et al.* 2008), and this constrains our ability to predict the consequences of biodiversity loss.

In this article we hypothesise that the insurance effect of biodiversity can be altered by climate change. We herein define insurance as the ability of herbivore species diversity to buffer food webs against effects of predation on herbivores that cascade to plants. Our hypothesis links predictions based on the insurance hypothesis of biodiversity, with predictions about the roles of environmental warming and CO₂-enrichment for plant-herbivore interactions. In theory, high herbivore diversity should weaken trophic cascades by increasing the chance that some herbivores are inedible to predators and maintain trophic control (Strong 1992; Duffy *et al.* 2007). However, even though prey diversity can weaken direct predation effects (Hillebrand & Cardinale 2004; Edwards *et al.* 2010), evidence for a reduction in the strength of trophic cascades is mixed (Duffy *et al.* 2005; Kurle & Cardinale 2011), potentially because predation resistance often trades off with consumption rate (Gruner *et al.* 2008; Sieben *et al.* 2011). Climate change may strengthen or weaken these processes: in many ecosystems environmental warming increases metabolism and growth of both primary producers and ectotherm herbivores (Nemani *et al.* 2003; Chavez *et al.* 2011). Since respiration of ectotherm herbivores is more temperature-limited than photosynthesis (Allen *et al.* 2005), sub-lethal warming can strengthen top-down control (solid black line in Fig. 1d) (O’Connor 2009; O’Connor *et al.* 2011). It can also be predicted that even though trophic

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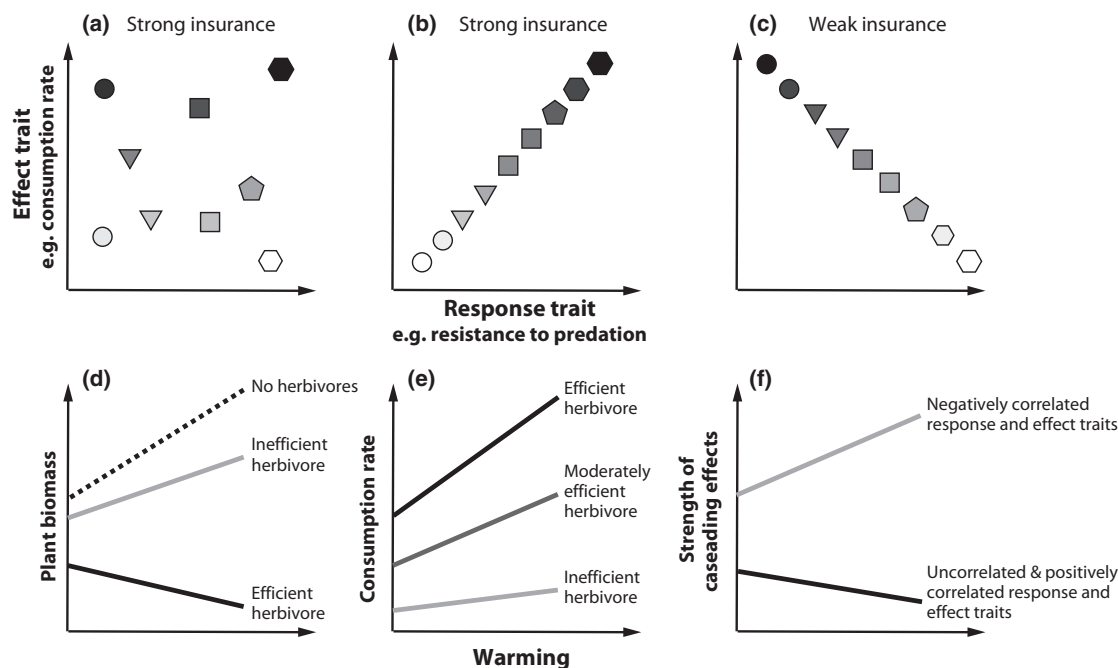


Figure 1 The insurance effect of biodiversity is mediated by the interaction between (i) the correlation between species response and effect traits, and (ii) climate change. The effect of losing vulnerable species depend on whether response and effect traits are (a) uncorrelated, (b) positively correlated, or (c) negatively correlated (symbols = species; symbol colour = consumption rate; symbol shape = predation resistance). (d) Warming strengthens herbivore control over plant biomass, but also increases *relative* differences in trophic control between efficient and inefficient herbivores (based on O'Connor 2009). (e) Warming amplifies differences in herbivore consumption rate. (f) When combined, these predictions suggest trophic cascades should *strengthen* with climate change when herbivore traits are negatively correlated. See text in *Introduction* for details.

control from inefficient herbivores increases with warming (dashed vs. grey solid line, Fig. 1d), their *relative* efficiency can still decrease (grey vs. black solid line, Fig. 1d) (O'Connor 2009). This is partly because warming will amplify relative differences in trophic control between efficient and inefficient herbivores (Fig. 1e), and partly because high plant growth can outstrip consumption from inefficient herbivores also under warming.

Against this background, we hypothesise that the effect of warming on trophic cascades will depend on how response traits (here, predation resistance) correlate with effect traits (here, consumption rate; see Fig. 1f). First, if predation resistance trades off with consumption rate, warming should *strengthen* trophic cascades by reducing the relative efficiency of predation-resistant, but inefficient, herbivores (grey line in Fig. 1f). (It is important to note here that we are referring to the *relative* efficiency of the herbivores, not the *absolute* efficiency.) Conversely, if grazing rate is either uncorrelated or positively correlated with predation resistance (Fig. 1a and b), warming should instead have zero effect or *weaken* trophic cascades (black line in Fig. 1f). In addition to warming, climate change involves increasing CO₂ concentrations in air and water (Caldeira & Wickett 2003; IPCC 2007). CO₂-enrichment can increase photosynthesis and biomass of many plants, especially in the absence of efficient consumers and in combination with warming (Connell & Russell 2010; Kroeker *et al.* 2010; Anthony *et al.* 2011). Consequently, warming and CO₂-enrichment should (i) *weaken* the insurance effect of herbivore diversity if response traits are traded-off against effect traits, or (ii) *increase* the insurance effect if traits are positively correlated or uncorrelated.

