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Global alteration of ocean ecosystem functioning due to increasing human CO₂ emissions

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Classification: Biological Sciences – Ecology

Rising anthropogenic CO₂ emissions are anticipated to drive change to ocean ecosystems, but a conceptualisation of biological change derived from quantitative analyses is lacking. Derived from multiple ecosystems and latitudes, our meta-analysis of 632 published experiments quantified the direction and magnitude of ecological change resulting from ocean acidification and warming to conceptualise broadly based change. Primary production by temperate non-calcifying plankton increases with elevated temperature and CO₂, whereas tropical plankton decreases productivity due to acidification. Temperature increases consumption by and metabolic rates of herbivores, but this response does not translate to greater secondary production, which instead decreases with acidification in calcifying and non-calcifying species. This effect creates a mismatch with carnivores whose metabolic and foraging costs increase with temperature. Species diversity and abundances of tropical as well as temperate species decline with acidification, with shifts favouring novel community compositions dominated by non-calcifiers and microorganisms. Both warming and acidification instigate reduced calcification in tropical and temperate reef-building species. Acidification leads to a decline in dimethylsulfide production by ocean plankton, which as a climate gas contributes to cloud formation and maintenance of the Earth's heat budget. Analysis of responses in short- and long-term experiments and of studies at natural CO₂ vents reveals little evidence of acclimation to acidification or temperature changes, except for microbes. This conceptualization of change across whole communities and their trophic linkages forecast a reduction in diversity and abundances of various key species that underpin current functioning of marine ecosystems.

Keywords: ocean acidification, climate change, meta-analysis, productivity, diversity, species communities, ecosystem processes, acclimation

Significance

People are not only concerned about climate change and its effects on plant and animal diversity, but also about how humans are fundamentally changing the globe's largest ecosystem that sustains economic revenue and food for many countries. We show that many

species communities and ocean habitats will change from their current states. Ocean acidification and warming increase the potential for an overall simplification of ecosystem structure and function with reduced energy flow among trophic levels and little scope for species to acclimate. The future simplification of our oceans has profound consequences for our current way of life, particularly for coastal populations and those that rely on oceans for food and trade.

We have entered an era of increasing uncertainty about the effect of human activities on the function and services of ecological systems, particularly the effect of human greenhouse gas emissions on marine ecosystems (1–4). Progress on understanding of how climate change affects marine ecosystems has been slower than that of terrestrial ecosystems (4), partly because of the vast coverage of the oceans and renowned complexity of species interactions. Until now, there has been almost total reliance on qualitative reviews and perspectives about potential global community and ecosystem change. Where quantitative assessments exist, they typically focus on single global stressors, single ecosystems, single species assessments, or small subsets of species interactions that provide information on species performance and key species interactions (5). Recent assessments of multi-stressor effects at global scales show that more than half of the world's ocean has experienced an increase in cumulative human impact over a five-year time span, predominantly driven by increasing climate stressors such as sea surface temperature, ocean acidification and UV radiation (6). Under a business-as-usual emission scenario, these stressors elevate the risk of substantial change to marine organisms and ecosystem services by 2100 (7).

The effects of warming on ecological processes and ecosystem functioning is substantially researched, but there is a tremendous knowledge gap in terms of the effects of ocean acidification. This gap is exacerbated by the inevitable combination of increasing ocean acidification and temperature and their potential interactive effects (8). Previous meta-analyses on the combined effects of climate change and ocean acidification typically targeted single-species responses (9,10), single ecosystems (11) or life-stages (8). Such analyses detected a lack of difference between the effect sizes of acidification alone and the combined effect of acidification and elevated temperature (9), or identified variation in single-species responses, such as calcification, growth, photosynthesis, reproduction, and survival (10). Because species interactions play a key role in how organisms and their communities respond to global change (12), there remains a critical need for multi-species studies. Yet, a quantitative meta-analysis of community level responses and insights in the potential underlying processes is absent. We here conceptualize change, based on peer-reviewed outcomes, by quantitatively assessing the direction and magnitude of near-future change from the perspective of system-wide productivity, diversity and function.

Our meta-analysis builds on previous analyses of single species by studying the combined effects between global stressors, incorporating species interactions, evaluating key ecosystem processes not previously considered, and evaluating scope for acclimation, to demonstrate how this may alter global species abundances and diversity and modify species community structures and food webs. Our meta-analysis used a statistical approach that calculated a weighted mean effect size of the stressor response and its significance (95% confidence interval using bootstrapping) across 632 different experiments published through to early 2014, restricted to studies that used experimental CO₂ or temperature elevations as predicted for around year 2100. Response to stressors was quantified on the basis of the natural logarithm of the Response ratio, a metric commonly used in meta-analysis (9).

Results

Acclimation to warming, acidification and their combination was small across the main effects we studied. In general, there was a trend of the effect sizes of longer-term experiments being equal or stronger than those of short-term experiments (Fig. 1, Fig. S1). Likewise, suppressed species abundances and diversity at natural CO₂ vents, where organisms have been exposed to elevated CO₂ over extended time periods, are comparable to declines within laboratory experiments (Figs. 2a, c). Only microorganisms, which are taxa with short generation times and occupy a wide range of (extreme) niches, showed significant population abundance increases at CO₂ vents in (sub)tropical regions (Figs. 2c).

