

Ocean acidification can mediate biodiversity shifts by changing biogenic habitat

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The effects of ocean acidification (OA) on the structure and complexity of coastal marine biogenic habitat have been broadly overlooked. Here we explore how declining pH and carbonate saturation may affect the structural complexity of four major biogenic habitats. Our analyses predict that indirect effects driven by OA on habitat-forming organisms could lead to lower species diversity in coral reefs, mussel beds and some macroalgal habitats, but increases in seagrass and other macroalgal habitats. Available *in situ* data support the prediction of decreased biodiversity in coral reefs, but not the prediction of seagrass bed gains. Thus, OA-driven habitat loss may exacerbate the direct negative effects of OA on coastal biodiversity; however, we lack evidence of the predicted biodiversity increase in systems where habitat-forming species could benefit from acidification. Overall, a combination of direct effects and community-mediated indirect effects will drive changes in the extent and structural complexity of biogenic habitat, which will have important ecosystem effects.

Ocean acidification (OA) is projected to affect all areas of the ocean, with varying consequences for marine species, ecosystems and their function¹. Direct physiological effects of decreased pH or increased CO₂ are readily detectable and typically include changes in survival, calcification, growth, development, reproduction and abundance². More difficult to project are the indirect effects of OA, which are important for understanding and anticipating the scope of ecosystem responses³.

Changes to biogenic habitat structure associated with OA represent a key alteration to benthic systems, with potentially large indirect effects on biodiversity. Relationships between the structural complexity of habitats and the diversity of organisms that they support are well documented for many habitat types (Supplementary Fig. 1). Typically, species richness increases with the structural complexity, or often the local density, of the habitat (Supplementary Fig. 1). Direct effects of declining pH on habitat-forming organisms are expected to vary depending on organism physiology and life history, but generalities are emerging from both laboratory and *in situ* studies. For example, growth and calcification tend to decrease among habitat formers that rely on calcification for structure (for example, oysters, mussels and corals²), while the growth of non-calcifying autotrophs that rely on CO₂ as a resource often increases⁴. However, scaling direct effects on growth up to

ecosystem-level parameters such as habitat complexity or density is problematic⁵.

We use *in situ* observations of four habitat types across temporally or spatially varying pH gradients to indicate how complexity (when available) or local density of biogenic habitat is affected at the local ecosystem scale. We then use relationships between complexity and/or density of the habitat and local species richness, to project ecosystem-level changes in species richness, to illustrate possible impacts on biodiversity.

In a coral reef, habitat complexity declines along a naturally decreasing pH gradient maintained by a CO₂ seep in Papua New Guinea (Fig. 1a). This trend occurs as a result of transitions to coral species with lower intrinsic complexity⁶. Projecting this outcome through known positive relationships between habitat complexity and species richness in tropical coral reefs (Fig. 1b) leads to the prediction that species richness will decline with expected changes in carbonate chemistry associated with OA (Fig. 1c).

In mussel beds of the US Pacific Northwest, the percentage of cover of large *Mytilus* mussels is projected to decline with declining pH, to be replaced by species that lack the structural complexity of large *Mytilus* for supporting interstitial fauna (for example, encrusting sponge, ephemeral and filamentous algae, and barnacles; based on inter-annual transitions across a temporal gradient in pH;