We tested the first of these two predictions in marine seagrass (eelgrass *Zostera marina* L.) beds; a globally threatened ecosystem

where predation-induced loss of small algal-feeding invertebrate herbivores (often referred to as 'mesograzers') contributes to ecosystem shifts to algal-dominated, degraded states (Duarte 1995; Eriksson *et al.* 2011; Nyström *et al.* 2012). We first tested if resistance of herbivores to predation and the herbivores' trophic control of macroalgae differed between two common groups of herbivores. For this purpose we used meta-analyses of published predation experiments. We then used an experiment with seagrass communities to test if the effect of removing an efficient, but predation-vulnerable, herbivore species was influenced by near-future levels of ocean warming and acidification. We hypothesised that under simulated climate change, loss of herbivore diversity would increase the risk for ecosystem shift from seagrass to macroalgal dominance.

MATERIAL AND METHODS

Study system

Eelgrass (the seagrass *Z. marina* L.) is a clonal angiosperm that forms highly productive, valuable and globally threatened marine ecosystems in the Northern hemisphere (Waycott *et al.* 2009). Eelgrass loss is often caused by shading from fast-growing epiphytic and floating, mat-forming macroalgae. As a result, the ecosystem can shift to an algal-dominated state characterised by high turbidity and loss of ecosystem services (Duarte 1995; Eriksson *et al.* 2011; Baden *et al.* 2012; Nyström *et al.* 2012). Such shifts were for long primarily attributed to eutrophication, but could in fact be triggered by loss of mesograzers (a diverse group of invertebrate herbivores like amphipods and gastropods) which, when sufficiently abundant and diverse, control algae and buffer eutrophication effects (Duffy

et al. 2005; Moksnes *et al.* 2008). In Sweden, recent declines in populations of coastal top predators (e.g. cod *Gadus morhua* L. and perch *Perca fluviatilis* L.) have increased predation pressure on efficient herbivores from a diverse group of mesopredators (invertivorous fish, shrimp and crabs) (Eriksson *et al.* 2011; Baden *et al.* 2012). As a consequence, near-shore, benthic ecosystems like eelgrass and perennial macroalgal beds (*Fucus* spp.) have become less resilient to eutrophication-induced algal blooms (for review, see Eriksson *et al.* 2011).

Meta-analyses

We searched the literature for field and laboratory experiments testing the effects of predation (predator presence vs. absence) on invertebrate communities in vegetated benthic systems, that reported simultaneous effects on amphipod and gastropod biomass or density (using ISI Web of Science and the search strings: 'predat* AND amphipod* AND gastropod*'; 'seagrass* AND predat*'; 'macroalg* AND predat*'). From 18 suitable experiments in 9 publications we then extracted data (mean, SD and *n*, see Appendix S1 in *Supporting Information*) from tables or graphs (using GraphClick™). We then calculated log response ratios (LRR) for amphipods and gastropods separately, using MetaWin 2.0 (Rosenberg *et al.* 1999). We chose this effect size metric because it is (i) dimensionless (allowing for comparison between the studies, which used different methodologies and/or units), (ii) easily interpretable and biologically meaningful and (iii) currently the most common metric in ecological meta-analysis (Hillebrand & Cardinale 2004; Gruner *et al.* 2008; Edwards *et al.* 2010; Kroeker *et al.* 2010). We then assessed the potential influence of eight moderator variables (publication, research group, absolute latitude, size of experimental units, experiment length, experimental nutrient enrichment, predator type and relative density of other herbivore types) on LRR using a multiple linear regression model. As no moderator variables were influential ($P \gg 0.05$ for both response variables), we calculated predation effects on each herbivore type using random-effects meta-analysis (Fig. 2a).

To estimate the extent to which the two herbivore taxa differed in grazing efficiency (and, indirectly, contributed to cascading effects of predation), we selected those predation studies that also reported responses of macroalgae (four studies from Sweden, see *Appendix S2*). We then fitted a mixed multiple regression model with 'macroalgal biomass' (treatment means) as a response variable, and 'amphipod bio-

mass', 'gastropod biomass', 'nutrient enrichment' (a treatment in several studies) and 'publication' (random factor) as predictor variables (Fig. 2b–c). We first standardised biomass variables as [mean per treatment/mean across treatments within studies] to be able to compare between studies, and controlled for assumptions of normal error distributions and multicollinearity. Predictor variables were considered significant at $\alpha = 0.05$.

Mesocosm experiment

We tested the separate and joint effects of simulated herbivore diversity loss, ocean warming and ocean acidification in 60 flow-through mesocosms in a semi-open greenhouse facility at the Sven Lovén Center for Marine Sciences, Kristineberg, SW Sweden (58.25° N, 11.45° E). The experiment ran for 5 weeks (20 July–24 August 2010). Replicates ($n = 5$) were randomly distributed across mesocosms.

The mesocosms were 30 L semi-transparent buckets ($\varnothing = 37.5$ cm, see Fig. S1A–F) filled with 10 L wet-sieved surface sediment (0.5 mm) from a *Z. marina* bed mixed with cleaned beach sand (ratio 1 : 2). Mesocosms received surface seawater from the nearby Gullmar Fjord (average salinity: 24‰, flow rate: 30 L h⁻¹). Herbivore contamination (which was minimal, see Fig. 4) was reduced by filtering the incoming water (200 µm). One week before start, 28 gently cleaned eelgrass (*Z. marina* L.) shoots collected in a nearby area were weighed (WW to nearest 0.001 g) and planted in each mesocosm. The resulting shoot density (350 m⁻²) was within the range of that in nearby shallow areas (Moksnes *et al.* 2008). On the first day of the experiment, we added ~2.0 g WW (~0.2 g DW 0.1 m⁻²) of the common green algae *Cladophora* to each unit to mimic natural conditions. Mesocosms and seawater outlets were covered with plastic mesh (3 and 1 mm respectively) to contain herbivores and simulate the light climate at 1 m depth (~30 × 10¹⁵ quanta) respectively. The inside walls of mesocosms were cleaned daily to prevent fouling.