Phytoplankton generate nearly half the planetary net primary production (13), which maintains the diversity and abundance of marine life, ecosystem services, and capacity for fishery yields, and influences climate processes *per se*. Increasing temperature and CO₂ could enhance terrestrial primary production (14), although suitable plant growing days, for example, decreases when changes in other abiotic factors are considered as well (15). In the ocean, elevated temperature has been predicted to increase primary production in polar regions and decrease production in tropical areas (16). Our meta-analysis reveals no effects of ocean acidification on pelagic production by tropical or temperate phytoplankton communities (Fig. 1a, Tables S1, S2). Single species experiments, in contrast, show that ocean warming and acidification have a positive effect on primary production by temperate non-calcifying species but that acidification has a negative effect on production by tropical species (Figs. S2a, S2b). However, warming also enhances oceanic stratification, exposing phytoplankton to the negative effects of greater levels of harmful ultraviolet light (17) and reduced transport of nutrients from ocean depths (18,19). The disproportionately large global contribution of phytoplankton to primary productivity (13) contributes substantially to the ocean's net CO₂ uptake from the atmosphere (20). Changes in phytoplankton productivity due to ocean warming, through the contrasting direct effects of temperature and indirect effects of stratification could, therefore, be a mechanism through which primary production might be altered in surface oceans. This could consequently modify the demand for atmospheric CO₂ as a resource. However, there is no simple relationship between net primary production and net CO₂ uptake between the ocean and atmosphere, and a fraction of the production is rapidly respired to CO₂ and thus does not contribute to a net CO₂ sink.

Predicting the consequences of changing primary productivity is not simple because of the complex interplay among species interactions and their multiple drivers. Nevertheless, whereas warming increases consumption of primary productivity through higher metabolic rates (Figs. 1c, d), secondary production by invertebrates in tropical as well as temperate regions decreases due to ocean acidification as established by both single-species and multi-species studies (Fig. 1b, Table S1). Loss of secondary productivity under future scenarios forms a contrast with changing energetic demands of their predators, whose foraging and metabolic rates increase due to acidification as well temperature in tropical, temperate, and polar regions (Figs. 1c, d, Table S1). Warming can intensify trophic cascades leading to stronger control by top consumers (21) while a reduction in pH imposes energetic costs on acid-base balance (22) that may act as a stressor on many carnivores. Collectively, ocean warming and acidification showed contrasting effects on productivity and consumption at multiple trophic levels, but with higher-order carnivores at clear risk of not meeting increased energetic demands.

Our meta-analysis shows an overall decrease of tropical and temperate (but not polar) species abundances and diversity across multiple functional and species groups due to ocean acidification (Fig. 2, Tables S1, S2). Ocean acidification increases the potential for simplification of species communities for calcifying and non-calcifying species alike (Fig. 2a). Of all taxa, benthic (sub)tropical microorganisms are the clearest 'winners' from the effects of ocean acidification (Figs. 2a, c). Simplification of trophic structure and reduced

species diversity has been shown to lead to diminished functional redundancy which has been coupled to lower ecosystem resistance and resilience to future stress that are both part of natural cycles and human intervention (23,24).

Ocean acidification has a greater negative effect on abundances of calcifying taxa (e.g. various species of crustaceans, molluscs and calcifying macroalgae) than non-calcifiers (e.g. various species of non-calcifying macroalgae, sponges, autotrophic and heterotrophic plankton, and benthic invertebrates) (Figs. 2c, d). A potential community shift towards non-calcifiers is reinforced by the differential effects that the combination of ocean acidification and increasing temperature have on primary and secondary production of non-calcifiers vs. calcifiers (Figs. 1a, b). Such potential shifts to communities dominated by non-calcifying organisms have profound implications for pelagic and benthic systems.

For pelagic species, warming causes a shift towards smaller pico- and nanoplankton species (to the detriment of microplankton; Fig. S2c) which are less suitable as a food source for zooplankton (25). Furthermore, our results reveal a significant direct negative effect of CO₂ on dimethylsulfide (DMS) production by temperate phytoplankton communities (Fig. 1f, Table S1). DMS is a driver of food web structure (26), acting as an anti-grazing defence mechanism in phytoplankton (27), while also providing chemical cues to attract predators (e.g. fishes, large zooplankton, birds) to prey that forage on phytoplankton (26,28). DMS has the potential to mediate trophic interactions that span distances of millimetres (e.g. mesozooplankton attracted to grazing microzooplankton) to thousands of kilometres (e.g. seabirds attracted to oceanic areas with high plankton productivity). Alterations to oceanic DMS release can, therefore, alter the complex trophic interactions in the ocean (29). Reduced DMS production is also linked with potential increases in global temperature because it contributes to cloud formation as a climate gas (30,31).

For tropical as well as temperate benthic species (Table S1), our analyses show a significant negative effect of acidification, warming, or their combination on calcification rates of key calcifying taxa that construct reefs, such as molluscs and tropical as well as cold water corals, and of calcareous algae that serve as a settlement substratum for coral larvae (Fig. 1e, Fig. S2d). While there is broad agreement that calcification and abundance of tropical corals will decrease (9,32) there is uncertainty of the overall effects on other foundation species. Mussel and oyster beds are the dominant reef-building taxa in estuaries and temperate coastal seas (33), while cold water corals construct large biogenic deep water reefs (34). A decline in such habitat-forming species at lowered pH and/or elevated temperature is likely to result in loss of secondary productivity, local extinctions and reduced taxonomic distinctness (35,36). The extent to which these indirect effects drive future change relative to direct effects is largely unknown (3,21), although negative effects on habitat-formers is likely to affect a greater number of species. Whilst our meta-analysis highlights negative effects for both habitat-formers and users, it remains unclear how these effects will coincide.

Discussion

Ocean warming and acidification have received increasing focus as global change stressors, but marine species will also be impacted in their performance by other emerging stressors such as changes in sea surface height, UV, underwater irradiance, water salinity, and seawater oxygen content (6). Hypoxic zones are becoming widespread in oceanic as well as shelf environments due to climate change and local stressors such as eutrophication (37). Many species will be challenged by the interactive effects of ocean warming, acidification and deoxygenation, but at present hardly any (multi-stressors) studies exist to evaluate the effects of anoxia on marine species and ecosystems (8,38). For some species there are opportunities to move to deeper waters or extend their ranges to higher latitudes, but not all species will be

able to keep up with the pace of climate change leading to alterations in current species distributions (39,40). Moreover, species that have fewer generations (e.g. *k*-strategists with greater longevity and later maturation) have fewer opportunities to adapt to rapidly changing conditions forecast for the next ~85 years. Unless longer-lived species relocate to climate refugia, their persistence will rely more on mechanisms of acclimation than adaptation. Importantly, if acclimation and adaptation to climate have low potential, the probability for community change is heightened. Hence, variance for adaptation among species (41), combined with low scope for acclimation (this study), jointly emphasise the potential for community change.

