

Multiple and cumulative impacts on the GBR: assessment of current status and development of improved approaches for management: Final Report Project 1.6

Uthicke, S. , Fabricius, K. , De'ath, G. , Negri, A. , Smith, R. , Warne, M. St. J. , Noonan, S. , Johansson, C. , Gorsuch, H. and Anthony, K.

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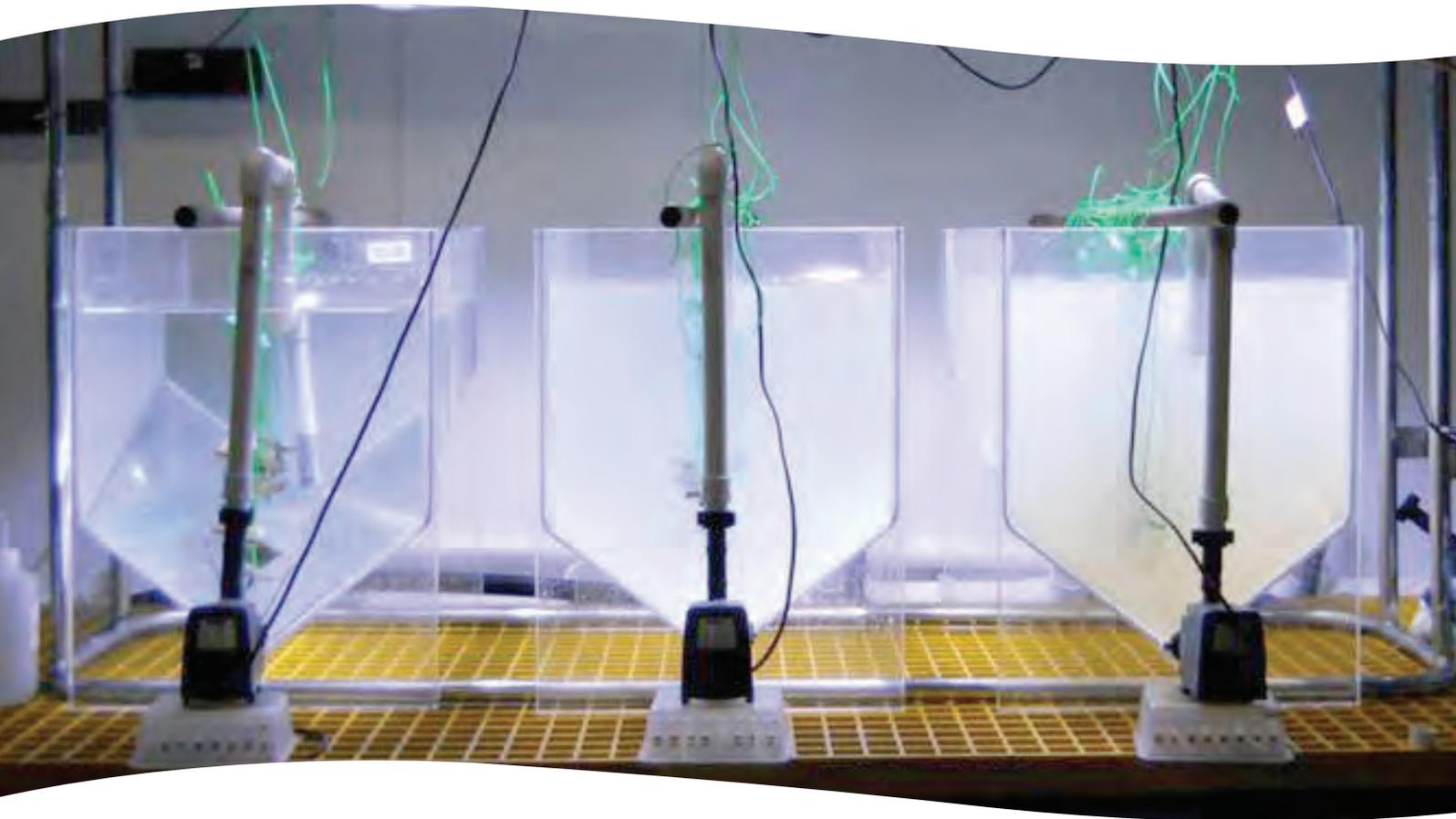
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Sven Uthicke¹, Katharina Fabricius¹, Glenn De'ath¹, Andrew Negri¹, Rachael Smith², Michael Warne³, Sam Noonan¹, Charlotte Johansson¹, Hayley Gorsuch¹, Ken Anthony¹

¹ Australian Institute of Marine Science

² Department of Science, Information Technology and Innovation

³ Centre for Agroecology, Water and Resilience, Coventry University, Coventry, United Kingdom



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ACRONYMS

BBNs	Bayesian Belief Networks
BTs	Boosted trees
CA	Chemical Addition
CDFs	Cumulative Distribution Functions
CI	Cumulative Impact
CIRA	Cumulative Impacts Risk Analysis
CoTS	Crown of Thorns Seastar
DotE	Department of the Environment
DPSIR	Driving-Pressures-State-Impacts-Responses framework
EC	Effect concentrations
EC10	10% Effect Concentration
EC50	50% Effect Concentration
GAMs	Generalised additive models
GBR	Great Barrier Reef
GBRMPA	Great Barrier Reef Marine Park Authority
GBRWHA	Great Barrier Reef World Heritage Area
GLMs	Generalised Linear Models
HUs	Hazard Units
LOEC	Lowest observed effect concentration
ML	Machine learning
MoA	Mode of action
ms-PAF	Multisubstance-potentially affected fraction
NERP	National Environmental Research Program
NESP	National Environmental Science Programme
NOAA	National Oceanic and Atmospheric Administration
NOEC	No Observed Effect Concentration
OA	Ocean Acidification
PAFs	Potentially Affected Fractions
PC95	95% species protection
PC99	99% species protection
RA	Response Addition
RIMReP	Reef 2015 Integrated Monitoring and Reporting
RRRC	Reef and Rainforest Research Centre Limited
SCIRA	Spatial Cumulative Impacts Risk Analysis
SSDs	Species sensitivity distributions
SST	Sea Surface Temperature
TTI	Thermal Tolerance Interval
TUs	Temperature units
TWQ	Tropical Water Quality

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EXECUTIVE SUMMARY

The outlook of the Great Barrier Reef (GBR) was recently assessed as poor and declining (Great Barrier Reef Marine Park Authority [GBRMPA], 2014a; GBRMPA, 2014b). Impacts on the Region's values do not occur in isolation but overlap in time and space, thus reducing the overall resilience and health of the Reef. Understanding cumulative pressures and their impacts has become a priority for environmental policy, management and conservation globally. In Australia, a fuller understanding of cumulative impacts from global and local stressors, and the ability to attribute those impacts to specific drivers and activities, is now a priority, as reflected in the Reef 2050 Long-Term Sustainability Plan. Despite such prioritisation, reef managers currently rely largely on qualitative tools to assess risks from cumulative impacts associated with development proposals (GBRMPA, 2009).

This Report focuses on coral reef environments and provides: (i) a comprehensive review and synthesis of existing tools and qualitative and quantitative studies that describe the cumulative impacts of local and global pressures on reef organisms and processes, (ii) an overview of important knowledge gaps and future research priorities, and (iii) a roadmap to develop a practical framework (incorporating quantitative approaches for assessing risk of multiple stressors) to support the assessment and management of cumulative impacts on the GBR.

To provide a clearer understanding of the concepts and problems around the science of cumulative impacts on coral reef environments, we reviewed and evaluated the existing knowledge of the cumulative effects of specific pressure combinations. This review also identified essential gaps in the information needed to guide effective management decisions and potential solutions.

We identified existing limitations in the interpretation of interactive effects, and propose a toolset to assess cumulative impacts, using approaches from statistical, ecotoxicological, conceptual, semi-quantitative and quantitative mechanistic models, and structured decision analyses.

We identified the generation of risk and exposure maps, together with the assessment of pressure and value thresholds, as key approaches to a greater understanding of the accumulation of pressures on specific locations or ecological communities to better inform management decisions (e.g. for the purpose of assessing permit applications). We present a prototype for an improved method to produce risk maps, through incorporating: (i) spatially explicit data (such as those available via eReefs and eAtlas) on the temporal variability of pressures, and (ii) improved mechanistic understanding of how multiple pressures interact and what the ecological consequences are.

This Report concludes that combinations of tools from different disciplines are essential to advance our understanding of cumulative impacts.

We summarise our findings into a **Roadmap** (Section 3) to provide a practical framework for incorporating quantitative approaches for assessing risk of multiple stressors to support the assessment and management of cumulative impacts on the GBR.

Simple, linear changes in ecosystems are rare, and it is likely that ecological thresholds under multiple pressures are different to physiological thresholds observed under single or even multiple pressures. It is also likely that thresholds and responses change over ecologically relevant time frames, through either acclimatisation of organisms that ameliorate pressures, or accumulation of effects that exacerbate the responses to pressures. Predictions without experimental or field confirmation of responses may lead to false conclusions, and hence suboptimal management investment.

Addressing these complexities is recommended as an immediate focus of further research to provide an improved knowledge base for the assessment of cumulative impacts on coral reef environments in the GBR and the development of a toolset to specifically identify:

- Pressure combinations that represent high risk;
- Analysing spatial distribution and intensity of cumulative pressures in exposure and risk maps;
- Key value-based environmental responses; and
- Critical pressure thresholds for these responses.

The recently commenced Project NESP 2.1.6 “From exposure to risk: novel experimental approaches to analyse cumulative impacts and determine thresholds in the GBRWHA” has been designed to address some of these key knowledge needs

Summaries of the four detailed review, synthesis and evaluation chapters presented as Appendices are as follows:

The **review of existing knowledge** presented in **Appendix A** summarises case studies of cumulative impacts of global and local pressures on coral reef organisms. It reveals that in most cases the joint effects of a global and a local pressure is aggravating organism responses. For most organisms, including corals, very few combinations of pressures have been investigated, and even fewer studies have quantified the combined effects of pressures. Given the management relevance, prioritisation of future work to understand these interactions is essential to: (i) quantify cumulative pressures on reefs (e.g. for permit assessments), (ii) predict future thresholds of individual pressures under climate change, and (iii) model scenarios to reduce cumulative pressure by reducing individual pressures. The **pressures** of greatest priority for GBR communities are those ranked as ‘very high’ by the Outlook Report, namely altered weather pattern (especially storms, floods), temperature rise, ocean acidification, sea level rise, nutrient run-off, sediment run-off, outbreaks of crown-of-thorns starfish, and illegal fishing. Given strong management interest in dredging and sediment runoff, along with a paucity of relevant data, we recommend light/turbidity and sediment-bound pollutants (including nutrients) as the priority of local pressures to test. The **pressure combinations** of greatest concern for management are those that combine ‘manageable’ pressures, and/or a ‘manageable’ pressure in combination with global pressures. Because global pressures (ocean acidification and warming) will continue to increase, these factors will both remain essential components in future multiple pressure studies.

The problem of cumulative impacts is so complex that additional modelling tools are needed in support of cumulative impact assessments. In **Appendix B**, we first present a structured approach to show how cumulative impact assessments can **inform decision making**,

building on the Drivers-Pressures-State-Impacts-Responses (DPSIR) framework. We then briefly review models that can comprise the analytical toolset of cumulative risk assessments, ranging from conceptual to highly quantitative models. Lastly, we present a new **dynamic mechanistic model** that enables predictions of cumulative risk in space and time for complex environmental scenarios. This model integrates knowledge of biological stress responses in corals with experimental and observational data to provide quantitative estimates of risk and associated uncertainty. We apply the model to a cumulative impacts problem for corals on inshore reefs and produce cumulative impact risk maps for a set of environmental scenarios driven by run-off and climate change. We show how these maps, in combination with summary results of model outputs, can guide management decisions around development proposals, or test environmental scenarios that can quantify risks or cumulative impacts.

