



The indirect effects of ocean acidification on corals and coral communities

Tessa S. Hill¹ · Mia O. Hoogenboom¹

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Abstract Ocean acidification (OA) is a major threat to marine calcifying organisms. This manuscript gives an overview of the physiological effects of acidification on reef-building corals from a cellular to population scale. In addition, we present the first review of the indirect effects resulting from altered species interactions. We find that the direct effects of acidification are more consistently negative at larger spatial scales, suggesting an accumulation of sub-lethal physiological effects can result in notable changes at a population and an ecosystem level. We identify that the indirect effects of acidification also have the potential to contribute to declines in coral cover under future acidified conditions. Of particular concern for reef persistence are declines in the abundance of crustose coralline algae which can result in loss of stable substrate and settlement cues for corals, potentially compounding the direct negative effects on coral recruitment rates. In addition, an increase in the abundance of bioeroders and bioerosive capacity may compound declines in calcification and result in a shift towards net dissolution. There are significant knowledge gaps around many indirect effects, including changes in herbivory and associated coral–macroalgal interactions, and changes in habitat provision of corals to fish, invertebrates and plankton, and the impact of changes to these interactions for both individual corals and reef biodiversity as structural complexity declines. This research highlights the potential of indirect effects to contribute to alterations in reef ecosystem

functions and processes. Such knowledge will be critical for scaling-up the impacts of OA from individual corals to reef ecosystems and for understanding the effects of OA on reef-dependent human societies.

Keywords Coral · CO₂ · Indirect effects · Ecological interactions · Ecosystem · Review

Introduction

Species interactions occur in every ecosystem and can be pivotal in ecosystem functioning and services (Jordano 2016). Nevertheless, much of the research that identifies how environmental change affects biological communities is based on the direct physiological and behavioural changes of individuals. While understanding the effects on individuals is important, biological communities can also be indirectly affected by environmental change. This occurs when direct effects on one or more species alter the extent or outcome of interactions between species. Such indirect effects, which affect both individuals and ecosystem functions and processes, can manifest over a far greater scale than that of direct effects (e.g. Connell et al. 2013; Alva-Basurto and Arias-González 2014) with small changes to an interaction resulting in substantial impacts (Mumby 2017). Furthermore, ecological interactions can be more vulnerable to environmental change than the biology of individuals (Jordano 2016). For instance, a recent review of extinctions as a result of climate change concluded that nearly 60% of both extinctions and declines in abundance were the result of a lost interaction rather than physiological tolerances of individuals being surpassed (Cahill et al. 2013). Consequently, understanding how ecosystems are likely to change under

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✉ Tessa S. Hill
tess.hill@my.jcu.edu.au

¹ College of Science and Engineering, and ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

future climate scenarios requires understanding alterations in the extent and outcome of ecological interactions.

Ocean acidification (OA) is one component of the ongoing global environmental change resulting from increases in atmospheric carbon dioxide concentrations (Gattuso et al. 2015). These increases are buffered by oceanic absorption of carbon dioxide which result in falling oceanic pH (Zeebe 2012; IPCC 2014). This uptake of atmospheric carbon dioxide has already caused a 0.1 unit decline in oceanic pH since the industrial revolution and is likely to cause up to an additional 0.3–0.32 unit decline by the end of the century (IPCC 2014; Gattuso et al. 2015). Changes in pH also result in a change in the concentrations of carbonate and bicarbonate ions in seawater which can affect fundamental organism physiology, such as calcification (Erez et al. 2011). As a result, OA is widely recognised to be a pervasive threat to marine biodiversity (Garrard et al. 2013; Harvey et al. 2013).

While the effects of OA are ubiquitous, they are of particular concern for calcifying organisms such as scleractinian corals, which use carbonate ions to build their skeleton (Hofmann et al. 2010). This potential for OA to reduce calcification in corals has identified coral reefs as one of the most vulnerable ecosystems to OA (National Research Council 2010). The change in calcification and a suite of other physiological effects on corals have the potential to result in indirect effects through altered interactions with other reef organisms. This paper provides a short overview of the direct physiological effects alongside a detailed review of the indirect effects of OA on shallow water tropical and temperate corals, to gain new insights about how corals and coral communities may be affected under future acidified conditions. Specifically we aim to: (1) review the direct, physiological effects of OA on reef building corals across different levels of biological organisation; (2) identify the indirect effects of OA through changes to ecological interactions and provide evidence of how these manifest at an ecosystem level; (3) identify priority areas for future research on indirect effects. While we acknowledge the importance of symbionts and microbial communities in influencing coral responses to environmental change, this review focuses on the responses of, and impacts on, the coral host.

Methods

We completed a literature search on ISI Web of Science for studies that identified the direct and indirect effects of ocean acidification on corals (completed October 2021). We focused primarily on tropical shallow water corals with some temperate corals included to capture research from naturally acidified field sites in temperate regions. Deep water corals were excluded from this review on the basis that other

variables such as temperature and light that also change with depth would confound comparisons of OA effects.

To review the literature on the physiological effects of acidification on corals, papers were selected using search terms for ocean acidification ('ocean acidification', ' $p\text{CO}_2$ ', 'pH', 'carbon dioxide'), 'coral' and a direct, physiological metric. These metrics were the eight broad headings presented here (Fig. 1): 'tissue biomass' OR 'lipid' OR 'protein'; 'calcification'; 'photosynthesis'; 'survival' OR 'mortality'; 'growth' OR 'skeletal density' OR 'porosity'; 'reproduction'; 'abundance'; and 'species richness' OR 'species diversity' OR 'community composition'. Where possible, all relevant studies found in the search were included with the exception of calcification and photosynthesis due to the vast body of literature on these metrics which have already been the subject of several reviews and meta-analyses (e.g. Erez et al. 2011; Kornder et al. 2018). Therefore, for these metrics, we focused on papers published in the last 10 years. To ensure there was no bias in the data from this particular selection of publications, additional observations of calcification under OA were recorded from studies focusing on another metric where calcification was also measured. Observations were excluded if they considered variations in other environmental variables (e.g. temperature, nutrients, light), although if possible, we included comparisons between 'ambient'/'control' conditions with the acidified treatment/s.

For every study selected, the statistical outcomes of comparisons between acidification treatments for each metric were recorded as 'significant increase', 'significant decrease', or 'no significant change'. Effects which were not statistically analysed were excluded. Many studies used $p\text{CO}_2$ treatments or field sites with acidification levels well beyond that expected in the near future (i.e., up to 5000 μatm). To ensure the trends in significance were not driven by these extreme conditions we compared the full dataset to two subsets of the data where we excluded observations involving $p\text{CO}_2$ 1) $> 1000 \mu\text{atm}$; and 2) $> 2000 \mu\text{atm}$. As there were no consistent differences in the proportions of observations reporting positive, neutral or negative effects of OA among these different datasets, the results presented here include the full range of $p\text{CO}_2$ treatments ($N = 902$ observations from 93 studies) (Fig. 1). To account for the often non-linear physiological responses of coral to acidification (e.g. Bove et al. 2019), we included only sequential, non-overlapping comparisons between $p\text{CO}_2$ treatments (e.g. low $p\text{CO}_2$ to mid, mid to high).

Studies on indirect effects were similarly identified using search terms for ocean acidification ('ocean acidification', ' $p\text{CO}_2$ ', 'pH', 'carbon dioxide'), 'coral' and an indirect effect. The effects considered here were selected using the terms: 'compet*'; 'predat*' OR 'coralliv*'; 'crustose coralline algae' OR 'CCA', 'bioero*'; 'habitat provision' then

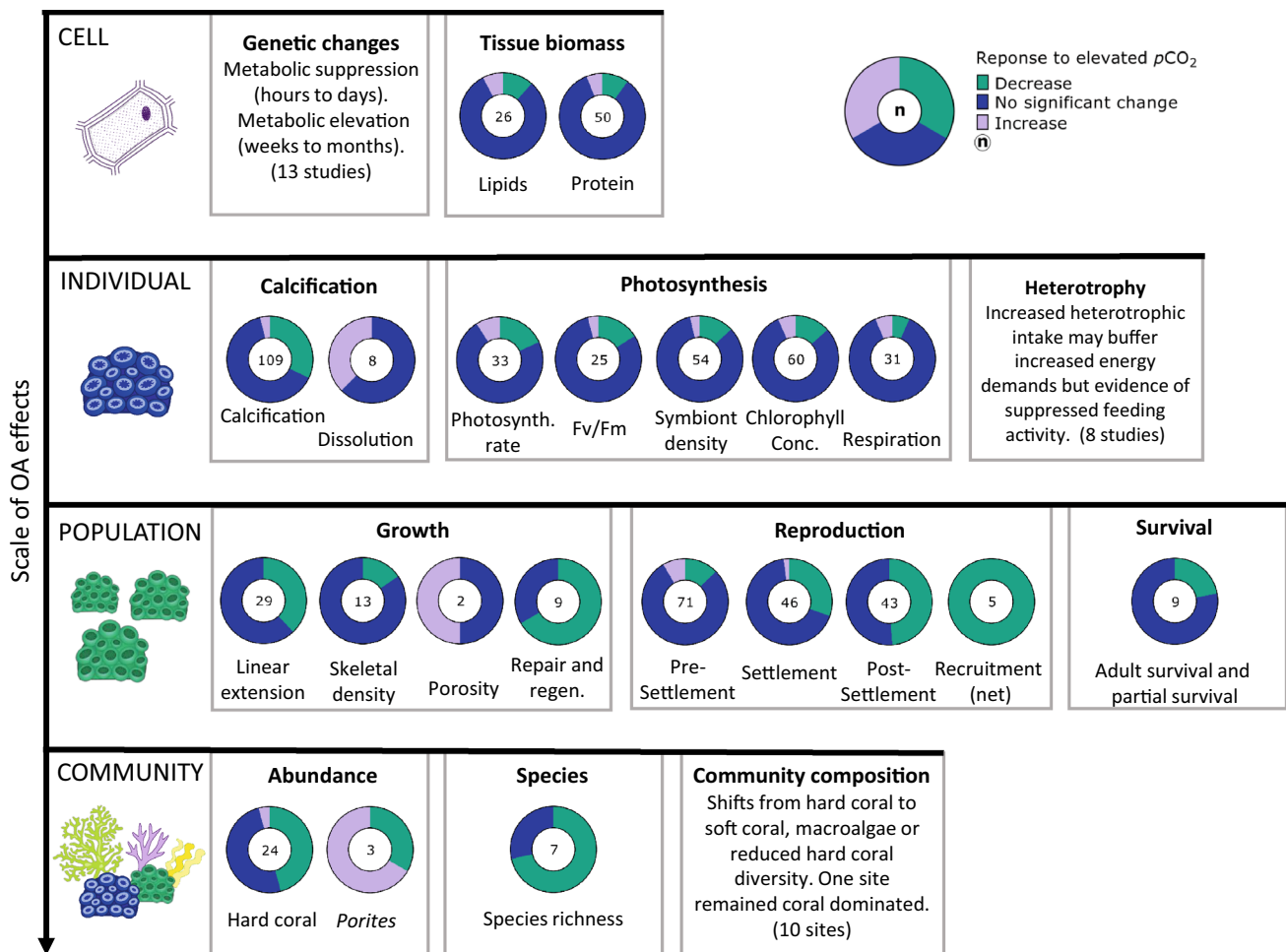


Fig. 1 A summary of the physiological effects of ocean acidification from a cell to community scale. Pie charts summarise the proportion of observations taken from the literature showing a significant decrease (green), no significant change (blue) or a significant increase

(purple) in response to elevated $p\text{CO}_2$. From within any study, only sequential, non-overlapping $p\text{CO}_2$ step comparisons are presented. Number within each pie chart denotes the number of observations for that metric. $N=902$ observations from 93 studies

‘habitat’ AND ‘structural complexity’ and; ‘disease’). An overarching search also included the term ‘indirect’ with the acidification and coral terms. However, as indirect effects are rarely labelled as such, it was necessary to include other broader search methods. Additional searches were therefore conducted around these topics for studies on other marine taxa (e.g. macroalgae and bioeroders) to gain broader understanding of potential non-specified indirect effects of OA. Lastly, the reference section of papers which included relevant information were reviewed for additional studies. All relevant studies found in the search are included; however, due to the limited recognition of indirect effects, we acknowledge that some relevant studies that did not explicitly refer to indirect effects would not have been captured in our search.