By integrating multi-species with multi-factor experiments of differing acclimation periods, we produce a conceptual insight into how human greenhouse gas emissions may drive change to pelagic and benthic ecosystems from different latitudes. Many of the studies included in our meta-analysis manipulated temperature or CO₂ to levels predicted for the end of this century (Tables S1, S3). It is notable that despite variation in choice of experimental temperatures and CO₂ levels among studies, these differences did not translate into detectable differences in the effect size of most processes under study (Table S2). This finding suggests that experimental outcomes are not only robust to such experimental choices, but also that the magnitude of our forecast responses are likely to be similar across the range of temperatures and CO₂ levels anticipated at the end of the century. While the magnitude of future change in ocean temperature and pH will be variable at local scales – potentially leading to different outcomes at specific locations and for some species – there are emerging patterns of change in ecosystem processes and species occurrences. We find that ocean warming and acidification increase the potential for an overall simplification of ecosystem structure and function with reduced energy flow among trophic levels with little scope for acclimation. Ocean acidification *per se*, appears to have the potential to bring penetrating modifications to ecological systems through changes in ecosystem processes and shifts in species community structures. While some ecosystem processes are affected by ocean acidification only, others are affected by warming alone or by the combination of the two stressors. These results, therefore, provide a conceptual framework towards more inclusive forecasts of future ecological change (Fig. 3).

Materials and Methods

Data selection. We searched the literature for studies published through to early 2014 on effects of ocean acidification on marine biota using Thomson Reuters' Web of Science. By using the search string 'ocean acidification', we explicitly incorporated studies that placed their experimental designs and results within this broader context of climate change as distinct from those testing the effects of changes in pH *per se*. We screened the titles and abstracts of ~2,300 published articles, of which 150 studies (covering 632 experiments) met the requirements for inclusion (Dataset S1). We selected studies that investigated the effect of ocean acidification on species diversity, species community abundances, and DMS production, and studies that investigated the effects of ocean acidification and warming on species performance (primary production, secondary production, foraging, metabolism, calcification). In addition to our own literature survey, we also cross-referenced our database with some more taxon targeted meta-analysis on ocean acidification (5,9,10,42), but this added only a limited number of studies, suggesting that our search string in Web of Knowledge was very effective.

We focussed our analyses on studies that used increases in CO₂ and temperature as predicted for year ~2100, typically based on the representative concentration pathway (RCP) 8.5 emission scenario (business-as-usual). Under this scenario, global ocean surface

temperatures are predicted to rise by an average (± 1 SD) of $\sim 3.7 \pm 0.7$ °C (43) as compared to the 1990s, while CO₂ into the atmosphere will more than triple relative to pre-industrial conditions, increasing from the current levels of ~ 400 ppm to ~ 936 ppm by the end of the century. This will lead to a decrease in ocean-surface pH of $\sim -0.33 \pm 0.003$ units by 2100 compared to the 1990s (43). Regarding the less likely high mitigation scenario RCP2.6, corresponding changes would be $+0.7 (\pm 0.5)$ °C and $-0.07 (\pm 0.001)$ pH units, respectively. A few studies that we included used somewhat higher values than predicted for the RCP8.5 emission scenario, because their present-day conditions already showed above average values for these stressors (e.g. enhanced acidification due to seasonal upwelling, or shallow coastal areas that warm up faster during summertime), reflecting the variability as typically observed across ecosystems, latitudes, and water depths. Studies that used extreme temperature elevations or pH reductions that are well beyond the predictions for year 2100 were excluded from the analyses, following previous approaches (9). Average (SD) reduction in pH and enhancement of CO₂ and temperature levels across all studies included in our meta-analysis were $-0.3 (0.1)$ units, $+508 (230)$ ppm CO₂, and $+3.8 (1.1)$ °C, respectively, which closely match the average and range in projections for RCP8.5. Nevertheless, there was variability across studies in the treatment levels used. Elevation levels (Δ treatment vs. control of the experiment) and their standard deviation for CO₂ and temperature per main factor tested are shown in Table S1 and values per experiment are shown in Dataset S1. We did not normalise the data for experimental elevation of CO₂ and temperature levels, because in almost all cases regression analyses (see procedure description below under “Meta-analysis”) showed lack of a significant correlation between the response variables and stressor levels (see regression results in Table S2).

Whilst initial studies primarily focussed on single-species experiments, there has been a rapid increase in multi-species experiments in *in situ* as well as laboratory-based mesocosms in the last few years. These studies have not been specifically tested yet using meta-analysis, even though they are much more realistic than single-species experiments as they incorporate complex species interactions. Where present, we therefore included multi-species (i.e. ‘community’ level) experiments that manipulated CO₂ even if they were not tested in a factorial design with temperature. For species-level studies, we focussed predominantly on factorial experiments on ocean acidification and warming.

We focussed on several key processes that underpin the persistence, functioning, health and productivity of ocean ecosystems. Primary production at community level involved experiments using multi-species phytoplankton assemblages and typically measuring ¹⁴C fixation rates across the entire assemblage. Primary production at a species level involved experiments on mono-cultures of phytoplankton and were primarily based on cellular growth rates followed by changes in cell biomass (Dataset S1). Secondary production at community level was measured as changes in the total density or biomass of all animals combined within the type of assemblage under consideration. At a species level, production was predominantly based on changes in biomass of single species. Foraging rates were based on per capita consumption rates. Metabolic rates were largely measured as resting/routine metabolic rates. Calcification rates at community level were measured as the net accumulation of CaCO₃ or ¹⁴C uptake for the entire assemblage, whereas at species-level this was usually measured as accumulation of CaCO₃ for individual species. Where studies selected solely calcifying or non-calcifying species to test community-level effects, we refer to these groups as calcifying species and non-calcifying species, respectively. In cases where both groups were present in the experiment and their responses were not separated, we refer to them as mixed communities of calcifiers and non-calcifiers. For DMS, studies on dimethylsulphonioacetate (DMSP) or dimethylsulphoxide (DMSO) were not included as photolysis and DMS gas exchange are linear functions of the DMS concentration (30).

