

# Ecological complexity buffers the impacts of future climate on marine consumers

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**Ecological complexity represents a network of interacting components that either propagate or counter the effects of environmental change on individuals and communities<sup>1–3</sup>. Yet, our understanding of the ecological imprint of ocean acidification (elevated CO<sub>2</sub>) and climate change (elevated temperature) is largely based on reports of negative effects on single species in simplified laboratory systems<sup>4,5</sup>. By combining a large mesocosm experiment with a global meta-analysis, we reveal the capacity of consumers (fish and crustaceans) to resist the impacts of elevated CO<sub>2</sub>. While individual behaviours were impaired by elevated CO<sub>2</sub>, consumers could restore their performances in more complex environments that allowed for compensatory processes. Consequently, consumers maintained key traits such as foraging, habitat selection and predator avoidance despite elevated CO<sub>2</sub> and sustained their populations. Our observed increase in risk-taking under elevated temperature, however, predicts greater vulnerability of consumers to predation. Yet, CO<sub>2</sub> as a resource boosted the biomass of consumers through species interactions and may stabilize communities by countering the negative effects of elevated temperature. We conclude that compensatory dynamics inherent in the complexity of nature can buffer the impacts of future climate on species and their communities.**

The web of life is classically considered as a network of organisms interlinked to each other and their environment through biotic and abiotic processes<sup>1</sup>. These networks not only drive population dynamics but also shape the ecological imprint of human activities at multiple levels of biological organization<sup>2,3</sup>. Individuals possess remarkable plasticity in using the complexity of their environment to persist through abiotic stress<sup>6–9</sup>. Yet, their interactions with other species can propagate<sup>10,11</sup> or stabilize against change<sup>12</sup>, giving rise to strong and complex indirect effects<sup>13,14</sup>. In turn, species diversity enhances function<sup>15</sup> and stability within ecosystems<sup>16,17</sup>. Consequently, as it manifests from individuals to ecosystems, ecological complexity has the potential to alter or stabilize local communities during global change.

Predictions of ecological responses to future ocean acidification and warming remain largely based on simplified laboratory systems and species in isolation<sup>4</sup>. The metabolic rates of marine ectotherms are directly affected by warming<sup>18</sup>, which accelerates growth in some species when sufficient food is provided<sup>19</sup>. However, in nature, temperature-driven regime shifts can negate such direct benefits by eroding the resources on which they rely<sup>20</sup>. Ocean acidification can raise the energetic costs involved in calcification and acid–base regulation<sup>21,22</sup> and impair neural functioning causing disturbed responses in ecologically relevant behaviours<sup>5</sup>. An intensification of

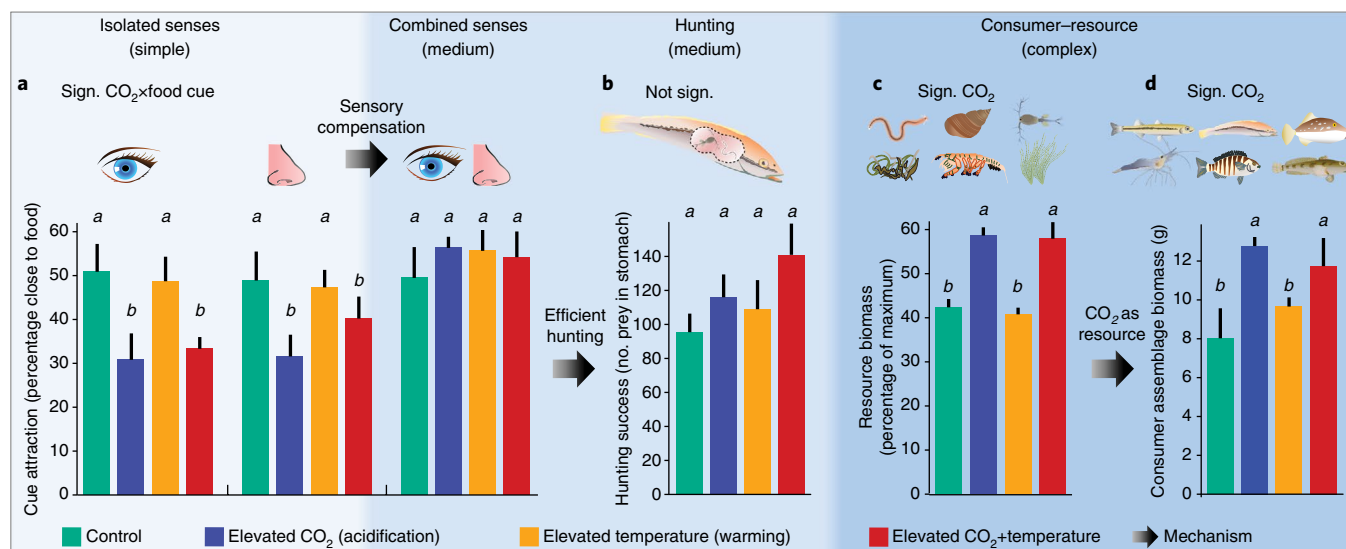
these direct effects from ocean acidification might be expected when animals are exposed to the pressures and complexities of nature. In contrast, fish, crustaceans and calcifying herbivores can flourish at natural analogues of ocean acidification<sup>23,24</sup>. These counter-intuitive findings suggest the existence of mechanisms that reverse the direction of change within the complexity of ecological communities.