Herbivore diversity loss

To simulate predation-induced loss of gammarid herbivores as observed in the study area (e.g. Moksnes *et al.* 2008) and in our meta-analysis (Fig. 2a), we added three combinations of herbivores using an additive design: (i) 'All herbivores', comprising 20 adult gammarid amphipods *Gammarus locusta* L. (♀:♂ 1 : 1, length = 10–15 mm), seven adult *Littorina littorea* L. gastropods (1.44 ± 0.18 g DW ind⁻¹,

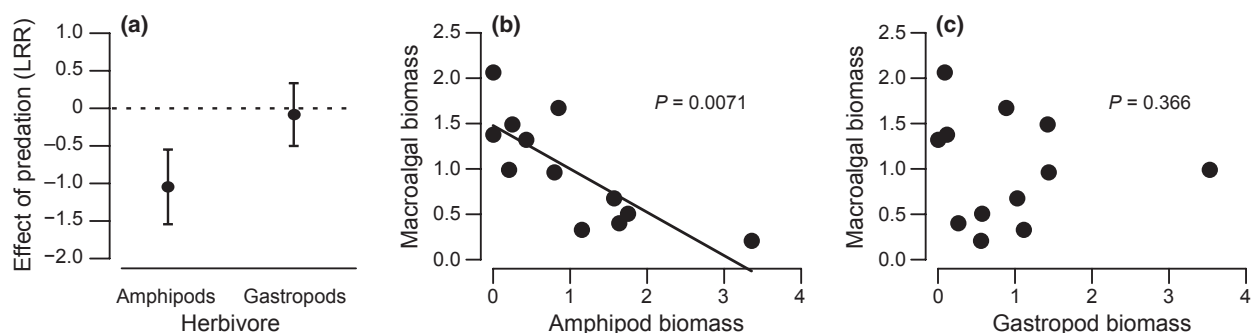


Figure 2 Resistance of herbivores to predation is associated with low trophic control. (a) Meta-analysis on effects of experimental predation on amphipods and gastropods in vegetated benthic ecosystems (mean LRR abundance or biomass ± 95% confidence intervals, $n = 18$). Effect of (b) amphipod and (c) gastropod biomass on macroalgal biomass (mean LRR biomass) in four trophic cascade experiments. Note that the regression line depicts the fixed linear effect model, which does not include random variation between studies.

mean \pm SEM, $n = 20$) and five adult *Rissoa* sp. gastropods (0.22 ± 0.02 g, DW ind⁻¹, mean \pm SEM, $n = 17$); (ii) 'No *Gammarus*', including only the two gastropod species (at same density as in the 'All herbivore' treatment); and (iii) 'No herbivores' (control without herbivores). To control for the potentially confounding effect between herbivore diversity and herbivore biomass, we included 'herbivore biomass' (final g, ash-free dry weight [AFDW] herbivores per mesocosm) as a covariate in statistical analyses (see below).

Simulated ocean warming

The effects of near-future ocean warming were tested by contrasting the levels 'No warming' (control with normal water temperature) vs. 'Warming' (+3.4° C). These treatment levels were crossed with two levels of ocean acidification (see below under *Simulated ocean acidification*). The climate conditions were manipulated so that the mean differences (ΔT and ΔpH) corresponded to mean predicted changes over the next century (Caldeira & Wickett 2003; IPCC 2007), while maintaining natural temporal variation in temperature and pH (Fig. S2). Filtered seawater was first pumped into two elevated 1000 L header tanks (IBC®). A top-mounted immersion-heater (6 kW) in one tank was controlled by a computerised thermostat with sensors placed in one 'No warming' and one 'Warming' mesocosm, set to maintain $\Delta T = 4.0^\circ$ C (Alsterberg *et al.* 2011). Weekly measurements using a Beckman Coulter pHi 460 data logger showed $\Delta T = 3.4 \pm 0.2^\circ$ C (mean \pm SEM, $n = 30$ per time period; Fig. 3). Temperature in the 'No warming' mesocosms was similar to that at 1.6 m depth in the nearby Gullmar Fjord (paired *t*-test, $P = 0.39$, $n = 6$). The temperature measurements revealed a slight systematic temperature variation between replicate mesocosms within each of the 12 treatment combinations (range: 0.6–1.2° C). To reduce the added variation caused by this temperature variation, we included 'temperature deviation' (the observed mean temperature [°C] per mesocosm over seven measurement periods, minus the mean temperature of that treatment combination) as a second covariate in statistical analyses.

Simulated ocean acidification

The 'No warming' and 'Warming' water were pumped into 80 L header tanks; two bubbled with air ('Non-acidified', pH \approx 8.10) and two

with air enriched with gaseous CO₂ ('Acidified'). The CO₂ injection rate was set to maintain pH 7.70 (using an AquaMedic pH-control system). Properties of the carbonate system in the four climate combinations were measured on experiment day 15 (Table 1) and 26 (Table S1). Total carbon dioxide content (TCO₂) was measured from 100 μ L water samples using an automated carbon dioxide analyser (CIBA Corning 965 UK). Water pH and temperature were measured using a freshly calibrated Beckman Coulter pHi 460 data logger (accurate to 0.01 units, controlled for accuracy against a pH electrode; Mettler Toledo LE413). Salinity was measured using a conductivity salinometer (WTW LF197) accurate to 0.01 psu. The remaining carbonate parameters were calculated using CO₂SYS (Pierrot & Wallace 2006), using the constants supplied by Mehrbach *et al.* (1973) refitted by Dickson & Millero (1987) and the KSO₄ dissociation constant from Dickson (1990). These calculations showed that mean pH in the 'acidified' mesocosms was \approx 7.75 (resulting in $\Delta pH = 0.35$). Hourly measurements over 24 h-periods showed diel pH fluctuations driven by production vs. respiration (for examples, see Fig. S2C).