Species diversity was largely based on changes between treatments in total number of species, number of operational taxonomic units, or the Shannon-Wiener diversity index for complete species assemblages. Community species abundances reflect the changes in abundances (typically measured as densities, cover, or abundances) of individual species in multi-species experiments, providing a more realistic measure of species changes as it incorporates species-interactions. In cases where multiple response variables were reported within a study for the processes we considered, only one response variable was included to avoid pseudo-replication. For example, if a study reported growth rate for an organism as a change in length and biomass, biomass was selected as the more meaningful response variable (9).

Meta-analysis. For each experiment, we calculated both the individual and combined effect sizes of acidification and warming using the natural logarithm of the response ratio (LnR), a response metric commonly used in meta-analyses (9,10). The effect size based on LnR represents the ratio of the response variable measured in an experimental group to that of the control group. The effect size of individual experiments were weighted by the reciprocal of their sampling variance, followed by a random-effects model to calculate the mean ('overall') effect size for comparisons across treatments for the various response variables (see Table S2). The mean effect size is thus a weighted average of individual effect sizes to reduce bias due to studies with few vs. large sample sizes (44). Confidence intervals around mean effect sizes were generated using bootstrapping methods (4999 iterations). We used biased-corrected bootstrap confidence intervals to reduce bias due to small sample sizes. If the confidence intervals do not overlap zero, then the effect size is considered significant.

The total heterogeneity of a weighted mean effect size is represented by the Q_T statistic which is a weighted sum of squares, comparable to the total sum of squares in an ANOVA. For each mean effect size Q_T was calculated and tested against a χ^2 -distribution (see Table S2). A significant Q_T indicates that the variance among individual effect sizes is larger than expected by sampling error, and that there may be an underlying structure to the data and therefore other explanatory variables should be tested. Consequently, we investigated several categorical factors for the overall mean effect sizes that showed significant heterogeneity using a categorical random-effects model, which is analogous to a mixed-effects model in ANOVA. For this model, total heterogeneity Q_T can be partitioned in the variance explained by the model (Q_M) and the residual error variance not explained by the model (Q_E). Q_M was tested against a χ^2 -distribution using a randomization procedure (4999 iterations), with a significant Q_M (see Table S2) indicating statistical differences in the mean effects sizes among categories (within a factor).

We first tested for the effect of latitude as a categorical factor for all main response variables that showed a significant Q_T (see Table S2). Except for primary production, the response for the various main factors considered was similar for the different latitudes and the respective Q_M was non-significant and/or very low indicating other factors were more important. Hence, for secondary production, calcifiers vs. non-calcifiers was tested as a categorical factor instead (Table S2). For calcification rate, taxon was tested as a categorical factor and the results are shown in Fig. S2d; in Fig. 1e aggregated results are shown for comparative purposes only. For species diversity, functional group was tested as a categorical factor and taxon level responses shown for comparative purposes only. For ocean acidification effects on species abundances, functional group was tested as a categorical factor and taxon level responses shown for comparative purposes only. For effects of temperature on species abundances, taxon was tested as a categorical factor. For primary productivity of single-species studies, either latitude or calcifiers vs. non-calcifiers or both categories were significant in independent categorical analyses, and therefore calcifiers vs. non-calcifiers was tested for the different latitudes separately (i.e. category calcifier within category latitude; the

results are shown in Figs. S2a, S2b, while the aggregated results for calcifiers vs. non-calcifiers (across latitudes) are shown in Fig. 1a for comparative purposes only). In all other cases where Q_T was non-significant this implies that the various categories (functional groups/latitudes) showed a similar direction of response as the main effects analysis (either all positive or all negative); nevertheless, these responses are also plotted for some categories (Fig. 1) and reported (Table S2) to facilitate the understanding of the complex data set.

To assess whether normalisation of effect sizes to particular levels of altered pH or temperature would improve interpretive value, we performed a continuous random-effects meta-analysis on effect-sizes across their different combinations using the relative differences between treatment and control as the explanatory variable. The relationship between effects sizes and predictor variables is calculated on the basis of a least-squares regression. In almost all cases, no significant correlations were detected (see regression results in Table S2) and the original data was analysed without normalising to pH or temperature.

To test for the potential of species to acclimate to changing stressors, we compared short-term experiments (<1 month) to longer-term experiments (>1 month; range 4–56 weeks; mean \pm SD: 11.6 ± 11.6 weeks) as well as data collected from natural CO₂ vents where many sessile or low-motility species have typically been exposed to decreased pH conditions over significant parts of their life cycle. For this specific analysis alone, we combined the data from single-species and multiple-species studies, and our interpretation is based on comparing the mean effect size and their 95% confidence intervals between short- and long-term experiments (rather than testing if their means differ from 0).

Sensitivity analyses. Because data selection and weighing might affect the outcome of the overall effect size (44) we also calculated the unweighted effect sizes using a fixed-effects model. As both approaches revealed similar trends and significances (test outcomes reported in Table S2) we report the weighted mean effect sizes. We tested for publication bias for main effects that were significant using Rosenthal's method of fail-safe numbers. The fail-safe number represents the number of studies with a non-significant outcome that needs to be added to change the effect sizes from significant to non-significant. Fail-safe numbers ranged between 7 and 1151 with almost all cases >19 (Table S2), which is relatively large compared to the sample sizes of main effects tested in our study.