Understanding the response of actively foraging animals to global change is particularly challenging because, compared to plants or sedentary animals, they consume a diversity of biological resources<sup>25</sup> and are able to react through their mobility and complex behaviour<sup>7,26</sup>. Interactions between an individual and its environment are mediated by behaviour; acting as a first line of defence against rapid human-induced change<sup>27</sup>. Exceptional plasticity in behaviour draws upon building blocks of ecological complexity such as space, time or environmental information to initiate compensatory responses<sup>6,7</sup>. For example, animals that are impaired in one sense through abiotic change (for example, olfaction impaired by ocean acidification) may retain their capacity for relevant decision-making when provided with more complete information about their environment through additional sensory cues<sup>28,29</sup>. Therefore, a deeper understanding of the role of behavioural plasticity and the indirect effects that operate within communities is critical to bridge the gap between the effects of future climate in the laboratory and their consequences in nature<sup>3–5</sup>.

The first step of our investigation experimentally tested whether ecological complexity can modify the effects of ocean acidification and warming on active consumers. In 1,8001 mesocosms harbouring a mosaic of habitats, we assessed the response of an assemblage of 8 species of omnivorous and carnivorous fish and shrimp (Supplementary Table 10) at the organism to community levels. The consumers were supported by a self-sustaining and highly diverse food web including microflora and fauna, macrophytes (20+ species) and macroinvertebrates (70+ species). Elevated CO<sub>2</sub> (910  $\mu$ atm, pH = 7.89) and temperature (+2.8 °C, baseline 21 °C) were maintained for 4.5 months according to end-of-century projections (Representative Concentration Pathway 8.5)<sup>30</sup>. Warming was simulated on the basis of summer temperatures because climate extremes are key drivers of community structure<sup>20</sup>; temperatures remained nevertheless within the thermal limits of the consumer species (see Supplementary Table 12).

This mesocosm approach showed that the direct negative effects of elevated CO<sub>2</sub> can be buffered and even reversed by ecological complexity. Consumers under elevated CO<sub>2</sub> were less attracted to either olfactory or visual food cues in isolation—the simplest level of complexity (Fig. 1a and Supplementary Tables 1 and 2). However, when both olfactory and visual cues were present, consumers fully

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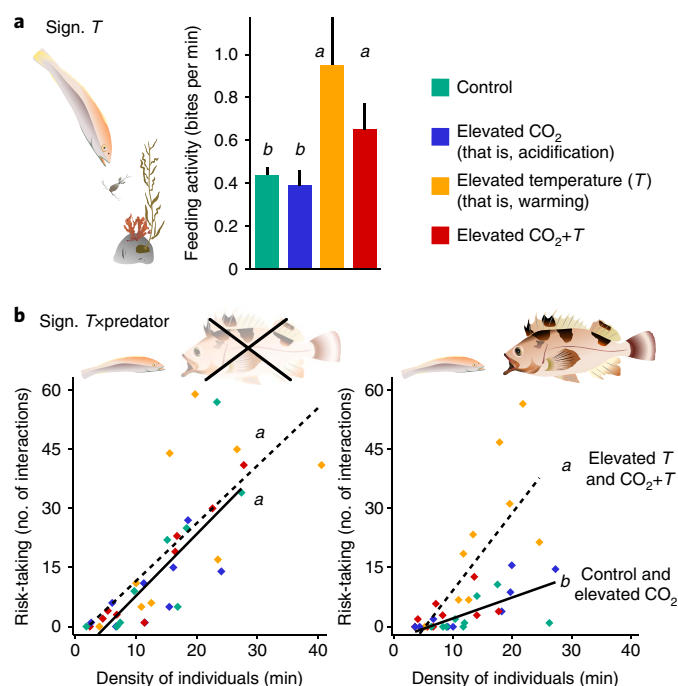


**Fig. 1 | Mesocosm study showing how the negative effects of ocean acidification on consumers can be buffered and reversed through ecological complexity.** **a**, Sensing of visual, olfactory and combined visual-olfactory food cues ( $n=6$  behavioural trials from 3 mesocosms). **b**, Invertebrate prey captured during foraging ( $n=53, 62, 49$  and  $54$  fish). **c,d**, Availability of resources (**c**) and overall performance of consumers (**d**) estimated as biomass after long-term exposure ( $n=3$  mesocosms). Different superscripts mark significantly different groups of means according to main effects (via analysis of variance (ANOVA), plots **b–d**) or interaction (via post hoc tests, plots in **a**). All data are shown as mean + s.e.m. Organism symbols (except tanaid and hardy head) are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science ([ian.umces.edu/symbols/](http://ian.umces.edu/symbols/)).