Sample analyses

After 5 weeks, mesocosm contents were sieved (0.5 mm for eelgrass and macroalgae and 1 mm for sediments) to collect all macroscopic organisms. All *Gammarus* were measured (tip of rostrum to last uropod, to nearest 0.25 mm). After obtaining length-weight relationships by drying and weighing 25 individuals from three of the five mesocosms from each climate combination (60° C to constant dry weight, g, DW), the total *Gammarus* biomass (g, DW) per mesocosm was calculated. The gastropod herbivores were counted, cleaned and dried. Following incineration (450° C for 3 h) of 10–5 individuals per species, total *Gammarus* and gastropod g, AFDW per unit was calculated using DW:AFDW conversions ($R^2 = 0.66$ – 0.92 , $P < 0.05$, $n = 10$ – 15). Eelgrass (leaves, roots and rhizomes) and macroalgae were cleaned and dried. Eelgrass biomass was standardised before analyses (final/initial DW biomass, the latter estimated using a WW:DW conversion: $R^2 = 0.86$, $P < 0.001$, $n = 25$). We then calculated 'macrophyte dominance' [eelgrass DW biomass / (eelgrass + macroalgal DW biomass)]; a proxy for ecosystem func-

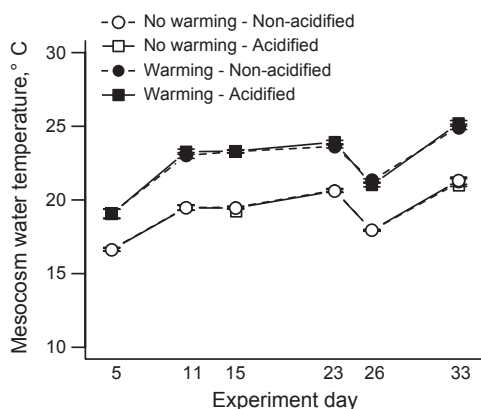


Figure 3 Mesocosm water temperature in the four climate combinations throughout the experiment (after pooling the three herbivore diversity levels). Data are means \pm SEM, $n = 15$.

Table 1 Properties of the carbonate system in four experimental climate combinations after 15 days (mean \pm 1 SD, $n = 15$)

Warming Acidification	No warming Non-acidified	Warming Non-acidified	No warming Acidified	Warming Acidified
Salinity (psu)	22.89 \pm 0.1	23.07 \pm 0.1	22.88 \pm 0.1	23.13 \pm 0.1
Temperature(°C)	19.45 \pm 0.3	23.31 \pm 0.4	19.50 \pm 0.3	23.29 \pm 0.4
TA(mmol kg SW ⁻¹)	1635 \pm 76.4	1707 \pm 71.6	1708 \pm 107.0	1726 \pm 145.9
tCO ₂ (mmol kg SW ⁻¹)	1442 \pm 62.3	1473 \pm 59.4	1620 \pm 101.4	1620 \pm 137.3
pH	8.21 \pm 0.01	8.22 \pm 0.01	7.86 \pm 0.01	7.86 \pm 0.1
HCO ₃ ⁻ (mmol kg SW ⁻¹)	1220 \pm 52	1302 \pm 50.4	1528 \pm 95.1	1517 \pm 128.3
CO ₃ ²⁻ (mmol kg SW ⁻¹)	137.2 \pm 11.0	164.5 \pm 13.9	73.22 \pm 8.6	85.08 \pm 15.4
CO ₂ (mmol kg SW ⁻¹)	7.15 \pm 0.3	6.42 \pm 0.5	18.68 \pm 1.9	17.16 \pm 2.9
Ω Calcite	3.56 \pm 0.3	4.32 \pm 0.4	1.90 \pm 0.2	2.23 \pm 0.4
Ω Aragonite	2.22 \pm 0.2	2.72 \pm 0.2	1.18 \pm 0.1	1.40 \pm 0.3
pCO ₂ (ppm)	204 \pm 7.8	204 \pm 15.5	534 \pm 55.9	545 \pm 93.1

tioning where 1 is total eelgrass dominance and 0 is total algal dominance (e.g. Duffy *et al.* 2005). Finally, since we expected that climate change would alter the relative efficiency of herbivores, we also calculated 'herbivore efficiency' [macroalgae DW biomass/herbivore AFDW biomass]; a standard measure negatively proportional to efficiency (e.g. Duffy *et al.* 2005).

Statistical analyses

Treatment effects on univariate response variables were primarily tested with analyses of covariance (ANCOVA) with *herbivore biomass* and *temperature deviation* as covariates (see above), using linear modelling in the R environment (CRAN 2011). For each response variable, we first confirmed that linear *temperature deviation* effects were comparable across treatment combinations (as a lack of significant interactions with the three treatment factors in four-factor linear models). Assumptions of normality of the error distribution were assessed by inspecting plots of expected vs. actual quantiles (Q–Q plots) and with the Shapiro-Wilk's test, and homoscedasticity using the Bartlett's test. If necessary, data were transformed (log or square root). Where relevant, significant effects were explored with Tukey's HSD *post hoc* test. Herbivore densities followed a Poisson distribution. Therefore, effects of warming and acidification on *Gammarus* density were tested with a three-way Generalised Linear Model (GLM) with *temperature deviation* as a covariate, a quasi-Poisson error distribution (due to over-dispersion) and a log-link function. Effects

of presence of *Gammarus*, warming, and acidification on the density of added *L. littorea* and *Rissoa* sp. (excluding *No herbivores* treatments, i.e. $n = 40$) were tested with four-way GLMs with *Warming*, *Acidification*, and *Gammarus presence* as factors, *temperature deviation* as a covariate, and a Poisson error distribution and a log-link function. Finally, treatment effects on macroalgal community composition (as biomass of six taxa) were tested using a permutated analysis of variance (PERMANOVA) with 4999 permutations, using PERMANOVA v.6 for Windows (Anderson 2005). Where relevant, significant effects were explored with pair-wise *post hoc* tests. In all analyses, factors were considered significant at $\alpha = 0.05$.