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Figure Legends

Figure 1 Effect of ocean acidification and warming on ecosystem processes and functional groups, and scope for acclimation. Mean effect size and direction of impacts from ocean acidification (OA; blue) on species tested in multi-species experiments (Com OA), and of impacts from ocean acidification, warming (T; orange), and their combined effects (OA × T; red) on species tested in single-species experiments, for a) primary production, b) secondary production by invertebrates, c) foraging rate, d) metabolic rate, e) calcification rate, and f) dimethylsulfide (DMS) production. Scope for acclimation (Acclim.) compares short (< 1 mo.) vs. long (1–13 mo.) experiments on the combined effects of warming and acidification. Error bars represent 95% confidence intervals. Numbers between brackets indicate sample size (# of experiments); * $P \leq 0.05$.

Figure 2 Effect of ocean acidification on species diversity and abundances based on multi-species experiments. Mean effect size and direction of impacts of ocean acidification on a, b) species diversity, and c, d) abundances of species within communities, for multi-species studies only. Figures 2a, c: left-hand panels: overall mean effects; central panels: categorical effects where data are split for various functional groups – calcifying species alone (Cal), non-calcifying species alone (eukaryotes; N-Cal), mixed communities of calcifiers and non-calcifiers (Mix), and microorganisms (Micro; blue circles with grey filling); right-hand-panels: effect sizes for short-term (<1 mo.) vs. longer-term (1–13 mo.) vs. *in situ* studies on natural CO₂ vents, separated for microbes and all other species. Figures 2b, d show effect sizes for different species groups. Error bars represent 95% confidence intervals. Numbers between brackets indicate sample size; * $P \leq 0.05$.

Figure 3 Conceptual diagram illustrating the main effects of ocean acidification, warming, and their combination on ecosystem processes and species groups, based on the meta-analysis results as shown in the various figures of our study. Circled arrows indicate the direction of change, question marks (?) indicate less certain responses. The most likely feedback responses that exacerbate the direct effects of these two global stressors are indicated with white arrows. Two model ecosystems are shown here (reefs and surface-ocean) to visually capture potential change (present day – top left and right panels vs. future – bottom left and right panels) in species abundance, species diversity, and community shifts, as revealed by our meta-analysis for ecosystems in general. The changes shown here for reefs and surface-ocean are not exact outcomes of future states but merely emphasize overall responses for (relative) abundance of species.