Finally, we review the effects of acidification on the abundance and diversity of corals at naturally acidified reef sites (Table 2), as well as evidence of any indirect effects at

such sites (Table 3). Observations of coral abundance and diversity were only taken from one study per site to avoid over-representation of a limited set of intensively studied locations within the data set. We focus on the effect of $p\text{CO}_2$ as a ‘catch-all’ measure of OA effects. However, we note that other measures of water chemistry, such as aragonite saturation (Ω) and the relative abundance of carbonate (CO_3^{2-}) and bicarbonate (HCO_3^-) ions, are correlated with $p\text{CO}_2$ and that OA effects encompass changes in all of these variables.

Direct effects of OA on coral

Corals employ a range of biological responses to counteract the adverse effects of acidification. These stress responses can manifest at multiple levels of biological organisation ranging from molecular or cellular processes to whole organism responses (Edmunds et al. 2016). The cumulative effect

of these physiological responses can translate into effects on populations by altering key demographic rates. This includes population growth through reproduction, recruitment, and colony growth, and population shrinkage through mortality. Ultimately, these demographic parameters then affect coral communities through changes in coral cover, and altered community composition and species diversity.

At the molecular and cellular level, corals have a variety of processes that allow them to survive and grow under acidified conditions. While mechanisms such as the ability to internally regulate pH (McCulloch et al. 2012, 2017) allow corals to adjust to acidic conditions, they are thought to be energetically costly (Allison et al. 2018). However, increased $p\text{CO}_2$ does not always result in depletion of energy reserves (measured via tissue biomass; e.g. Strahl et al. 2016) (Fig. 1). This suggests that at least some coral species can maintain growth under OA via regulating pH at the site of calcification (see: Comeau et al. 2022).

At the ‘whole colony’ level, both calcification and photosynthesis can be affected by ocean acidification. For photosynthesis, effects of OA are highly variable among studies (Fig. 1). The majority of observations considered here showed no significant changes in the rates or efficiency of photosynthesis under OA (e.g. Bedwell-Ivers et al. 2017; Bahr et al. 2018), nor in the density of symbionts or the chlorophyll within each symbiont (e.g. Bedwell-Ivers et al. 2017; Rivest et al. 2017). Changes in photosynthetic acquisition of energy under OA are therefore unlikely to be the limiting factor for coral persistence in the future.

The effect of acidification on calcification is the most widely recognised threat to corals and there is a substantial body of research showing declines in calcification (Erez et al. 2011; Chan and Connolly 2013; Kornder et al. 2018), as well as some evidence of increased dissolution (e.g. Fine and Tchernov 2007; Kline et al. 2019). However, calcification responses are highly variable, and both species and colony specific (e.g. Sekizawa et al. 2017; Bahr et al. 2018), with the overall majority of observations showing no significant effect of acidification (e.g. Carbonne et al. 2021) (Fig. 1). Furthermore, corals continue to calcify and grow in naturally acidified reefs (e.g. Inoue et al. 2013; Camp et al. 2017) (Fig. 1) under conditions far more acidic than the theoretical limits for calcification and net carbonate accretion (560 ppm atmospheric CO_2 , Silverman et al. 2009; 2.3 to 3.5 Ω aragonite, Kline et al. 2019) (Table 2).

At the population level, negative effects of OA are more apparent (Fig. 1) suggesting that small changes in multiple aspects of physiology might accumulate to comprise a significant impact when summed across all individuals in the population. There is some evidence of a shift in growth strategies under acidification, with some corals maintaining linear extension by building less dense, more porous, skeletons (Mollica et al. 2018; Teixidó et al. 2020). This strategy is

unlikely to drive changes in coral cover under acidification; however, there may be significant indirect effects through increased vulnerability to breakages in weaker skeletons (Hennige et al. 2015). In contrast, other colonies maintain skeletal density/porosity at the expense of linear extension (Enochs et al. 2015a), which can reduce lifetime reproductive because slower growth means corals are more likely to die before reaching the largest, most fecund, colony sizes.

For reproduction metrics, the effect of acidification is again variable among studies. Overall, the early stages of reproduction (production of gametes, fertilisation, and larval development, growth and survival) appear to largely be unaffected by acidification (e.g. Rivest et al. 2018; Pitts et al. 2020). Conversely, the later stages of reproduction (settlement, metamorphosis, recruit growth and survival) show more consistent negative effects (e.g. Jiang et al. 2018; Yuan et al. 2018), suggesting that recruits are more vulnerable to acidification than gametes or larvae. This is of concern because even a moderate (20%) decline in recruitment was estimated to reduce coral cover by 15% over 7 year period (Evensen et al. 2021). However, declines in recruitment are estimated to potentially rise as high as 52% by mid-century conditions ($\sim 560 \mu\text{atm}$), and 73–91% by end of century conditions ($\sim 800 \mu\text{atm}$) (Albright et al. 2010; Fabricius et al. 2017). Such reductions are therefore likely to present a significant threat to the persistence of corals and coral communities under acidified conditions. Finally, despite the described physiological effects, increased $p\text{CO}_2$ does not consistently reduce adult colony survival, under acute experimental or naturally acidified conditions. Rather, OA appears to result in sub-lethal effects, defined here as “physiological effects that reduce coral fitness (e.g., cause slower growth or lower reproductive output) but do not result in mortality”. The accumulation of such sub-lethal effects on growth and reproduction may suppress population growth rates in the future, contributing to changes in abundance, species richness and/or diversity, and community composition at an ecosystem level.

Overall, we find the direct effects of acidification on corals are highly variable. This variation may result from differences in experimental methodology or $p\text{CO}_2$ levels; however, it is also likely to represent the significant variation both between individuals, species and sites. In total across all scales 52% of observations included here found no significant difference with acidification (Fig. 1). Interestingly however, it appears that consistently negative effects are more often seen at a population level (26% of 274 observations), rather than cell (10% of 80 observations) or colony level (16% of 388 observations). This suggests that while the acidification has largely sub-lethal physiological effects on individuals, coral populations and communities may still be altered. We therefore stress the importance of researching the effects of acidification on coral populations

and communities in addition to effects on individual coral colonies.

Indirect effects of OA on corals

Indirect effects are defined here to be a change in an ecological interaction between species. This may occur when a physiological or behavioural change affects either the extent or outcome of an interaction with another species or taxon. Indirect effects can occur as a result of physiological changes to one or both of the interacting taxa, changes to the interaction itself or changes in environment in which the interaction occurs and, consequently predicting indirect effects is challenging, and requires knowledge of both the stressor and all individuals involved (Connell et al. 2011; Sunday et al. 2016). In the following section we review the indirect effects of OA for reef-building corals, including interactions between corals, and between corals and other taxa (see Table 1).

Competition

For sessile benthic organisms, competition is primarily for resources such as space and light (Lang and Chornesky 1990) and helps to structure communities and determine species distributions (e.g. Connell et al. 2004). OA may affect competition dynamics through; (1) a change in the frequency of competition as coral cover changes, resulting in either intensification or competitive release (Hofmann et al. 2010); (2) a change in the identity of competitors as species composition changes; (3) an altered outcome of an existing competitive interaction, resulting from differences in the magnitude to which different species are affected by OA; (4) an altered outcome of an existing competitive interaction due to changes in availability of resources, or; (5) novel competitive interactions as a result of shifting distributions (e.g. Alexander et al. 2016).

Competition between hard corals

To date, there has been limited investigation of the impact of ocean acidification on competition between hard corals (Table 1). However, given the physiological and population-level effects outlined above, we may expect a number of possible changes. Firstly, competitive interactions only occur when colonies are in close proximity (Edmunds et al. 2016) therefore, the occurrence of coral–coral interactions is likely to be lower under acidified conditions if coral cover is reduced. However, lower coral cover does not necessarily correspond to fewer competitive interactions if the remaining colonies are spatially aggregated due to microhabitat requirements, or if only a small proportion of

free space is actually colonisable. There are currently no studies that demonstrate how the prevalence of competition changes as a result of OA.

Secondly, if there are changes in species richness under OA, different intensity of intra- compared with inter-specific competition may occur in the future (Table 1). To date, three studies have examined changes to inter- and intra-specific coral competition under high $p\text{CO}_2$, all of which report that while interspecific competition significantly suppressed growth, the addition of high $p\text{CO}_2$ conditions caused no additional suppression under that kind of competition (Evensen et al. 2015; Evensen and Edmunds 2016; Horwitz et al. 2017; Table 1). However, these studies show different trends for intraspecific competition. One study found no additional suppressive effect of OA above that of intraspecific competition on growth (Evensen et al. 2015), another reported significant declines in growth in five out of the six species (Horwitz et al. 2017). One potential explanation for this difference is the experimental duration, with additional suppressive effects only seen in the longest duration study (1 year; Horwitz et al. 2017). Nevertheless, the scarcity of research on this topic means that it remains unclear whether and how release from interspecific competition will affect coral communities on reefs in the future.

Finally, the physiological cost of competition under OA could be higher in acidified conditions (Table 1) if costs of maintaining growth reduce the ability of corals to invest energy in winning competitive interactions. The single study that has investigated this to date found that corals (*Galaxea fascicularis*) responded more rapidly to competition under acidified conditions but that net tissue necrosis was the same between treatments (Evensen and Edmunds 2018). While the effect of competition on growth suggests there is a greater physiological cost of competition under OA, the lack of impact on competitive ability potentially indicates a change in allocation of resources to maintain competitive ability. However, while Evensen and Edmunds (2018) focused on mesenterial filaments, these are only one of a number of competitive mechanisms corals use, and the effect of OA on other competitive methods has not been considered as yet.

How the effects of competition under acidification scale up to an ecosystem level is largely unknown. Early evidence of the effect of competition at an ecosystem level found that recovery on coral reefs under the combination of OA and competition reduced recovery an additional 14% compared to OA alone (Evensen et al. 2021). However, competition was found to be less important than coral growth in recovery. Therefore, to understand how OA-induced changes to coral–coral interactions play out at an ecosystem level requires additional research on the extent to which corals compete, their competitive ability or aggression, and the impacts of competition on colony growth and survival.