We recommend that further experimental work will be essential to define thresholds and understand response mechanisms. To support the selection of the best methods to analyse and interpret complex ecological data, the Report reviews a selection of ecotoxicological and biostatistical tools.

Ecotoxicology has its own set of tools to investigate cumulative pressures of several stressors (usually chemicals). **Appendix C** contains a review of existing ecotoxicology methods to deal with multiple stressors and cumulative effects. It identifies two methods that can assist in the analysis of multi-factor experiments that can be transferred from ecotoxicology to ecological questions. We show that (i) the formal methods and criteria of ecotoxicology can be applied to GBR-relevant environmental pressures; (ii) the models used to investigate responses to multiple pressures can be applied to both single species and ecological communities, and (iii) data generated in ecotoxicology experiments can be used to parameterise and validate broader risk models (e.g. those presented in Appendix B).

In **Appendix D**, we revisit and review the **statistical methods** suitable for analyses of cumulative pressures, using case studies to illustrate possible pitfalls in the analyses of multiple pressure experiments and field data. Machine learning methods can complement traditional statistical methods and are useful for the analysis of complex data. Examples of one experimental dataset and two field studies are used to illustrate how these techniques can help to (i) choose the appropriate models for analysis, (ii) tease out the most important pressures influencing communities in field data, and (iii) quantify the effects of multiple pressures.

1.0 INTRODUCTION

1.1 Operational definition of cumulative pressures

Understanding cumulative pressures and their impacts has become a priority for environmental policy, management and conservation globally (Halpern, Walbridge et al., 2008; GBRMPA, 2014a; GBRMPA, 2014b). In Australia, a fuller understanding of cumulative impacts from global and local stressors, and the ability to attribute those impacts to specific drivers and activities, are now a priority at both federal and state (Queensland) government levels, as reflected in the Reef 2050 Long-Term Sustainability Plan (Commonwealth of Australia, 2015). Despite such prioritisation, however, reef managers currently rely largely on qualitative tools to assess risks from cumulative impacts associated with development proposals (GBRMPA, 2009).

Coastal marine ecosystems are subjected to a multitude of natural and anthropogenic pressures (Jackson et al., 2001; Duarte, 2014). Historically, overfishing including intertidal harvesting is likely to be the first anthropogenic pressure to marine systems dating back hundreds if not thousands of years (Jackson et al., 2001). Over time, other pressures such as eutrophication and pollution, physical habitat destruction and marine invasive species added to the spectrum of pressures. Today, most areas of the coastal seas and open ocean are exposed to cumulative pressures caused by human activities or natural pressures. Cumulative pressures from human activities have increased demonstrably over just 5 years from 2008 to 2013 in over 60% of the world's oceans (Halpern, Frazier, et al., 2015). This is attributed mainly to increasing climate change and ocean acidification resulting from the build-up of greenhouse gasses in the atmosphere (Jackson et al., 2001; Duarte, 2014).

Because many of the past pressures continue to persist as new pressures are being added, the overall outcome could be conceptualised simply as a 'stacking up' or a growing set of *cumulative pressures* (Figure 1). While illustrative, this schematic assumes a simple additivity of pressures and neglects acute impacts, two assumptions that may not always apply. We discuss this problem in detail in Appendix D.

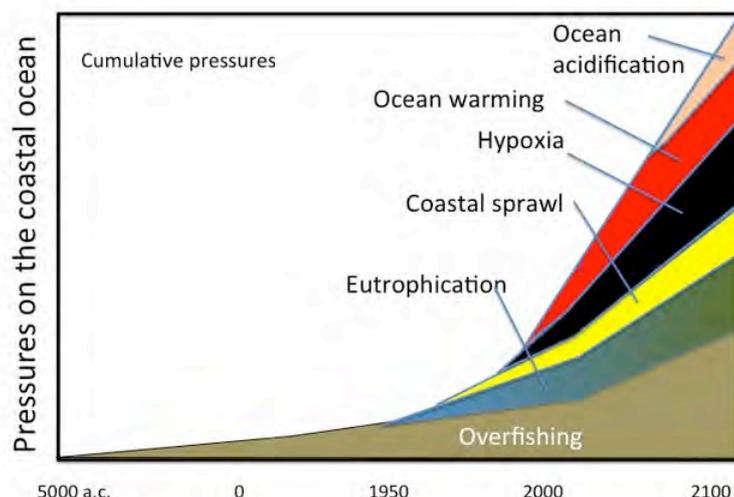


Figure 1: Pressures on coastal ecosystems, modified from Duarte (2013).

A suite of pressures, also sometimes (erroneously) referred to as impacts (GBRMPA, 2014b) or (more correctly) threats (GBRMPA, 2014a) affect coastal ecosystems like the GBR (Table 1). The causes (drivers or activities) of these pressures can be global or local. Many global pressures are due to increased greenhouse gasses in the atmosphere through fossil fuel burning, which leads to climate change and ocean acidification (OA). The GBR Outlook Report 2014 acknowledges that climate change is likely to represent the greatest threat to the GBR (GBRMPA, 2014a). Addressing climate change requires international collaborations and commitments to a shift to alternative and renewable energy sources (IPCC, 2014). Many other pressures on the GBR are local or regional, caused by changing land-use practices, fishing, coastal developments and human population growth in the coastal zone. Both the GBR Outlook Report 2014 (GBRMPA, 2014a) and the Strategic Assessment (GBRMPA, 2014b) provide an analysis of pressures, the drivers and activities giving rise to these pressures and their current threat to the GBR (see short summary in Table1).

A set of general principles to help understand the relationships linking human activities and ecological outcomes can be derived by applying the *Driving Forces-Pressures-State-Impacts-Responses* (DPSIR) framework to represent the linked social-ecological system and associated ecosystem-based management for the GBR (Atkins et al., 2011; Gregory et al., 2013; Gari et al., 2015). Firstly, co-occurring or sequentially occurring individual drivers or activities can result in cumulative pressures, which can lead to cumulative effects via multiple pathways. For example, land clearing and poor land-use practices associated with cane farming and grazing can increase the sediment, nutrient and pesticide load on the GBR, consequently affecting multiple biological and ecological processes (e.g. Brodie et al., 2012; Schaffelke et al., 2013; Thorburn et al., 2013). Secondly, multiple drivers and activities can amplify one or several pressures, leading to a convergence or accumulation of effects. For example, over-application of fertiliser on farmlands coinciding with storm activity leading to floods combine to exacerbate the nutrient export from agricultural areas and, hence, the nutrient load on the GBR (Lough et al., 2002). The same floods are likely to simultaneously export recently applied pesticides, sediments from soil erosion and freshwater into the coastal zone where effects accumulate further.

Table 1: List of pressures relevant for the Great Barrier Reef World Heritage Area. Only those threats identified in the GBR Outlook Report (GBRMPA, 2014a) as “Very High” or “High” risks to the GBR Region’s ecosystem are listed. L = local, G = global, A = acute, C = chronic.

Pressure/Threat	Local vs. Global cause	Acute/Chronic	Risk to ecosystem
Ocean warming	G	C/A	Very High
Ocean acidification	G	C	Very High
Cyclones/altered weather patterns	L (G)	A/C	Very High
Illegal fishing and poaching	L	C	Very High
Incidental catch of species of conservation concern	L	A	Very High
Nutrient runoff	L	C/A	Very High

Outbreak of Crown of Thorns Seastars	L	A	Very High
Sediment runoff	L	C/A	Very High
Coastal habitat modification	L	C	Very High
Sea level rise	G	C	Very High
Pesticide pollution	L (G)	C/A	High
Barriers to flow	L	C	High
Discarded catch	L	A	High
Extraction of predators	L	A/C	High
Disposal of dredge material	L	A/C	High
Marine debris	L (G)	A/C	High
Extraction from spawning aggregations	L	A/C	High
Outbreak of disease	L (G)	A	High

Inconsistent terminology has slowed progress on the topic of cumulative impact assessments and current needs are not being met. This Report **defines** the most critical used terms such as cumulative pressures, interactive effects and synergistic responses.

1.1.1 Definition of Terms

Term	Approximate Equivalents/ Synonyms/ Proxies	Definition and Comments
Acute	'Pulse'/episodic disturbance	Pressure acting at a time scale that is short relative to the life expectancy of an organism (causing a rapid adverse response e.g. death or reduced growth). Typically less than 2 weeks duration for invertebrates and less than 3 weeks for fish.
Additivity		In a statistical sense – models without interactions. In a general sense – a term used to describe the overall response of an organism or ecosystem to multiple pressures that do not interact.
Antagonism	Mitigating factor	'Acting in opposition' or 'an action/process/feature that counteracts the other one, the agonist' or 'a drug or chemical substance that interferes with the physiological action of another, especially by combining with and blocking its receptor'. The combined effect of several pressures is smaller than the sum of the individual effects. A commonly used term in multiple pressure studies for mitigating interactions, indicating that the presence of one pressure ameliorates the response to another pressure. Comment: The same caveats apply as for synergism. This term

		is too ill defined to be of any use, and should be avoided. We propose to instead report on the direction and intensity of the joint effects.
Chronic	'Press' disturbance	Lingering or continuing exposure to a pressure (can be at the same or variable intensity) over a substantial proportion of an organism's life span. Typically longer than 2 weeks for invertebrates and 3 weeks for fish.
Cumulative impact (CI)	Cumulative effect	'Cumulative effects are changes to the environment that are caused by an action in combination with other past, present and future human actions' (Hegman et al. 1999).
Cumulative pressure	Cumulative stressor, multiple stressor	Single pressure acting in the same space repeatedly over time or over prolonged periods of time, and/or multiple pressures that coincide in space and/or time.
Driver	Stress source	Natural or anthropogenic root cause or process. An overarching cause of change in the environment (GBRMPA, 2014b) Comment: Includes activities in DPSIR framework
Effect size		Magnitude of response, compared to control conditions.
Ecological Risk Assessment		The process for evaluating how likely it is that the environment may be impacted as a result of exposure to one or more environmental stressors such as pollution or temperature.
Ecological threshold		The point or range in a non-linear response in ecological or biological systems to pressures caused by human activities or natural processes, after, or outside of which, the system enters into an undesirable state. Comment: When an ecological threshold has been passed, the ecosystem is considered to be under increased risk of no longer being able to return to its original state. Knowing environmental values of major transitions can help optimise ecosystem management actions
Management response		Action/decision taken by environmental managers
Multiplicative		In a statistical sense – models containing an interaction, thus not additive
Pressure	Stressor, Disturbance, Agent, Threat,	An environmental factor that is tested for its effect on biological performance/biological systems. Comment: Consequence of a driver or activity in the DPSIR framework
Response	Effect, Impact	A measure of biological performance following an event/perturbation (responses may be at the level of genetics, biochemistry, energetics, physiology, population and community ecology, etc). Comment: Note that 'response' here is different from management response in DPSIR framework.
State		A measure of an ecosystems or biological system health or condition. Examples can be coral cover, physiological performance and biodiversity.