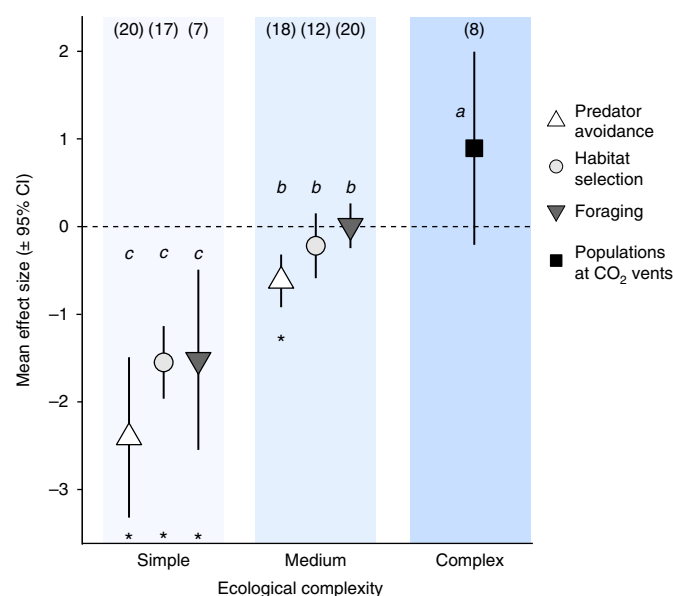
restored their attraction to food cues under elevated  $\text{CO}_2$  (Fig. 1a). Accordingly, the success of consumers during hunting was not affected by elevated  $\text{CO}_2$ , estimated through the number of live prey captured while foraging freely amongst structured habitats (Fig. 1b and Supplementary Table 3a). Consumer–resource interactions operated over long terms in the mesocosms, as consumers had to search and compete for the self-replenishing resources. At this ecologically more complex level, resource availability was boosted by elevated  $\text{CO}_2$  (Fig. 1c and Supplementary Table 3b), and correspondingly, consumer assemblages showed higher biomass (Fig. 1d and Supplementary Table 3c). This response was not altered by the identity of the consumer species (Supplementary Table 4).

While elevated temperature did not affect cue sensing in consumers (Fig. 1a and Supplementary Table 1), it intensified risk-taking behaviours that could increase their exposure to predators in nature. Consumers invested more effort in acquiring food under elevated temperature (Fig. 2a and Supplementary Table 3d), but this was not converted to increased biomass (Fig. 1d and Supplementary Table 3c). In the absence of a predator, consumers of all climate treatments aggressively competed for food in unsheltered habitat (Fig. 2b and Supplementary Tables 5 and 6). Only consumers under ambient temperature reduced these interactions when facing a live predator, while consumers under elevated temperature maintained high levels of risk-taking. In contrast,  $\text{CO}_2$  did not affect the response of consumers to a live predator that provided the full range of predator cues (Fig. 2b and Supplementary Table 5).

The second step of our investigation related these experimental responses to ocean acidification with responses of other study systems ( $n=102$  experiments) that similarly included fish or decapod crustaceans. The performance of consumers was considered in three key ecological traits—predator avoidance, habitat selection and foraging—under different levels of ecological complexity. Meta-analysis suggested a steady reduction in the impacts of ocean acidification on consumers from ecologically simple to complex experiments (Fig. 3 and Supplementary Table 8a), which is in agreement with our mesocosm study. Elevated  $\text{CO}_2$  had a strong negative effect on



**Fig. 2 | Mesocosm study showing how warming can increase risk-taking behaviour in consumers.** **a**, Hunting effort (mean + s.e.m.) required to meet food demand ( $n=3$  mesocosms). **b**, Willingness to take risks in the absence and presence of a live predator ( $n=18$  behavioural trials per regression line from 6 mesocosms). Different superscripts mark significantly different groups of means according to main effect (via ANOVA, plot **a**) or interaction (via post hoc tests, plots in **b**). Organism symbols are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science ([ian.umces.edu/symbols/](http://ian.umces.edu/symbols/)).