Figure 1

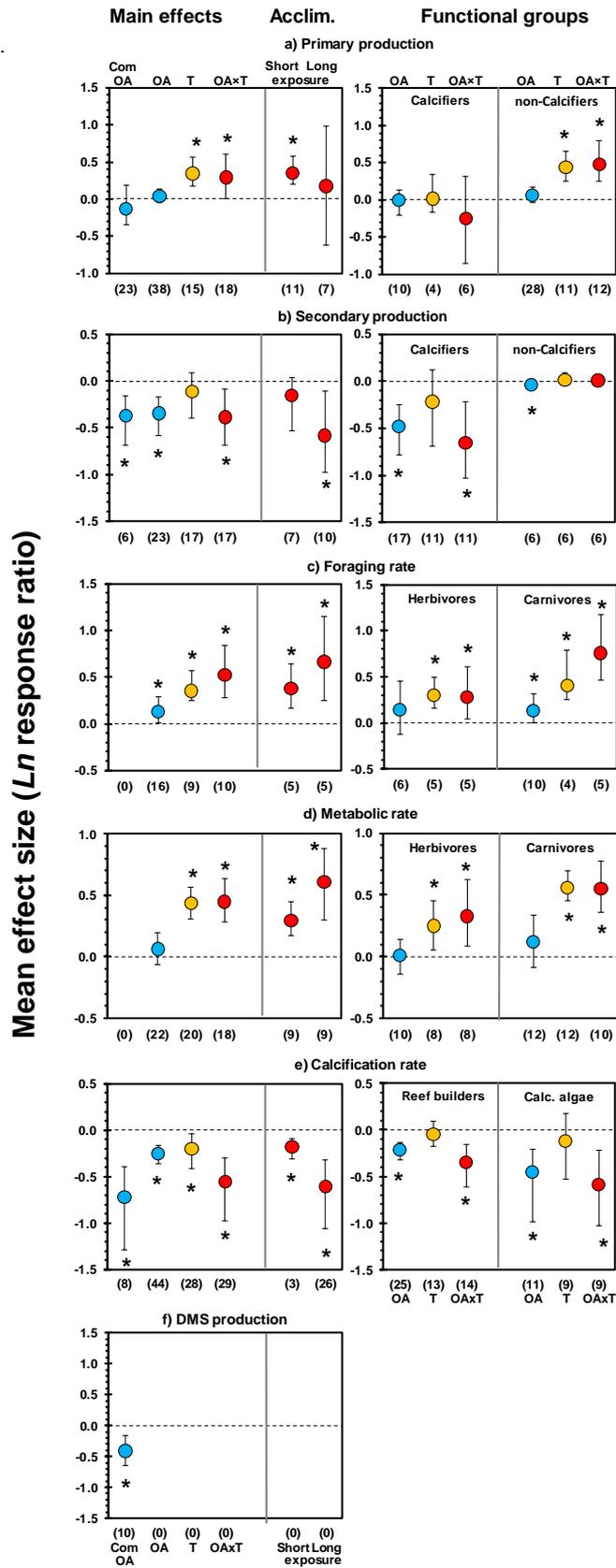


Figure 2

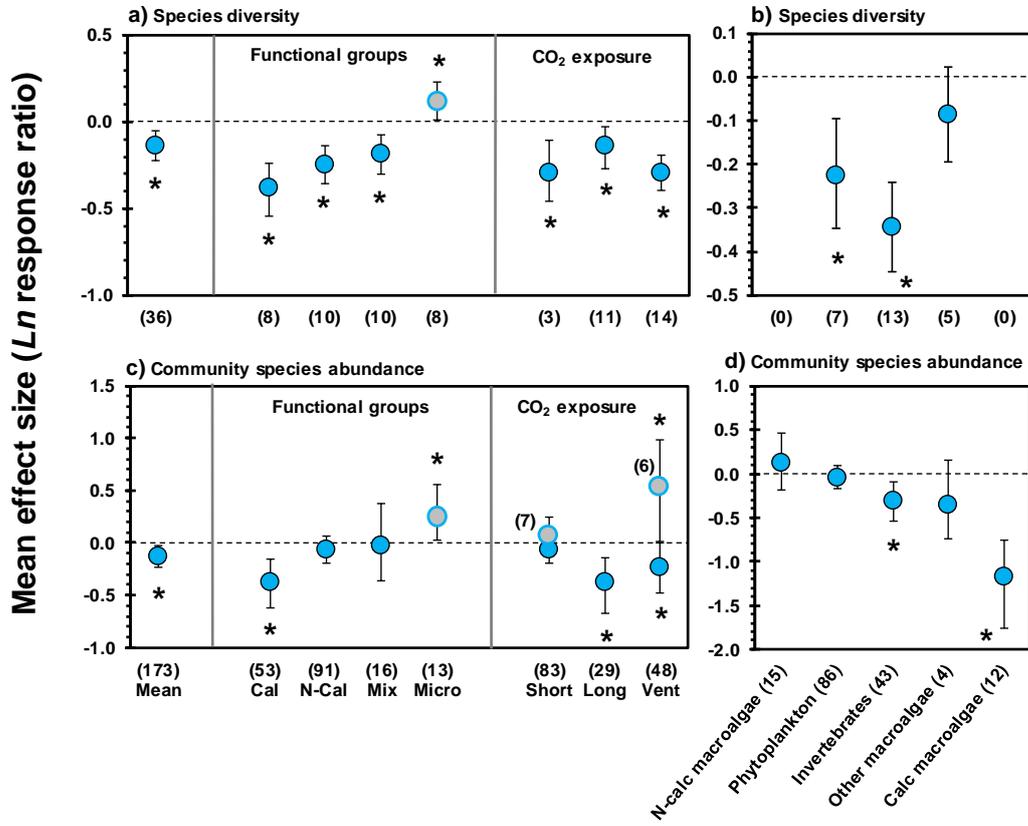
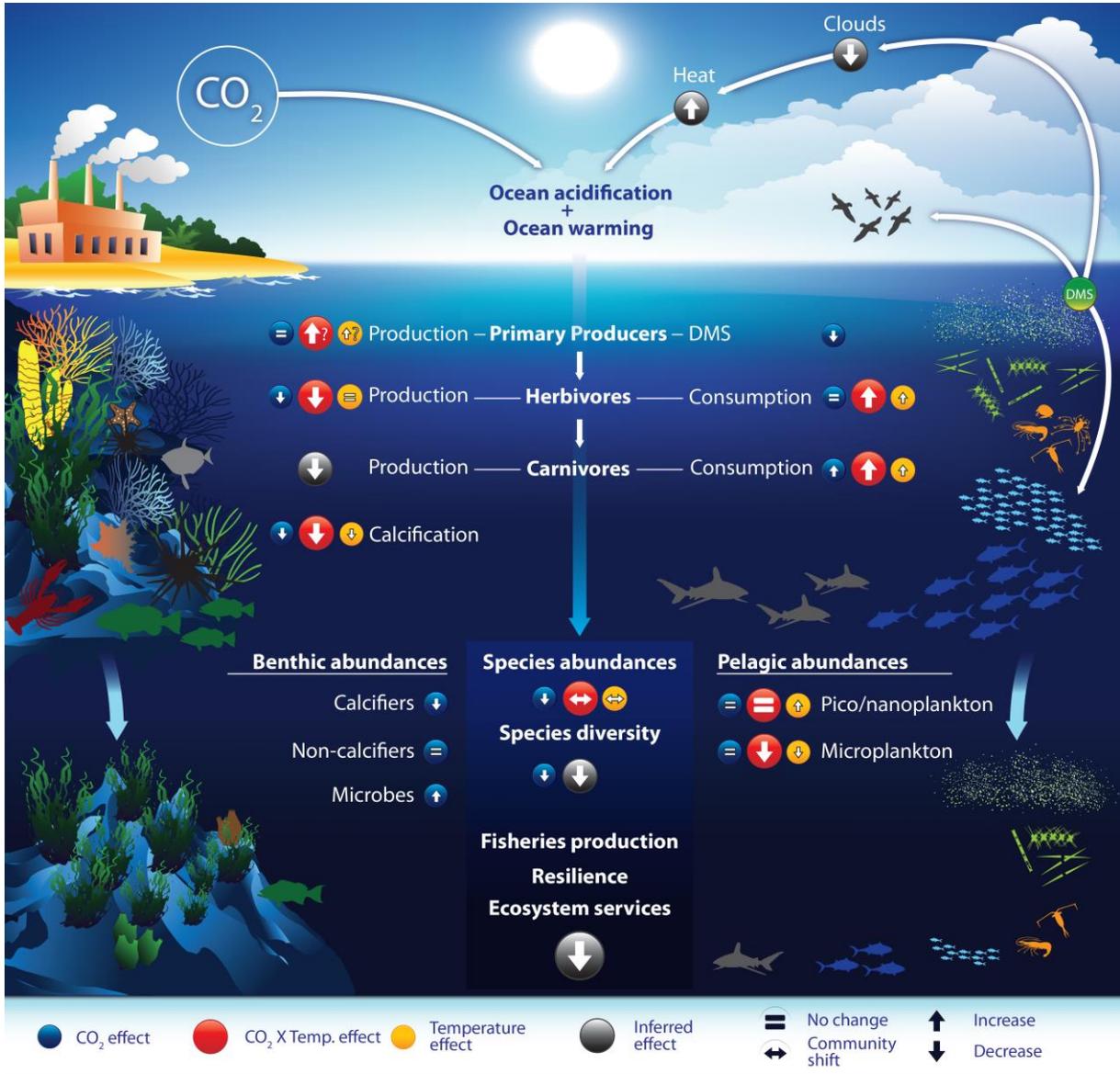


Figure 3



Supplemental Figure and Table Legends

Table S1. Overview of the processes studied (main effects) and number of studies used. For each main effect the number of studies is shown for each stressor, followed by the mean experimental decrease in pH and increases (enrich.) in CO₂ and temperature, respectively. Also shown are the duration of experimental CO₂ exposure (weeks) and the distribution (#) and trends (positive, negative, no change) of studies across latitudes and biomes.