		<p>Comment: State is not necessarily indicative of ecosystem health as a poor state can be transitory (e.g. recovering from a disturbance).</p>
Statistical Interaction		<p>Two or more independent pressures interact if the effect of one of the pressures differs depending on the presence/intensity of another pressure (on the modelled scale).</p> <p>Comment: We will show in Appendix D that the presence of an interaction <i>on the observed scale</i> can only be assessed in linear models, i.e. for unbounded data. For others, interactions are assessed <i>on the modelled scale</i>. For example, a response that shows an interaction on the observed scale in a linear model in response to two environmental factors, may show no interaction in a generalised linear model or on the log scale (here, effects are additive). Hence, the model type and scales need to be specified when assessing the presence of interactions.</p>
Synergism	Aggravating factor	<p>A commonly used term in multiple pressures studies for aggravating interactions: the combined effect of several pressures on a response is greater than the sum of the effects of the individual pressures. Opposite: antagonism.</p> <p>Comment: We will show in Appendix D that this term is ill defined, and should be avoided. For example, multiplicative effects are additive on the log scale, and both synergistic, additive and antagonistic relationships are found along logistic response curves. We propose to not use the term 'synergism', and instead report on the direction and intensity of the joint effects at any one level of pressure.</p>

1.2 Types of cumulative pressures

In addition to the temporal perspective discussed above, a variety of different types of cumulative pressures are discussed in the literature or used in environmental impact statements (Crain et al., 2008; Halpern, McLeod, Rosenberg, and Crowder, 2008; Anthony et al., 2013; Brown et al., 2013; Halpern, Frazier, et al., 2015). These include relatively simple cases such as the addition of a pressure on a group of species or a system that is already under pressure from human activities, e.g. the impact of increased boating operations associated with harbour expansion on already declining populations of bottlenose dolphin (Parra et al., 2006) and dugong (Grech and Marsh, 2008). More complex cumulative impacts can be predicted in response to multiple pressures (e.g. Anthony et al., 2013).

Cumulative effects caused by **the same pressure** (Figure 2A) accumulate in a range of ways through time and space. Some examples include:

- Sequential acute events of the same pressure, such as those caused by repeated maintenance dredging campaigns in the same area or seasonally occurring runoff events affecting the same coral reefs, year after year.
- Subsequent acute effects occur before full recovery from the previous stress event.
- Simultaneous pulses of the same pressure, such as sediment plumes from dredging of multiple terminals within the same development.

- Chronic (long term) exposure to the same pressure, for example ocean warming leading to supra-optimal temperatures for growth and reproduction (De'ath et al., 2009) and ocean acidification effects on early life-history processes (Albright and Langdon, 2011; Byrne et al., 2013; Uthicke et al., 2013).

Cumulative effects by **multiple pressures** are even more complex. Some examples are given in Figure 2B. A simultaneous or successive effect by two or three (or more) acute events may lead to reduction in ecosystem health. On the GBR it is not unusual for reefs to be successively affected by Crown of Thorns Seastar (CoTS), cyclones and bleaching from thermal stress. In a DPSIR framework, this means that numerous drivers and activities, as diverse as atmospheric changes in carbon dioxide concentrations, fisheries and agriculture, may interact to lead to cumulative pressure. Combined effects from land runoff and climate change have been much debated (e.g. Wooldridge and Done, 2009; Fabricius et al., 2013) and were the subject of several recent NERP projects (summarised in Appendix A). Some of these pressures (especially the global and mostly chronic pressures of ocean acidification and global warming) can be seen as slowly ramping up over decades, while other pressures simultaneously affect the community in an acute or chronic fashion.

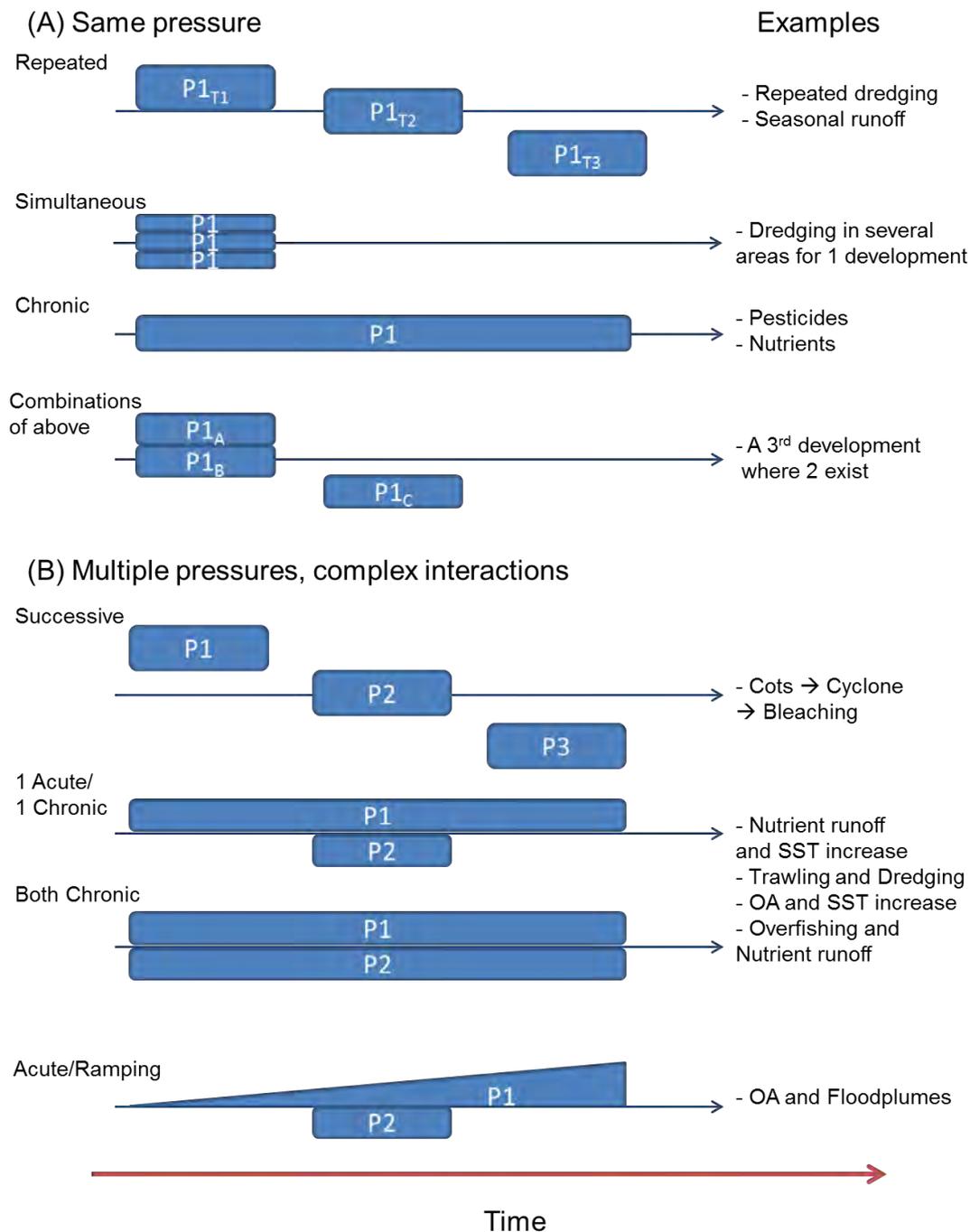


Figure 2: Different types of cumulative pressures (P1, P2) on marine ecosystems. Pressures with different subscript (e.g., P1A, P1B) denote similar pressures derived from different drivers or activities.

From a scientific perspective, cumulative effects from an individual pressure on single species are relatively straightforward to investigate because responses to only one pressure need to be quantified. For example, whether a coral is exposed to sedimentation from one or several dredging events at the same time is immaterial, as long as the total exposure is known, which can be derived by simple addition. Similarly, the effect of chronic exposure can be established in time-course experiments with individual pressures on individual species. However, understanding the community or ecosystem effects of the cumulative effects from an individual pressure is a challenge. Furthermore, most pressures do not act in isolation.

For example, a development project may exert a new acute or chronic pressure on a reef that is potentially already weakened by warming sea temperatures and OA. Therefore, one could argue that all new and previous pressures (whether continuing or not) should be considered in the context of a multiple pressures or cumulative effects framework (see Appendix B) (Brown et al., 2013).

Two main descriptors are needed to quantify exposure to these pressures. These factors are their **intensity** (concentration or level) and their **duration or frequency**. For the latter, pressures may be classified as **acute** (Table 1), e.g. bleaching after a few weeks of unusually high temperatures or **chronic**, e.g. eutrophication/overfishing. However, the classification of pressures into instantaneous acute (pulse-type) and chronic (press-type) categories can be blurred for some pressures that are variable in intensity (e.g. turbidity, sedimentation and heat stress/warming) and will vary spatially and across levels of organisation (individuals versus ecosystem).

In the field, multiple pressures will also exert different effects depending on their timing, i.e. whether they occur simultaneously or sequentially. If they are sequential, the attribution of effects will be co-determined by the sequence of events, i.e. which pressure comes first. For example, once a reef has lost significant coral cover from a storm, then predation by CoTS will not cause much additional damage, and vice versa. Another crucial factor to determine the effects by sequential pressures is recovery time and successional processes. For example, if a coral community is in an early stage of recovery and dominated by small colonies, then that community is less fragile to storm damage. Many chronic and acute disturbances are not amenable to management on a local scale (storms, bleaching events, OA etc.). Thus, it is important to determine which factors determine rates of recovery, and to what extent these factors can be managed. Determinants for rates of recovery may be chronic environmental conditions, which in turn are chronic pressures that also accumulate, such as high turbidity and consequently low light, high rates of sedimentation, nutrient enrichment, as well as species composition (vs. massive coral morphologies), and specific coral traits that can differ between species and locations (rates of growth, recruitment and fecundity).

Some combinations of pressures are typically independent (e.g. CoTS outbreaks and storms), except where storms, for example, lead to floods and nutrient pulses that in turn can lead to the facilitation of CoTS outbreaks in subsequent years (Fabricius et al., 2010). However, other pressures are typically confounded (e.g. sediments, dissolved inorganic nutrients, pesticides and reduced salinity typically co-occur in flood plumes)(Devlin and Brodie, 2005; Devlin and Schaffelke, 2009; Brodie et al., 2010). In the latter case, it is often difficult to attribute the measured effect to any specific pressure based on field data. In situations where a manager or a regulator is charged with the task of identifying the activity most likely to cause the observed effect, insight into the processes that led to the effect can be informed by mechanistic models calibrated by multifactorial experiments and parameterised by the relevant environmental variables. We address this more specifically in Appendix B.

1.3 Cumulative Risk Maps

Risk maps are useful to assess correlations between human pressures and their potential ecological consequences. Risk maps also provide an intuitive and visual way to illustrate risk to the cumulative effects as a result of exposure to multiple pressures. These are often generated by summing up individual pressures for each pixel on a map. Although individual pressures are often weighted, interactions between individual pressures are usually assumed to be additive. Better knowledge of how pressure interact would allow for the creation of improved risk maps but at present ‘...the default additive model remains the only feasible option’ (Halpern and Fujita, 2013).

One of the first examples of a risk map of cumulative pressures for marine ecosystems on a world-wide scale was produced by Halpern, Walbridge, et al. (2008, Figure 3). This study developed a cumulative effect index by simply summing the severity of unique types of pressures (log-transformed and scaled) that coincided per pixel in space, to identify the areas at greatest risk. A similar approach was applied to assess the cumulative pressures from human activities on more regional scales, such as a Hawaiian Marine Protected Area (Selkoe et al., 2009), the Mediterranean Sea (Micheli et al., 2013), the Baltic Sea (Andersen et al., 2015), Western Canada (Ban et al., 2010) or the California Current (Halpern et al., 2009). Risk maps can also be produced to describe cumulative risks to species or species groups arising from various human activities (Maxwell et al., 2013). For example, the global assessment of human-induced effects presented by Halpern, Walbridge, et al. (2008) showed weak but significant negative correlations to species richness (Tittensor et al., 2010).

The same research group also developed a global ocean health index in which the oceans of each marine nation are assessed against 10 ‘public goals’ taking into consideration status, trend, pressure and resilience (Halpern et al., 2012; Halpern, Longo, et al., 2015). Australia’s score (77) in 2013 was distinctly better than the average global score of 67 (Halpern, Longo, et al., 2015).

Within the GBR region, Johnson et al. (2013) presented a cumulative exposure map based on regional differences in the exposure to freshwater inundation, temperature increase and past cyclone frequency. The large-scale assessments of cumulative risks through exposure maps typically focus on chronic pressures, and provide poor insight into more stochastic acute pressures.