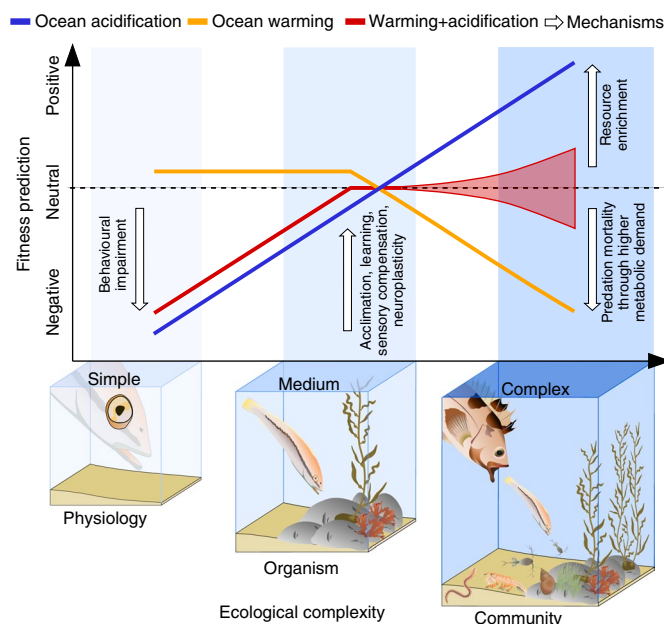


**Fig. 3 | Meta-analysis on the effects of ocean acidification on the performance of fish and decapods at different levels of ecological complexity.** Effect sizes are standardized mean differences (Hedges's *g*) and should be interpreted as multiples of standard deviations. Within each of the three ecological traits, different superscripts mark effect sizes that differ significantly between levels of complexity. Means that differ significantly from 0 are marked by asterisks, and the number of experiments included is given in brackets.

multiple behaviours in simpler experiments (Supplementary Table 9a). However, negative effects on behaviour, growth or survival were less severe (for predator avoidance) or absent (for habitat selection and foraging) in experiments with medium complexity (Supplementary Table 9a). While we defined these two levels of complexity through the presence of sensory cues ('simple' for an isolated cue and 'medium' for multiple cues), they were probably representative of ecological complexity in a broader context (see Supplementary Table 16). At natural CO<sub>2</sub> vents, the most complex level that integrated ecological traits and allowed for biotic interactions, population densities of consumers remained on average unaffected (Fig. 3 and Supplementary Table 9a), but showed an increase for several individual experiments (Supplementary Fig. 1).

After accounting for ecological traits and levels of complexity in the meta-analysis, the amount of remaining heterogeneity indicated that responses of consumers to elevated CO<sub>2</sub> differed substantially among experiments (*I*<sup>2</sup> and *Q* statistics in Supplementary Table 9a). While the CO<sub>2</sub> effect appears to be variable across species and contexts, the consumer responses from our mesocosm are close to the mean effect sizes from the literature and may thus be seen as representative (Supplementary Fig. 1).

We show that ecological complexity buffers the influence of future climate on marine consumers and highlight the importance of compensatory processes within complex communities. We not only provide an experimental demonstration for this phenomenon, but also show how widely spread it may occur across multiple systems. Physiological responses to ocean acidification were compensated at the organismal level, and indirect effects subsequently acted as principle pathways towards negative (via ocean warming) or positive change (via ocean acidification) (Fig. 4). Such successive incorporation of increasing ecological complexity may explain why global change can be dampened at larger spatio-temporal scales<sup>2</sup>. It may also assist us in understanding the widespread nature of observations in the stability–biodiversity debate: for example, why plant



**Fig. 4 | Conceptual framework of how increasing ecological complexity can buffer the direct negative effects of future climate on marine consumers and drive community dynamics through biotic interactions.** Fitness predictions are based on a multi-species assemblage tested in a foraging context in mesocosms (acidification and warming) and on a global meta-analysis considering multiple ecological traits (acidification alone). Organism symbols (except tanaid) are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science ([ian.umces.edu/symbols/](http://ian.umces.edu/symbols/)).

diversity reinforces the resistance of grassland productivity to abiotic stress<sup>17</sup>, and why increasing trophic diversity provides stability to food webs<sup>16</sup> and enhances ecosystem services<sup>15</sup>. From homeostasis within individuals to interactions among species, these lower-level processes may contribute to emergent properties of stability and resistance at the scale of complex food webs and ecosystems<sup>12</sup>.

