

# Sensitivities of extant animal taxa to ocean acidification

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**Anthropogenic CO<sub>2</sub> emitted to the atmosphere is absorbed by the oceans, causing a progressive increase in ocean inorganic carbon concentrations and resulting in decreased water pH and calcium carbonate saturation. This phenomenon, called ocean acidification, is in addition to the warming effects of CO<sub>2</sub> emissions. Ocean acidification has been reported to affect ocean biota, but the severity of this threat to ocean ecosystems (and humans depending on these ecosystems) is poorly understood. Here we evaluate the scale of this threat in the context of widely used representative concentration pathways (RCPs) by analysing the sensitivities of five animal taxa (corals, echinoderms, molluscs, crustaceans and fishes) to a wide range of CO<sub>2</sub> concentrations. Corals, echinoderms and molluscs are more sensitive to RCP8.5 (936 ppm in 2100) than are crustaceans. Larval fishes may be even more sensitive than the lower invertebrates, but taxon sensitivity on evolutionary timescales remains obscure. The variety of responses within and between taxa, together with observations in mesocosms and palaeo-analogues, suggest that ocean acidification is a driver for substantial change in ocean ecosystems this century, potentially leading to long-term shifts in species composition.**

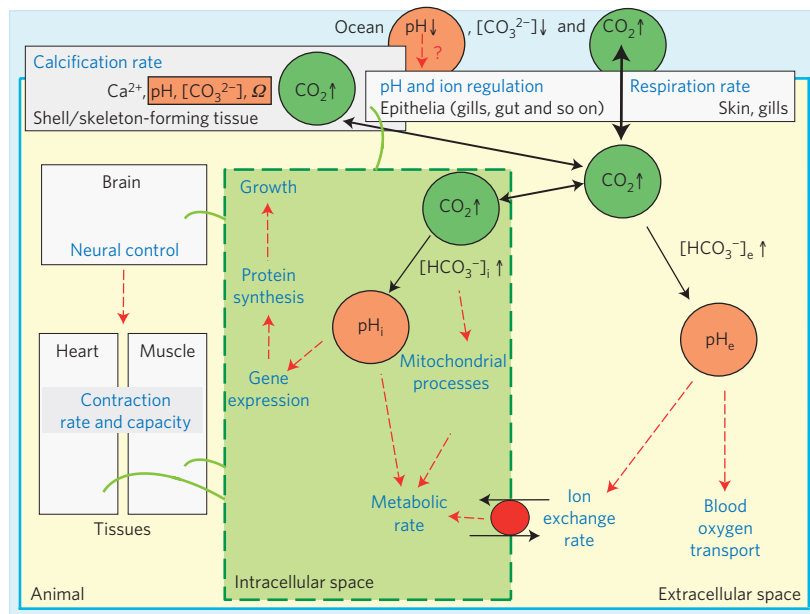
The extent of ocean acidification that occurs this century will largely follow changes in atmospheric CO<sub>2</sub> concentrations. These changes have been projected in a suite of scenarios (RCPs; refs 1,2). Until 2050 the resulting CO<sub>2</sub> concentrations are similar across RCPs (443–541 ppm), but range from 421 to 936 ppm in 2100 (RCP2.6: 421 ppm, RCP4.5: 538 ppm, RCP6: 670 ppm, RCP8.5: 936 ppm; ref. 2). This corresponds to a possible decrease in global average ocean pH by about 0.26 units below pre-industrial (0.14 below present) values by 2050 and by 0.4–0.5 (0.3–0.4 below present) units in 2100 in the SRES (Intergovernmental Panel on Climate Change Special Report on Emissions Scenarios) scenario A2, which resembles RCP8.5 (refs 3,4). Ocean acidification is projected to be accompanied by a rise in global mean sea surface temperature by 1.5 to 2.6 °C by 2100 relative to 1980–1990, depending on the scenario (SRES B1 to A2; ref. 5).

Marine ecosystems host a large diversity of species with distinct body plans and functional specializations. These relate to differential rates of energy turnover and capacities of physiological systems, which in turn may shape species sensitivities to ocean warming, hypoxia and acidification<sup>6,7</sup>. Multiple factors changing at the same time represent an additional challenge to qualify and quantify the sensitivity of species to climate change<sup>8</sup> and the resulting threat to marine ecosystems and their services for humankind.