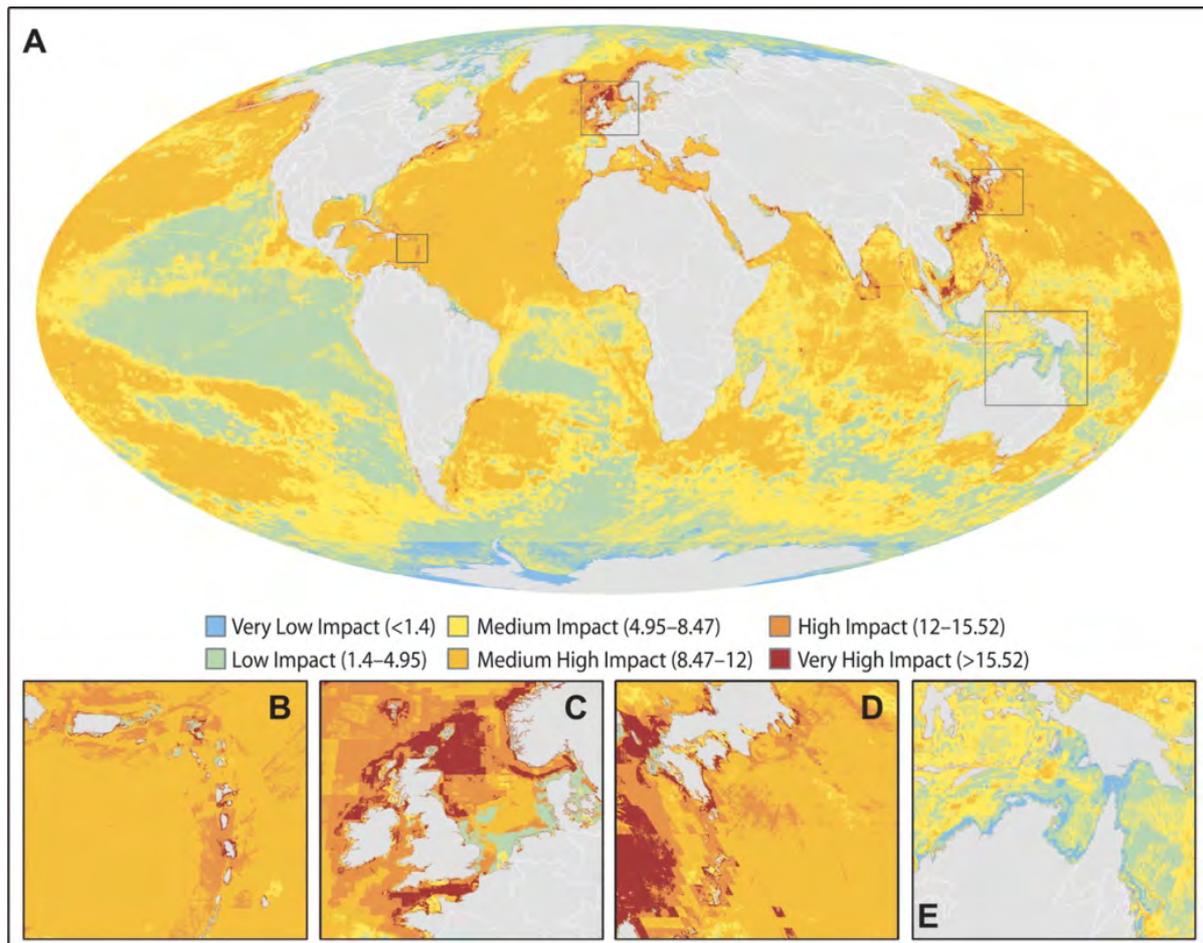


Figure 3: Maps of cumulative risks to the oceans ecosystems derived by Halpern, Walbridge et al. (2008).

1.4 Cumulative impacts of multiple pressures

The question of whether **the effect of one pressure is independent of the presence of another pressure** (or previous exposure to the same pressure) is a key challenge for cumulative impact assessments. The complexity of this question is due to a number of factors:

- The large **number of pressure** types that potentially co-occur (Table 1).
- The **wide range of exposure intensities and their temporal and spatial variability**, and changes that may range from a few percent (e.g. mean summer maximum sea surface temperature) versus changes of several orders of magnitude (e.g. benthic irradiance).
- The **different types of responses** (from gene expression to survival of different life-history stages of multiple species). **Both direct (physical or physiological) and consequential (ecological) effects to multiple pressures** need to be considered. Laboratory experiments typically investigate the direct effects of one or multiple pressures (e.g. on the physiology/survival of individual organisms). However, in ecosystems the same pressures will exert a multitude of indirect and flow-on effects through ecological changes such as altered species interactions or habitat quality (e.g. high nutrients and sediments not only stress corals directly, but they also increase competition with macroalgae). Such flow-on effects may cause more severe effects on the organisms, populations and the ecosystem under investigation than

predicted from experimental experiments. This highlights the importance of combining experimental studies with field data for validation.

- The importance of **relevant co-variables** when assessing cumulative impacts. For example, the effect of a certain concentration of toxins on a species may differ as a function of body size/ age or sex.
- **Different timing of multiple pressures** (simultaneous or sequential exposure) will also lead to different impacts, which is especially relevant for field data. For **simultaneous** exposures, most critical would be the intensity of the pressures, and their duration. Effects of **sequential** exposures to the same or different types of pressures are only cumulative if recovery is incomplete before the next exposure occurs (e.g. genetic damage after exposure to a carcinogen). If the pressures occur sequentially, their relative effects may also depend on their temporal sequence, e.g. after a storm has destroyed most branching corals, only a few corals will be destroyed by a consecutive CoTS outbreak, and vice versa. Indeed, if they occur sequentially, the earlier pressure may make the system temporarily more 'resilient' to the next effect, because the most sensitive components have already been removed (Maynard et al., 2008).
- Joint exposures to multiple pressures may lead to **unexpected effects**. An example from medicine would be the administration of two types of medications that interact, which may not only lead to additive effects but also to unexpected side effects. An example from marine systems would be the exposure to elevated levels of CO₂ and predators, which leads to behavioural impairment and higher predation mortality in prey fishes (Dixson et al., 2010). Another example is if CO₂ decimates structural corals, leading to the disappearance of CO₂-tolerant crabs because their habitat is lost (Fabricius et al., 2014). Higher CO₂ concentrations under near future scenarios may promote macroalgal growth, which in turn improve rates of growth in sea urchins, perhaps offsetting their CO₂ sensitivity (Uthicke et al., 2016).

Due to the complexities outlined above, general conclusions about the frequency with which various interactions types occur in nature are difficult (Crain et al., 2008). Because of this, it will remain impossible to address fundamental questions on multiple pressures exclusively through experimental work. Indeed this would require a nearly infinite number of experimental studies. Griffen et al. (2016) propose a framework to more strategically focus experimental studies on multiple pressures:

- the studies should be designed to lead to a **mechanistic understanding** of the observed responses (rather than just cataloguing responses);
- the studies should be **designed to inform population and ecosystem models**, to allow upscaling from the experiments to field populations, communities and ecosystems;
- the studies should be conducted at a **sufficient number of pressure levels** to conclude whether responses are linear, or whether there are thresholds or other non-linear responses to pressures; and
- conclusions about effect sizes and interactions (additive or multiplicative) need to consider the model used to test the data, as transformation changes the statistical model being tested.

Further research on the combined effects of multiple pressures should aim to address these four points, which would enhance our ability to better predict outcomes under conditions that have not yet been studied experimentally.

1.5 Interactions between pressures: additive, synergistic and antagonistic effects

Investigation of multiple pressure scenarios is complex, even if only two pressures are considered. It is important to know whether one factor reinforces/worsens or mitigates/reduces the effects of another factor. Many experiments have focussed on only two pressures and few exposure levels so far (see Appendix A). Although this has been a necessary step to gain insight into whether and how stressors interact, i.e. whether they are additive or synergistic, full response curves (or response surfaces) for individual and combined pressures are needed to accurately assess cumulative impacts.

It is essential to understand whether the presence of one pressure affects the magnitude of the response of another pressure effect for understanding and assessing of cumulative impacts (Figure 4). The effects of multiple pressures on an organism, community or ecosystem can be **additive**, i.e. there is no statistical interaction and the combined effect is similar to the sum of the effects from individual pressures and can be readily predicted. Alternatively, if the effect by one of pressure differs depending on the presence or intensity of other variables (statistical **interaction**), then it will be important to know whether their joint effect is greater than (**synergistic**) or less than expected for additivity, i.e. (**antagonistic**) (Figure 4). However, the definition of synergistic and additive depends strongly on the model chosen, and which parts of a response curve have been investigated (see Appendix D). Thus, until full response curves are available to predict impacts at different levels of pressure combination, we argue in Appendix A that responses might more simplistically be grouped into 'aggravating' and 'mitigating' (Figure 4).

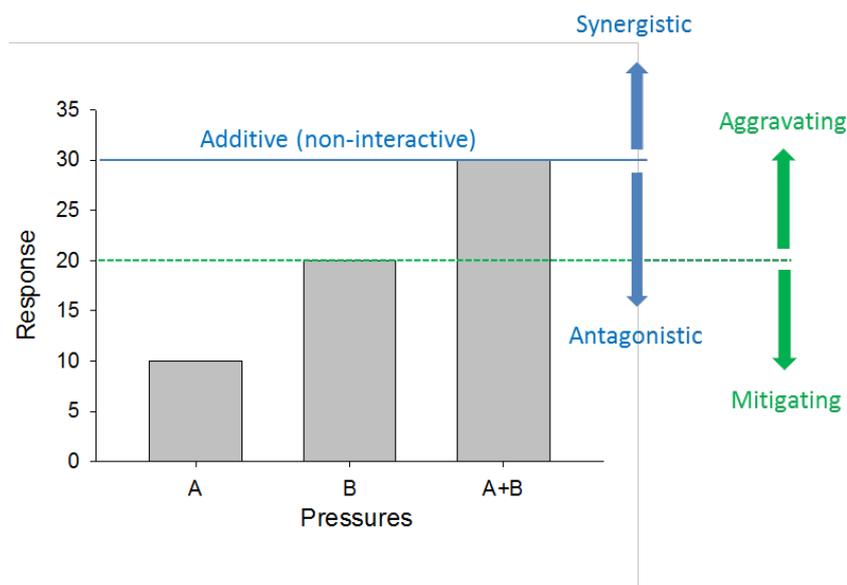


Figure 4: Effects of individual effects of pressures A and B and their potential interactions. Additivity = no interaction. Synergistic is when an interaction between A and B causes an effect greater than predicted for additivity and, antagonistic is when the interaction between A and B causes an effect less than predicted for additivity.

2.0 KNOWLEDGE SYNTHESIS AND EVALUATION OF EXISTING APPROACHES TO ASSESS CUMULATIVE IMPACTS OF LOCAL AND GLOBAL PRESSURES ON REEFS

The main aim of this Report was to: 1) provide a comprehensive review and synthesis of existing tools and qualitative and quantitative studies that describe the cumulative impacts of local and global pressures on reef organisms and processes, and 2) identify knowledge gaps and future research priorities. This has been achieved in four detailed desktop studies that are presented as four Appendices. A summary for each of these studies is presented in this section.

2.1 Review of existing knowledge on combined pressures on coral reefs – Summary of Appendix A

Relatively few laboratory and field studies have investigated the effect of multiple pressures on physiological, whole-organism or ecosystem processes. Due to the lack of data, many analyses of multiple pressures assume that responses are additive (Clarke Murray et al., 2014). However, a recent meta-analysis for the marine environment suggested that only a minority of all interactions between two pressures (26%) were additive, whereas 38% are antagonistic and 36% synergistic. However, these proportions differed for different sub-groups of data (antagonistic effects are common in community-level data, while synergistic effects are common for population-level data)(Crain et al., 2008). Figures were similar in another meta-analysis including marine, freshwater and terrestrial studies (Darling and Côté, 2008), which concluded that ‘...ecological surprises are more common than simple additive effects’. Similarly, a study summarising the combined effects of ocean acidification and seawater temperature concluded that most (four out of five) biological variables responded synergistically under the combined effect of these two pressures (Harvey et al., 2013). By contrast, a recent meta-analysis on multiple pressures in freshwater environments concluded that most pressures in that ecosystem interacted antagonistically or additively (Jackson et al., 2016).