While isolated sensory modalities were often compromised by ocean acidification—a result that on its own would predict population decline—consumers could restore their performances through compensatory responses at the organism level. For instance, sensory compensation may occur via two mechanisms based on the cognitive flexibility of animals<sup>6,28,29</sup>: an impaired sensory modality is replaced by a functioning one (sensory redundancy) or, as demonstrated in our mesocosms with vision and olfaction, two impaired modalities complement each other (sensory complementation). In the broad ecological context of our meta-analysis, neuroplasticity and learning may also form part of the repertoire of processes that buffer against the negative effects of ocean acidification<sup>7,31</sup>. However, the full compensatory potential may be accomplished only if animals are offered choices (for example, in resources and habitat) under long-term selective pressure (for example, competition and survival). These criteria are met at natural CO<sub>2</sub> vents and in our mesocosms and might have favoured the development of behavioural strategies to maintain increasingly difficult tasks such as hunting. By drawing upon the complexity that characterizes ecological niches, behavioural plasticity can improve the fitness of animals during unprecedented environmental change including ocean acidification and buy genetic adaptation time for physiological recalibration<sup>8,27,32</sup>.

At the community level in our mesocosms, an increase in resources supported greater consumer biomass, reversing the direct negative effect of ocean acidification. Primary producers can utilize

anthropogenic CO<sub>2</sub> as a nutrient<sup>33</sup> that propagates to secondary<sup>24</sup> and tertiary producers<sup>23,34</sup>. Alterations to consumer–resource interactions are generally regarded as powerful drivers of food web structure and function<sup>3,11</sup>, and we show that CO<sub>2</sub> enrichment can benefit an entire assemblage of consumers, including eight species of omnivores and carnivores. CO<sub>2</sub> enrichment may similarly be responsible for the increase in fish numbers at CO<sub>2</sub> vents in the Mediterranean, the tropical Pacific and the temperate Pacific as documented by several studies in our meta-analysis. While our findings provide a broader framework in which to consider ocean acidification—a field dominated by reports on negative effects—ecosystems as a whole still seem likely to experience losses in species and functional diversity<sup>18</sup>. As such, ocean acidification may: impair other life stages including reproduction and early life history that are not fully considered at CO<sub>2</sub> vents due to the subsidy of individuals from nearby control areas; enable generalist species to displace specialist species<sup>14</sup>; threaten calcifying consumers including molluscs and echinoderms<sup>22</sup>; and impact foundation species such as corals, causing degradation of habitats and the species they support<sup>35</sup>.

Ocean warming may counter the positive effects of acidification on consumers by increasing their vulnerability to higher-order predation. In our mesocosms, the rising metabolic demand at elevated temperature<sup>18</sup> may have favoured competition for food over vigilance in the trade-off between growth and survival<sup>36,37</sup>. Through increased risk-taking in consumers and raised food demands in their predators<sup>18,19</sup>, warming would intensify predator–prey interactions. These findings are unlikely to reflect short-term stress responses, as the thermal niche of our consumer assemblage was not exceeded by the warming treatment. This possibly explains the absence of any negative effects of warming on foraging behaviours and biomass. In contrast, species loss and a substantial reorganization is forecast for consumer assemblages closer to their upper thermal limits, which is more often the case in the subtropics<sup>38</sup>. Trophic complexity that incorporates resources (gain) and predators (loss)<sup>11,25</sup> propagates change via indirect effects<sup>3,10,34</sup> that may dominate over direct effects of human stressors<sup>13</sup>. Accordingly, our findings suggest that changes in consumer assemblages in future oceans can depend on the relative balance between the negative effect of predation through warming and the positive effect of resource enhancement through acidification (Fig. 4). This consideration challenges the view of ocean acidification as an overwhelming stressor and, instead, indicates its potential to buffer some impacts of coinciding ocean warming. Consumers may consequently maintain function under future climate to support some ecosystem services, such as the trophic transfer of benthic production towards fisheries.

Here, we bridge the knowledge gap between direct effects of future climate and the dynamics of species assemblages in natural environments. Our findings reveal processes that counter the propagation of change, both at simple (via sensory compensation) and elevated levels of complexity (via resource enrichment and interacting stressors). Therefore, we highlight the potential of ecological complexity to buffer or reverse the responses of species to future climate and mediate change or stasis in ecological communities.

## Methods

Methods, including statements of data availability and any associated accession codes and references, are available at <https://doi.org/10.1038/s41558-018-0086-0>.

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## Author contributions

S.U.G., I.N. S.D.C. and C.M.F. designed the study, S.U.G., E.M., A.B. and C.M.F. performed the research, S.U.G. analysed the data, S.U.G. conducted the meta-analysis, S.U.G., I.N. and S.D.C. wrote the manuscript and all authors contributed to writing the manuscript.

## Competing interests

The authors declare no competing financial interests.