Identifying the specific sensitivities to individual drivers may provide a basis for unravelling effects associated with the complete set of climate-associated factors. With respect to ocean acidification, physiological studies on extant species and palaeo-observations have developed convergent hypotheses: metazoans with higher metabolic rates or levels of activity, a higher capacity to adjust body fluid pH, and less expressed calcified structures (crustaceans and fishes) cope better than more inactive, sessile groups with heavier skeletons and a lower capacity to regulate pH (corals, echinoderms and molluscs<sup>9–11</sup>). This capacity also varies within taxa depending on mode of life (for example, between and within bivalves, gastropods and cephalopods among molluscs). The ability

to compensate for CO<sub>2</sub>-induced changes in extracellular pH may play a pivotal role in the tolerance of an organism during short- and long-term exposures to elevated  $p_{\text{CO}_2}$  (ref. 12; Fig. 1) and thus its persistence in CO<sub>2</sub>-exposed environments<sup>13</sup>. Shifts in acid–base chemistry of various body compartments are mediated by the weak acid distribution characteristics of CO<sub>2</sub>, such that these shifts develop in parallel to the changing chemistry of sea water, unless they are compensated for by acid–base regulation<sup>8</sup>. Uncompensated changes in extracellular pH ( $\text{pH}_e$ , for example in blood plasma) and intracellular pH ( $\text{pH}_i$ , for example in erythrocytes or tissues) may lead to metabolic depression (through decreasing  $\text{pH}_e$  and  $\text{pH}_i$ ) or hamper the function of blood oxygen transport (through falling  $\text{pH}_e$  or  $\text{pH}_i$  of erythrocytes). CO<sub>2</sub>-induced acidification of calcification fluids decreases the rate of precipitation of calcium carbonates (Fig. 1). Compensation for hypercapnic acidosis in body fluids and calcification compartments occurs by pH and ion regulation across the epithelia of gills, gut and kidney, driven by energy-consuming ion pumps. The resulting accumulation of  $\text{HCO}_3^-$  and equimolar decrease of  $\text{Cl}^-$  concentration support carbonate formation and calcification. Owing to the associated energetic costs, exposure to ocean acidification may cause shifts in the energy budget of cells, tissues or the whole organism<sup>7,10,12,14</sup>. The extent to which aerobic performance, growth and overall fitness are hampered by ocean acidification may depend on feedbacks on tissue energy consumers through shifted set points in acid–base regulation<sup>12</sup>. Changing acid–base parameters may also affect synaptic transmission<sup>15</sup>, the levels or function of neurotransmitters or their receptors, for example, adenosine<sup>16</sup> or GABA ( $\gamma$ -aminobutyric acid; ref. 17), and thereby elicit behavioural changes.

Quantitative reviews or meta-analyses of published findings have synthesized available information and identified small, but significantly negative, ocean acidification effects on survival, growth and calcification of marine animals<sup>18,19</sup>. However, meta-analyses may come with a set of drawbacks such as the constrained representation of comparative data<sup>20</sup>. Previous meta-analyses



**Figure 1 | Schematic summarizing effects of ocean acidification on animals.** The increase in atmospheric  $p_{\text{CO}_2}$  causes an increase of ocean  $p_{\text{CO}_2}$  (highlighted in dark green) and a decrease of water pH (highlighted in red).  $p_{\text{CO}_2}$  readily distributes by diffusion (black arrows) across an animal's body, in turn causing pH disturbances in extra- and intracellular compartments ( $\text{pH}_e$  and  $\text{pH}_i$ , respectively) and directly or indirectly influencing (red broken arrows) tissues, cells and their inherent processes and functions (in blue), as well as calcium carbonate saturation state ( $\Omega$ ) at calcification sites. The ability to compensate for these changes by acid-base and ion regulation may determine the sensitivity of an animal in response to ocean acidification. Note that the depiction of mechanisms is schematic and not comprehensive. Modified after refs 8,12,48.

calculated an effect size, which varied depending on taxon, process (for example, survival, growth, calcification) and life-history stage<sup>18–20</sup>. They have either focused on only one taxon<sup>21</sup>, or on processes such as calcification and metabolism, while pooling either taxa or  $p_{\text{CO}_2}$  values<sup>18</sup>, or have evaluated processes at only one pH value<sup>19</sup>. These analyses calculated a mean effect size, but did not support differentiated statements on the proportion of future winners and losers within taxa. In contrast, our analysis identifies the sensitivity of each species to a range of  $p_{\text{CO}_2}$  values.