Table 1 Published studies which consider, or raise the potential for, indirect effects of acidification on corals and coral communities. ‘-’ negative effect, ‘=’ neutral or no effect, ‘+’ positive effect

Indirect effect	Impact or percent change compared to control	Effect on hard corals	Reference
<i>Coral competition</i>			
Physiological effects of competition	39% (<i>Montipora aequituberculata</i>) and 71% (<i>Porites lutea</i>) reduction in growth of non-competing corals but in competing corals, there was no additional suppressive effect over that of OA	-/=	Evensen et al. (2015)
	32% decrease in calcification in corals under paired interspecific competition compared to control. No decrease in calcification in interspecific groups, heterospecific pairs or heterospecific groups	-/=	Evensen and Edmunds (2016)
	Competition between hard coral <i>Porites cylindrica</i> and soft coral <i>Sinularia</i> sp. had no significant effect on growth but significant decreased photosynthesis in both species	-/=	Brien et al. (2016)
	Intraspecific competition significantly decreased growth (5 of 6 sp.). No additional suppressive effect of interspecific competition over that of OA (5 of 6 sp.)	-/=	Horwitz et al. (2017)
	Modelled predictions of recovery of coral communities showed 43% recovery under OA when only considering coral growth, but only a 29% recovery when competition was also included. Under OA, coral growth rate decreased exponentially as the proportion of colony competition increased	-	Evensen et al. (2021)
Competitive capacity	No change in the competitive capacity of <i>Galaxia fascicularis</i> under OA, shown through comparable extrusion of mesenterial filaments	=	Evensen and Edmunds (2018)
<i>Macroalgal interactions</i>			
Physiological effects of coral–algae interactions	Two-to threefold increase in mortality of <i>Acropora intermedia</i> when in contact with <i>Lobophora papenfusii</i> macroalgae	-/ =/+	Diaz-Pulido et al. (2011)
	Presence of macroalgae had no effect on coral growth but presence of corals significantly reduced macroalgal growth		
	Macroalgae (<i>Dictyota</i> spp.) and pH individually reduced recruit survival and settlement of <i>Porites astreoides</i> ; however, there was no interactive effect	-/=	Olsen et al. (2015)
	<i>Porites astreoides</i> recruit survival decreased with <i>Styopodium zonale</i> presence. Settlement was decreased by combination of low pH and <i>S. zonale</i> presence	-	Campbell et al. (2017)
	Competition with <i>Halimeda heteromorpha</i> did not affect survival of <i>Acropora intermedia</i> but did decrease calcification (includes seasonal temperature effects)	=	Brown et al. (2019)
	Macroalgal (<i>Dictyota</i> sp.) presence had no significant effect on <i>Siderastrea radians</i> coral growth in paired interactions. Macroalgal biomass decreased with acidification both with and without an interaction with coral	=/+	Page et al. (2021)

Table 1 (continued)

Indirect effect	Impact or percent change compared to control	Effect on hard corals	Reference
Macroalgal competitive abilities	Mat-forming algae had enhanced productivity and 50% increase in cover. Likely to become competitively superior to corals	–	Connell et al. (2013)
	Altered allelopathy of some macroalgae species (1 of 3), increased rate of tissue death in corals in contact with macroalgae	–	Del Monaco et al. (2017)
<i>Corallivory</i>			
Physiological effects of corallivory	Some evidence of declines in calcification due to damage but no significant difference in wound healing	=	Edmunds and Yarid (2017)
	<i>Acropora</i> spp. were 10 times more likely to suffer mortality following 1 week predation by COTs, but subsequent growth and survival were unaffected by $p\text{CO}_2$	–/=	Kamya et al. (2018)
Corallivory rate	COTs feeding rate was unaffected by $p\text{CO}_2$	=	Kamya et al. (2018)
<i>Herbivory</i>			
Herbivore abundance	Increased density of urchins (<i>Diadema savi-gnyi</i> and <i>Echinothrix spp.</i>)	=/+	Fabricius et al. (2014)
	Decreased density of urchins (<i>Paracentrotus lividus</i> and <i>Arbacia lixula</i> urchins)	–/=	Hall-Spencer et al. (2008)
<i>CCA</i>			
Induction of coral settlement by CCA	42–63% reduction in CCA cover, resulting in 46–57% reduction in coral settlement	–	Doropoulos et al. (2012)
	Pre-exposure of CCA to high $p\text{CO}_2$ reduced larval settlement success in <i>Acropora millepora</i> and <i>Acropora tenuis</i> by 54%	–	Webster et al. (2013)
	Larval settlement decreased 87% with <i>Titano-derma</i> sp. and 50% with <i>Porolithon onkodes</i> and <i>Sporolithon</i> sp. due to altered chemical cues	–	Doropoulos and Diaz-Pulido (2013)
	Both CCA cover and the density of juveniles decreased with coastal acidification across the Great Barrier Reef continental shelf. However, there is no evidence that this is causal, as other factors such as suspended sediment also increased along the gradient		
<i>Habitat provision</i>			
Impact of habitat interactions on coral	The presence of <i>Trapezia</i> (crab) and <i>Alpheus</i> (shrimp) species reduced calcification in ambient but not in acidified conditions, suggesting a shift from parasitic to mutualistic interactions	+	Doo et al., 2018

Table 1 (continued)

Indirect effect	Impact or percent change compared to control	Effect on hard corals	Reference	
<i>Bioerosion</i>				
Abundance of bioeroders	50-fold increase and eightfold increase in abundance of boring <i>Lithophaga</i> bivalve and Vermetid gastropods respectively (associated with increased abundance of <i>Porites</i>)	–	Fabricius et al. (2014)	
	No significant difference in external bioeroder abundance in massive <i>Porites</i> colonies	=	Valentino (2014)	
	Significant increase in presence of macrobioeroders in <i>Porites</i> colonies	–	Barkley et al. (2015)	
	No significant difference in abundance or community composition of bioeroding endolithic green algae in <i>Porites</i> colonies with $p\text{CO}_2$	= –	Marcelino et al. (2017)	
	Endolithic community was less diverse in <i>Pocillopora damicornis</i> and <i>Seriatopora hystrix</i> , indicating lower buffering potential and resilience to acidification in these species			
Rate of bioerosion	No significant difference in percent area with internal bioerosion in massive <i>Porites</i> colonies	=	Valentino (2014)	
	78% increase in erosion and predation by boring organisms in <i>Porites astreoides</i>	=	Crook et al. (2013)	
	11 fold increase in percent volume of skeleton removed in <i>Porites</i> colonies, largely by bioeroding bivalve <i>Lithophaga</i>	–	Barkley et al. (2015)	
	Skeleton cores from live <i>Porites</i> colonies showed significant increase in rate of bioerosion with decreasing aragonite saturation	–	DeCarlo et al. (2015)	
	Total bioerosion and chemical bioerosion rates from <i>Cliona Caribbaea</i> (sponge) increased with $p\text{CO}_2$. No change in mechanical bioerosion	–	Webb et al. (2017)	
	Physiological effect of bioeroder on coral	Excavating sponge <i>Cliona varians</i> exacerbated declines in calcification in <i>Porites furcata</i> resulting from increased $p\text{CO}_2$	– =	Stubler et al. (2014)
		No significant effect of <i>Cliona varians</i> on <i>Porites furcata</i> survival		
Significant increases in net dissolution and bioerosion in <i>Porites furcata</i> under high $p\text{CO}_2$ but no further increase with the presence of <i>Cliona varians</i>		–	Stubler et al. (2015)	
	Encrusting/excavating sponge did not alter growth rate in <i>Siderastrea radians</i> between ambient and acidified conditions	=	Page et al. (2021)	
<i>Coral disease</i>				
Disease virulence	Optimal growth of pathogen <i>Aurantimonas corallicida</i> causing white plague type II, was at pH 7, with no growth below pH of 6	=	Remily and Richardson (2006)	
	Black band disease on <i>Orbicella faveolata</i> had lower progression rates under acidification	+	Muller et al. (2017)	

Table 1 (continued)

Indirect effect	Impact or percent change compared to control	Effect on hard corals	Reference
Abundance of pathogens	Shift in microbiome towards being more pathogenic, with increased abundance of disease-associated <i>Flavobacteria</i> and fungi under acidification	–	Vega-Thurber et al. (2009)
	Microbial community of <i>Acropora eurystoma</i> had increased abundance of <i>Vibrionaceae</i> and <i>Alteromonadaceae</i> like-pathogens, which are associated with diseased and stressed corals	–	Meron et al. (2011)
	No change in microbial communities between ambient and acidified conditions, with absence of microbial pathogens under acidification	+	Meron et al. (2012)

Competition between hard and soft corals

In general, soft corals appear to be more resistant to high $p\text{CO}_2$ than hard corals (Gabay et al. 2014) suggesting that soft corals could win more competitive interactions with hard corals in the future. Under recent historical ambient conditions, adult soft corals were often the subordinate competitors (Dai 1990), although chemical defences used by soft corals have been shown to affect hard corals through inhibiting recruitment (Atrigenio and Alino 1996) and growth, as well as causing significant tissue necrosis and mortality (Sammarco et al. 1983). However, ambient oceanic $p\text{CO}_2$ has increased dramatically since these studies were published and it is not known whether these interactions still occur or result in the same outcome under today's or future $p\text{CO}_2$ conditions. Only one study has experimentally tested the physiological effects of competition between hard and soft corals under high $p\text{CO}_2$ conditions. This study found that the presence of a soft coral competitor had a negative effect on photosynthesis but not growth of the hard coral (*Porites cylindrica*), and negligible changes in competitive ability in response to changing $p\text{CO}_2$ conditions (Brien et al. 2016; Table 1). In contrast, the cytotoxicity of the soft coral *Sarcophyton* spp. declined with increasing $p\text{CO}_2$ (Januar et al. 2016) potentially indicating a reduced capacity for competition. However, this decline coincided with a decrease in overall coral cover and may therefore represent a decreased need to compete. Similarly, at all three naturally acidified sites that reported abundances for both soft and hard corals, soft corals increased in abundance from ambient to mid $p\text{CO}_2$ before declining again under high $p\text{CO}_2$ (Inoue et al. 2013; Januar et al. 2017; Agostini et al. 2018). However, this result could reflect opportunistic colonisation of space as hard coral abundance declined rather than altered competitive ability. Studies that directly quantify how the

prevalence and outcomes of competition change between corals at natural CO_2 seeps compared to control sites will help to resolve knowledge gaps about how OA will affect reef ecosystems in the future.

Competition between hard corals and macroalgae

Competition on reefs also occurs between corals and other sessile benthic organisms such as macroalgae. Calcifying macroalgae (e.g. *Halimeda*) can decline in abundance and diversity under OA in a similar way to corals (Johnson et al. 2014; Zunino et al. 2017). While fleshy macroalgal species (hereafter, macroalgae) can also suffer negative effects of OA on their physiology, diversity or abundance (e.g. Page et al. 2021), overall the observed effects on this taxon are predominantly positive (Connell et al. 2013; Kroeker et al. 2013; Johnson et al. 2014; Zunino et al. 2017).

Coral–algal interactions are commonplace, especially in temperate environments, and under ambient conditions are not a significant threat to corals (Vieira 2020). However, under acidification a disparity between the predominantly negative physiological effect on corals and the predominantly positive effect on macroalgae has the potential to shift this balance, affecting coral–algal competition in two ways. Increases in macroalgae abundance (Connell et al. 2013) are likely to increase the frequency of coral–algal interactions. This increase of interactions has not been explicitly tested under acidification but has been shown under ambient conditions where macroalgae increased in abundance due to fishing pressure removing herbivorous fish (Bonaldo and Hay 2014). Furthermore, there is some evidence that coral–algal interactions are more detrimental to corals under high $p\text{CO}_2$ (Table 1). For example, direct contact between corals and macroalgae under high $p\text{CO}_2$ conditions results in significantly greater and faster coral mortality than under

ambient conditions, in both adult colonies (Del Monaco et al. 2017) and coral larvae (Campbell et al. 2017). Furthermore, acidification is anticipated to result in smaller colony sizes (e.g. Teixidó et al. 2020) which have been shown to suffer greater mortality than larger corals when interacting with macroalgae under ambient conditions (Ferrari et al. 2012). The mechanisms behind these effects include enhanced macroalgal allelopathy (Del Monaco et al. 2017) and/or elevated production of DOC (dissolved organic carbon) which encourages microbial activity with negative consequences for coral (Diaz-Pulido and Barrón 2020).