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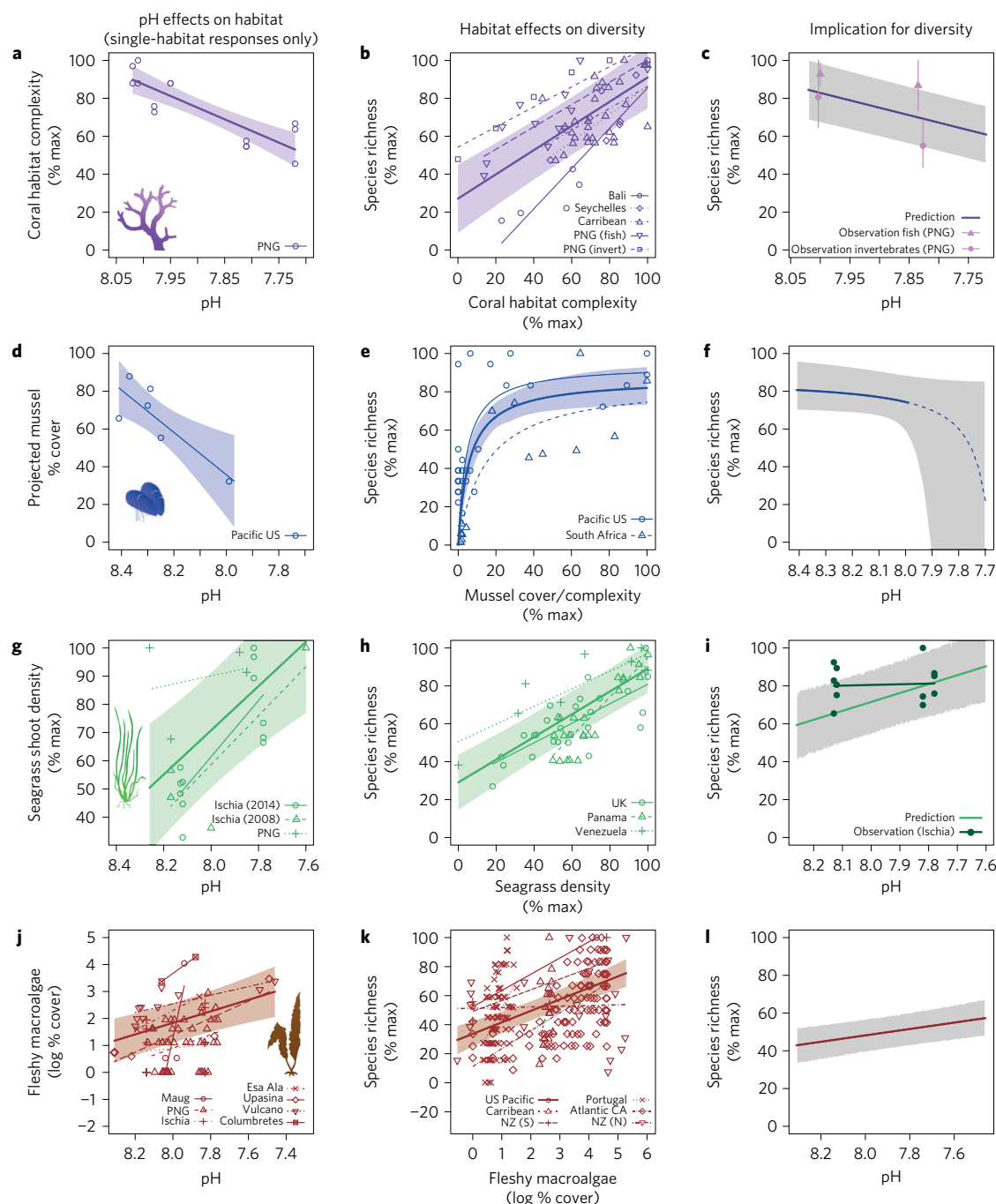


Figure 1 | Observed and predicted relationships between pH, habitat structure and community richness in four focal habitats, based on published data.

a–l. Relationships in coral reefs (**a–c**), mussel beds (**d–f**), seagrass meadows (**g–i**), and macroalgae (**j–l**). Changes in habitat complexity/density along spatial gradients from high to low pH regimes (**a,d,g,j**), and effects of habitat complexity/density on species richness of associated taxa (**b,e,h,k**) are shown in each row, with the fitted line from the linear models within studies (thin lines), and across studies (thick lines, with shaded regions showing the 95% confidence interval). **c,f,i,l**, Implied effects of pH on species richness projected from linear models (lines, with shaded regions showing 95% confidence interval, see Methods), and observed relationships between species richness and pH (points in **c** and **i**, with standard errors in **c**). Dashed line in **f** represents extrapolation of relationship beyond observed pH values within the time series of ref. 7. Data sources by panel: **a**, ref. 12; **b**, refs 12,21–24; **c**, refs 12,15; **d**, ref. 7; **e**, refs 14,25; **g**, refs 16,26,27; **h**, refs 28–30; **i**, ref. 16; **j**, refs 6,26,31–33; **k**, refs 23,34–38.