For coral reefs, Ban et al. (2014) recently summarised the data of over 170 studies. Out of these, 111 used quantitative statistical methods allowing quantification of the types of interactive effects. Most studies (60) described a synergistic effect, with additivity (33) and antagonism (17) being less common. However, this review is heavily biased towards corals, and the high degree of synergism is probably because the review was dominated by temperature and irradiance interactions as factors for coral bleaching. Our own review (Appendix A) confirmed that corals are, not surprisingly, the most studied organisms for multiple pressures on coral reefs. Within that group, temperature, irradiance, ocean acidification and temperature interactions were the most commonly investigated pressures. However, large knowledge gaps exist even for corals, with less than five studies investigating several important interactions such as ocean acidification and salinity, or ocean acidification and pollution. For the other species groups (mainly algae, seagrasses, foraminifera, echinoderms and sponges) most pressure combinations have not been investigated at all, and no interaction has been studied in more than five studies. In the non-coral groups,

temperature and CO₂ interactions are the most commonly studied. Based on the assessment by the authors of the individual studies, hardly any of the pressure interactions between global and local pressures on coral reefs are antagonistic, but most were additive or synergistic. To simplify, we grouped all studies providing sufficient information into two groups, ameliorating or aggravating, and found that only 4% were in the former group and more than 50% in the latter.

Given the high level of aggravation between local and global stressors, it is imperative for management to understand these interactions to: a) quantify cumulative pressures on reefs, b) predict future thresholds for individual pressures under climate change, and c) identify the best strategies to reduce cumulative pressure by reducing individual pressures. The limited existing information requires prioritisation of studies to address the most pressing knowledge gaps. In the conclusion of Appendix A we recommend:

- A strategic focus on several model organism and priority pressures, due to the vast possibilities of factor and organism combinations.
- A fixed combination of temperature and CO₂ levels as global pressures could be used as a simplification of experimental designs, given that the global pressures of OA and temperature are predicted to further increase simultaneously.
- Light/turbidity and sediment-bound pollutants as priority local pressures to test, given the strong management interest in dredging and sediment runoff, along with a paucity of relevant data.
- Experiments should be designed to include sufficient levels to allow describing full response curves. This would improve management because thresholds for combined pressures could be predicted, and benefits from reducing individual pressures modelled.
- Similar to the above point, regional and climate adjusted thresholds for priority local pressures can be determined.
- Determine GBR-specific thresholds for pressures under combinations of the highest priority pressures outlined in the GBR Outlook Report, especially for the ecosystem health indicators measured to be developed through the Reef Integrated Monitoring and Reporting Program (RIMReP).

2.2 Cumulative effect models and analyses to inform management and policy – Summary of Appendix B

Managing cumulative impacts is a priority issue for GBR management (GBRMPA, 2014a; GBRMPA, 2014b). Despite this priority, reef managers currently rely largely on qualitative tools to assess risks from cumulative impacts associated with development proposals (GBRMPA, 2009). However, since 2009, GBRMPA has used a range of tools from checklists, matrices, conceptual models to risk maps (GBRMPA, 2014b). Without quantitative analytical tools that can provide insight into how risks accumulate in space and time, and how they can be ameliorated or prevented effectively via management actions on key environmental drivers, environmental decision-making around cumulative impacts is at risk of bias and subjective judgement.

In Appendix B, we present a structured approach to understanding the risks from cumulative impacts. Firstly, we build on the DPSIR framework (Atkins et al., 2011) combined with models of the linked social-ecological system (Schlüter et al., 2012; Anthony et al., 2013, 2015), to identify the sources of stress (drivers), the environmental scenarios that may play out to produce complex sets of pressures, and identify potential management levers for intervention or risk prevention.

Secondly, we review models that can represent useful and complementary parts of the analytical toolset for cumulative risk assessments, ranging from conceptual to highly quantitative models. Of these, the concept of risk maps consisting of multiple exposure layers (Halpern, Walbridge et al., 2008; Maynard et al., 2015) is promising and has received increasing attention. However, exposure mapping lacks the ability to translate exposures into risk prediction in a dynamic environment, including the ability to identify thresholds.

To fill this gap, we present a new mechanistic model that enables predictions of cumulative risk in space and time under complex environmental scenarios. This dynamic, mechanistic model integrates knowledge of biological stress responses in corals with experimental and observational data to produce quantitative estimates of risk and associated uncertainty. We apply the model to a cumulative impacts problem for corals on inshore reefs and produce cumulative impact risk maps for a set of environmental scenarios driven by run-off and climate change. Using coral bleaching and mortality risk, we demonstrate that, when used as a risk assessment tool, the model can inform management decisions around actions to mitigate or prevent stressor combinations that lead to cumulative impacts and/or the exceedance of thresholds. Briefly, the Spatial Cumulative Impacts Risk Analysis (SCIRA) model uses dynamic environmental layers as input variables (Figure 5), using data sources including eReefs and eAtlas, and produces estimates of bleaching and mortality risk as outputs (Figure 6). Because the model integrates uncertainty from all sources of variation, e.g. from environmental variables to mortality risk, the output layers (risk maps) and summary data for a given area are amenable to statistical analysis. Therefore, cumulative impact assessments using multiple scenarios that represent alternative management options can be compared directly to inform transparent decision-making.

We devote the last section of the Appendix to illustrate how these dynamic risk maps in combination with synoptic model results can be used as a decision support tool. We focus on scenarios around land runoff and climate change (ocean warming), specifically the relative importance of warming, turbidity and nutrients in driving coral bleaching and mortality risks. We demonstrate that exposure time and environment x time interactions are critical determinants of whether thresholds for coral survival are likely to be exceeded under different scenarios. By presenting the results of 12 scenarios with varying combinations of warming, sediment and nutrient influences in a consequence table, the results are directly amenable to a decision analysis that, for example, compares risks against costs of interventions or prevention. This is of direct relevance to any water quality management strategy or policy aiming to proactively assess and manage risks in an uncertain environment.

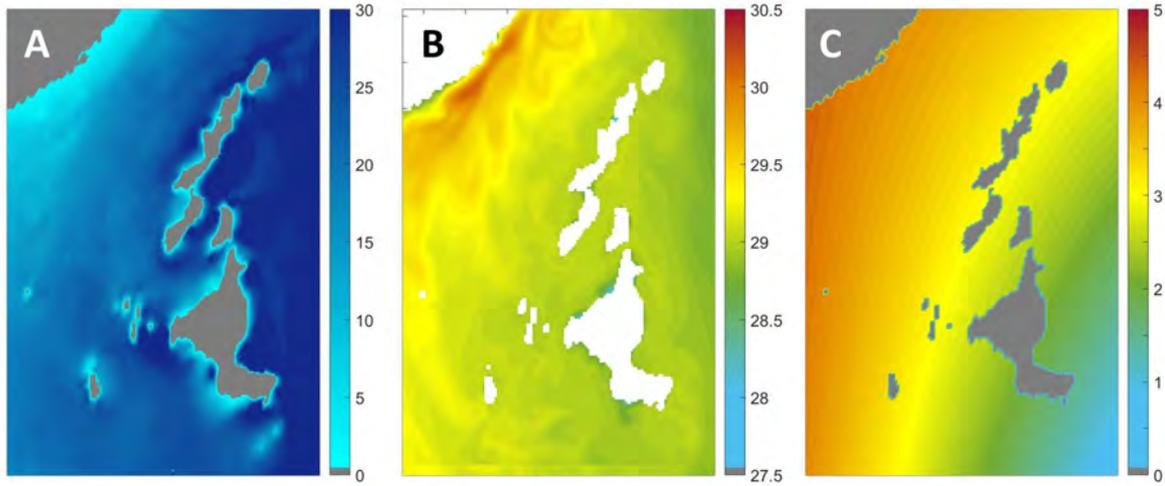


Figure 5: **A:** Bathymetry for the focus area (m below lowest astronomical tide), **B:** sea surface temperatures ($^{\circ}\text{C}$) for late February 2015 (eReefs), and **C:** modelled gradient of suspended particulate matter (mg L^{-1}) used in scenario analyses.

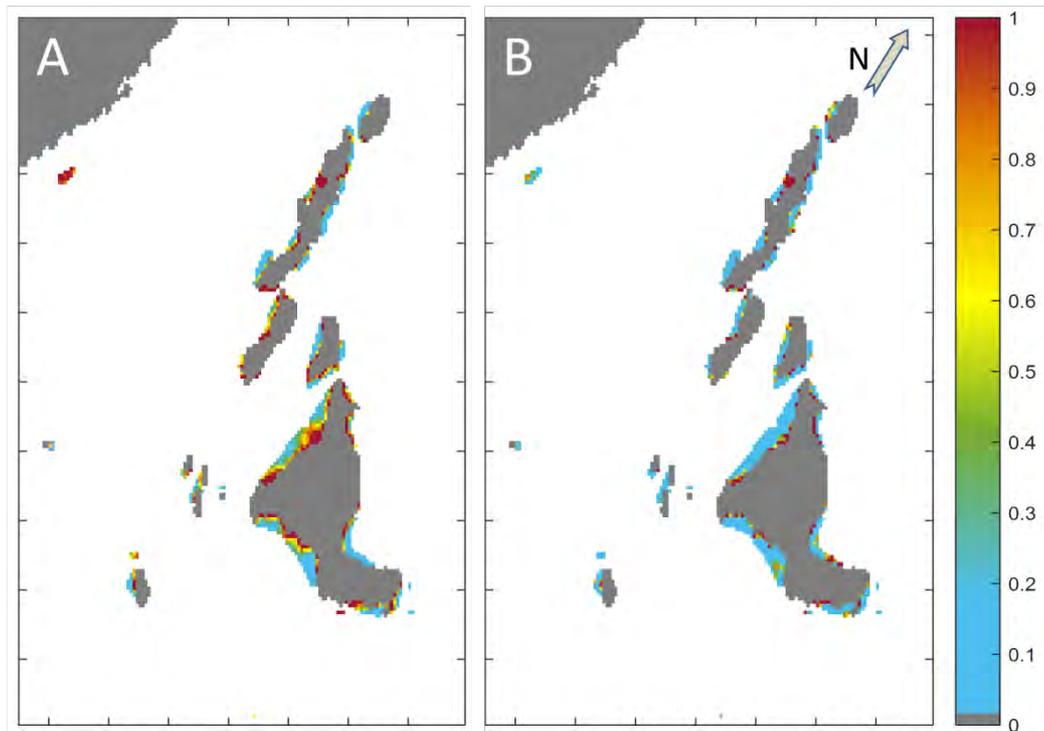


Figure 6: Result of bleaching (left panel) and mortality (right panel) risk predictions for example scenario for reefs in the Palm Islands groups in warm conditions ($27.5 - 32.0^{\circ}\text{C}$) under moderate turbidity (mean of 1.8 mgL^{-1} at peak of the event) and elevated chlorophyll *a* concentrations ($\sim 0.5 \text{ ug L}^{-1}$). Note that bleaching here is in shallow water and due to high irradiance, whereas mortality is in deep areas and driven by turbidity and light limitation (exhaustion of energy reserves).