Table S2. Statistical output of the meta-analyses performed for Figures 1 and 2. Weighted and unweighted effect sizes of a random-effects model and the total heterogeneity and p-value for the weighted main effect size for each stressor. Test statistics for the subsequent categorical random-effects model are reported for various categorical factors. Also shown are the test for publication bias (Rosenthal's) and the output of continuous random-effects models (CO₂/T correlation columns) to test for the correlation with experimental level of CO₂ or temperature increase, respectively.

Dataset S1. Details of the studies included in the meta-analysis.

Figure S1. Mean effect sizes and direction of impacts of ocean acidification (OA; blue) and ocean warming (T; orange) and their combined effects (OA × T; red) showing the effect of experimental exposure time. Short = duration of experiment <1 month, long = duration of experiment 1–13 months. Error bars represent 95% confidence intervals. Numbers between brackets indicate sample size (# of experiments); * $P \leq 0.05$. For main effects see Figures 1 and 2.

Figure S2. Mean effect sizes and direction of impacts of ocean acidification (OA; blue) and ocean warming (T; orange) and their combined effects (OA × T; red) for various categorical effects. a, b) primary production by calcifiers vs. non-calcifiers in (sub)tropical and temperate regions, c) community species abundances of various species groups, d) calcification rates of several species groups. Error bars represent 95% confidence intervals. Numbers between brackets indicate sample size (# of experiments); * $P \leq 0.05$. For main effects see Figures 1 and 2.

Table S1

Study level	Stressor	N	pH reduction	CO ₂ /temp. enrich.	CO ₂ exposure	Latitude			Biome	
			Mean ± SD	Mean ± SD	Mean ± SD	(sub)Tropical	Temperate	Other	Benthic	Pelagic
Primary production										
communities	OA	23	0.3 ± 0.1	441 ± 99 ppmv	1.8 ± 2.7	11 =	11 =	1 *	2	21
species	OA	38	0.3 ± 0.1	410 ± 198 ppmv	10.8 ± 14.6	7 ↓	27 ↑	4 ↓	17	21
species	T	15		4.5 ± 1.1 °C		1 *	13 ↑	1 *	6	9
species	OA x T	18				4 =	13 ↑	1 *	8	10
Secondary production										
communities	OA	6	0.3 ± 0.1	752 ± 266 ppmv	5.1 ± 0.9	3 *	3 *		6	
species	OA	23	0.3 ± 0.1	690 ± 331 ppmv	6.2 ± 4.0	10 ↓	12 ↓	1 *	23	
species	T	17		3.6 ± 1.2 °C		7 =	10 =		17	
species	OA x T	17				7 =	10 ↓		17	
Foraging rate										
species	OA	16	0.3 ± 0.1	569 ± 362 ppmv	7.5 ± 7.0	7 ↑	9 =		16	
species	T	9		4.0 ± 1.2 °C		2 *	7 ↑		9	
species	OA x T	10				2 *	8 ↑		10	
Metabolic rate										
species	OA	22	0.3 ± 0.1	634 ± 223 ppmv	4.1 ± 4.5	7 =	10 =	5 ↑	15	7
species	T	20		4.4 ± 1.1 °C		5 ↑	9 ↑	6 ↑	14	6
species	OA x T	18				4 ↑	9 ↑	5 ↑	12	6
Calcification rate										
communities	OA	8	0.4 ± 0.1	512 ± 87 ppmv	1.2 ± 1.4	2 *	6 ↓		3	5
species	OA	44	0.3 ± 0.1	546 ± 288 ppmv	9.7 ± 11.6	22 ↓	22 ↓		44	
species	T	28		3.7 ± 1.0 °C		16 =	12 ↓		28	
species	OA x T	29				17 ↓	12 ↓		29	
DMS production										
communities	OA	10	0.4 ± 0.1	540 ± 144 ppmv	2.6 ± 1.2	2 *	7 ↓	1 *	2	8
Species diversity										
communities	OA	36	0.3 ± 0.1	487 ± 224 ppmv	8.2 ± 7.9	20 ↓	9 ↓	7 =	28	8
Species abundances										
communities	OA	173	0.3 ± 0.1	482 ± 194 ppmv	5.0 ± 8.3	78 ↓	73 ↓	22 =	87	86
communities	T	20		3.4 ± 0.7 °C			20 =		6	14
communities	OA x T	32				4 =	28 =		10	22

OA = ocean acidification; T = temperature; N = sample size; SD = 1 standard deviation; values for experimental pH reduction reflect pH units; CO₂/temp. enrich. = levels of experimental CO₂ and temperature enrichment, respectively; values for experimental CO₂ exposure reflect duration in # of weeks; Other = polar or cosmopolitan; ↑ = increase; ↓ = decrease; = = no change; * insufficient replicates to investigate trends.