To date, the balance of evidence suggests that algae can often outcompete corals under acidification. At a colony level this may result in an increased likelihood of coral overgrowth (Diaz-Pulido et al. 2011); however, there are also wider ecosystem level effects. For example, changes in coral–algal interactions under acidified conditions in favour of macroalgae can create a density-dependent negative feedback loop where increased macroalgal abundance results in more coral mortality which creates more space for macroalgal colonisation. This can result in ecosystem phase shifts from coral to macroalgal dominated states (Diaz-Pulido et al. 2011), which has been seen in at least one naturally acidified site (Enochs et al. 2015b). However, the maintenance of coral dominance at some naturally acidified sites, despite increased abundance of macroalgae (e.g. Fabricius et al. 2011) suggests that the (chronic) effect of acidification on coral–macroalgal interactions is not sufficient, on its own, to cause this phase shift. There may be a number of explanations for this. Firstly, competition can have negative effects for macroalgae as well as corals (Diaz-Pulido et al. 2011), and the presence of coral–algal competition does not always have additional suppressive effect on growth (Page et al. 2021) or tissue loss from allelopathy (2 out of 3 species; Del Monaco et al. 2017) above that of acidification alone. Secondly, the effect and outcome of coral–algal competition differs between species (e.g. Del Monaco et al. 2017; Vieira 2020) suggesting phase shifts towards macroalgae are dependent on the macroalgal community composition. Thirdly, other environmental factors such as temperature may play a role. For example, coral–algal interactions vary temporally due to seasonal changes in temperature (Brown et al. 2019). Finally, additional indirect effects, such as decreasing herbivory (see section below), can determine the likelihood of a phase shift (Enochs et al. 2015b). Therefore, we suggest that while altered coral–algae competitive interactions have significant implications for coral communities, broader knowledge of species-specific tolerances to OA for both corals and algae, and better knowledge of the mechanisms and costs of competitive interactions, are required before the outcomes of such encounters can be accurately predicted in the future.

Corallivory

Under ambient conditions ($\sim 390\text{--}420 \mu\text{atm } p\text{CO}_2$, based on the approximate global average $p\text{CO}_2$ concentrations from 2010 to 2022), corallivory (predation) of corals can be a chronic stressor to coral communities (Cole et al. 2011), potentially affecting species abundance and diversity (e.g. Littler et al. 1989; Lenihan et al. 2011). Changes in the rate of corallivory are likely based on demonstrated changes in fish behaviour under OA (Ferrari et al. 2011; Munday et al. 2014). Moreover, the potential effect of acidification on fish physiology, such as bone strength/mineralisation (Di Santo 2019; Mirasole et al. 2021) and skeletal deformities (Pimentel et al. 2014), may alter the impact of corallivory. However, to the best of our knowledge, only two studies have considered how corallivory changes as a result of ocean acidification (Table 1). One study found that very high $p\text{CO}_2$ (1608 μatm) conditions did not affect the rate of coral consumption, or further reduce coral survival, following predation from Crown-of-Thorns starfish (COTs, *Acanthaster planci*; Kamyra et al. 2018). A second study showed that injuries made on small corals to simulate bite scars of corallivorous parrotfish healed at the same rate under ambient (420 μatm) and high (1050 μatm) $p\text{CO}_2$ conditions (Edmunds and Yarid 2017), suggesting acidification does not affect recovery from predation. However, potential changes in rates of predation by different corallivores remains a significant knowledge gap. While as yet untested, acidification could also result in secondary impacts of predation. For example, bite scars from parrotfish are larger on low-density substrate than on high-density substrate (Bruggemann et al. 1994) and, therefore, if coral skeletal density declines as a result of acidified conditions (Tambutté et al. 2015; Mollica et al. 2018) the potential size and impact of predation scars might increase.

Corallivory is an important driver of changes in coral cover. Models of future coral cover on the Great Barrier Reef found managing predation by COTs to be one of the most effective strategies in delaying declines in coral cover (Condie et al. 2021). However, the cumulative impacts of changes to corallivory on coral populations and communities under OA are, as yet, unknown. Despite this, we suggest that predation pressure on individual coral colonies could increase under OA due to potential decreases in coral abundance (Enochs et al. 2015b) reducing food supply, a shift in community composition to a species less preferred for predation (e.g., *Porites* spp.; Fabricius et al. 2011), but little to no change in corallivorous fish community (Munday et al. 2014). Detailed investigation of both the rates and the impact of corallivory will be important to reveal the implications of changes in predation pressure for corals and coral communities in the future.

Herbivory

Herbivory has been shown to be a critical function in the resilience of coral reefs (Hughes et al. 2007). Under ambient conditions, a loss of herbivory has been noted as significant factor in the occurrence of a number of coral to macroalgal phase shifts (Vieira 2020). Fortunately, under acidified conditions, the abundance of herbivores is expected to be equal or greater than ambient conditions, due to the increased availability of food and a simplification of coral reef food webs (Kroeker et al. 2011; Alva-Basurto and Arias-González 2014; Vizzini et al. 2017; Harvey et al. 2019). Therefore herbivory is likely to continue being a major benthic structuring process under acidification (Baggini et al. 2015). However, where the herbivores are themselves negatively affected by acidification (e.g. sea urchins; Hall-Spencer et al. 2008) or the algal community becomes less palatable to herbivores (e.g. Harvey et al. 2019), this can reduce the top-down control of macroalgae and result in shifts in the benthic community. These effects are ‘secondary’ indirect effects where the impact on corals occurs via the impact of herbivores on the macroalgal community. In addition, herbivory can also affect corals directly. For example, under acidified conditions coral recruits had significantly higher post-settlement mortality and a higher size-escape threshold from grazing herbivorous fish (Doropoulos et al. 2012). Although we were unable to find any studies explicitly testing the secondary effects of herbivory on coral communities, we suggest changes in herbivory may be a significant factor in moderating the impacts of acidification on corals, and highlight the need for additional research on this topic.

Crustose coralline algae (CCA)

CCA, like corals, are calcifying organisms and are therefore likely to be negatively affected by acidification. For example, increased $p\text{CO}_2$ on CCA has been shown to cause declines in recruitment (Ordoñez et al. 2017), competitive ability (Kuffner et al. 2008; Crook et al. 2016), growth (Johnson et al. 2014), calcification and recovery following injury (Manning et al. 2019). Ultimately, these changes result in up to 70 to 90% declines in CCA abundance (Kuffner et al. 2008; Fabricius et al. 2015; Vogel et al. 2016), however, these effects are species specific with some species persisting while others suffer reduced abundance or are lost completely (e.g. Peña et al. 2021). Therefore, acidification is also likely to cause shifts in community composition of CCA on reefs.

CCA play a number of vitally important roles for corals. CCA cement and stabilise the reef substratum (Guinotte and Fabry 2008) which provides stable and suitable habitat for juvenile corals to settle on. However, reef pavement (solid carbonate substratum covered with CCA, turf algae

and other sessile invertebrates), has been found to have dissolution rates 86% higher in acidified compared to ambient conditions. Similarly, reefs with low cementation rates under natural acidification suffered an almost complete loss of reef framework following a disturbance, with very low rates of coral recovery (Manzello et al. 2008). Furthermore, like corals, CCA are likely susceptible to increased bioerosion under OA. In addition to reduced abundance, this may contribute to a decrease in reef cementation in the future, reducing the available substrate for settlement of coral recruits.

CCA are often used as a suitable settlement substrate, with declines in CCA abundance therefore reducing available settlement space. For example, during an in situ experiment at naturally acidified reefs in Papua New Guinea, 81% of coral recruits settled on CCA, despite it only accounting for 12% of substrate (Fabricius et al. 2017). This will therefore compound the effects of reduced reef cementation, further reducing the availability of suitable space for larval settlement. Finally, CCA act as an important settlement cue for coral larvae (Heyward and Negri 1999) and increased $p\text{CO}_2$ can disrupt the response of corals to CCA (Table 1). For example, when CCA were pre-exposed to high $p\text{CO}_2$, larval settlement declined between 54 to 87% (Doropoulos and Diaz-Pulido 2013; Webster et al. 2013). In addition, a loss of affinity has been shown between coral larvae and the most favourable CCA species (*Titanoderma* sp.) which may further reduce settlement (Doropoulos et al. 2012). To exacerbate this effect, CCA species are differentially affected by increased $p\text{CO}_2$ (see review: Hofmann and Bischof 2014) resulting in altered community compositions, with preferred settlement species such as *Titanoderma* sp. thought to be less tolerant of acidified conditions (Fabricius et al. 2015). These effects suggest loss of CCA, or changes to the community composition of CCA, is a major pathway of indirect effects of OA on coral communities.

Habitat provision

Corals are ecosystem engineers that build three-dimensional structures that provide habitat, shelter and food for many other reef organisms. This structural complexity they create affects species richness and abundance of many reef organisms, and is a driver of reef ecosystem functioning (Graham and Nash 2013). Consequently, degradation of structural complexity from acidification (Fabricius et al. 2011; Manzello et al. 2014; Enochs et al. 2015b) can have significant implications for a wide variety of taxa and the functioning of acidified reefs. Here we consider the interactions between corals with fish, invertebrates and zooplankton.

Under ambient conditions, fish–coral interactions are often mutually beneficial. For example, associations with fish have been shown to benefit corals through enhanced colony growth (Chase et al. 2014) and photosynthesis

(Garcia-Herrera et al. 2017), reduced sedimentation and sediment-induced partial mortality (Chase et al. 2018), and protection from predation (Chase et al. 2014). Furthermore, provision of habitat and shelter for herbivorous fish also benefit corals through maintenance of algal populations. For instance, herbivory pressure was > 7 times higher in high-complexity areas compared to low-complexity areas (Santano et al. 2021). Moreover, declines in structural complexity at naturally acidified sites can drive a shift in fish community composition (Cattano et al. 2020), and altered abundances of some fish species at acidified compared with ambient areas (Munday et al. 2014). To the best of our knowledge, the effect of ocean acidification on interactions between corals and fish have not yet been investigated, and therefore, how changes in fish abundance or community composition indirectly affect corals ability to persist under acidified conditions remains unknown.

Many invertebrates use coral for habitat, with almost 1,000 known coral–invertebrate associations (Stella et al. 2011), although this number is likely to have increased over the last decade. This includes species which live in the branches and crevices coral provide, and boring organisms who reside within the coral tissue/skeleton (Stella et al. 2011). Overall, invertebrate communities appear to be negatively affected by acidification and the associated loss in structural complexity (Fabricius et al. 2014). The implications of changes in invertebrate communities or coral–invert interactions depend on the interacting taxa. For example, populations of the herbivorous urchin *Diadema savignyi*, increased dramatically at the acidified site in Papua New Guinea (PNG; Fabricius et al. 2014) which could benefit corals through increased herbivory. In contrast, increased abundance of vermitid gastropods which bore into large *Porites* colonies (Fabricius et al. 2014), may negatively affect corals through weakening their structure. Finally, the mutualistic relationship between the coral host (*Pocillopora verrucosa*), and two ectosymbionts *Trapezia* spp. crabs and *Alpheus*, spp. shrimp reduced the impact of acidification on calcification in the host coral (Doo et al. 2018; Table 1). However, it is not clear whether this is because the ectosymbionts reduced the sensitivity of the coral to acidification or provided a resource or service that prevented the reduction in calcification seen in the corals without ectosymbionts. Due to high diversity of coral-associated invertebrates and the range of responses in interactions to acidification, it is hard to predict the potential changes in interactions and what the outcomes of those may be for corals. Furthermore, additional changes in the physical (water flow and temperature) and chemical (e.g. dissolved nutrients and oxygen) conditions of the ocean as a result of acidification and climate change could further exacerbate changes in interactions between the organisms involved in these symbioses.