## Additional information

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## Methods

**Mesocosm study.** *Mesocosms.* We simulated a shallow temperate coastal ecosystem with an enhanced level of realism using 12 circular mesocosms of 1,800 l each (see Supplementary Figs. 2 and 5 for photos; width = 169 cm and depth = 80 cm), maintained indoors from February to July 2015. Each mesocosm comprised a mosaic of the three dominant local habitats (Gulf St Vincent, South Australia)<sup>39</sup>: 'rocky reef' made of natural rocks collected from the sea and including associated macrophytes and invertebrates; 'artificial seagrass' colonized by epiphytes and planted into fine silica sand; and 'open sand' composed of the same fine silica sand. Natural sediment collected among seagrass meadows and including all infauna and flora was used to seed the soft-bottom habitats (25 l per mesocosm). Primary production was fuelled by a lamp that simulated a local water depth of ~6–7 m (14/10 light–dark cycle, 30 min dawn and dusk dimming). A flow-through of unfiltered seawater provided each mesocosm with nutrients and planktonic propagules at 2,300 l day<sup>-1</sup>.

**Climate treatments.** CO<sub>2</sub> (levels: ambient and elevated) was crossed with temperature (levels: ambient and elevated) using three replicate mesocosms per treatment combination. Climate manipulations followed end-of-century projections under a business-as-usual emission scenario (Representative Concentration Pathway 8.5)<sup>30</sup> (see Supplementary Table 13 and Supplementary Fig. 3 for details on water parameters). An ambient temperature of 21 °C was applied corresponding to local summer conditions (average over two loggers: 5 m depth, 5-year data set 2010–2015, SA Water). To achieve elevated CO<sub>2</sub>, the seawater was pre-conditioned with pure CO<sub>2</sub> to treatment levels (1,000 µatm p<sub>CO2</sub>) and then continuously circulated between each mesocosm and an associated bin heavily aerated with CO<sub>2</sub>-enriched air (at 1,000 µatm p<sub>CO2</sub>). These bins also contained heaters in the elevated temperature treatments. As expected from shallow coastal systems, community metabolism produced diurnal variability in pH and reduced p<sub>CO2</sub> to 910 µatm due to net autotrophy (Supplementary Fig. 4).

**Consumer assemblage.** We studied an assemblage of highly mobile omnivorous and carnivorous consumers, including juveniles of six species of fish and two species (same genus) of shrimp (Supplementary Table 10). To start, 7–10 individuals of each fish species and 10 shrimps (total of  $n = 55$  per mesocosm, 10–40 mm in length) were introduced to each mesocosm, which was then exposed to the climate treatments for 4.5 months. This long-term exposure not only ensured an advanced level of acclimation in the consumers but also allowed trophic and competitive forces to act on the consumer assemblage. Correspondingly, the consumers adjusted to their specific environmental conditions through growth and survival, with an average of  $25.1 \pm 4.4$  ( $\pm$  s.d.) individuals remaining per mesocosm at the end of the experiment (Supplementary Table 11).

The effects of ocean warming on ecological communities is forecast to vary considerably between regions, depending on the specific thermal niches of component species<sup>38</sup>. As indicated by latitudinal distributions, the eight consumer species used in our mesocosm probably differ in their thermal niches (Supplementary Table 12). While all species also occur in considerably colder regions relative to the location of our study, their ranges extend differently towards warmer regions. Yet, we found no evidence for a species-specific effect of warming on biomass or abundance after long-term exposure in the mesocosms (Supplementary Table 4). A change in composition was possibly not observed as our study location is not at the upper thermal limit of any of the consumer species.

**Consumer behaviour.** Cue sensing and decision-making in the context of foraging and predation were tested inside the mesocosms after 2.5 months of exposure to the climate treatments. To study potential sensory compensation, the attraction of the consumers to three distinct food cues was tested: isolated visual cue; isolated olfactory cue; and combined visual and olfactory cue. A 'food cue provider' provided the visual (highly active brine shrimps, 2–5 mm length), olfactory (mix of various invertebrates) and combined cues without a change in appearance (Supplementary Fig. 5). To study consumers under predation risk, a live predator (*Gymnapistes marmoratus*, ~9 cm total length,  $n = 3$  per treatment, for thermal niche see Supplementary Table 12) was presented in a cage emitting the natural range of predator cues (Supplementary Fig. 5). The predators were acclimated to the climate treatments for one month in separate tanks and fed daily *ad libitum* with a mix of local prey fish and shrimps.

Behavioural trials with all combinations of 'food cue' (levels: visual, olfactory and visual + olfactory) and 'predator' (levels: absent and present) were conducted in each mesocosm in random order on different days, totalling six trials per mesocosm. The food cue provider was placed in front of the predator cage to start the trials and the surrounding area was video-recorded from the top (field of view 90 × 50 cm) for 7 min. During the subsequent video analysis, a circular overlay centred on the provider divided the field of view into an area 'close' and 'distant' to the food cue (Supplementary Fig. 5). The behaviour and location of individuals was manually recorded for every second from entering until exiting the field of view using the software Solomon Coder. Hardyheads were not considered because they often stayed in the water column out of camera view. For each trial, the sum across all individual observations was used as consumer response.