2.3 Assessment of cumulative impacts from multiple pressures: Approaches from ecotoxicology – Summary of Appendix C

Field monitoring provides crucial data for risk assessments and this information should be augmented with precise thresholds for single and combined pressures derived from experimental approaches. Toxic thresholds are determined in ecotoxicology by modelling experimental data from multi-level concentration-effect treatments. The toxic thresholds for communities can then be estimated by generating sensitivity distributions for multiple species. These techniques are used to develop water quality guidelines and to parameterise risk maps. The methods applied in ecotoxicology can be adapted to calculate precise stress thresholds for other pressures including ocean warming and acidification, turbidity and nutrient exposures. The ecotoxicology approaches used to explore the cumulative effects (joint action) of simultaneous pressures are also well established but have mostly been applied to test the combined toxicity of multiple chemical contaminants. In Appendix C we outline the basis and application of several methods that may be applied to examine cumulative pressures relevant to the GBR. Specifically we:

- Introduce experimental criteria and methods for accurately quantifying single pressure thresholds, including examples on how this can be applied to climate pressures.
- Describe methods for deriving single pressure thresholds and water quality guidelines for communities.
- Present two commonly applied “Joint Action” models to investigate whether responses to simultaneous pressures are independent (additive) or interactive (synergistic or antagonistic). Chemical Addition (CA) assumes identical modes of action and is applicable to chemicals such as a suite of pesticides that act on the same receptor. Response Addition (RA) assumes the opposite, with each pressure acting on different and completely independent stress pathways.
- Work through an example to examine how the RA model could be applied to test the combined effects of thermal stress and copper exposure on coral larval metamorphosis. This example shows how different combinations of pressure levels can result in a range of additive and synergistic outcomes (Figure 7).
- Introduce the multisubstance-potentially affected fraction (ms-PAF) method, which can be used to predict the response of marine communities to multiple pressures. We develop a species sensitivity distribution for the effects of thermal stress on reef organisms and demonstrate how simultaneous exposure to the herbicide diuron is predicted to affect the sensitivity of the community to temperature stress.

Figure 7: Observed vs. expected responses from a simultaneous exposure of coral larvae to thermal stress and copper using the Response Addition model of joint action.

Only a handful of marine experimental studies have applied ecotoxicological approaches to explore the combined effects of multiple stressors, including water quality and climate pressures. Most of the results have revealed the combined effects are aggravating (e.g. sub-additive, additive or synergistic, see Appendix A) and this can often be explained by the modes of action of each pressure. However, given many of the pressures affecting the GBR have multiple modes of action (e.g. thermal stress, eutrophication, turbidity) the likelihood of accurately predicting the total response of an organism or community to cumulative pressures without empirical data is low. Nevertheless, straightforward models such as CA and RA can be used to assess deviations from responses in organisms and communities to multiple pressures caused by interactions and inform the choice of more complex statistical models.

2.4 Statistical tools to detect cumulative temporal and spatial changes in ecological systems – Summary of Appendix D

This Appendix reviews available statistical tools to identify and estimate the effects of multiple pressures on marine organisms and communities using both laboratory and field data. It focuses on the definitions and interpretations of interactions from a statistical and ecological perspective. It outlines pitfalls in past classifications of environmental effects as synergistic, additive and antagonistic, and resolves this issue by defining these terms in a statistical sense.

Appendix D first contrasts the use and interpretation of various statistical models that can serve to detect and interpret interactions. It shows how additivity and interactions are model- and scale-dependent in all but linear models. That is, multiplicative relationships may become additive through data transformation or the use of most generalised linear models. For example, effects that would be classified as multiplicative prior to data transformation (i.e. they would show interactions on the observed scale) are classified as additive (no

interaction) with a log-linear model or log-transformed response. This problem, which is often ignored in the ecological literature, is outlined using a graphical example.

Testing for interactions between multiple pressures is most readily achieved under controlled laboratory conditions. In well-designed laboratory studies, responses can be clearly attributed to one or more pressures, and the scale of the response to combined pressures can be accurately measured (Dunne, 2010; Griffen et al., 2016; Van den Brink et al., 2016). An example is presented in this Appendix to illustrate the use of statistical models to interpret the presence of interactions in a fully orthogonal set of ecotoxicological data on coral larvae jointly exposed to varying temperatures and copper levels (Negri and Hoogenboom, 2011). In studies that are less comprehensive than this, determining antagonistic versus synergistic effects from two-factor laboratory experiments could be misleading if only a few pressure levels/intensities are tested and hence, the shapes of the response curves are unknown. Typical response curves may be linear, proportional to the pressure, exponential, logit or modal, or responses may show hysteresis or acclimatisation; the conclusion of interaction or not, and type of interaction will then entirely depend on the choice of exposure levels. This indicates that that more comprehensive experiments need to be conducted to reflect the whole curve and not just a subset.

In field data, identifying the specific contributions from each pressure is even more challenging. Appendix D illustrates solutions to these complex problems based on two examples of published field data. The first example, based on De'ath et al. (2012), demonstrates how the cumulative effects of different types of disturbances affect GBR coral cover, and how the models can be used to calculate spatially explicit rates of losses and rates of recovery in the presence and absence of each of these disturbances. The second example contrasts the use of parametric models with boosted trees (a machine learning [ML] approach) to show how the latter can be used to identify complex interactions between ecological drivers. The boosted tree outputs can be used to select optimal models that include all relevant pressure variables and their interactions. The performance of both methods (third example) is demonstrated on a data set on changes in GBR octocorals richness along environmental gradients (Fabricius and De'ath, 2008).

The three examples in combination demonstrate that the joint use of classical statistical models and modern ML methods can be extremely effective for analysis of ecological and environmental data to identify the cumulative impacts of multiple pressures at the ecosystem level.

3.0 ROADMAP TO IMPROVE UNDERSTANDING, ASSESSMENT AND MANAGEMENT OF CUMULATIVE IMPACTS

The last aim of our project was to provide a roadmap to develop a practical framework to incorporate quantitative approaches for assessing the risk of multiple pressures to support the assessment and management of cumulative impacts on coral reefs of the GBR. This roadmap is presented below, and is based on conclusions from our detailed desktop studies, and informed by discussions at a stakeholder consultation workshop and with other scientists.

3.1 Where we are now

This Report has achieved the following objectives:

1. Improved understanding of the cumulative effects of specific pressure combinations.
2. Identified existing limitations in the interpretation of interactive, synergistic and additive effects, and then proposed toolsets to better inform about CI (including statistical, ecotoxicological, conceptual, semi-quantitative and quantitative mechanistic models and structured decision analyses).
3. Conducted a gap analysis and identified priority questions that need to be addressed through experimental and field studies, and modelling.
4. Developed a prototype for a new Dynamic Risk Map of CI in complex environmental scenarios on inshore reefs, to inform adaptive management. This Dynamic Risk Map builds on the approach taken by Halpern et al. (2008a, b), but also accounts for temporal dynamics, specific mechanistic understanding of responses, and uncertainty.

3.2 The Roadmap

Simple predictable responses in reef systems following anthropogenic and natural disturbances are uncommon, and ecological thresholds under multiple pressures are likely to differ from physiological thresholds observed under single or even multiple pressures. Thresholds and responses are also expected to change over ecologically relevant time frames, through either acclimatisation of organisms that ameliorate the pressures, or accumulation of effects that exacerbate the responses to the pressures. Predictions of future impacts without empirical (experimental or field) confirmation of responses may lead to false conclusions, and hence suboptimal management investment. Addressing these complexities is recommended as an immediate focus of further research to provide an improved knowledge base for the assessment of cumulative impacts on coral reef environments in the GBR and the development of a toolset to specifically identify:

- Pressure combinations that represent high risk;
- Analysing spatial distribution and intensity of cumulative pressures in exposure and risk maps;
- Key value-based environmental responses; and
- Critical pressure thresholds for these responses.

Managers and scientists need to work collaboratively to further improve the understanding, assessment and management of cumulative impacts. The recently commenced Project NESP 2.1.6: “From exposure to risk: novel experimental approaches to analyse cumulative impacts and determine thresholds in the GBRWHA” has been designed to address some of these key knowledge needs through the following steps, which will be further refined in consultation with key stakeholders:

1. Determine **GBR-specific thresholds** for pressures under combinations of the priority pressures outlined in the GBR Outlook Report, especially for the ecosystem health indicators measured by the Marine Monitoring Program and global pressures. Light/turbidity and sediment-bound pollutants are suggested as top-priority local pressures to test, given the strong management interest in dredging and sediment runoff, along with a paucity of relevant data. The complexity of the problem will require a combination of:
 - a. **Multi-level laboratory experiments** to characterise response curves, identify thresholds for pressures and understand physiological mechanisms that underpin responses to multiple pressures;
 - b. Multi-species, longer term, **mesocosm experiments** investigating ecological, as well as physiological, responses to multiple pressures; and
 - c. **Field investigations** along environmental gradients and changes over time from monitoring programs.
2. Develop **environmentally realistic exposure maps**, dynamic risk maps and obtain data validation of these maps. The models have to take into consideration environmental variability, GBR-specific thresholds, and improved mechanistic understanding of ecosystem, community or species responses. Improved hindcasting of the changes the GBR has already undergone over the last 50 years of intensifying cumulative pressures is needed. This work will need to be set up as a new collaboration between physiologists, ecologists, biostatisticians, eAtlas staff and modellers, and will need to be conducted in partnership with GBRMPA, Department of the Environment (DotE) and other key stakeholders. Further funding allocations are required for this research task.
3. **Inform the GBR Outlook Report 2019** on how CI from water quality, climate change and ocean acidification will affect the ability to meet Reef 2050 Long-Term Sustainability Plan goals and targets, and identify which management targets will yield the greatest benefits under a scenario of cumulative pressures from global changes.
4. **Inform managers** on data needs and analysis methods required from proponents for cumulative risk assessments in environmental impact assessments of development proposals (GBRMPA permitting section objectives).
5. **Inform RIMReP** about specific monitoring requirements and additional indicators for monitoring programs that may contribute to populating cumulative risk maps.

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5.0 APPENDICES

APPENDIX A: REVIEW OF EXISTING KNOWLEDGE ON COMBINED PRESSURES ON CORAL REEFS

Sven Uthicke, Sam Noonan, Charlotte Johansson, Andrew Negri

A.1 Introduction

The previous Chapters in this report have outlined that a multitude of pressures exist in the marine environment, and several reviews on the interaction of these pressures exist (Crain et al., 2008; Clarke Murray et al., 2014). For coral reefs, Ban et al. (2014) recently summarised the data of over 170 studies. Out of these, 111 used statistical methods allowing quantification of the types of interactive effects. Most studies (60) described a synergistic effect, with additivity (33) and antagonism (17) being less common. Most of the studies on corals were on the interactions of temperature and irradiance in the context of coral bleaching. Reflecting the overall dataset, most effects between that pair of environmental pressures were synergistic. A quantitative analysis for this pair of pressures on several photosynthetic parameters found that average responses to the combined effects were above the expected effect under the assumption of additivity, but this difference was not significant. Ban et al. (2014) identified several research gaps, mainly between the pressure pair's nutrients and irradiance (including UV) and nutrients and chemical pollutants such as herbicides and pesticides.

Ban et al.'s (2014) study mainly investigated corals. To complement this study we focussed on interactions between global pressures (sea surface temperature [SST] increase and ocean acidification) and local pressures (land runoff) and included important reef organisms other than coral. Because the previous study focussed on irradiance and temperature interactions, we omitted that pressure pair from the analysis, but still listed the findings in our results.

A.2 Methods

Similar to Ban et al. (2014), we conducted a Web of Science search for each individual pressure pair (Table A1). Initial tests showed that 'coral reef' as a search term in the search was too restrictive. Thus, we chose to run the search without that term initially and refined the search to include the term 'coral reef' in a second step. At least the title and abstract of each remaining paper was checked and included if it described research on the relevant pressure pair. We included all fully experimental studies, but also some correlative studies if these seemed of relevance.

Table A1: Summary of the Web of Science searches and search terms. All search terms are preceded by the name of the organisms, “(echinoderm* OR porifer* OR microb* OR Zoanthid* OR Crustacea* OR mollusc*)” was used for the term ‘Others’. Numbers given are actual results for the initial search (‘Not Restricted’), refining the search to ‘Coral Reef’, those relevant after checking the papers, and the final number used after adding some publications not in the search. All searches were ‘Topic Searches’ (TS).