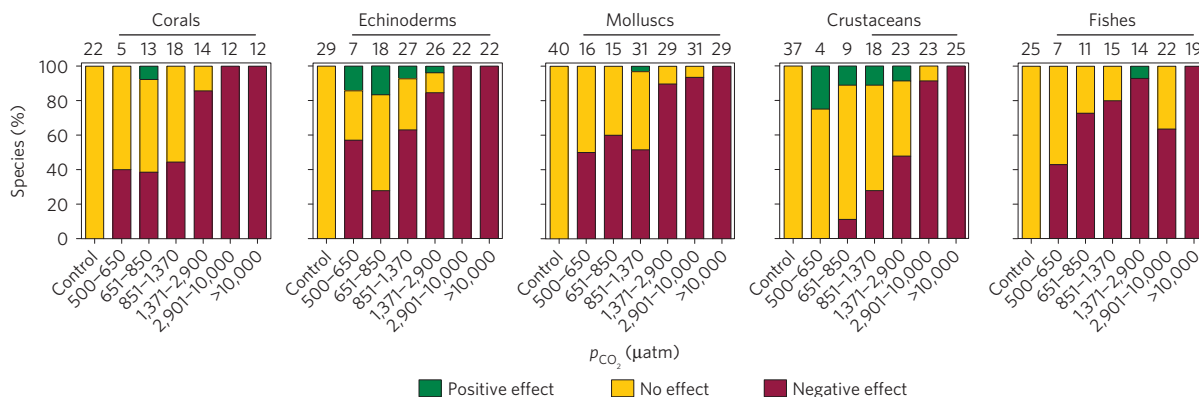
For a comprehensive look into the sensitivity distribution among species of a taxon, our meta-analysis uses indicators of physiological performance as criteria of sensitivity, such as standard metabolic rate, aerobic scope, growth, morphology, calcification, maintenance of acid–base balance, immune response, fertilization, sperm motility, developmental time, changes in gene expression patterns, behavioural changes and abundance in response to ocean acidification exposure. We included information on various life-history stages where possible. Our assessment does not quantify the effects observed and does not distinguish between developmental stages and processes. Our analysis rather assesses the sensitivity of individual taxa by accounting for responses of individual species to different levels of elevated  $p_{\text{CO}_2}$ . As a rationale, any relevant effect, be it small or large, will yield its ecological consequences; however, timescales may differ until the consequences become visible or severe. For each species, we noted significantly positive, negative or no effects across a wide range of seawater  $p_{\text{CO}_2}$  levels from present to projected future values and beyond. We interpreted increases in a parameter or process as positive if beneficial effects result for fitness, and the respective decreases as negative. If in doubt we assessed and adopted the respective interpretations by the authors.

In total, we found 167 studies (listed in the Supplementary Information) reporting effects on physiological performance parameters in 153 species (Supplementary Table S1). Most information was available for adult, juvenile and larval life stages, and information was relatively scarce for embryos and gametes. The distribution of species studied per life stage and  $p_{\text{CO}_2}$  category varied among taxa

(Supplementary Table S1 and Fig. S1). Many experiments targeted the RCP8.5 scenario for 2100; few species were studied at the lower  $p_{\text{CO}_2}$  values, which may characterize the near future (Supplementary Fig. S1). This lack of information is evident especially for larvae, embryos and gametes of corals, crustaceans and fishes (Supplementary Table S1 and Fig. S1). Most studied species were sampled from the benthos in tropical or temperate climate zones (Supplementary Table S1). Fifty-two species were investigated over short periods (<8 d), 31 species for 8–28 d, and 62 species for 29–180 d. Seven species were studied for longer than 180 d (1 species with unknown study duration, Supplementary Table S1). Most fishes studied were from tropical areas. In these studies experimental periods were short, in line with short life cycles at tropical temperatures.

Increased  $p_{\text{CO}_2}$  significantly affects the distribution of responses in all taxa (Fig. 2 and Supplementary Tables S2 and S3). The number of species negatively affected is significantly related to  $p_{\text{CO}_2}$  even in the lowest bin of 500–650  $\mu\text{atm}$  ( $p < 0.0001$  to  $p = 0.0285$ ) in all taxa except for crustaceans. Crustacean response distributions are significantly different from controls in the  $p_{\text{CO}_2}$  range 851–1,370  $\mu\text{atm}$  ( $p = 0.0025$ ) and beyond (Supplementary Table S3). The variability of responses is high in all taxa at low  $p_{\text{CO}_2}$ , but almost all species are negatively affected at  $p_{\text{CO}_2} > 2,900 \mu\text{atm}$  (Fig. 2). These values are far beyond what is projected for 2300 in RCP8.5 (1,962 ppm; ref. 2), but may be relevant for scenarios addressing  $\text{CO}_2$  injection into the deep sea<sup>14,22</sup>.

On a linear  $p_{\text{CO}_2}$  scale, the fractions of negatively affected species were fitted best by sigmoidal dose–response curves (Fig. 3a–d, Table 1). The  $p_{\text{CO}_2}$  at which 50% of the species are negatively affected ( $P_{50}$ ) ranges from 632 to 1,003  $\mu\text{atm}$  in corals, echinoderms molluscs and fishes and is substantially higher (2,086  $\mu\text{atm}$ ) in crustaceans (Fig. 3c,d). The curves do not differ significantly depending on whether only reported results are used in the models or whether the models include extrapolations following our assumptions described in the Methods and figure captions (Fig. 3a–d; for all taxa  $p > 0.05$ ). However, including such extrapolations improves the quality of the fits ( $R^2$ , Table 1). Overall,



**Figure 2 | Sensitivities of animal taxa to ocean acidification.** Fractions (%) of coral, echinoderm, mollusc, crustacean and fish species exhibiting negative, no or positive effects on performance indicators reflecting individual fitness (see text) in response to the respective  $p_{CO_2}$  ranges ( $\mu\text{atm}$ ). Note that it was not possible to determine the response of each species for each  $CO_2$  range, such that variable species numbers (on top of columns) result, even though the following assumptions were used to compensate at least for some of the missing information: species that exhibit negative effects at low  $p_{CO_2}$  will exhibit negative effects at the higher  $p_{CO_2}$  levels as well; if a species exhibits a positive/negative/no effect at both, a low and a high  $p_{CO_2}$ , it will exhibit the same effect at a medium  $p_{CO_2}$  (see also Supplementary Table S2). Bars above columns denote count ratios significantly associated with  $p_{CO_2}$  (according to Fisher’s exact test,  $p < 0.05$ , used to analyse species counts of pooled groups of negatively affected species versus not negatively affected species (sum of positively affected and unaffected species); see Supplementary Table S3 for exact  $p$  values).