ref. 7, Fig. 1d). In the same region, species richness in mussel bed interstitial invertebrate communities has a positive but saturating relationship with percentage of cover of mussels (Fig. 1e), such that we predict no change in species richness over the range of habitat loss associated with the observed pH values (solid lines in Fig. 1d–f). However, future declines in mean annual pH due to OA may lead to habitat loss beyond this range. We cautiously extrapolate the

linear relationship between environmental pH and mussel cover to demonstrate possible nonlinear effects on mussel bed biodiversity in a future acidified ocean (dashed line, Fig. 1f). Thus, as mean pH declines beyond observed values, richness may decline linearly, or may switch to a precipitous decline. Emerging evidence suggests that the positive effect of food availability on mussel growth can overcome the negative effects of pH (refs 8,9); this may be important

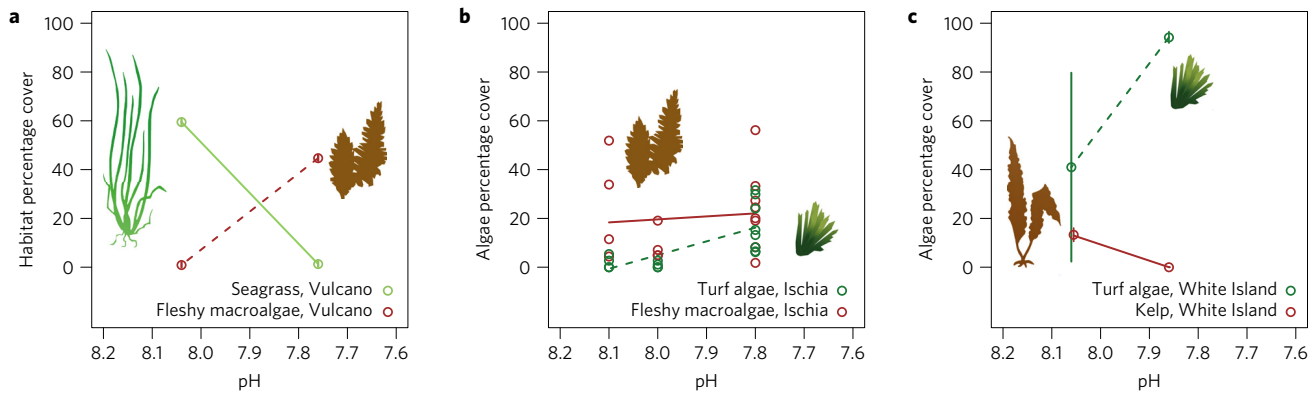


Figure 2 | Changes in habitat density along spatial gradients from high to low pH regimes, showing cases where alternative habitat types were reported. a–c, Solid lines show responses in dominant structure-forming species, dashed lines show responses in less-dominant or less-structural species. Data sources: a, ref. 11; b, ref. 39; c, ref. 11.

as coastal food supplies can co-vary with expected changes in carbonate chemistry. This highlights the potential for alternative responses to those predicted.

For seagrass and fleshy erect macroalgae, we observe two divergent scenarios. In most cases, we observe increasing biomass of dominant structural macroalgae and seagrass with decreasing pH (Fig. 1g,j). Positive relationships between density and species richness in both seagrass and macroalgae (Fig. 1h,k) lead to the prediction in these cases—all else being equal—of a potential local increase in species richness with decreasing pH (Fig. 1i,l). However, there are some cases where the dominant photosynthetic habitat type was not found to increase, but instead decreased or showed no change in local density, while potentially competing photosynthetic species increased (Fig. 2a–c). In these cases we expect a more complicated change in associated fauna and diversity, which we do not attempt to predict here.

The divergent responses observed in seagrass and fleshy macroalgae are consistent with a model of competitive replacement associated with enhanced CO_2 concentrations, where the unequal effects of OA on species competing for space drive shifts in dominance. Conceptually, such changes may have predictable effects on structural complexity (Fig. 3). For example, macroalgal species with simpler body forms, faster growth and/or generational times may benefit more from additional CO_2 compared with large canopy-forming kelps¹⁰, leading to an overall loss of structural complexity for associated biodiversity, despite increases in the performance of individual kelps¹¹ (Fig. 3c). Recognizing such community context dependency is critical for prediction of ecosystem-level responses, given its potential to accelerate¹², buffer¹³ or even reverse¹⁴ the effects of changing climate.