Table S2

Study level	Stressor	Weighted			Unweighted			Heterogeneity (weighted)			Categorical effects				Rosenthal's fail-safe #	CO ₂ /T correlation	
		mean <i>LnR</i>	95% CI		mean <i>LnR</i>	95% CI		Q _T	df	p-value	Q _M	Q _E	p-value	category		slope	p-value
Primary production																	
communities	OA	-0.1	-0.3	0.2	-0.1	-0.3	0.2	34.6	22	0.043	0.05	34.4	0.819	latitude	NA	0.000	0.913
species	OA	0.0	0.0	0.1	0.0	-0.1	0.1	49.5	37	0.083	15.4	49.0	<0.001	latitude	NA	-0.001	<0.001
species	T	0.3	0.2	0.6	0.4	0.2	0.6	14.7	14	0.400					56	0.024	0.807
species	OA x T	0.3	0.0	0.6	0.4	0.0	0.8	28.6	17	0.039	4.1	18.6	0.043	latitude	23		
Secondary production																	
communities	OA	-0.4	-0.7	-0.2	-0.5	-0.9	-0.2	4.7	5	0.459					10	0.000	0.621
species	OA	-0.3	-0.6	-0.2	-0.3	-0.6	-0.1	16.3	22	0.799					46	0.000	0.642
species	T	-0.1	-0.4	0.1	-0.2	-0.6	0.0	28.4	16	0.028	1.1	23.9	0.289	calcifier	NA	-0.207	0.029
species	OA x T	-0.4	-0.7	-0.1	-0.5	-0.8	-0.2	30.1	16	0.017	11.4	30.0	0.001	calcifier	64		
Foraging rate																	
species	OA	0.1	0.0	0.3	0.1	0.0	0.3	18.4	15	0.245					7	0.000	0.368
species	T	0.4	0.2	0.6	0.4	0.2	0.6	10.7	8	0.220					62	-0.049	0.573
species	OA x T	0.5	0.3	0.8	0.5	0.3	0.8	5.7	9	0.767					19		
Metabolic rate																	
species	OA	0.1	-0.1	0.2	0.1	-0.1	0.2	27.8	21	0.147					NA	0.000	0.428
species	T	0.4	0.3	0.6	0.5	0.3	0.6	17.9	19	0.526					290	-0.012	0.865
species	OA x T	0.4	0.3	0.6	0.5	0.3	0.6	16.9	17	0.458					142		
Calcification rate																	
communities	OA	-0.7	-1.3	-0.4	-1.7	-3.2	-0.7	9.4	7	0.225					34	-0.002	0.296
species	OA	-0.2	-0.4	-0.2	-0.7	-1.2	-0.3	174.2	43	<0.001	44.8	88.6	<0.001	taxon	1151	0.000	0.296
species	T	-0.2	-0.4	0.0	-0.1	-0.4	0.3	51.7	27	0.003	18.6	33.1	0.001	taxon	62	-0.157	0.034
species	OA x T	-0.6	-1.0	-0.3	-0.6	-1.0	-0.4	33.1	28	0.232					122		
DMS production																	
communities	OA	-0.4	-0.6	-0.2	-0.4	-0.6	-0.2	6.7	9	0.671					20	0.000	0.701
Species diversity																	
communities	OA	-0.1	-0.2	-0.1	-0.2	-0.4	-0.1	47.1	35	0.082	31.3	34.3	<0.001	funct. group	191	-0.001	0.025
Species abundances																	
communities	OA	-0.1	-0.2	0.0	-0.2	-0.3	-0.1	346.2	172	<0.001	20.2	332.3	<0.001	funct. group	838	0.000	0.289
communities	T	0.1	-0.1	0.3	0.0	-0.2	0.3	30.1	19	0.050	20.0	20.7	<0.001	taxon	NA	-0.122	0.521
communities	OA x T	-0.1	-0.4	0.2	0.0	-0.3	0.3	40.5	31	0.117					NA		

LnR = mean effect size based on the natural logarithm of the Response Ratio; OA = ocean acidification; T = temperature; CI = confidence interval; Q_T = total sample heterogeneity (of the weighted *LnR*); Q_M = variance explained by the categorical model (performed when Q_T was significant); Q_E = residual error variance not explained by the model; df = degrees of freedom; NA = not applicable. CO₂/T correlation = correlation between effects sizes and CO₂ and temperature enhancement, respectively.

Figure S1

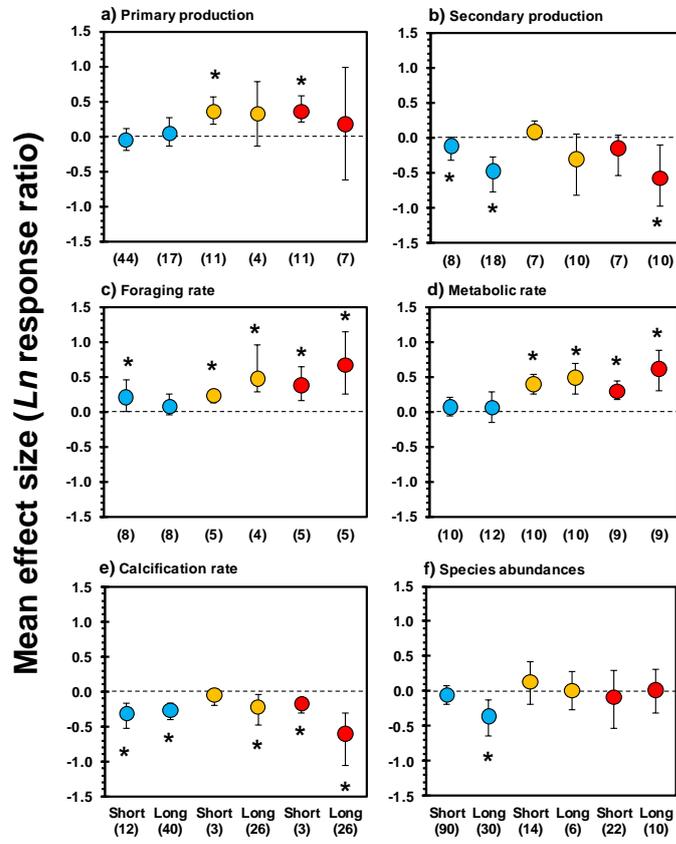


Figure S2