RESULTS

Meta-analyses of herbivore resistance to predation and trophic control

Meta-analyses showed that predation negatively affected amphipods (LRR = -1.08 ± 0.49 , mean \pm 95%) but had no effect on gastropods (LRR = -0.0852 , ± 0.428 , mean \pm 95%) (Fig. 2a). Meanwhile, amphipods negatively affected macroalgae ($P = 0.0071$, Fig. 2b), but gastropods had no such effect ($P = 0.366$, Fig. 2c). The non-significant effect of gastropods was most likely explained by the relative dominance of floating, mat-forming macroalgae in productive environments, which are difficult for the inefficient and relatively immobile gastropods to access and control (Moksnes *et al.* 2008;

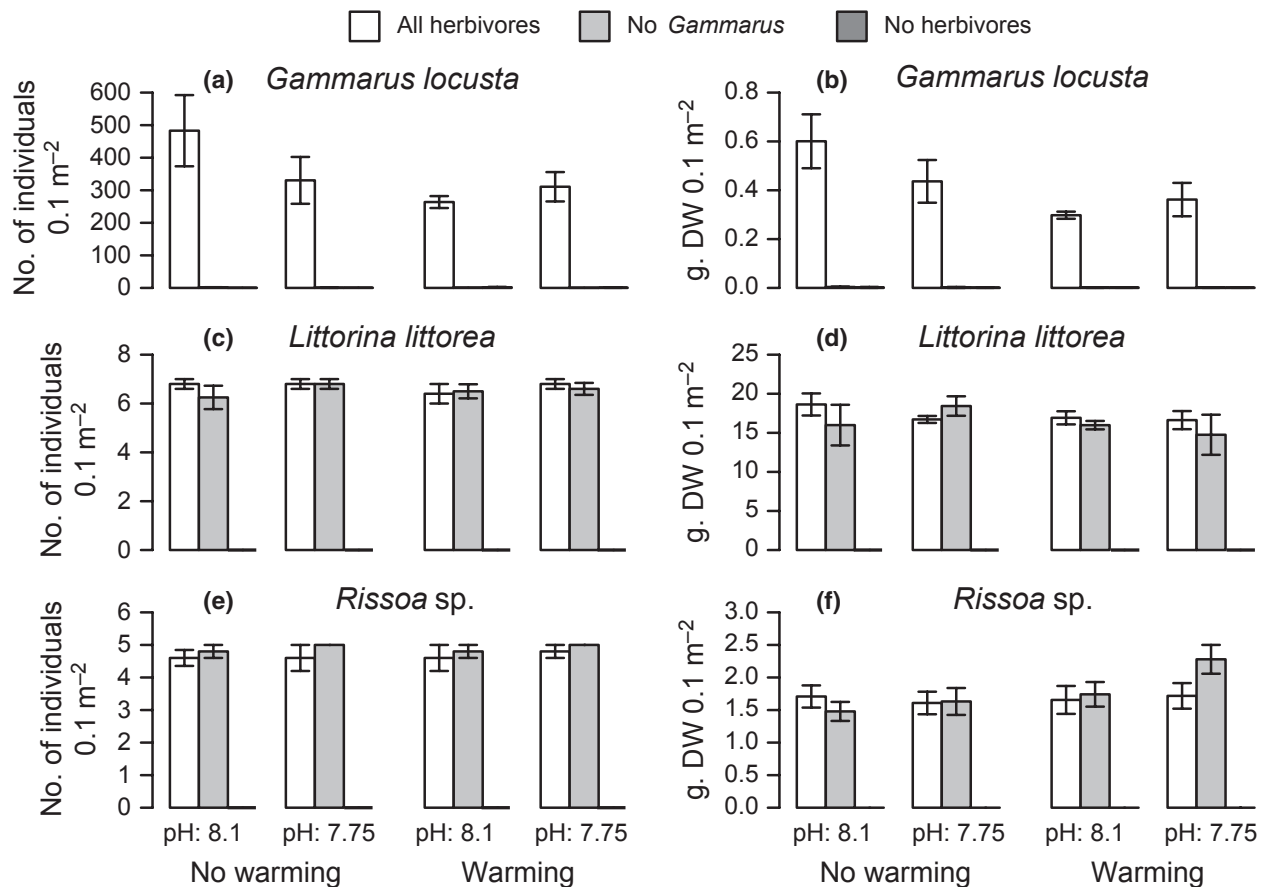


Figure 4 Effects of experimental ocean warming and acidification on (a, c, e) density and (b, d, f) total biomass of the herbivores *Gammarus locusta*, *Littorina littorea* and *Rissoa* sp. Data are means \pm SEM, $n = 5$.

Baden *et al.* 2010). Consequently, the herbivores most impacted by predation (gammarid amphipods) were the most influential in controlling macroalgae.