**Table 1 | Parameters, goodness of fit and resulting  $P_{50}$  values of the taxon sensitivity curves in Fig. 3.**

Taxon	A	B	$R^2$	$P_{50}$ ( $\mu\text{atm}$ )
Fig. 3a,b reported				
Corals	3.058	1.597	0.9157	1,143
Echinoderms	3.021	1.627	0.7991	1,050
Molluscs	2.924	1.448	0.7152	840
Crustaceans	3.361	1.830	0.9731	2,298
Fig. 3c,d including estimates				
Corals	3.001	1.973	0.9378	1,003
Echinoderms	2.892	1.998	0.8582	870
Molluscs	2.892	1.953	0.8638	781
Crustaceans	3.319	2.097	0.9888	2,086
Fishes	2.801	4.391	0.7653	632

Curve equation  $Y = 100 / (1 + 10^{(A-X)^B})$ ,  $A = \log_{10} P_{50}$ .  $P_{50}$ :  $p_{CO_2}$  at which 50% of the species were negatively affected.

our extrapolations match the trends of reported results, except for in fishes. The reported data for fishes are strongly biased by the large number of behavioural studies in coral reef species, which indicate high sensitivities within  $p_{CO_2}$  ranges of 651–850 and 851–1,370  $\mu\text{atm}$ . Other studies have not reported such sensitivities, even at  $p_{CO_2}$  in the ranges 1,371–2,900 and 2,901–10,000  $\mu\text{atm}$ . This leads to a small number of affected species in the graph and failure to fit a model to these data (Fig. 3b).

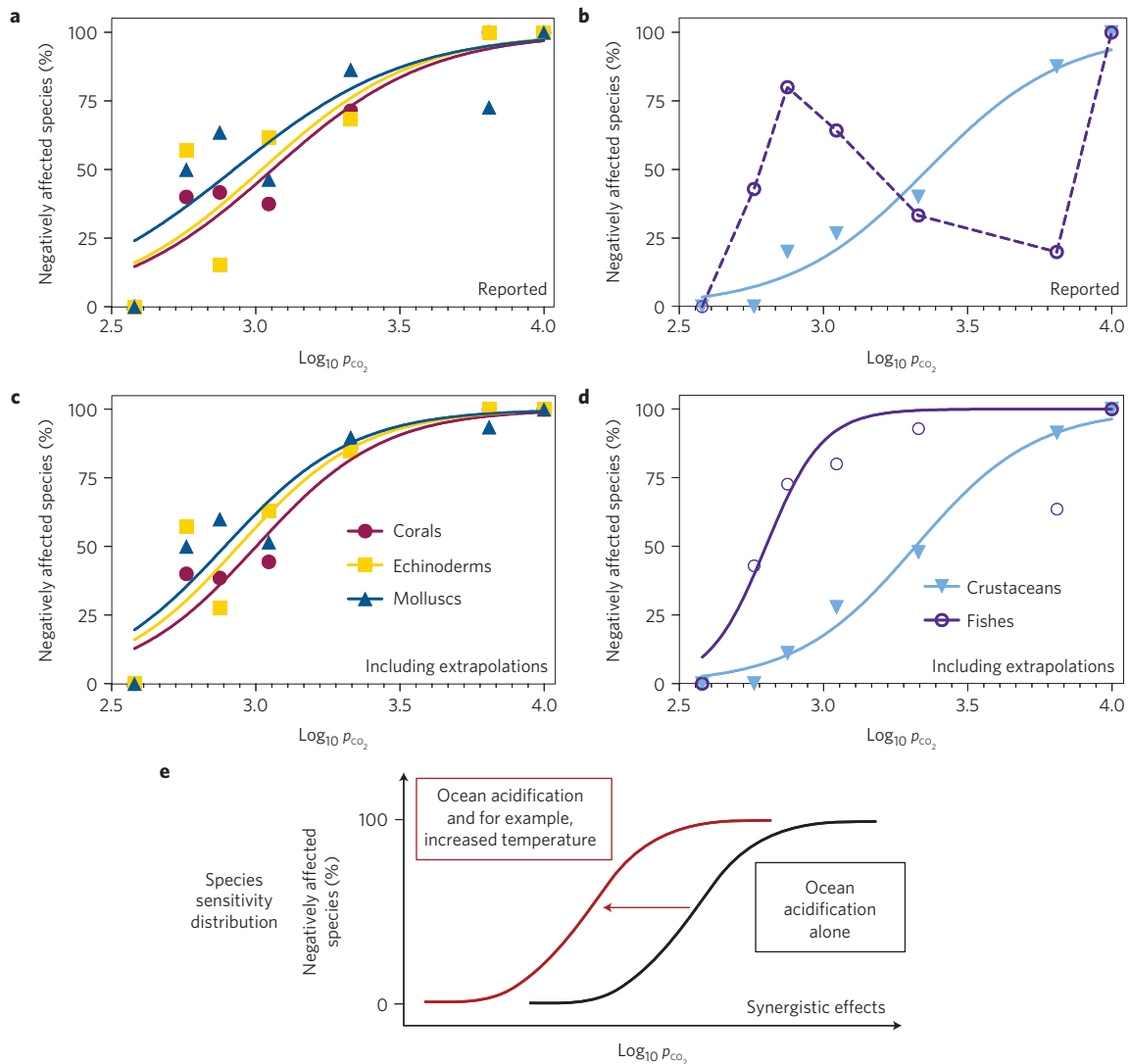
The meta-analysis shows taxon-specific vulnerabilities, resembling findings on evolutionary timescales during earth history, for example, during the mass extinctions of the Permian–Triassic transition or the Palaeocene–Eocene Thermal Maximum (PETM). Both periods were characterized by rates of  $CO_2$  accumulation one order of magnitude slower than present accumulation rates; therefore, resulting rates and amounts of acidification may have been moderate<sup>23,24</sup>. However, even in these cases,  $CO_2$  may have had profound consequences for marine biodiversity. The outcomes of such evolutionary crises were proposed to be the result of differential sensitivities of phyla that stem from their physiological characteristics (for example, refs 9,25,26). Our analysis confirms the patterns proposed for corals, echinoderms, molluscs and crustaceans, but identifies extant teleost fishes to be remarkably different and more sensitive than suggested by studies of the palaeo-record.