Demersal zooplankton use coral to shelter from predation during the day (Alldredge and King 1977). Similarly to fish, declines in structural complexity under acidified conditions have also been shown to result in reduced biomass and abundance of zooplankton (Smith et al. 2016; Allen et al. 2017). However, zooplankton are an important heterotrophic food source for corals (Houlbrèque and Ferrier-Pagès 2009) and declines in their abundance has the potential to impact corals, through altered availability of food. The extent of this impact is likely to be species specific, depending on the reliance of each species on heterotrophic food sources. Moreover, some species are capable of mitigating the effects of acidification by increasing heterotrophic energy contributions (Towle et al. 2015). A decline in zooplankton may therefore reduce the resilience of some corals to acidification.

Overall, we suggest that the changes in habitat interactions reviewed here are likely to have only sub-lethal consequences for corals. However, they highlight the possibility of multiple small shifts in the functioning of coral reef ecosystems to accumulate, which may ultimately contribute to a shift in communities greater than that expected from the physiological stressors. This may be particularly be the case where changes affect mutually beneficial relationships, creating the possibility of a negative feedback loop. In this case, fewer beneficial habitat associations reduce physiological coral health and/or survival, which further affects habitat associations. Such effects are extremely hard to predict and with the current paucity of data on the indirect effects on corals of changes to habitat associations, this remains a significant knowledge gap.

Bioerosion

Bioeroders are a diverse range of organisms including bacteria, algae, sponges, molluscs and fish, which cause erosion through grazing of, attachment to, or embedding in, the coral skeleton (Wisshak et al. 2012; Glynn and Manzello 2015; Schönberg et al. 2017). There is significant evidence from naturally acidified reefs that bioeroder abundance increases under high $p\text{CO}_2$ (Crook et al. 2013; Enochs et al. 2016b) (Table 1). This may be the result of reduced competition for space between settling bioeroders such as sponges (Schönberg and Ortiz 2008) or an increase in dead coral habitat which supports a high number of invertebrates (Tribollet and Golubic 2011; Valentino 2014). Increased bioeroder abundance may have additional indirect effects on coral populations by reducing the available space for settlement. However, increased bioeroder abundance is not found for all bioeroding species (e.g. grazers; Schönberg et al. 2017) or where other factors like habitat are limiting (Valentino 2014).

The bioerosive capacity of many species is increased under high $p\text{CO}_2$ (Table 1). Chemical bioerosion is less physiologically costly under high $p\text{CO}_2$ (Wisshak et al. 2012) which may increase the bioerosive capacity of boring species. For example, it is estimated that rates of chemical bioerosion by an excavating sponge (*Cliona caribbaea*) could double by the end of the century (Webb et al. 2017). In addition, taxa using mechanical bioerosion may have increased bioerosive capacity where coral skeletons are weaker, less dense/more porous. While corals with lower density were more likely to have evidence of bioerosion than high density corals (Barkley et al. 2015), this correlation has not been explicitly tested under acidification. Furthermore, under ambient conditions, skeletal density does not always result in increased bioerosion. For example, the highest rates of bioerosion were found in the coral genus with the highest skeletal density (*Pavona*; Cosain-Díaz et al. 2021). These contrasting findings may be explained in part by variable rates of bioerosion between morphologies, with the most dense coral also being the morphology with the highest rates of bioerosion (massive; Cosain-Díaz et al. 2021). However, where density does affect bioerosive capacity, we are likely to underestimate the net effect of OA on coral growth by considering the direct effects in isolation. Finally, bioeroders may have increased biomass and faster growth (Fang et al. 2013; Uthicke et al. 2016), ultimately allowing an individual to have a greater rate of bioerosion or lifetime erosive capacity. The combination of increased bioeroder abundance and bioerosion capacity is expected to result in a large increase in total bioerosion under high $p\text{CO}_2$. By the end of this century, these increases in bioerosion from sponges alone are estimated to be 7% under RCP 4.5, 16% under RCP6 and 31% under RCP8.5 compared to ambient conditions (393 μatm ; Wisshak et al. 2012; IPCC 2014). Similarly, total volume removed by bioerosion under Ω aragonite saturation < 2 (comparable to RCP8.5) may increase up to 78% compared to ambient aragonite (Ω aragonite > 3.5 ; Crook et al. 2013). Such increases in bioerosion rates have been shown to result in significant declines in net calcification (Stubler et al. 2014) and even a switch from net calcification to net dissolution (Enochs et al. 2016a). Therefore, in conjunction with the predicted changes in net accretion, bioerosion could be a significant contributor to coral cover declines in the future.

Coral disease

Coral disease results from interactions between the host corals and the pathogen causing the disease. Worldwide, the prevalence of coral diseases has increased in recent decades due to a number of factors, such as rising water temperatures (Tracy et al. 2020), and decreasing water quality including nutrient enrichment (Vega-Thurber et al. 2014), plastic pollution (Lamb et al. 2018) and metal pollution (Tracy et al.

2020). However, the effect of acidification on coral diseases is largely unknown and remains a significant knowledge gap (Vega Thurber et al. 2020). To date, only one study has empirically shown an impact of acidification on disease dynamics, which found that low pH (7.7) decreased the progression of black band disease on *Orbicella faveolata* under experimental conditions (Muller et al. 2017). This suggests that future acidified conditions may be less favourable to black band disease and result in decreased prevalence and/or progression. However, coral diseases are caused by a range of pathogens including marine and terrestrial bacteria, cyanobacteria and viruses (Sokolow 2009; Vega Thurber et al. 2020), meaning the results from Muller et al. (2017) cannot easily be extrapolated to diseases caused by other pathogens.

Despite limited information on coral disease under acidification, there are some indications that pathogen abundance and virulence, and coral susceptibility may change (Table 1). Increased abundances of disease-associated bacteria within the coral microbiome have been found experimentally (Meron et al. 2011; Grottoli et al. 2018; Table 1; Vega Thurber et al. 2020), and at the seep site in PNG (Morrow et al. 2015), however, this did not result in an increase in infections. Furthermore, microbial pathogens were absent entirely at the seep site in Ishia, Italy (Meron et al. 2012). In addition, there is some evidence that pathogen virulence may be affected by acidification, potentially due to pathogen pH tolerance limits. For example, growth in the bacterium *Aurantimonas corallicida*, which causes white plague type II, was strongly affected by pH with a clear lower limit beyond which no growth occurred (Remily and Richardson 2006). Finally, corals have shown decreased immunity under acidification, which may result in an increase in susceptibility (see review: Traylor-Knowles and Connelly 2017). Regardless of this potential decrease in virulence, we note that reduced growth and calcification in corals may reduce the ability of corals to recover if infection does occur and this could heighten the impacts of diseases on coral populations. Additional research is required on the prevalence of disease at naturally acidified sites, as well as both pathogen abundance and virulence, as well as coral susceptibility and recovery, to understand the effect of acidification on coral–pathogen interactions.

Coral communities under acidified conditions

Ultimately, the coral communities we see in the future will be the result of the combined impacts of both the direct and the indirect effects on corals. With consistent variability in findings between species, location and experimental studies, as well as the paucity of data on many indirect effects, our ability to accurately scale up our current knowledge to an

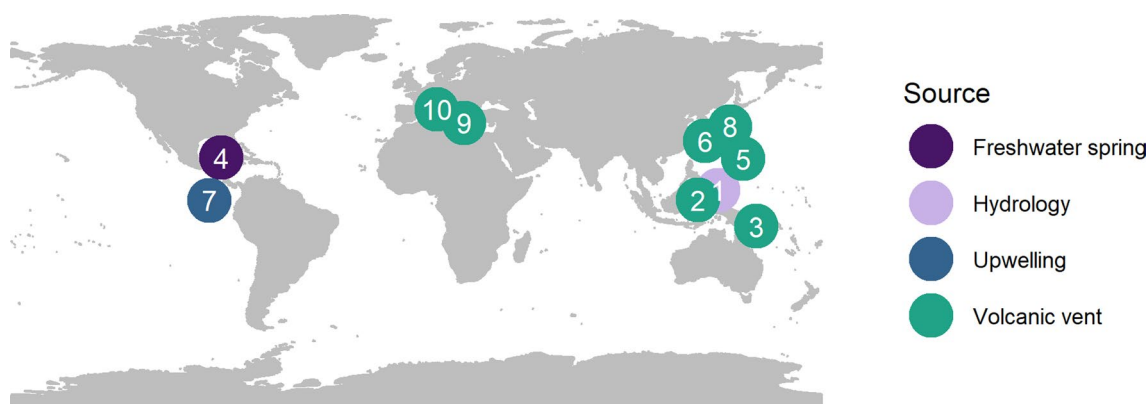


Fig. 2 The location of the ten natural acidified sites with associated corals which are reviewed here, ordered by smallest to largest decrease in coral cover. 1- Rock Island Bays, Palau; 2- North Sulawesi and Maluku Provinces, Indonesia; 3- Dobu, Esa'Ala and

Upa-Upasina, Papua New Guinea (PNG); 4- Puerto Morelos, Mesoamerica; 5- Maug, Commonwealth of Northern Mariana Islands (CNMI); 6- Iwotorishima, Japan; 7- Galapagos, Eastern Tropical Pacific (ETP); 8- Shikine, Japan; 9- Panarea, Italy; 10- Ishia, Italy

ecosystem scale is limited. However, globally, there are a number of locations with naturally low pH/high $p\text{CO}_2$ conditions as a result of volcanic gas seeps, hydrographic processes and localised low pH submarine springs. The natural gradients of $p\text{CO}_2$ around these sites reveal how the direct and indirect effects of OA that are reviewed above could manifest at an ecosystem level. We review the evidence of indirect effects and the result of both direct and indirect effects on ecosystem level metrics, at ten naturally acidified coral communities or coral reefs (Fig. 2, Table 3). Seven of these sites occur around volcanic vents, where gas containing a high percentage of CO_2 seeps through the seafloor and acidifies the surrounding waters. Of these seven, three occur in tropical coral reef ecosystems, in North Sulawesi and Maluku Provinces (Indonesia), Dobu, Esa'Ala and Upa-Upasina (PNG), and Maug (Commonwealth of Northern Mariana Islands [CNMI]), and one on a sub-tropical reef in Iwotorishima (Japan). The remaining three vents are in temperate rocky shore environments where corals occur, in Shikine (Japan), and Panarea and Ishia (both Italy). Carbonate chemistry at vent sites is variable depending on the composition of the vent gases; however, $p\text{CO}_2$ conditions close to the vent can be high and well in excess of what is predicted under end of century conditions, particularly in temperate regions (e.g. 5066 μatm in Ishia, Italy; Hall-Spencer et al. 2008). The remaining three sites occur as a result of three different processes. In Rock Island Bays in Palau, acidification occurs in tropical lagoonal reefs where there is restricted circulation of water in semi-enclosed bays (Golbuu et al. 2016). Acidification here is less extreme ($\sim 600 \mu\text{atm}$) than at some of the vent sites. In Puerto Morelos (Mesoamerica) submarine springs (or 'Ojos') discharge low-pH, low aragonite saturation groundwater, through natural localised springs in close proximity to the tropical Mesoamerican Barrier Reef. This results in high levels of acidity (pH 7.05,