Mesocosm experiment

Herbivore density, size and biomass

The final density and biomass of *Gammarus* were 300–500 individuals (15–25 times higher density than that at start) and 0.3–0.6 g dry weight per 0.1 m² respectively (Fig. 4a–b). Experimental warming and acidification did not affect *Gammarus* density (GLM with Poisson distribution, $P = 0.10–0.17$) or individual length ($F_{1,15} = 2.66$, $P = 0.123$, Fig. S3), but warming reduced their total biomass by ~30% (ANCOVA, $F_{1,15} = 5.92$, $P = 0.028$).

The gastropod herbivores (*L. littorea* and *Rissoa* sp.) did not reproduce during the experiment, and showed a ~5% mortality across treatments (Fig. 4c–f). Neither warming, acidification, nor presence of *Gammarus* affected density and biomass of the two species ($P > 0.2$ for all factors in all tests).

Macroalgal community structure

Herbivore diversity loss and experimental warming had an interacting effect on the macroalgal community (PERMANOVA; $F_{2,52} = 2.27$, $P = 0.021$). In the presence of *All herbivores* the added green algae were completely grazed down (Fig. 5), the epiphytic *Polysiphonia* (primarily *P. fibrillosa*) dominated and warming and acidification had no effects (the apparent increase in *Ectocarpales* in the

Warming + Acidification treatment occurred only in one mesocosm). In the *No Gammarus* treatment the green algae *Cladophora* spp. dominated instead. In *No warming* conditions, gastropods reduced algal biomass by ~50% in relation to that in *No herbivores* treatment. With warming, however, the gastropod effect disappeared completely, most likely because *Cladophora* biomass increased by ~300% (in relation to the *No warming* conditions with *No Gammarus*). In *No herbivores* controls, warming increased algal biomass by ~100%. Finally, acidification had no single instance of interactive effects ($P \gg 0.05$).

Eelgrass biomass

Eelgrass biomass (Fig. 6a) depended on two interaction effects; one between herbivore diversity loss and warming (ANCOVA; $F_{2,50} = 10.10$, $P = 0.0002$), and one between warming and acidification (ANCOVA; $F_{1,50} = 6.67$, $P = 0.013$). First of all, presence of herbivores (regardless of *Gammarus* presence) increased eelgrass biomass by ~30% in *No warming* conditions, but with warming, the effect remained only in the *All herbivores* treatment and was weakened (~10% biomass increase). Thus, warming removed the ability of gastropods to alone facilitate eelgrass growth. Second, acidification increased eelgrass biomass by ~15% in *No Warming* conditions (regardless of herbivore presence), but with warming the effect disappeared.

Macrophyte dominance

Herbivore diversity loss and warming had an interacting effect on the relative dominance of eelgrass over macroalgae (ANCOVA; $F_{2,46} =$

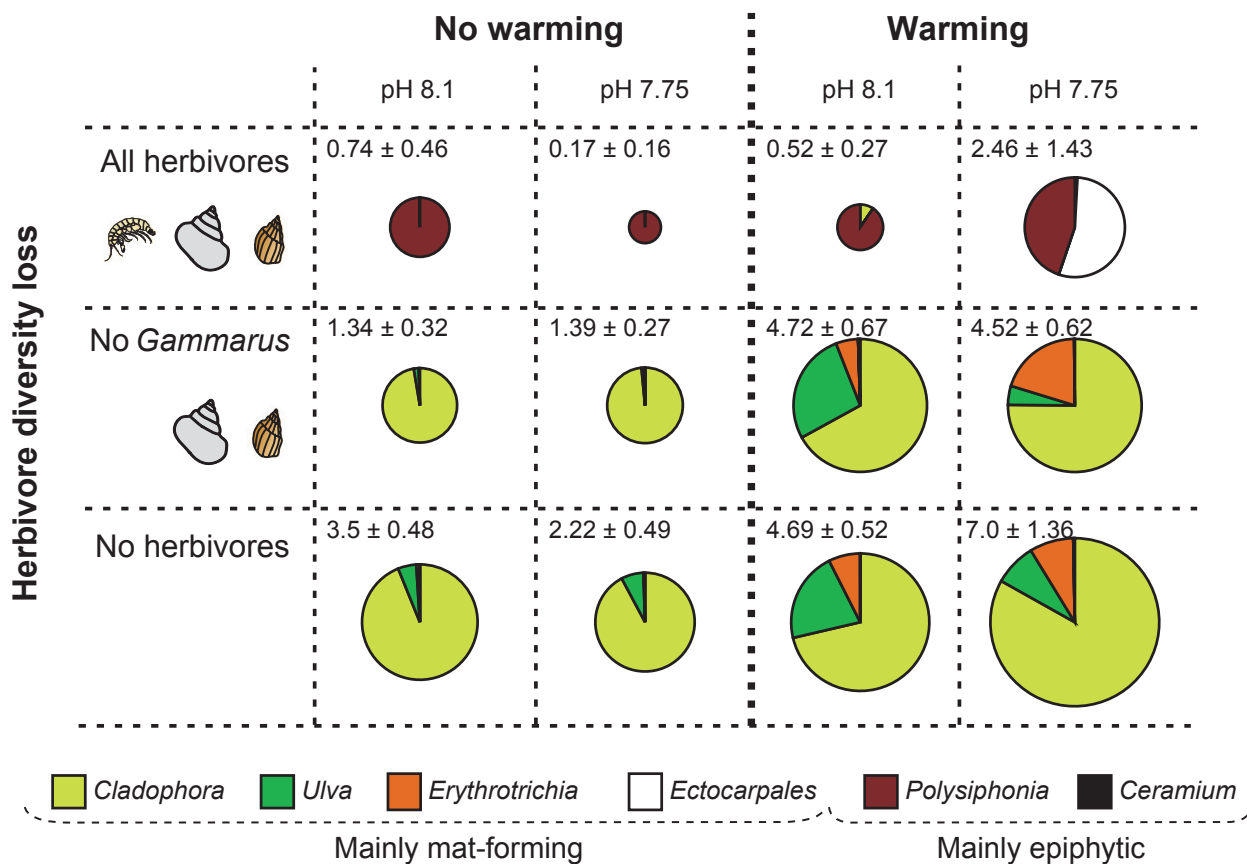


Figure 5 Effects of experimental herbivore diversity loss, ocean warming and acidification on macroalgal community structure (g. DW biomass of six taxa). The size of circles is proportional to total algal biomass in that treatment combination (also noted ± SEM on the upper left side of circles, $n = 5$).