Consideration is thus required whether all or only some of the results collected in experimental studies of ocean acidification effects on timescales of weeks to months bear importance for the projection of long-term effects over decades and centuries.

The PETM may best illustrate ecological consequences of differential sensitivities of corals and planktonic marine calcifiers to climate change including ocean acidification<sup>24</sup>. During the PETM, atmospheric  $p_{CO_2}$  was approximately 3,000 ppm (ref. 27 and references therein), which implies that ocean chemistry was markedly different from today even if pH changes may have been compensated for to some extent by weathering<sup>24</sup>. Although evidence for the acidification of surface waters is still lacking (for example, ref. 28 and references therein), increases in temperature and nutrient input do not seem to explain entirely the changes in coral reef production<sup>27</sup>, which may rather relate to consequences of elevated  $CO_2$  partial pressures. Coral diversity changed only slightly, but latitudinal extension and the volume of reefs declined by a factor of about 100 (refs 26,27). Despite negative effects on reef-building capacity (that is, calcification), some PETM corals were able ‘to colonize the substrate, maintain biodiversity, and act as locally important carbonate-sediment producers, suggesting broad environmental tolerance limits’<sup>27</sup>. The diversity of responses and resilience observed in extant corals indicates potential for similar phenomena in the future.

Some extant coral species seem surprisingly resistant to  $p_{CO_2}$  levels projected by RCP scenarios 6 and 8.5, leading to an estimated  $P_{50}$  of 1,003  $\mu\text{atm}$  for the whole group (Figs 2 and 3). However, sensitivity is highly variable in these ranges of  $p_{CO_2}$  where 38.5 and 44.4% of the species were negatively affected (Fig. 2). Resilience may depend on a significant capacity for the upregulation of pH at calcification sites<sup>29</sup>, which increases internal aragonite and calcium carbonate saturation states ( $\Omega$ ), and facilitates carbonate precipitation (Fig. 1). Further study needs to compare species and demonstrate whether their capacity to compensate for pH disturbances and sustain calcification relates to coral fitness under ocean acidification<sup>30</sup>.

Most extant echinoderms and molluscs exhibit relatively low metabolic rates and do not compensate well for acid–base disturbances; furthermore, they build heavy skeletal structures and shells made of aragonite and calcite<sup>21,31,32</sup>. A large fraction of species is negatively affected even by the lowest levels of experimental  $p_{CO_2}$  (500–650  $\mu\text{atm}$ ). Our analysis suggests that most (63.0 and 51.6%, respectively) echinoderm and mollusc species