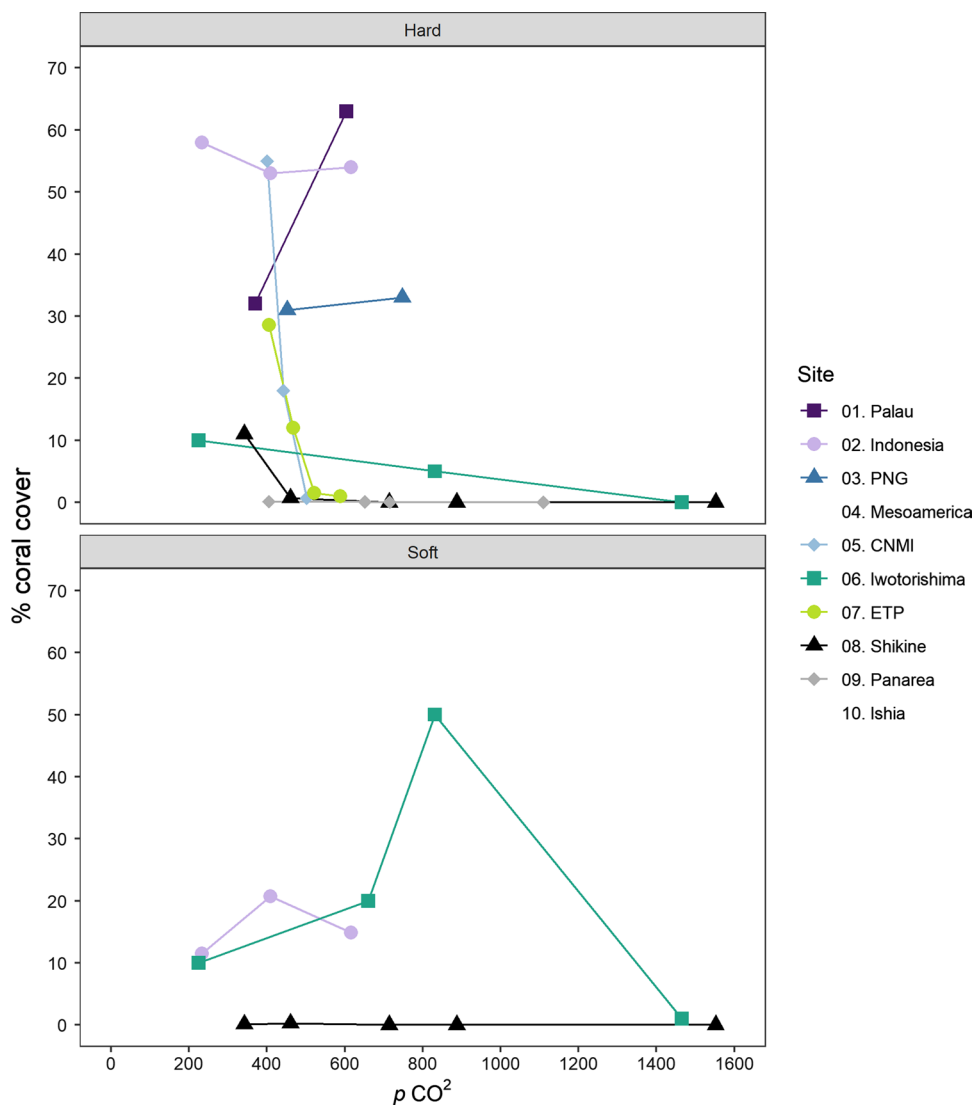
$p\text{CO}_2$ data is not stated) as well as reduced salinity and total alkalinity (Crook et al. 2012). Finally, seasonal upwelling results in mild acidification (588 μatm) at the southern-most reefs in the subtropical Galapagos Islands (Eastern Tropical Pacific [ETP]), as well as exposure to cool waters and elevated nutrient levels. Reefs further north are less affected by the upwelling and experience more ambient ocean conditions (Manzello et al. 2014).

A number of other acidified sites have also been described in the literature, however, they are excluded here because they also experience elevated temperatures and/or deoxygenation (Bouraké, New Caledonia; Mangrove lagoons, northern Great Barrier Reef; Bahia Concepcion, California), or because there are no ecological records of coral communities at those sites, (Ambitle Island, PNG; Mayreau Gardens, Caribbean) or where the $p\text{CO}_2$ gradient occurs and dissipates daily (Moorea, French Polynesia).

Changes in coral abundance (coral cover) with increasing $p\text{CO}_2$

The effect of acidification on hard coral abundance, with the exception of *Porites* spp., is largely negative (Fig. 3). Seven of the ten naturally high $p\text{CO}_2$ sites showed reduced hard coral cover compared with adjacent control sites (Fig. 3, Table 2). Nevertheless, the effect is not always negative, and there is limited evidence of a physiological 'tipping point' or threshold response to increasing $p\text{CO}_2$. While the three temperate/sub-tropical coral communities, as well as the CNMI and Mesoamerican coral reefs, showed rapid declines in coral cover at $\sim 500 \mu\text{atm}$ $p\text{CO}_2$, coral cover at similar concentrations increased significantly at Palau ($\sim 31\%$), was maintained at seep locations in Indonesia ($\sim 4\%$ increase) and PNG ($\sim 2\%$ increase) and shifted from hard to soft coral cover at Iwotorishima (Fig. 3, Table 2). This suggests that

Fig. 3 The percentage cover of hard corals (top) and soft corals (bottom) along a $p\text{CO}_2$ gradient at eight of the ten naturally acidified sites reviewed here. Coral cover data are not shown for two sites because of lack of stated $p\text{CO}_2$ values (Mesoamerica, site 4) and coral cover (Ishia, site 10); however, both studies note significant to total loss of coral cover. Abundances for Iwotorishima (Japan) are approximate, based on broad percentage categories. Site numbers in legend correspond to Fig. 2



effects of $p\text{CO}_2$ on coral abundance are likely to be influenced by other indirect effects and/or environmental factors, and also by the species composition of coral present at each site (see below). Overall, whereas all of the temperate/sub-tropical coral communities showed a complete loss of corals between control and seep sites, only two of the seven warm water coral reefs showed a significant loss of coral cover across a similar $p\text{CO}_2$ gradient (Inoue et al. 2013; Enochs et al. 2015b; Fig. 3). Therefore, the high light levels available in warm tropical waters, and the increases in metabolic rates that accompany moderate increases in water temperature, could allow certain species of corals (e.g. *Porites*) to maintain growth rates on tropical reefs despite changes in $p\text{CO}_2$. In contrast, increasing $p\text{CO}_2$ has major effects on coral growth under more marginal conditions.

Differences in local species composition may also influence the impact of $p\text{CO}_2$ on abundance. Among-species

variation in sensitivity to acidification has been widely discussed (e.g. McCulloch et al. 2012; Agostini et al. 2021) with the premise that declines in abundance are driven in part by declines in less tolerant, ‘loser’ species. However, ‘winners’ and ‘losers’ are not consistent between sites. For example the abundance of *Acropora spp.* declined at many of the acidified sites (e.g. Palau) but increased ~65% under high $p\text{CO}_2$ at the Indonesia seep site (Barkley et al. 2015; Januar et al. 2016). Despite the suggested resilience of soft corals to acidification, of the four sites that reported soft coral abundance, only two noted a significant increase in at seep sites with intermediate $p\text{CO}_2$ conditions compared to the control sites. Furthermore, at these locations, soft coral cover subsequently declined at the highest $p\text{CO}_2$ conditions surveyed (Fig. 3, Table 2).

Table 2 A summary of the physical site characteristics of the naturally acidified sites in this review ‘*’ = data extracted from a figure in source publication, ‘–’ = no data available

	(1) Rock Island Bays, Palau			(2) North Sulawesi and Maluku Provinces, Indonesia,			(3) Dobu, Esa’Ala and Upa-Upasina, PNG		(4) Puerto Morelos, Mesoamerica	
<i>Site description</i>										
Community type	Tropical coral reef			Tropical coral reef			Tropical coral reef		Tropical coral reef	
Source	Biological & hydrographic processes			Volcanic seeps			Volcanic seeps		Low-pH submarine springs	
Unique/confounding factors	Semi-enclosed, restricted circulation. Acidified = lagoonal reef, Control = outer reef			Nutrient enrichment/eutrophication					Decreased salinity and total alkalinity	
% CO ₂ from vent gas	NA			–			> 99%		NA	
<i>Physical features</i>										
# Site replicates	11 sites along acidification gradient			Replicate sites at 3 acidified reefs			Replicate sites at 3 acidified reefs		Replicate Ω saturation gradients surrounding 10 springs. No true control site	
Site (n)	<i>Control</i> (Ngaremlen-gui Barrier)	<i>High</i> (Nikko Bay)	<i>Control</i> (3)	<i>Low</i> (3)	<i>High</i> (3)	<i>Control</i> (3)	<i>High</i> (3)	<i>Control</i> (10)	<i>High</i> (10)	
Mean pCO ₂ (µatm)	392	586	233	409	616	452	748	–	–	–
Mean pH	8.03	7.84	8.20	8.01	8.00	8.00	7.83	8.03	7.05	7.05
Mean aragonite saturation (Ω)	3.60	2.34	4.70	3.43	2.60	3.45	2.67	3.6	0.68	0.68
<i>Biological features</i>										
Dominant reef taxa	Hard coral			Hard coral			Hard coral		Hard coral	
% change hard coral cover	–	33.9%*	–	–15%*	6.7%*	–	6.5%	–	–	Signif. decline
Reference	Shamberger et al. (2014); Barkley et al. (2015)			Januar et al. (2016); (2017)			Fabricius et al. (2011)		Crook et al. (2012)	
	(5) Maug, Commonwealth of Northern Mariana Islands (CNMI)			(6) Iwotorishima, Japan			(7) Galapagos, Eastern Tropical Pacific (ETP)			
<i>Site description</i>										
Community type	Tropical coral reef			Sub-tropical coral reef			Temperate reef/community			
Source	Volcanic seeps			Volcanic seeps			Upwelling			
Unique/confounding factors				Semi-enclosed reef, and presence of low salinity hot springs			Exposure to cool, nutrient rich waters Affected areas are no longer true reefs after failing to recover from El Niño disturbance event (1982–83)			
% CO ₂ from vent gas	61.10%			> 40%			NA			
<i>Physical features</i>										
# Site replicates	Single vent site			Single vent site			7 sites along acidification gradient			
Site (n)	<i>Control</i> (1)	<i>Low</i> (1)	<i>High</i> (1)	<i>Control</i> (1)	<i>High</i> (1)	<i>Extreme</i> (1)	<i>Control</i> (Darwin)	<i>Low</i> (Marchena)	<i>Mid</i> (Devil’s Crown)	<i>High</i> (Urvina)
Mean pCO ₂ (µatm)	401*	442*	502*	225	831	1465	406	468	521	588
Mean pH	8.04	7.98	7.94	–	–	–	8.02	7.98	7.95	7.90

Table 2 (continued)

	(5) Maug, Commonwealth of Northern Mariana Islands (CNMI)					(6) Iwotorishima, Japan			(7) Galapagos, Eastern Tropical Pacific (ETP)				
Mean aragonite saturation (Ω)	3.84*	3.64*	3.38*	–	–	–			3.28	3.02	2.83	2.42	
<i>Biological features</i>													
Dominant reef taxa	Hard coral		Macro-algae		Hard coral	Soft coral	Few corals	Hard coral					
% change hard coral cover	–	–68%*	–99%*	–	–5%*	–10%*	–	–58%	–93%	–97%			
Reference	Enochs et al. (2015a, b)				Inoue et al. (2013)			Manzello et al. (2008); Manzello et al. (2014)					
	(8) Shikine, Japan					(9) Panarea, Italy			(10) Ishia, Italy				
<i>Site description</i>													
Community type	Temperate coral community					Temperate coral community			Temperate coral community				
Source	Volcanic seeps					Volcanic seeps			Volcanic seeps				
Unique/confounding factors	Some vents release hydrogen sulphide (H ₂ S)												
% CO ₂ from vent gas	–					98–99%			90.1–95.3%				
<i>Physical features</i>													
# Site replicates	Replicate sites at 2 acidified reefs					Single vent site			Single vent site				
Site (n)	<i>Control</i> (3)	<i>Low</i> (1)	<i>Mid</i> (1)	<i>High</i> (1)	<i>Extreme</i> (1)	<i>Control</i> (1)	<i>Mid</i> (2)	<i>High</i> (1)	<i>Control</i> (2)	<i>Mid</i> (1)	<i>Extreme</i> (1)		
Mean <i>p</i> CO ₂ (μ atm)	342	460	714	888	1552	405	684	1110	323	768	10,314		
Mean pH	8.22	8.11	7.94	7.9	7.66	8.1	7.9	7.7	8.16	7.9	6.9		
Mean aragonite saturation (Ω)	2.75	2.23	1.6	1.68	0.94	3.6	2.3	1.5	3.99	2.68	0.86		
<i>Biological features</i>													
Dominant reef taxa	Rocky shores with corals		Rocky shores, no corals, dominated by turf and low profile algae			Rocky shore & cold water corals		Rocky shore, no corals	Rocky shore & cold water corals	Rocky shore, no corals, increased seagrass & macroalgae			
% change hard coral cover	–	–94%	–100%	–	–	–41 to 71%	100%	–	100%	100%			
Reference	Agostini et al. (2018)					Goffredo et al. (2014); Fantazzini et al. (2015)			Hall-Spencer et al. (2008)				