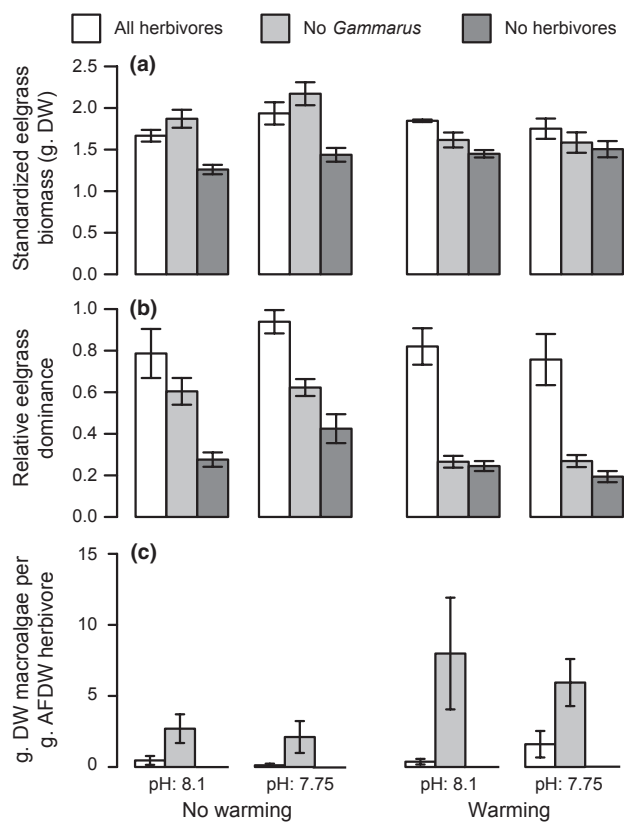


Figure 6 Effects of experimental herbivore diversity loss, ocean warming and acidification on (a) eelgrass biomass (standardised against initial biomass), (b) macrophyte dominance (relative dominance of eelgrass vs. macroalgae) and (c) herbivore relative efficiency (macroalgal biomass per herbivore biomass). Data are means \pm SEM, $n = 5$.

4.11, $P = 0.023$, Fig. 6b). In *All herbivores* treatments eelgrass dominated (indicated by values close to 1), and warming and acidification had no effects. Exclusion of *Gammarus* did not alter this pattern in *No warming* conditions, because gastropods halved green algal biomass (see Fig. 5) and facilitated higher eelgrass biomass (see Fig. 6a). With warming, however, this gastropod effect disappeared completely, the system shifted to macroalgae domination (index values closer to 0 than to 1), and became statistically indistinguishable from the *No herbivores* treatments. Acidification had no statistically significant effects ($P \gg 0.05$).

Herbivore efficiency

Herbivore diversity loss and warming had an interacting effect on herbivore efficiency, estimated as the biomass ratio of macroalgae to herbivores (ANCOVA; $F_{1, 30} = 4.45$, $P = 0.043$; Fig. 6c). In *No warming* conditions, the biomass ratio in *All herbivores* treatments was $> 20\%$ of that in the *No Gammarus* treatment. In other words, the presence of *Gammarus* increased herbivore efficiency by a factor of five. Warming had no effect in the *All herbivores* treatment, but increased the biomass ratio in the *No Gammarus* treatment by $\sim 350\%$. This corresponds to a $\sim 70\%$ decrease in herbivore efficiency; an effect most likely caused by the positive warming effect on algal biomass (see Fig. 5), since warming had no effect on gastropod density or biomass (Fig. 4). Finally, acidification had no detectable effects ($P \gg 0.05$).

DISCUSSION

The insurance hypothesis states that biodiversity maintains ecosystem functioning in the face of disturbance and environmental fluctuations, by increasing the likelihood that there are some well adapted or resistant species that maintain functioning (Yachi & Loreau 1999). We show that in food webs where the effect trait of interest (herbivore trophic control) trades off with a response trait (resistance to predation) climate change can reduce the relative efficiency of resistant species, and weaken the insurance effect of biodiversity.

The meta-analyses showed that the benthic herbivores most impacted by predation (amphipods) were also the most effective at controlling macroalgae. This supports evidence for a trade-off between herbivore consumption rate and predation resistance (see also Gruner *et al.* 2008; Sieben *et al.* 2011). The mesocosm experiment then showed that three regionally common herbivores together controlled algal biomass (mainly *Cladophora* and *Ulva*), facilitating eelgrass dominance under both ambient and climate-change conditions. However, total algal biomass did not decline with warming (as shown by e.g. O'Connor 2009). This result is explained by the fact that at least two taxa (*Polysiphonia* spp. and *Ectocarpales* spp.) are unpalatable to most grazers, and most likely benefitted from herbivore removal of competitively superior green algae (see Duffy *et al.* 2005; Moksnes *et al.* 2008 for similar results). When *G. locusta* was excluded to simulate predation effects, the algal community composition shifted to a mix of epiphytic and floating algae, but the gastropods still maintained eelgrass dominance (Fig. 5). Under warming, however, the gastropods were unable to control the floating, mat-forming algae and the system shifted from eelgrass to algal dominance.