**Figure 3 | Sensitivities (fractions (%) of species) of corals, echinoderms, molluscs, crustaceans and fishes negatively affected within each p<sub>CO<sub>2</sub></sub> range (depicted as Log<sub>10</sub> of mean p<sub>CO<sub>2</sub></sub> in μatm). a–d.** Species sensitivities were derived from reported results (a,b) and complemented by extrapolated estimates using the following assumptions (c,d): species that exhibit negative effects at low p<sub>CO<sub>2</sub></sub> will exhibit negative effects at higher p<sub>CO<sub>2</sub></sub> levels as well; if a species exhibits a positive/negative/no effect at both a low and a high p<sub>CO<sub>2</sub></sub>, it will exhibit the same effect at a medium p<sub>CO<sub>2</sub></sub> (see also Supplementary Table S2). Data were fitted to the equation  $Y = 100 / (1 + 10^{(A-X)*B})$ ,  $A = \log_{10} P_{50}$ .  $P_{50}$ : p<sub>CO<sub>2</sub></sub> at which 50% of the species were negatively affected (Table 1). Key in c (d) also applies to a (b), respectively. e. Schematic of sensitivity distribution in response to ocean acidification combined with other adverse drivers. The sensitivity of species and taxa increases once factors such as thermal extremes, hypoxia, reduced food supply and/or pollution combine with ocean acidification. The fraction (%) of negatively affected species for a taxon is increased at lower p<sub>CO<sub>2</sub></sub> values, which results in a left-shift of the curve.

investigated so far are vulnerable to ocean p<sub>CO<sub>2</sub></sub> values projected for the year 2100 (851–1,370 μatm) in the RCP8.5 scenario, but will start to be affected even earlier (Fig. 2 and Table 2 and Supplementary Table S3).

Crustaceans build lighter skeletons than the aforementioned groups and seem less sensitive to ocean acidification than echinoderms and molluscs ( $P_{50} = 2,086$  μatm, compared with 870 and 781 μatm, respectively; Fig. 3 and Tables 1 and 2), possibly through more efficient pH regulation<sup>33</sup>. Nevertheless, almost a third of the studied species (27.8%) are negatively affected between 851 and 1,370 μatm (Fig. 2). Therefore, future changes of ocean chemistry are likely to impact many crustacean species.

Marine ray-finned fishes are excellent osmotic and acid–base regulators with lightweight vertebrae well isolated from the surrounding medium<sup>34</sup>. This would suggest low sensitivity; however, Fig. 2 suggests that a large fraction (72.7%) of investigated species will be negatively affected by 2100, indicating high

vulnerability even to RCP6 (Table 2). The data on fishes are not representative across climate zones and do not cover similarly long timescales as the studies on invertebrates (Supplementary Table S1). Bias results from the fact that mainly coral reef fishes were studied at relevant near future p<sub>CO<sub>2</sub></sub>s and that their behaviour was very sensitive to even small changes in p<sub>CO<sub>2</sub></sub> ( $\leq 850$  μatm). According to a recent hypothesis, brain function seems to be affected in fishes that tightly regulate their acid–base balance. Concomitant changes in Cl<sup>−</sup> and HCO<sub>3</sub><sup>−</sup> gradients over neuronal membranes would cause GABA-A receptors to be excitatory instead of being inhibitory<sup>17</sup>. In support of this hypothesis, it was found that the application of a GABA-A receptor antagonist reverses behavioural effects of elevated p<sub>CO<sub>2</sub></sub> in reef fishes<sup>17</sup>. The association of behaviour with changes in pH and ion gradients needs to be tested further and across animal phyla.

The long-term nature of these effects remains unexplored. The high vulnerability of coral reef fishes contrasts observations in the fossil record from mass extinction periods (for example, the



**Table 2 | Assessment of taxon sensitivity to future ocean acidification under RCPs 6 and 8.5 in 2100.**

Taxon	RCP6		RCP8.5	
	Evidence	Sensitivity	Evidence	Sensitivity
Corals	Limited	Medium	Medium	Medium
Echinoderms	Medium	Low	Robust	Medium
Molluscs	Limited	Medium	Robust	Medium
Crustaceans	Limited	Low	Medium	Low
Fishes	Limited	High	Limited	High

RCP6: projected atmospheric  $p_{\text{CO}_2}$  = 670 ppm; RCP8.5: projected atmospheric  $p_{\text{CO}_2}$  = 936 ppm; ref. 2. The amount of evidence was rated limited, medium or robust, if <16, 16–20 or >20 species were studied, respectively. The sensitivity of a taxon was low, medium or high, if  $\leq 30\%$ , 31–70% or 71–100% of the species were negatively affected, respectively.

Permian–Triassic boundary), where fishes and other predatory taxa (for example, malacostracans and ammonoids) showed a large potential to adapt and increased in dominance<sup>35,36</sup>. Looking at evolutionary history from a physiological point of view also indicates the potential to overcome these limitations. Animal evolution repeatedly involved the transition from breathing in water to breathing in air, in various animal phyla<sup>37</sup>. Such transition involves a marked reduction in ventilatory volumes associated with improved oxygen uptake and causes an internal accumulation of  $\text{CO}_2$  to levels far above those effective in coral reef fishes. Normal behaviour in air would require compensation for any physiological challenges caused by elevated  $p_{\text{CO}_2}$ , indicating a potential for adaptation. Regular transition from water to air is still on-going in various metazoan phyla, evidenced by the existence of amphibious species able to swap respiratory media and undergoing internal  $\text{CO}_2$  oscillations. The neurological challenges involved with the transition to air have not been studied and the timescale of such adjustments remains unclear. Any assessments of the role of behaviour in shaping vulnerability of teleost fishes must therefore remain preliminary.