Three response variables were derived for further analysis. 'Cue attraction' was estimated as the percentage of time spent 'close' to the food cue relative to the time spent in the entire field of view. A procedural control preceding each trial showed no effect of the climate treatments on the attraction to the provider in the absence of a food cue (see the Consumer behaviour section in the Supplementary Methods). 'Risk-taking' was determined by counting all clearly identifiable competitive interactions between individuals in the area close to the food cue (that is, attacks, fights and chases). This area faced the predator cage and provided no habitat structure. 'Hunting activity' was measured as bite rate at the benthic habitat by the carnivorous fish (that is, little weed whiting, blue weedy whiting and longfin goby). To represent the general effort invested into hunting in the mesocosm environment, only the area distant to the food cue and trials without predator were considered here and pooled to obtain one replicate per mesocosm.

**Consumer biomass, hunting success and diet.** Over the final month of the study, the actual foraging outcome was assessed through stomach content analysis. Consumers were captured, starved for 20 h (that is, gastric evacuation) and then released back into their mesocosm to forage freely for 4 h. Finally, the stomachs of fish were assessed under a stereo microscope to identify their principal resources using biovolume estimation and to determine 'hunting success' through the number of prey invertebrates captured (see the Resources section in the Supplementary Information). Due to the temperature sensitivity of digestion rates, hunting success under elevated temperature was probably underestimated and should thus be compared only between levels of CO<sub>2</sub>. As shrimps masticate larger prey, we derived their diet from the literature. For each mesocosm, consumer biomass and abundance was calculated as the sum over all individuals. Both of these responses showed no evidence for a species-specific climate treatment effect (Supplementary Table 4), which validates the use of responses across a species assemblage in this study.

**Resource availability.** A high diversity of resources was introduced with the habitats and unfiltered flow-through seawater. This increased the likelihood of species more tolerant to low pH or high temperature that are essential for community dynamics that buffer against the loss of sensitive taxa such as density compensation and functional redundancy. Moreover, the long-term exposure allowed for advanced acclimation in larger and multiple generations in smaller-bodied resource taxa (see the Resources section of the Supplementary Information). Over the final month of the study, the principal resources of the consumers were sampled thoroughly in all habitats: small molluscs, annelids, copepods, macrofaunal crustaceans, mat-forming algae and detritus. The measures for each resource were then standardized to the maximum value observed for the respective resource in any mesocosm. The average across the different standardized resources provided a relative measure of resource availability for each mesocosm.

**Data analysis.** Two-way ANOVAs were conducted with CO<sub>2</sub> and temperature as fixed factors for response variables with mesocosm as the lowest level of replication. For 'hunting success', which was instead based on individuals as replicates, linear mixed models were fitted incorporating CO<sub>2</sub> and temperature as fixed factors and mesocosm as a random factor. The behavioural responses 'cue attraction' and 'risk-taking' were tested within each mesocosm under all six possible combinations of food cue and predator. Thus, linear mixed models were fitted on the basis of a conventional split-block design employing mesocosm as random blocking factor<sup>40</sup>. The fixed effects included CO<sub>2</sub> and temperature as between-block factors, food cue and predator as within-block factors and all of their interactions. Competition was expected to be influenced by the density of individuals in each behavioural trial. Thus, for the response 'risk-taking', the time individuals were present close to the food cue (that is, density) was added as covariate. To identify the key drivers of behaviour, sub-models with all possible combinations of the fixed effects were compared using the Akaike information criterion corrected for small sampling sizes<sup>41</sup>, while retaining the random model structure. The fixed effects of the most parsimonious sub-models were also tested using ANOVA.

In the case of a significant ( $\alpha = 0.05$ ) interaction, post hoc multiple comparisons adjusted by false discovery rate were conducted<sup>42</sup>. The testing of multiple responses in the same mesocosms probably did not alter our interpretation of the results through an inflation of Type I error (Supplementary Table 7). Deviations from normality of residuals and random effects were assessed with normal Q–Q plots and Shapiro–Wilk tests, homogeneity of variance with residual versus fitted plots and Levene's tests, and sphericity with Mauchly's tests. The heteroscedasticity and/or positive skewness in several response variables were corrected by transformation. More information on model diagnostics and transformations can be found in the corresponding statistic tables in the Supplementary Information. All data analyses were performed with R version 3.4.1<sup>43</sup>.

**Ethics.** Research was conducted under approval of the University of Adelaide animal ethics committee (projects: S-2012-193A). The collection of organisms and habitat was permitted by the Minister for Transport and Infrastructure and the Government Department of Primary Industry and Regions SA (exemptions: 9902676 and 9902752).