Data exist to test these projections in two of these habitat types. In a coral reef associated with the Papua New Guinea CO_2 seep system, invertebrate taxonomic richness declines, as predicted, with decreasing pH and accompanying decreasing structural complexity¹² (Fig. 1c). However, there was no change in fish species richness along the same gradient¹⁵ (Fig. 1c). The difference observed between invertebrates and fish in this system might be due to the small spatial scale of CO_2 seeps relative to greater mobility of adult fish, or to a slower rate of diversity decline in fish compared with invertebrates along the gradients of reef complexity, as suggested by Fig. 1b and ref. 15. Next, in seagrass beds in the temperate Mediterranean CO_2 seep system, no change in invertebrate species richness was observed in areas of reduced pH and increased seagrass shoot density¹⁶, contrary to the prediction of an increase in richness (Fig. 2c). Hence, either direct or indirect negative effects of OA on communities living in seagrass beds (for example, decreases of calcifying epibionts despite increases in seagrass shoot density¹⁷), or the small

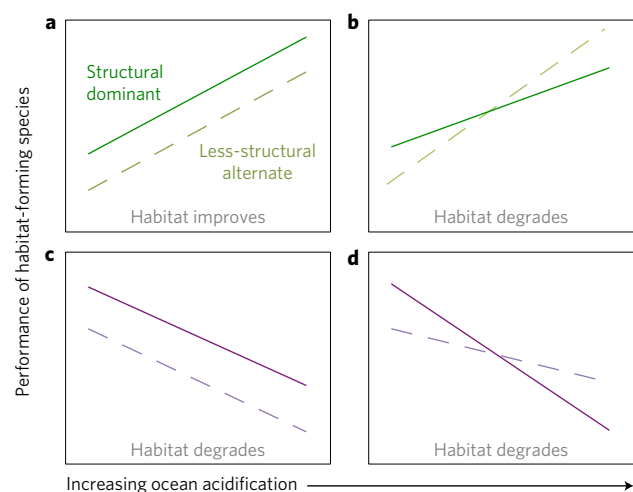


Figure 3 | Conceptual model showing potential effects of OA on relative performance on competing habitat-forming organisms. a, b, Effects of OA on non-calcifying photosynthesizers are expected to be generally positive but smaller and more ephemeral competitors (dashed line) may have faster rates of performance increases (solid line, b). At the local ecosystem level, the scenario in b may lead to a competitive shift in dominance towards species with lower intrinsic complexity, and thus a decline in habitat quality for associated taxa despite increasing performance in both groups of habitat-forming species. c, d, Effects on calcifying habitat formers are expected to be negative but less-structural forms (dashed lines) may be less negatively impacted compared with those forming greater structural complexity (solid lines). As a result, total habitat density may be less impaired than expected through species replacement, but there may be a decline in habitat quality for associated taxa due to replacement by species with lower structural complexity (scenario predicted from d).

spatial scale of the increased shoot density, override the expected positive effect of increased shoot density alone on species richness.

These test cases are few and early, and we caution that the space-for-time analogy required to interpret patterns around natural CO_2 seeps is limited; other features of the habitat may vary in CO_2 seeps such as seawater chemistry¹⁸ or substratum type, effects of ocean warming are not always included, and the small spatial scale and open nature of these habitats limits the potential for evolutionary responses¹⁹ and possibly of ecological responses of highly motile species. In addition, we have attempted to relate pH sensitivity observed in one location, with community diversity relationships at others, despite the expectation of context dependency and

interactions between multiple environmental drivers that influence ecological outcomes⁸. Furthermore, an additional imprint of OA on species diversity not explored here is its potential effect on habitat recovery after disturbance³. For example, because species diversity is theoretically unimodally related to the rate of recovery from disturbances, a delay in habitat recovery rates caused by OA may affect (increase or decrease) equilibrium diversity³. Nevertheless, these case studies, focused on complexity and density of biogenic habitats, demonstrate that the effects of OA on habitats may critically interact with direct effects on resident species, and alter our predictions of future ocean change.