Furthermore, the sensitivity patterns of fishes may be especially biased by lack of knowledge (that is, evidence is limited; Table 2) and a lack of publication of no-effect studies testing low  $p_{\text{CO}_2}$ s. The latter problem applies to all taxa (and even more so to all meta-analyses), but is a crucial drawback in vulnerability assessments. Publication of such results in peer-reviewed journals or databases (for example, PANGAEA, [www.pangaea.de](http://www.pangaea.de)) will ultimately improve future assessments.

The results on invertebrate sensitivities are consistent not only with the palaeo-record but also with benthic mesocosm studies, where abundances declined to a greater extent among echinoderms and molluscs than arthropods<sup>38</sup>. Such a differentiation between groups was observed with small changes in pH and was lost at strongly increased  $p_{\text{CO}_2}$  (>10,000  $\mu\text{atm}$ ) when all taxa showed negative effects (Fig. 2).  $\text{CO}_2$  levels as high as these are only conceivable in association with extreme hypoxia, leakage from seabed  $\text{CO}_2$  storage sites, or after purposeful injection of  $\text{CO}_2$  into the ocean. For comparison, natural  $\text{CO}_2$  vents in the Mediterranean Sea and the Indo-Pacific are virtually devoid of calcifying organisms at pH values of 7.7 and below<sup>39–41</sup>.

Acclimatization, epigenetic flexibility and evolutionary adaptation over generations may occur and mitigate or even compensate for effects of ocean acidification. Examples from the palaeo-record or natural analogues indicate some resilience and limited adaptation. Positive carry-over effects between life stages may be involved but here, again, our knowledge is very patchy<sup>42,43</sup> (Supplementary Table S1 and Fig. S1). Furthermore, a direct negative consequence for one species can also have consequences for dependent species or competing species, but little is known on

effects of elevated  $p_{\text{CO}_2}$  on species interactions, food web structure and other ecosystem changes.

$\text{CO}_2$  does usually not act in isolation but together with other environmental stressors such as temperature extremes, hypoxia and nutrient supply<sup>7,18,38,44</sup>. In several corals, fishes, crustaceans, echinoderms and molluscs, tolerance to warming was reduced under elevated  $\text{CO}_2$  levels, indicating a narrowing of species-specific thermal windows, which possibly is a unifying principle across animal taxa<sup>45</sup>. Conversely, sensitivity to ocean acidification will be higher during ocean warming (Fig. 3e) and probably greater than found in this study, which focused only on  $\text{CO}_2$ -induced changes. As a consequence, temperature-dependent biogeographical ranges of species will not only shift further with ongoing warming as observed at present in many ecosystems, but will also contract owing to ocean acidification, similar to observations on foraminifers and corals during the PETM (ref. 46). The combined effects of various drivers thus classify the present assessment of sensitivities to ocean acidification (Table 2) as conservative and applicable to within the thermal optimum of a species. Figure 3e and the palaeontological record suggest, however, that the interaction between climate drivers may shift the sensitivity threshold or critical  $p_{\text{CO}_2}$  to lower levels whereas the width of the sensitivity distribution within phyla remains unchanged. Sensitivity to ocean acidification and to thermal extremes may thus go hand in hand and may in fact involve the same mechanisms of effect<sup>6,8</sup>. Clearly, further studies are needed in all phyla from various climate zones to develop realistic scenarios of the ecological consequences.

Our analysis demonstrates that all considered groups are impacted negatively, albeit differentially, even by moderate ocean acidification. Among the invertebrates, corals, echinoderms and molluscs with heavily calcified structures and low capacities to defend the set points of acid–base regulation suffer the most, whereas crustaceans are relatively resistant to changes in ocean pH. With the exception of fishes, these observations in extant fauna are in line with conclusions drawn from palaeophysiological and palaeoecological studies<sup>9,25–27,35,36,47–49</sup>. Within phyla, species sensitivities are highly variable indicating that there will be winners and losers of climate change and associated shifts in community composition and species interactions. The diversity of responses at stable but elevated  $p_{\text{CO}_2}$  values projected under RCP6 and 8.5 scenarios may lead, on evolutionary timescales, to a quasi-stabilization of profoundly altered ecosystems.