**Meta-analysis. Literature search.** We searched for studies published between 2008 and 2017 in the field of ocean acidification that included experiments or observations on fish or decapod crustaceans in the laboratory or at CO<sub>2</sub> vents in the field (see the Search protocol section in the Supplementary Information). The primary search with Web of Science was complemented by scanning recent reviews/meta-analyses and unpublished data. Only experiments simulating realistic future scenarios were considered with a  $p_{\text{CO}_2}$  of on average ~1,000  $\mu\text{atm}$  (range 600–2,100  $\mu\text{atm}$ ), but extreme values were accepted for environments with naturally high  $p_{\text{CO}_2}$ . Finally, we identified 102 experiments from 57 studies (Supplementary Fig. 6) that matched 1 of 7 categories following the general framework of the mesocosm study. A detailed list of all experiments is provided in Supplementary Table 19.

Experiments at CO<sub>2</sub> vents that measured population sizes were classified as being ecologically ‘complex’ as they integrate over various ecological traits and include biotic interactions over long terms allowing for potential indirect effects. Experiments at ‘simple’ or ‘medium’ complexity could instead be assigned to one of the ecological traits ‘predator avoidance’, ‘habitat selection’ or ‘foraging’. ‘Simple’ was used for experiments on isolated sensory modalities typically tested with short-term behaviours and ‘medium’ was used for experiments in which individuals could use two or more sensory modalities in short-term behavioural tests or during longer-term growth or survival. More details on the types of experiment that were considered in the meta-analysis are given in Supplementary Table 14. Although increasing complexity was categorized on the basis of sensory modalities and the presence/absence of long-term biotic interactions, it represented also an increase in other potential measures of complexity (Supplementary Table 16).

**Effect sizes and analysis.** Information was extracted for each experiment from supplementary data or from figures through data-mining (web plot digitizer 3.12). We calculated the standardized mean difference as effect size for each experiment, which represented the mean difference in performance of consumers in control and elevated CO<sub>2</sub> conditions standardized by standard deviations (Hedges’s  $g$ )<sup>44</sup>. Standardized mean difference is popular in modern meta-analysis<sup>45</sup>, and better suited for our study than the log-transformed response ratio, as it can be applied to a wider range of data (but see Supplementary Tables 8b and 9b).

For each of the seven categories defined by trait and complexity, we conducted a random-effects meta-analysis<sup>45,46</sup> to estimate an overall mean effect size and to test its significance. These models were fitted with restricted maximum likelihood and weighted the effect sizes of individual experiments according to their uncertainty. The conservative Knapp–Hartung approach was employed for hypothesis tests and to construct confidence limits<sup>47</sup>. The heterogeneity statistics  $I^2$  and Cochran’s  $Q$ -test<sup>48</sup> were calculated to quantify and test for the variability in the data that is due to differences between individual effect sizes (that is, experiments) beyond what could be expected by chance alone. A substantial amount of unexplained heterogeneity was found for all mean effect sizes (Supplementary Table 9a), which was however not related to the specific degree of acclimation or  $p_{\text{CO}_2}$  increase that characterized individual experiments (Supplementary Table 17). A discussion on other factors that may have influenced the effect of elevated CO<sub>2</sub> can be found in the Potential moderators section of the Supplementary Information.

In addition, for each of the three ecological traits, we conducted a mixed-effects meta-analysis<sup>45,46</sup> that employed ecological complexity as a moderator

with its levels ‘simple’, ‘medium’ and ‘complex’. Although the ‘complex’ level did not distinguish between ecological traits, it was included in all three analyses as the comparison of population responses at CO<sub>2</sub> vents with the performance in specific traits at ‘simple’ and ‘medium’ complexity is meaningful. A significant moderator test was followed by post hoc multiple comparisons adjusted by false discovery rate<sup>42</sup>. The meta-analysis was conducted with the R package metafor (version 2.0-0)<sup>46</sup>.

**Data diagnostics.** Forest plots, normal Q–Q plots, residual versus fitted plots, and Cook’s distance were used to assess data properties and extreme outliers were subsequently winsorized (see the Data analysis section in the Supplementary Information and Supplementary Table 15). A ‘leave-one out’ analysis was conducted in which one individual effect size at a time was removed before retesting the significance of the model. This sensitivity analysis confirmed that our interpretation of the results was not driven by the presence of single, particularly influential experiments (Supplementary Table 9). Publication bias was assessed with funnel plots and ‘trim and fill’ analysis to test for funnel plot asymmetry<sup>49</sup>. Although this analysis indicated publication bias for some of the mean effect sizes, augmenting the data with the hypothetically missing experiments did not alter the significances (Supplementary Table 9).

**Data availability.** The data that support the findings of this study are available from the corresponding author upon request.

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