In other biodiverse biogenic habitats, we expect OA to affect structural complexity and biodiversity in a similar way. Structural complexity is nearly ubiquitously associated with increases in species richness, as demonstrated in seagrasses, macroalgae, sponges, ascidians, mussels, oysters, vermetid reefs, serpulid reefs and coral reefs (Supplementary Fig. 1). Effects of CO₂ on structural complexity have been studied in only some of these habitats *in situ* (Supplementary Fig. 2); however, changes in performance of habitat-forming species in laboratory and mesocosm studies¹⁰ suggest that we may see changes at the population and community levels either through changes in dominant species or through changes in recovery rates after disturbances. Such changes stand to have far greater effects on marine biodiversity than individual-level responses of each community member. This feature could accelerate direct negative effects on diversity, when OA decreases habitat complexity, but could retard or even reverse direct negative effects, when OA increases habitat complexity. While the call to focus on species interactions is a critical advance for OA research, the best research value will be gained by focusing on those species with relatively strong ecological interactions within their communities^{3,20}, such as those that form the structural habitat supporting local diversity.

Methods

Methods and any associated references are available in the [online version of the paper](#).

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Author contributions

All authors conceptualized and designed the paper; J.M.S., K.E.F., K.J.K., K.M.A., N.E.B., J.M.H.-S., M.M. and C.D.G.H. assembled the data; J.M.S. analysed the data,

produced figures and drafted the paper; all authors contributed discussion, writing and interpretation.

Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to J.M.S.

Competing financial interests

The authors declare no competing financial interests.

Methods

Effects of ocean acidification on biogenic habitat. We collated studies of effects of CO₂ on complexity or density of habitat-forming species, focusing on *in situ* studies across spatially varying pH gradients around CO₂ seeps or temporally varying pH gradients in a region of changing CO₂. Studies were included if percentage of cover, biomass density, or structural complexity was assessed as a function of pCO₂, pH, or aragonite saturation state. We noted studies of percentage of cover where a transition from the dominant habitat type to another within the same category (that is, within calcifiers or non-calcifying autotrophs) was explicitly reported, for example, changes from large fleshy macroalgae to turf algae, as these changes may (more likely) occur as a result of competition or differential recruitment. We found three cases and report these separately from the other data (Fig. 2).

Biogenic habitat and associated community richness. We gathered studies on associations between percentage of cover, biomass density, or structural complexity of habitat-forming species with richness or diversity of associated fauna. We excluded studies if the scale of structural complexity was different than the scale expected to be important to the associated biota (for example, coralline frond density and meiofauna richness⁴⁰).

Case studies. We chose case studies based on maximum reporting of relationships between habitat structure with pH, and habitat structure with species richness metrics. We included only relationships where the metric of habitat structure (as percentage of cover or structural complexity) was directly comparable between measures of pH concentration and species richness. Because most studies reported relationships between habitat structure and pH (rather than CO₂ or saturation state), we used this metric for the case studies and excluded those where pH was not reported from the case studies (for example, ref. 41).

Test cases. We searched for empirical relationships between community richness and pH within these four habitat groups, and found examples from a natural CO₂ seep in a coral reef ecosystem (invertebrates¹²; fish¹⁵) and in a seagrass ecosystem¹⁶. We present these examples next to predictions for visual comparison.

Analysis. We fitted linear models to all relationships using maximum likelihood estimation, and included grouping variables from the original studies as random effects in these linear models. If a relationship visually appeared nonlinear, we tested whether a nonlinear model fitted better (based on a lower Akaike information criterion) and if so, we present this relationship.

For the case studies, we present individual linear model fits, but we also pooled studies for each relationship and habitat type, and fitted a linear mixed effects model to the full data, using location of study as a random effect on the intercept. For the effect of mussel habitats on community richness, we fitted a nonlinear saturating relationship to the individual and pooled studies. We used these general (pooled studies) relationships to derive general predictions of habitat-mediated effects of pH on community richness. We used the model-predicted effects of pH on habitat structure as input variables for the model-predicted effects of habitat structure on community richness. We projected estimates of uncertainty in mean richness by drawing, for each pH value and habitat, 1,000 random estimates of habitat complexity (or density) from a normal distribution with a mean and standard deviation equal to the mean and standard error from the complexity (or density) model output. We then used each of these complexity estimates to predict another 1,000 estimates of richness, drawing from a normal distribution with a mean and standard deviation equal to the mean and standard error of the richness model output. For each pH value, the 95% confidence interval for mean richness was calculated as the 0.025 and the 0.975 interquantile of these 1×10^6 richness estimates. For the mussel community richness (nonlinear) model (Fig. 1g), we estimated 95% confidence intervals of community richness as a function of mussel percentage of maximum cover/complexity by bootstrapping the pooled data for 1,000 model fits, and used these bootstrapped models to project uncertainty in community richness as a function of pH.

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