Global Pressure	Local Pressure	Organism	Search Term	Not restricted	Coral Reef	Relevant	Final used
Acidification	Light	Algae	AND (acidification AND (irradiance OR light OR turbidity))	161	26	2	3
		Seagrass	AND (acidification AND (irradiance OR light OR turbidity))	23	4	0	1
		Foraminifera	AND (acidification AND (irradiance OR light OR turbidity))	24	8	0	0
		Coral	AND (acidification AND (irradiance OR light OR turbidity))	127	103	6	6
		Others	AND acidification AND (irradiance OR light OR turbidity))	64	6	1	1
	Pollution	Algae	AND (acidification AND (pollution OR contaminant*))	33	6	0	0
		Seagrass	AND (acidification AND (pollution OR contaminant*))	8	1	0	0
		Foraminifera	AND (acidification AND (pollution OR contaminant*))	17	2	0	0
		Coral	AND (acidification AND (pollution OR contaminant*))	47	40	1	1
		Others	AND acidification AND (pollution OR contaminant*))	101	3	0	0
	Salinity	Algae	AND (acidification AND (salinity OR hypersalinity))	22	0	0	0
		Seagrass	AND (acidification AND (salinity OR hypersalinity))	4	3	0	0
		Foraminifera	AND (acidification AND (salinity OR hypersalinity))	14	0	0	0
		Corals	AND (acidification AND (salinity OR hypersalinity))	50	38	0	0
		Others	AND acidification AND (salinity OR hypersalinity))	45	2	0	0
	Nutrients	Algae	AND (acidification AND (nutrient*))	119	22	3	4
		Seagrass	AND (acidification AND (nutrient*))	18	6	0	1
		Foraminifera	AND (acidification AND (nutrient*))	26	7	0	1
		Corals	AND (acidification AND (nutrient*))	122	113	4	6
		Others	AND acidification AND (nutrient*))	245	11	0	0
Temperature	Light	Algae	AND (temperature AND (irradiance OR light OR turbidity))	2525	173	2	2
		Seagrass	AND (temperature AND (irradiance OR light OR turbidity))	306	17	1	1
		Foraminifera	AND (temperature AND (irradiance OR light OR turbidity))	820	29	0	0
		Coral	AND (temperature AND (irradiance OR light OR turbidity))	780	627	26	26

	Others	AND temperature AND (irradiance OR light OR turbidity))	2255	35	1	1
Pollution	Algae	AND (temperature AND (pollution OR contaminant*))	233	17	1	1
	Seagrass	AND (temperature AND (pollution OR contaminant*))	18	5	0	0
	Foraminifera	AND (temperature AND (pollution OR contaminant*))	115	3	1	1
	Coral	AND (temperature AND (pollution OR contaminant*))	125	106	4	5
	Others	AND temperature AND (pollution OR contaminant*))	1168	9	0	0
Salinity	Algae	AND (temperature AND (salinity))	856	42	0	0
	Seagrass	AND (temperature AND (salinity))	148	33	0	0
	Foraminifera	AND (temperature AND (salinity))	909	17	0	0
	Corals	AND (temperature AND (salinity))	540	380	2	2
	Others	AND (temperature AND (salinity))	2107	35	0	0
Nutrients	Algae	algae AND (temperature AND (nutrient*))	1429	97	1	1
	Seagrass	seagrass AND (temperature AND (nutrient*))	190	23	0	0
	Foraminifera	foram* AND (temperature AND (nutrient*))	496	26	1	2
	Corals	coral AND (temperature AND (nutrient*))	427	374	7	7
	Others	(AND temperature AND (nutrient*))	5160	44	2	3
CO₂+Temperature	Algae	algae AND (temperature AND acidification))	171	51	8	11
	Seagrass	seagrass AND (temperature AND acidification))	21	6	0	0
	Foraminifera	foram* AND (temperature AND acidification))	75	23	3	4
	Coral	coral AND (temperature AND acidification))	452	384	22	24
	Others	(AND (temperature AND acidification))	374	28	3	6
SUM:			22970	2985	102	121

We restricted the search to the period of 1982 to the end of 2015. However, due to the relevance to this review we included some of our own studies as part of the NERP TE Hub that have been published in early 2016.

Within the set of fully factorial studies (77) we categorised the authors' observations and comments on whether results between the two pressures were antagonistic, additive, or synergistic. This information is usually not given for individual parameters, but for the overall study. However, some author's comment that the combined pressure found in their study were 'additive and synergistic', in which case we counted the study as being both. A more detailed analysis required a strict definition of the terms (Dunne, 2010) and testing how authors interpreted results and whether their data were transformed (Griffen et al., 2016; see Appendix D). Given that from a reef management perspective it is more relevant if pressures are aggravating (that would include, synergy, additivity and sub-additivity) or ameliorating (mainly antagonistic), we also grouped each study into those categories.

A.3 Results and Discussion

Initial literature searches gave very high numbers of hits (some > 2000, see Table A1), but the refinement to 'Coral Reef' resulted in more realistic numbers. However, investigating the actual publications showed that usually less than 10% of these truly investigated the targeted pressure pair in the context of interactions and cumulative impacts. The remaining studies often investigated one of the pressures, and a second one was only measured and reported to describe environmental conditions. For instance, an experiment investigating the effect of nutrients on algae growth may report the experimental temperature, without manipulating temperature. The studies thus identified ('Relevant' in Table A1) were complemented by additional studies based on our own knowledge of the literature ('Final used'). This resulted in 95 table entries (Table A2), based on 87 individual studies (because some studies worked on several organism types, these were entered multiple times).

Not surprisingly, most of the studies (64%, percentages given here include studies reviewed in Ban et al.'s (2014) numbers) are on coral. The most frequently investigated interactions in corals are between temperature x irradiance and temperature x CO₂ (Figure A1). However, even in this important group all other interactions have only been studied in six or less publications. Algae constitute the next most studied group (18%), with several studies focussing on crustose coralline algae and the effect of temperature and OA. Less than 10% of all studies on cumulative pressures were conducted on each of the remaining groups, including the pooled 'others' group containing crustaceans, molluscs, porifera (sponges) and several smaller invertebrate groups. Across all taxa, the most studied interaction was between OA and temperature (37% of all studies), followed by temperature and irradiance (25%).

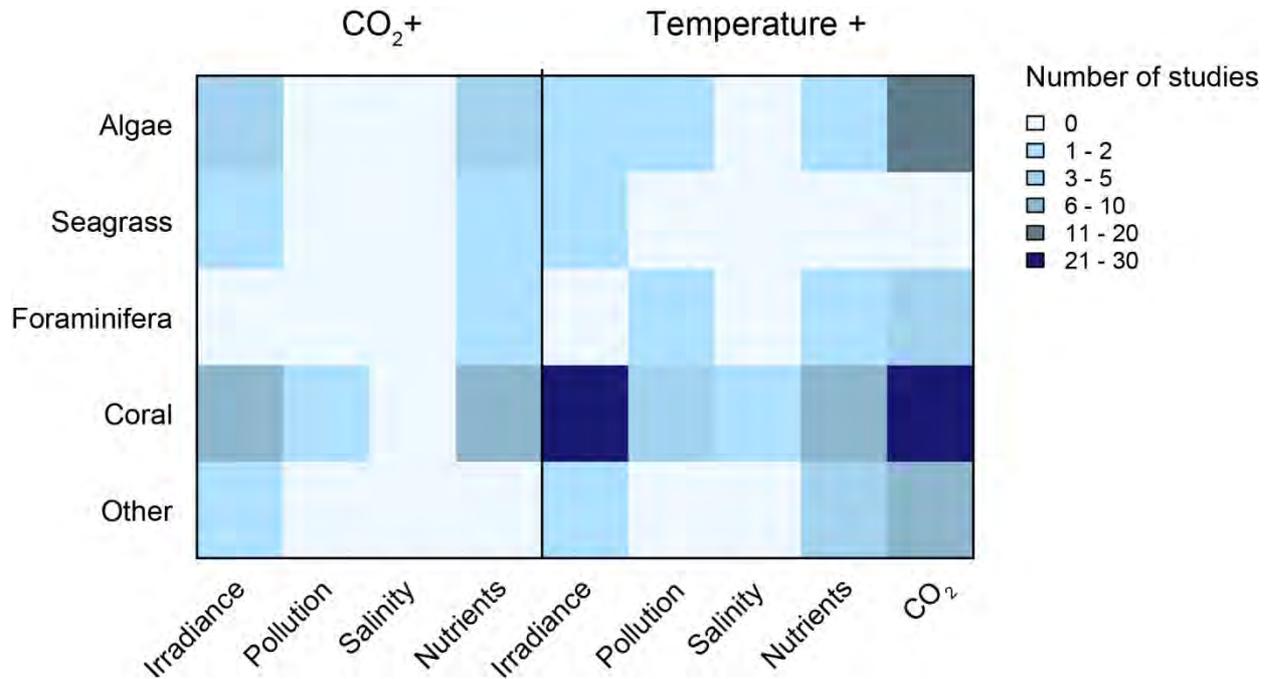


Figure A1: The number of studies identified for the combined Global vs. Local pressures for the five groups of organisms and included in Table A2. The combination of temperature and irradiance includes the 26 studies identified by Ban et al. (2014).

As a mode of interaction, antagonism was only reported in 2 of the 32 studies in which combined effects existed and the authors scored antagonism, additivity and synergism, while 15 studies each reported additivity or synergism. Ban et al. (2014) observed a much higher percentage (73%, i.e. 19 out of 26 studies) of synergism; it is likely that this was due to their focus on the light x temperature interaction. Similarly, Crain et al. (2008) in a study on general marine ecosystems observed a somewhat higher number of synergisms (36%) than additivity (26%) for human induced pressures on the marine organisms. Strikingly, that study scored a much higher percent of antagonisms (38%) than the present analysis. These antagonisms were observed in most pressure combinations. It is thus unlikely that the difference in results reflect that our study only focussed on interactions between global and local interactions.

Grouping the study results into ameliorating and aggravating provided further insight into the data. In 27 (37%) of the 73 studies we inspected, no pressure or only one was significant, thus no interaction existed. Only 4% of the studies exhibited pressures ameliorating each other. In 59% of the studies the joint effect was higher than the larger of the individual effects, and these were thus scored as aggravating. Two of the studies with ameliorating pressures contained light as one of the factors. For example, elevated irradiance levels compared to low light levels in inshore environments can reduce adverse effects of high temperature on seagrass growth (Collier et al., 2011). However, this example illustrates that care needs to be taken in grouping studies into broad categories. If *high* light and 'normal' temperature were assumed as the 'natural state' one could also argue that the combination of *low* light and high temperature have a negative effect on growth.