Locations are ordered from the smallest to the largest decrease in coral cover. Values presented are means of all sites in each category. ‘Control’ refers to sites that have ambient water chemistry and are used as reference sites in the source publication

Changes in species diversity, richness, and community composition with increasing *p*CO₂

Coral species richness at the ten acidified sites reviewed here consistently declined with increased *p*CO₂, likely driven by the loss of vulnerable species. Species richness

has been reported (or can be inferred) at eight of the ten high *p*CO₂ sites (Table 2), of which seven showed large declines in species richness, from –31% to –100%. The remaining site, Palau, had a 50% increase in species richness and a 10% increase in diversity (Shannon diversity index) between the least and most acidic site (Shamberger

Table 3 Evidence of indirect effects of acidification on corals and coral communities from the naturally acidified sites considered by this review

<i>1. Rock Island Bays, Palau</i>	
Coral–coral competition	The highest coral abundances were in the most acidic sites ^(1,2) , so competition may also be higher There were no soft corals in the most acidic sites, so hard-soft competition may be absent. ⁽³⁾
Coral–algal competition	Macroalgae abundance was low and did not vary with acidity ^(1,3)
CCA	CCA cover was low and did not vary with acidity. ^(1,3)
Bioerosion	11 fold increase in bioerosion, primarily from <i>lithophaga</i> bivalve, from least to most acidified site. Likelihood of bioerosion increased as skeletal density decreased ⁽¹⁾
<i>2. North Sulawesi and Maluku Provinces, Indonesia</i>	
Coral–coral competition	Cytotoxicity of soft coral <i>Sarcophyton</i> decreased with pH but not clear whether this was decreased capability of allelochemical production OR due to decreased demand from lower coral cover ⁽⁴⁾
Coral–algal competition	Non-calcifying algae did not appear to have a competitive advantage over corals and were more abundance in the control ⁽⁵⁾
Structural complexity and habitat provision	Reduced abundance of framework building corals ⁽⁴⁾
<i>3. Dobu, Esa'Ala and Upa-Upasina, PNG</i>	
Coral–algal competition	Increased macroalgae cover ⁽⁶⁾
Corallivory, food webs and herbivory	Little change in fish population but no evidence reported on corallivore abundance ⁽⁷⁾ Significant increase in herbivorous <i>diadema</i> urchins ⁽⁸⁾ Reductions in demersal zooplankton ^(9, 10)
CCA	CCA cover reduced by 43–85%, including a 60–85% reduction in <i>Titanoderma</i> sp., which are the preferred coral settlement substrate (11). 81% of coral recruits settled on CCA, despite it only accounting for 12% of the benthos. ⁽¹²⁾ This coincides with significant declines in coral recruitment. ^(6, 12) Declines resulted from vulnerabilities in early life stages of CCA, rather than a change in competition, which seems to be weaker with acidification. ⁽¹¹⁾
Bioerosion	Visible macrobioeroders were almost twice as abundant ⁽⁶⁾ <i>Echinometra</i> urchins which are important bioeroders grew faster and were larger bodied at the vents ⁽¹³⁾
Structural complexity and habitat provision	Reduced structural complexity. ⁽⁶⁾ Little change in fish population but those seen were driven by change in reef structure and habitat provision ⁽⁷⁾
Coral disease	Increased abundance of disease and stress-associated bacteria (<i>Flavobacteria</i>) ⁽¹⁴⁾
<i>4. Puerto Morelos, Mesoamerica</i>	
Coral–coral competition	Reduced coral cover, smaller and patchier colonies ⁽¹⁵⁾
Coral–algal competition	Fleshy macroalgal abundance was 42% higher than the controls due to altered competitive dynamics ⁽¹⁶⁾
CCA	Acidified sites had 82% less CCA cover than controls. Potential due to CCA being outcompeted by fleshy macroalgae ⁽¹⁶⁾
Bioerosion	Bioerosion was greater in the springs with 78% more volume eroded than the surrounding areas. ⁽¹⁷⁾
Structural complexity and habitat provision	None of 3 species present are major framework builders so structural complexity is reduced ⁽¹⁵⁾
<i>5. Maug, Commonwealth of Northern Mariana Islands (CNMI)</i>	
Coral–coral competition	Significant reductions in coral cover ⁽¹⁸⁾
Coral–algal competition	Shift to macroalgae dominance, presumed to be in part due to changes in competition ⁽¹⁸⁾
Corallivory, food webs and herbivory	Herbivores tend to avoid the dominant species of macroalgae, potentially explaining the shift to macroalgae abundance ⁽¹⁸⁾
CCA	Reduced CCA abundance and species richness at most acidic site but an increase from control to intermediate ⁽¹⁸⁾
Bioerosion	Greater settlement of microborers and rates of biogenic dissolution on calcite blocks ⁽¹⁹⁾
Structural complexity and habitat provision	Loss of carbonate reef framework near vent ⁽¹⁹⁾

Table 3 (continued)

<i>6. Iwotorishima, Japan</i>	
Coral–coral competition	Initial shift to soft coral dominance before almost complete loss of corals ⁽²⁰⁾
Coral–algal competition	Macroalgae were not observed ⁽²⁰⁾
Corallivory, food webs and herbivory	Hypothesised control of macroalgae through grazing invertebrates and fishes ⁽²⁰⁾
Structural complexity and habitat provision	Shift from complex 3D hard corals to less complex softs corals ⁽²⁰⁾
<i>7. Galapagos, Eastern Tropical Pacific (ETP)</i>	
Coral–coral competition	Significant reductions in coral cover ⁽²¹⁾
Coral–algal competition	Possible evidence of <i>Caulerpa</i> algae competing and overgrowing corals but no evidence of how this varies along acidification gradient ⁽²²⁾
Corallivory, food webs and herbivory	Sea urchin <i>Eucidaris galapagensis</i> predate on corals; however, fishing is removing their natural predators and resulting in trophic release, with implications for corals. No evidence of how this varies along acidification gradient ⁽²²⁾
CCA	Reefs have low carbonate cementation ⁽²³⁾
Bioerosion	Bioerosion rates are very high and is a major limiting factor to reef growth. High bioerosion may be due to skeletal density > 30% lower in the most acidic reefs, compared to ambient ⁽²¹⁾ and very poor rates of reef cementation. ⁽²³⁾ Bioerosion contributed to the initial disturbance event resulting in coral mortality, and then removed the reef framework. ⁽²²⁾ Bioeroding urchin (<i>Eucidaris galapagensis</i>) are preyed by fish, however fish abundance is reduced due to fishing resulting in trophic release of urchins ⁽²²⁾
Structural complexity and habitat provision	Complete loss of reef framework in areas most affected by upwelling ⁽²¹⁾ Coral reef degraded from reef to a coral community ⁽²²⁾
<i>8. Shikine, Japan</i>	
Coral–coral competition	Complete loss of corals ⁽²⁴⁾
Coral–algal competition	Fleshy and non-calcifying macroalgal abundance increased 53%–98% between ambient and high $p\text{CO}_2$ but with a 56% reduction in diversity ^(24, 25) Turf-like diatoms were absent in the control but up to 100% of the substrate at the acidified site with presumed competitive superiority ⁽²⁶⁾
Corallivory, food webs and herbivory	Decreased diversity of fish and community shifts towards species more tolerant of reduced complexity, driven by shifts in algae, corals and CCA. ⁽²⁷⁾ There was no evidence of herbivory on the turf-like diatom mats. Simplification of food web ⁽²⁶⁾
CCA	Significant decline in % cover and species diversity, thinner crusts with minimal associated faunal communities ^(24, 25)
Bioerosion	Coral boring serpulids absent in more acidic sites ⁽²⁴⁾
Structural complexity and habitat provision	Sixfold decrease in complexity with acidity, with a shift from corals, calcified organisms and complex CCA structures, to low-profile, turf and non-calcified organism dominance, with low complexity of CCA ^(24, 25, 27) Decreased diversity of fish and community shifts towards species more tolerant of reduced complexity, driven by shifts in algae, corals and CCA. ⁽²⁷⁾
<i>9. Panarea, Italy</i>	
Coral–coral competition	Reduced population density ⁽²⁹⁾
Corallivory, food webs and herbivory	Significant decline in skeletal density and increase in porosity ⁽²⁹⁾
Bioerosion	Significant decline in skeletal density and increase in porosity ^(28, 29)
<i>10. Ishia, Italy</i>	
Coral–coral competition	Complete loss of corals ⁽³⁰⁾
Coral–algal competition	Increased abundance and biomass of some non-calcifying algal genera ^(25, 30, 31) at the seep compared to the control, with only 5% of macroalgae unable to tolerate acidified conditions ⁽³²⁾
Corallivory, food webs and herbivory	Simplification of food web with a decrease in herbivores and heavily calcified invertebrates ^(31, 33)
CCA	Declines in CCA abundance, from > 60% to 0% ⁽³⁰⁾ and diversity. ⁽²⁵⁾ Declines thought to be due to CCA being outcompeted by fleshy macroalgae ⁽³⁴⁾ . Two species CCA increased due to high magnesium skeletons, a decrease in competition and decreased predation pressure ⁽³²⁾

Table 3 (continued)

Bioerosion	Boring microbioeroders were negatively affected by acidification with lower bioerosion on aragonite blocks than in ambient conditions ⁽³⁵⁾
Structural complexity and habitat provision	Loss of corals ⁽³⁰⁾ and 80% decrease in colony size. ⁽³⁶⁾ Some complexity given by increase in erect macroalgae ⁽³⁷⁾
Coral disease	Tissue necrosis increased from <0.5% to 13% under acidified conditions but no evidence this resulted from disease ⁽³⁶⁾ No change in microbial communities with no evidence of microbial pathogens ⁽³⁸⁾

Bold text shows where an indirect effect has been tested. Normal text highlights evidence of a change which may result an indirect effect on corals but which has not been explicitly tested

1. Barkley et al. (2015); 2. Shamberger et al. (2014); 3. Shamberger et al. (2018), 4. Januar et al. (2016); 5. Januar et al. (2017); 6. Fabricius et al. (2011); 7. Munday et al. (2014); 8. Fabricius et al. (2014); 9. Smith et al. (2016); 10. Allen et al. (2017); 11. Fabricius et al. (2015); 12. Fabricius et al. (2017); 13. Uthicke et al. (2016); 14. Morrow et al. (2015); 15. Crook et al. (2012); 16. Crook et al. (2016); 17. Crook et al. (2013); 18. Enochs et al. (2015a, b); 19. Enochs et al. (2016a, b); 20. Inoue et al. (2013); 21. Manzello et al. (2014); 22. Glynn et al. (2018); 23. Manzello et al. (2008); 24. Agostini et al. (2018); 25. Peña et al. (2021); 26. Harvey et al. (2019); 27. Cattano et al. (2020); 28. Goffredo et al. (2014); 29. Fantazzini et al. (2015); 30. Hall-Spencer et al. (2008); 31. Kroeker et al. (2011); 32. Porzio et al. (2011); 33. Foo et al. (2018); 34. Kroeker et al. (2013); 35. Tribollet et al. (2018); 36. Teixidó et al. (2020); 37. Porzio et al. (2013); 38. Meron et al. (2012)

et al. 2014; Table 2). While this site provides optimistic evidence on the effect of acidification, there are a number of potential reasons for an increase in species richness. For example, the retention of $p\text{CO}_2$ adapted larvae within the semi-enclosed lagoon, the duration and source of acidic exposure (hydrographic processes; Golbuu et al. 2016) which result in alterations to other water chemistry parameters such as low total alkalinity, and habitat differences between the control (outer reef) and acidified (lagoon) sites reflecting differences in community composition.