## Methods

**Data selection.** We surveyed the literature for studies on effects of altered seawater carbonate chemistry on marine corals (Anthozoa), echinoderms (Echinoidea, Asteroidea, Ophiuroidea, Holothuroidea), molluscs (Gastropoda, Bivalvia, Cephalopoda), crustaceans (Malacostraca, Maxillopoda) and fishes (Actinopterygii). We used ISI Web of Science, Google Scholar and published reviews to identify primary literature, which was collected for analysis until 29 February 2012. We selected studies reporting investigations of physiological rates or integrity sustaining fitness and reflected as, for example, standard metabolic rate, aerobic scope, growth, morphology, calcification, maintenance of acid–base balance, immune response, fertilization, sperm motility, developmental time, gene expression, behavioural integrity and abundance. As differences in fitness relate to physiological traits and cause shifts in species interactions, we also included mesocosm studies on changes in community composition. We collected all available studies that provided information on effects of  $p_{\text{CO}_2}$  set by  $\text{CO}_2$ -bubbling and ranging between 500–650, 651–850, 851–1,370, 1,371–2,900, 2,901–10,000 and above 10,000  $\mu\text{atm}$ . These  $p_{\text{CO}_2}$  bins include values projected by scenarios of anthropogenic  $\text{CO}_2$  emissions according to RCPs in ref. 2. They also include possible increases in deep-sea  $p_{\text{CO}_2}$  resulting from direct injections of  $\text{CO}_2$  as a mitigation strategy<sup>22</sup>. Control treatments varied in  $p_{\text{CO}_2}$ , but in most instances were close to 380  $\mu\text{atm}$ . If  $p_{\text{CO}_2}$  was not reported in a study, we estimated it from water pH (considering possible errors if the carbonate chemistry of the sea water used was not known). Where available, information on several life-history stages of one species was included in the analysis. If a study provided information on more than one species, all data were used, even if multiple species were examined in the same experimental tank. If other factors (for example temperature, salinity) were tested simultaneously, the effect of altered  $p_{\text{CO}_2}$  was evaluated at control levels of these additional factors.

**Assessing species sensitivity.** For each life stage of a species it was noted whether the response in the experimental treatment differed significantly from the control treatment in a positive or negative way or did not differ significantly (no effect). In most cases a positive effect corresponded to an increase in a parameter or process. If in doubt whether significant differences should be rated positive or negative, the interpretation of the data by the authors was assessed and used. In those cases when multiple parameters were recorded in a life stage, the most relevant parameter(s) were used to assess sensitivity (see Supplementary Fig. S2). If several studies reported on the same species/life stage (see Supplementary Fig. S3), the available information was combined to determine the overall effect within the investigated  $p_{\text{CO}_2}$  range. If effects differed between life stages within one  $p_{\text{CO}_2}$  range, the stage affected negatively was given priority when deciding whether the species was affected. For example, if the adult remained unaffected, whereas the larval stage showed a negative effect, it was concluded that the species would be negatively affected. If several studies investigated the same life stage and reported differing effects, priority was given to the study with the longest duration. To compensate for missing data across  $p_{\text{CO}_2}$  ranges, the following assumptions were made: species that exhibit negative effects at low  $p_{\text{CO}_2}$  treatments, will exhibit negative effects at the higher  $p_{\text{CO}_2}$  treatment(s) as well; if a species exhibits a positive/negative/no effect at two  $p_{\text{CO}_2}$  treatments, one at low and one at high  $p_{\text{CO}_2}$ , it will exhibit the same effect at a medium  $p_{\text{CO}_2}$ . Note that responses different from these assumptions are possible for individual processes and thus also for the sensitivity of a species. However, a transiently positive change in any one response should not be mistaken as clear evidence for increased fitness, as a (transient) increase in, for example, calcification may come with trade-offs at other levels. Therefore, these assumptions include hypotheses to be tested in further studies.

**Statistical analyses.** The  $\chi^2$ -test was used for each taxon (phylum) to test the null hypothesis, whether the frequencies of the response patterns were independent of  $p_{\text{CO}_2}$  at  $p < 0.05$ . Subsequently, Fisher's exact test was employed to test this same hypothesis considering one  $p_{\text{CO}_2}$  bin at a time and the control bin (Fig. 2). To meet the requirements of Fisher's exact test it was necessary to set up two groups, one with the number of species negatively affected and one with the number of species exhibiting no negative effects (pooling the species affected positively and those unaffected). The control group comprised all species from each taxon as not affected. The tests were carried out on actual species numbers, not percentages. However, percentages are given in Figs 2 and 3 to facilitate comparisons. For each taxon an F-test was used to compare the models fitted to results reported in the literature with models complemented by estimates obtained by extrapolation (Fig. 3). For an assessment of taxon sensitivity to RCPs 6 and 8.5, the amount of evidence was rated limited, medium or robust, if <16, 16–20 or >20 species were studied, respectively (Table 2). The sensitivity of a taxon was low, medium or high, if  $\leq 30\%$ , 31–70%, or 71–100% of the species were negatively affected, respectively.

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## Author contributions

A.C.W. surveyed the literature and analysed the data accounting for ideas by H-O.P. A.C.W. wrote a first draft of the manuscript, which was subsequently revised by both authors.

## Additional information

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## Competing financial interests

The authors declare no competing financial interests.