Multiple lines of evidence suggest that this interactive effect between herbivore diversity loss and warming was caused by warming-induced changes in the relative efficiency of the predation-resistant gastropods rather than differences in herbivore biomass or density; (i) we statistically controlled for effects of differences in herbivore biomass; (ii) *Gammarus* constituted only a fraction of total herbivore biomass even though they outnumbered gastropods (Fig. 4), and (iii) 85–95% of the *Gammarus* were juveniles, which are relatively ineffective herbivores (Moksnes *et al.* 2008). Since gastropod biomass and density were unaffected by warming (Fig. 4), it appears their lower relative efficiency was caused by faster accumulation of algal biomass (e.g. Fig. 6c). We identify two possible mechanisms to explain this: first, theoretically, if algal growth rate is high enough, herbivore relative efficiency will decrease with warming, even though their per capita consumption rate increases (grey vs. dashed line in Fig. 1d); second, even though warming has been shown to increase trophic control from these gastropods over macroalgae in other ecosystems (e.g. Lotze & Worm 2002), they are too sedentary and inefficient to control the floating algal mats that form under high-productivity conditions in our study system (Moksnes *et al.* 2008; Baden *et al.* 2010). Consequently, even if warming increased gastropod consumption rate (see e.g. Lotze & Worm 2002), the effect was outweighed by simultaneous effects on algal growth rate and accessibility.

The simultaneous manipulation of water temperature and acidification showed that these factors not only have interactive effects, but that the direction and strength of effects may be species-specific. The eelgrass benefitted slightly from acidification at normal temperature; an expected result given that it is naturally CO₂-limited (Kroeker *et al.* 2010). This effect disappeared, however, with warm-

ing; a well-known direct disturbance (Reusch *et al.* 2005). Similarly, the indirect positive effect of gastropod grazing on eelgrass seen under *No Warming* conditions disappeared with warming (Fig. 6a). These antagonistic effects of warming indicate that the often-assumed positive effects of (i) grazing on algae (Duarte 1995; Moksnes *et al.* 2008) and (ii) ocean acidification (Kroeker *et al.* 2010) on seagrass, could weaken in a warmer world. The main competitor to eelgrass – the green alga *Cladophora* – benefitted from warming when *Gammarus* was absent, but was unaffected by acidification (even though there was a trend towards a synergistic *Warming + Acidification* interaction in the absence of herbivores, see Fig. 5). These marked differences in responses between competing species (see also Diaz-Pulido *et al.* 2011) underscore the difficulty in using single-species studies to predict ecosystem-level effects of climate change.

Short-term studies of model systems like our mesocosms are inevitable simplifications, but often reveal important ecosystem processes (Benton *et al.* 2007). We therefore suggest that this study, taken together with long-term monitoring of predatory fish (Eriksson *et al.* 2011; Baden *et al.* 2012) and extensive predation experiments in the field (Moksnes *et al.* 2008; Baden *et al.* 2010; Sieben *et al.* 2011), has two important messages.

First, in ecosystems with trade-offs between herbivore predation resistance and trophic control, the insurance effect of biodiversity may weaken with climate change. The main reason is that the relative efficiency of resistant, but inefficient, herbivores could weaken with warming, even if their absolute consumption rate increases. An important implication is that high response diversity (Elmqvist *et al.* 2003) to disturbance (here, predation) under one set of conditions could provide poor insurance in a gradually changing climate or environment. Moreover, because of this context-dependence, the resulting vulnerability of the system may not become apparent until conditions change so much that the insurance effect has already been weakened. Conversely, in food webs where herbivore response and effect traits are uncorrelated or positively correlated, we predict that sub-lethal warming should instead *weaken* the effects from losing the vulnerable species (black line in Fig. 1f). This effect arises because resistant (and efficient) species become even more efficient relative to plant growth. Consequently, the nature of trait correlations and climate change should interact to regulate the functional consequences of diversity loss.

Second, from an applied perspective, our findings suggest that efficient and climate change-resistant herbivores may act as crucial 'escape valves' in a warmer world. By channelling primary production up the food web herbivores could buffer ecosystems against climate-induced vegetation shifts, just as they buffer against eutrophication effects (Duarte 1995; Eriksson *et al.* 2011). As a consequence, disturbances affecting such herbivores (e.g. increased predation due to mesopredator release) could reduce ecosystem resilience not only to eutrophication today, but also to climate change in the near future (this study). The extent of such effects should also depend on the responses of higher trophic levels to climate change, as well as the potential adaptation of the species involved. Although these last two aspects were beyond the scope of this study, the dominant mesopredators in these systems may in fact benefit from increasing temperature (Eriksson *et al.* 2011). Overfished populations of top predators on the other hand are likely to decline even further (Drinkwater 2005). Consequently, unless we facilitate efficient herbivores – for example, by protecting top predators and their nursery areas (Eriksson *et al.* 2011; Nyström *et al.*

2012) – climate change is likely to increase the risk for ecosystem shifts to socially undesirable states.

ACKNOWLEDGEMENTS

We thank V. Telemo, L. Ulvestad, J. Egardt, E. Norin, C. Magyar, I. Wallentinus and P.-O. Moksnes for assistance in the field and in the lab. We also thank H. Hillebrand, M. Bracken, B.K. Eriksson, M. Jonsson, P. Lundberg, K. Norén and three anonymous referees for comments that greatly improved the paper. Funding was provided by Formas (grant no. 2009–4007 to LG and JH, and grant no. 2007–401 to K.S.), VR (grant no. 2009–5457 to LG) and the Memorial Fund of Birgit and Birger Wählström to K.S. This work was partly performed within the Linnaeus Centre for Marine Evolutionary Biology (<http://www.cmeb.science.gu.se/>)

AUTHOR CONTRIBUTIONS

JSE, JNH and LG conceived research; all authors performed research; JSE analysed the data, JSE drafted the paper, and JSE, JNH and LG wrote the paper.

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Editor, Marcel Holyoak

Manuscript received 13 February 2012

First decision made 16 March 2012

Manuscript accepted 30 April 2012