A shift in coral community composition has been observed at every naturally acidified site studied to date compared to the control sites. This includes a shift from hard to soft coral (Iwotorishima, Japan), hard coral to macroalgae with corals still present (CNMI) or with corals absent (Shikine, Japan; Ishia, Italy), reduced richness of hard coral (PNG, Indonesia, Mesoamerica and ETP), and increased species richness of hard coral but a shift in dominant species (Palau; Table 2). This variety again shows the complexity of predicting the effect of acidification on coral communities but suggests that reefs are unlikely to retain their current composition in the future.

Evidence of indirect effects at naturally acidified locations

By reviewing studies of coral diversity and abundance at naturally acidified locations (Table 2), we identify some common indirect effects of OA that structure coral communities. The majority of sites (6 of 10) report an increase in macroalgal abundance as $p\text{CO}_2$ increases. These studies support interpretation of an increase in competitive dominance by algae, and overgrowth of corals (Enochs et al. 2015b; Glynn et al. 2018) and of CCA (Kroeker et al. 2013; Crook et al. 2016; Table 3) under OA, which in some cases resulted

in a complete phase shift to macroalgal abundance (Enochs et al. 2015b). In addition to changes in macroalgae, CCA consistently declines in abundance and diversity as $p\text{CO}_2$ increases (Table 3). Evidence from the PNG vents indicates that these declines in CCA abundance were the strongest predictor of recruit density (Fabricius et al. 2017) suggesting a reduction in CCA may have major implications for the long-term persistence of corals at this site. Effects on recruitment have yet to be investigated at any other site. However, acidification also appears to reduce reef cementation in the ETP (Manzello et al. 2008) and at the Shikine vent in Japan where the thick carbonate crusts formed in part by CCA were notably thinner (Peña et al. 2021). This indicates a potential reduction in substrate stability in the future, with further implications for additional declines in recruitment.

Bioerosion tends to be higher at the acidified sites compared to nearby control sites (Table 3). This is due to an increase in either the abundance of bioeroders (Fabricius et al. 2011) or their bioerosive capacity (Enochs et al. 2016a) and potentially exacerbated by decreased coral skeletal density (Manzello et al. 2014; Barkley et al. 2015). The extent of this bioerosion is variable but in the site where corals appear to fare best under acidification (Palau), bioerosion was still 11-fold higher than the control reefs (Barkley et al. 2015). Furthermore, at a reef with lower coral cover in the ETP, bioerosion resulted in the complete loss of the reef framework following a major coral mortality event and prevented recovery back to reef status (Manzello et al. 2014). Consequently, indirect effects of bioerosion on the integrity of coral skeletons and the reef substratum are a significant factor for long term persistence of reefs under acidification.

Linked to changes in coral cover and bioerosion, almost every site (8 of 10) exhibited a decrease in structural complexity with acidification (Table 3). These changes have indirect effects on other organisms, for example, changes in

abundance within the fish community from PNG were likely driven by changes in structure and habitat provision (Munday et al. 2014). However, the implications of such changes for corals have not been investigated. Without knowing whether the interactions with corals and fish and/or invertebrates had positive, negative or neutral effects on corals, it is hard to extrapolate what the impact of these changes might be. However, we stress that as the structural complexity of the reef plays a key role in ecosystem functions and processes, the indirect effects of loss of structural complexity on corals, and many other reef organisms, may be important.

Finally, the among-site differences in responses to changing $p\text{CO}_2$ highlight that there are many potential internal and external factors that moderate indirect effects and therefore may shape how coral communities respond to OA. For example, the indirect effects reported here for PNG and CNMI are similar (increased macroalgal abundance, decreased CCA, increased bioerosion and a decrease in structural complexity) yet in PNG coral cover is maintained and in CNMI coral cover decreases (Table 2). This difference may result from both direct physiological effects (calcification declined at CNMI but not at PNG) and indirect effects (in PNG there was evidence of an increase in herbivorous urchin (Fabricius et al. 2014), while in the CNMI, the herbivores avoided preying on the dominant algal species (Enochs et al. 2015b)). As highly complex environments, the number of potential external factors which may result in indirect effects is significant. For example, reefs are increasingly exposed to other anthropogenic stressors like rising water temperatures and decreasing water quality such as increased turbidity, pollution and/or eutrophication. Similarly, internal factors from within the coral holobiont, such as changes in both the microbial communities and zooxanthellae populations resulting from OA (Mason 2018; Biagi et al. 2020), may also act as a source of indirect effects on corals and coral communities. In conjunction with OA, these other factors may ultimately exacerbate the extent to which indirect effects affect corals and coral communities, either through compounding the effects highlighted here, or through additional indirect effects not yet considered. Clearly, potential feedbacks between changes in the physical environment as well as the diversity, abundance and behaviours of species in different coral reef trophic groups will shape coral reef futures.

The future of indirect effects research

In this review we have identified a range of indirect effects which have the potential to have significant impacts on coral and coral communities. Consequently, single-species studies that assess the effects of OA on coral physiology potentially underestimate the effects of OA on coral communities and limit our ability to extrapolate findings to an ecosystem

scale. We therefore recommend that the indirect effects of acidification be more widely considered in acidification research.

Indirect effects research can be done using a number of research methods. Small-scale, short-term experiments are the basis of much ocean acidification research and an effective method to establish the impact on simple or paired interactions. Larger-scale, long-term aquaria or mesocosm experiments allow us to potentially include more ecosystem functions/processes such as competition and bioerosion. However, these experimental set-ups are limited in ecological complexity and therefore need to target specific species, interactions or processes. *In-situ* manipulations are becoming more feasible through the use of FOCE (Free Ocean Carbon Enrichment; Stark et al. 2019) and SCoRE-FOCE (Shallow Coral Reef Free Ocean Carbon Enrichment; Srednick et al. 2020) experimental flumes. *In-situ* flumes use natural communities and therefore have greater ecological complexity; however, they may be unable to account for interactions with more mobile taxa such as fish and can be challenging/expensive to run over ecologically meaningful timescales. FOCE experiments may therefore be most useful for research on benthic indirect effects such as bioerosion.

At present, studies using naturally acidified sites remain the only method where it is possible to consider large-scale community and ecosystem level effects, including multi-species interactions and effects on food-webs, using corals which have experienced lifetime exposure to acidification. However, these sites are not perfect analogues of future acidified conditions. For example, these sites often have connectivity to ambient reefs which allows new recruits to arrive from ambient reefs and movement of mobile organisms in and out of the acidified area (Munday et al. 2014). Physically these sites may also differ from future acidified reefs. For example, the source of acidity may also result in other changes to the water chemistry such as elevated levels of DIC (dissolved inorganic carbon; Crook et al. 2012) or other volcanic gases or elements (see review; Gonzalez-Delgado and Hernández 2018). Nevertheless, these sites are useful proxies to identify indirect effects of potential concern. We suggest that a combination of all research methods will allow us the greatest progression in our understanding of the indirect effects of acidification on corals.

Here we focused specifically on how indirect effects affect corals and coral communities but our review of the literature illuminates many other potential indirect effects via other taxa, and potentially complex feedbacks among taxa in different trophic groups. For example the increased competitive success of fleshy algae over CCA (Crook et al. 2016) which may or may not be mediated by herbivory. Interactions such as these equally have the potential to affect structure and function of our future coral reefs and also need to be investigated. Understanding ecosystem trajectories is particularly

challenging when ecosystem functioning could change via a cascade of altered interactions, such as what might occur in response to an ecological tipping point or within a trophic chain (e.g. Ferreira et al. 2021). Clearly, however, the ecological impact of these indirect effects can be significant (Mumby 2017), and therefore identifying and understanding them is vitally important in our ability to scale up direct physiological effects of OA to an ecosystem level.

Future directions and knowledge gaps

Our review highlights multiple pathways of indirect effects of OA that have the potential to exacerbate the impact of the direct physiological effects on coral colonies (i.e. lower calcification, slower growth, decreased recruitment) and communities (reduced hard coral abundance and species richness). These direct effects, alone, can have flow-on effects to reef ecosystem services like food provisioning and coastal protection. Based on our synthesis of the literature, we propose that the indirect effects of greatest concern are that a decline in CCA, and the settlement cues and habitat they provide, is likely to drive a reduction in recruitment of corals and impede population replenishment after disturbances. We suggest that manipulative field experiments, such as controlled seeding of coral larvae at naturally acidified locations and monitoring of settlement success and post-settlement survival compared with nearby control locations, are needed to resolve existing data gaps. Moreover, declining CCA will lead to diminished levels of reef cementation which can cause coral mortality due to substratum instability (Madin et al. 2012). Detailed monitoring of coral survival after storms at naturally acidified locations compared with nearby control sites, accompanied by measurement of CCA abundance and substratum strength, will provide new insights about how CCA loss affects coral survival.

In addition to changes in CCA, increased bioerosion is likely to compound effects of decreased calcification and increase dissolution, to shift corals from net skeleton accretion towards net skeleton loss. While as yet there is limited evidence of a significant direct effect on coral abundance and diversity resulting from reduced structural complexity, a recent study indicates that coral biodiversity is highest at intermediate roughness (rugosity) of reef substrata (Torres-Pulliza et al. 2020). Field-based observations of the magnitude of bioerosion, and the diversity and abundance of bioeroding taxa, are required to link changes in bioerosion to differences in structural complexity on reefs, and to link these changes to coral diversity. A loss of structural complexity on reefs due to OA (via decreased cementation and increased erosion) is also likely to result in changes to reef functions more broadly. More complex reefs support higher

diversity and abundance of fishes and therefore OA could affect the critical reef ecosystem services of food provision.

Our review highlights the need to extend from single species studies, to studies that explicitly characterise how species interactions change, and how trophic linkages are altered, as $p\text{CO}_2$ increases. Key knowledge gaps in the literature include the effects of OA on: the prevalence and outcomes of competition between corals and other benthic organisms in the field; the prevalence and impact of predation by corallivores on corals, as well as effects on mutualistic interactions between corals and small fishes that live within their branches; the prevalence and virulence of pathogens that cause coral diseases; and the capacity for herbivorous fishes to reduce coral–macroalgal competition. We recommend that mesocosm experiments that manipulate seawater carbonate chemistry are used alongside field observations at naturally acidified sites to generate new knowledge of OA effects. Understanding how both the direct and indirect effects of OA impact the ecosystem engineers of coral reefs, and how these effects propagate throughout the entire reef foodweb, is critical to predicting coral reef futures as atmospheric and seawater $p\text{CO}_2$ continue to increase.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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