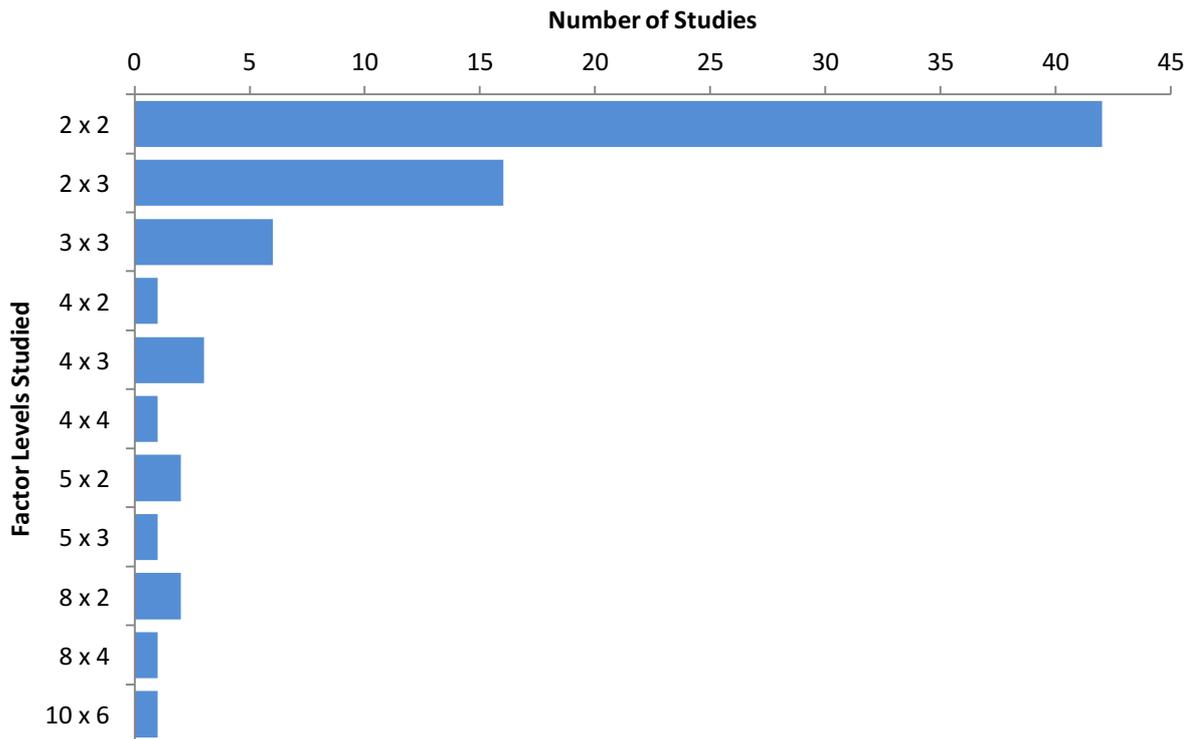


Figure A2: The number of studies in our review investigating different factor levels.

To describe the pressure-response relationship ideally experiments would include multiple levels of the pressures ('factor levels') under investigation. We also investigated the number of factor levels used by each study (Figure A2). The majority of studies used the minimum number of levels (two levels of a global pressure, two of a local one). These studies usually consist of 'control' (ambient, or average, or historical) conditions and some degree of elevation (or decrease, e.g. in the case of light). This finding is congruent with observations in Griffen et al. (2016). Particularly the studies investigating CO₂ and temperature and CO₂ and another pressure often have very few factor levels because facilities needed to manipulate these factors are not available at many institutes or research stations. Given that usually a minimum replication of 3 aquaria per treatment combination is used, even a 2 x 2 experiment already results in 12 aquaria per experiment, and this number rapidly increases with more factor levels. Very few studies exist with sufficient factor levels (~> 5) to describe full pressure-response curves, reliably identify thresholds for combined factors or predict future thresholds under elevated temperatures and pCO₂. Noticeable exceptions are several ecotoxicology studies investigating the effect of herbicides or copper at different temperatures. This is not meant to criticize studies using fewer factor levels: most of these were designed for a different purpose, namely to investigate if there are individual or combined effects of these factors at all.

A.4 Conclusions and recommendations

We identified many clear research gaps and highlighted several shortfalls of the data available at present. As research priorities for future experimental studies on cumulative impacts on coral reefs we recommend:

- A strategic focus on several model organism and priority pressures, due to the vast possibilities of factor and organism combinations.
- A fixed combination of temperature and CO₂ levels as global pressures could be used as a simplification of experimental designs, given that the global pressures of OA and temperature are predicted to further increase simultaneously.
- Light/turbidity and sediment-bound pollutants as priority local pressures to test, given the strong management interest in dredging and sediment runoff, along with a paucity of relevant data.
- Experiments should be designed to include sufficient levels to allow describing full response curves. This would improve management because thresholds for combined pressures could be predicted, and benefits from reducing individual pressures modelled.
- Similar to the above point, regional and climate adjusted threshold for priority local pressures can be determined.
- Determine GBR-specific thresholds for pressures under combinations of the highest priority pressures outlined in the GBR Outlook Report, especially for the ecosystem health indicators measured to be developed for the RIMReP.

Table A2: Summary table of cumulative effects of Global and Local pressures on coral reef organisms resulting from our Web of Science search. Study Type: (f)ex: (factorial)experimental, c: correlative field data, m: modelled data, treatment levels are given for all fully factorial studies. The organism category 'Others' is defined in Table A1.

Authors' conclusions: na = study did not specifically test for additive/synergistic/antagonistic effects; - = not specified by author, conclusion in parenthesis: conclusion not explicitly spelled out, but implied.

Global	Local	Organism	Species	Calcification	Production	General Effects/ Other parameters/ Comments	Study Type (levels)	Authors' conclusion	Literature
Temp	Nutr	Corals							
			7 species of coral	na	na	DIN can increase bleaching susceptibility and mortality	Ex	na	Wiedenmann et al., 2012
			<i>A. millepora</i> <i>M. tuberculosa</i>	na	T + OE = ↓Fv/Fm	Organic enrichment (OE) reduced bleaching threshold, DIN alone not. Outcomes depend on trophic status	m/ex	na	Fabricius et al., 2013
			<i>Turbinaria reniformis</i> <i>Stylophora pistillata</i>	na	na	Feeding corals increased bleaching threshold +Light = ↓Chla in <i>S. pistillata</i> Light + T = ↓Chla	Ex	na	Hoogenboom et al., 2012

						in <i>T. reniformis</i> +Light = ↓PSII protein in <i>T. reniformis</i>			
			<i>Diploria strigosa</i> planula	na	na	T + NH ₄ ⁺ = ↑mortality, ↓motility and ↓settlement	(f)ex (3 x 2)	Additive	Bassim and Sammarco, 2003
			Coral community	na	na	Reefs with high Chl <i>a</i> and DIN had higher bleaching during a thermal stress event	C	na	Wagner et al., 2010
			<i>Turbinaria reniformis</i>	Low DIN + T = ↓	Low DIN + T = ↓	Low DIN + T = ↓Pigments	(f)ex (2 x 2)	-	Béraud et al., 2013
			<i>Porites cylindrica</i>	na	NO ₃ ⁻ + T = ↓Prod Respiration ns	Chl <i>a</i> and zoox densities ns	(f)ex (2 x 2)	-	Nordemar et al., 2003
Temp	Nutr	Algae							
			<i>Gracilaria parvispora</i>	na	Ammonia = ↑biomass	Other environmental variables (water motion, temperature, salinity, nitrate and phosphate) did not correlate with growth.	ex	na	Glenn et al., 1999
Temp	Nutr	Seagrass							

			na	na	na	na	na	na	na
Temp	Nutr	Forams							
			Symbiodinium bearing (<i>M. vertebralis</i>)	T↓ DIN↓	T↓ (also Chl a)	Survivorship: T↓ DIN↓	(f)ex (3 x 3)	Additive	Uthicke et al., 2012
			3 Diatom bearing species	In 2 species: T↓ DIN ns	T↓ (also Chl a)	No effect of DIN addition	(f)ex (3 x 3)	-	Schmidt et al., 2011
Temp	Nutr	Others							
		Biofilms		na	Under high light: T + DIN = ↓prod	T and DIN alter microbial community composition	(f)ex (3 x 3)	Additive	Witt et al., 2012
		Echinoderms	<i>Acanthaster planci</i> (CoTS)	na	na	Increased DIN may increase planktonic algae. Algae + T = ↑larval development	(f)ex (3 x 3)	Additive to synergistic	Uthicke et al., 2015
		Microbial communities	Microbial communities on <i>Rhopaloeides odorabile</i> (sponge)	na	na	Microbial communities stable across all treatments	(f)ex (2 x 3)	-	Simister et al., 2012
Temp	Light	Corals							

						62 studies on temperature and light with 26 being fully factorial		26 (f)ex: 19 synergistic, two antagonistic	Ban et al., 2014
Temp	Light	Algae							
			<i>Hydrolithon reinboldii</i>	low light ↓	na		(f)ex (2 x 2)	-	Comeau et al., 2014
			Endolithic cyanobacteria	na	Light + T = ↓Fv/Fm		(f)ex (2 x 2)	-	Fine et al., 2005
Temp	Light	Seagrass							
			<i>Zostera muelleri</i> <i>Halodule uninervis</i>	na	Halodule: T + light ↑ Zostera: T + (high & low) light ↓	Depending on species: T and light effects, for <i>Z. muelleri</i> high light can ameliorate negative effects of T	(f)ex (3 x 2)		Collier et al., 2011
Temp	Light	Forams							
			na	na	na	na	na	na	na
Temp	Light	Others							
		Zooanthid	<i>Palythoa caribaeorum</i>	na	na	T + UV (but not irradiance) = ↓zoox (i.e. bleaching) T = ↓Chla/zoox T + light = ↑enzyme activity	(f)ex (2 x 2)	Synergistic	Lesser et al., 1990

Temp	Pollut	Corals							
			<i>Acropora millepora</i>	na	T + Diuron & Atrazine = ↓ Photosynth. Efficiency, MQY	T = ↓Chla (i.e. bleaching)	(f)ex (2 x 8)	Additive/synergistic	Negri et al., 2011
		Larvae	<i>Acropora millepora</i> <i>Acropora tenuis</i>	na	na	Cu contamination increases T stress on metamorphosis. Depending on T	(f)ex (6 x 10)	Additive/synergistic	Negri and Hoogenboom, 2011
		Symbiodinium	several <i>Symbiodinium</i> clades	na	T ↓ + Diuron = ↓Fv/Fm		(f)ex (4 x 8)	Additive	van Dam et al., 2015
			<i>Pocillopora verrucosa</i>	na	LAS + T = ↓Fv/Fm and ↑tissue loss Diesel ns T = ↓Fv/Fm	T + diesel = ↑respiration	(f)ex (2 x 2)	-	Kegler et al., 2015
		Larvae	<i>Platygyra acuta</i>	na	na	Copper = ↑mortality and ↓motility	(f)ex (2 x 5)	-	Kwok and Ang, 2013
Temp	Pollut	Algae							
			<i>Neogoniolithon fosliei</i> (CCA)	na	T = ↓Fv/Fm no Diuron or interactive effect	T = ↓Chla	(f)ex (2 x 8)	-	Negri et al., 2011
Temp	Pollut	Seagrass							
			na	na	na	na	na	na	na

Temp	Pollut	Forams							
			Several species with different symbionts	na	T + Diuron = ↓Fv/Fm, ↑bleaching		(f)ex (5 x 3)	Additive	van Dam et al., 2012
Temp	Pollut	Others							
			na	na	na	na	Na	na	na
Temp	Salinity	Corals							
			<i>Montastrea annularis</i>	na	T + Sal = ↑	12 h: T + Sal = ↑prod 30 h: T + Sal = ↓prod	(f)ex (2 x 2)	Additive	Porter et al., 1999
		Early life history	<i>Platygyra acuta</i>	na	na	T + ↑salinity = ↑fertilisation and development	(f)ex (4 x 3)	Antagonistic	Chui and Ang, 2015
Temp	Salinity	Algae							
			na	na	na	na	na	na	na
Temp	Salinity	Seagrass							
			na	na	na	na	na	na	na
Temp	Salinity	Forams							
			na	na	na	na	na	na	na
Temp	Salinity	Others							

			na	na	na	na	na	na	na
CO₂	Nutr	Corals							
			Reef community	Low Ω_{Ar} and low T decreases calc. Some evidence that more distinctly so at higher NO ₃		Strength of effect cannot be teased out	c	na	Silverman et al., 2007
			<i>Porites compressa</i> <i>Montipora verucosa</i> , Community rates	CO ₂ ↓ DIN/P ns	CO ₂ ↑ Nutris ↑	CO ₂ and NO ₃ not given simultaneously	ex	na	Langdon and Atkinson, 2005
			<i>Portites compressa</i>	pH ↓ NO ₃ ↓	na	pH change through HCl NO ₃ effect: m.s. Single source colony Extreme pH (~7.2)	(f)ex (2 x 4)	-	Marubini and Atkinson, 1999
			<i>Porites</i> spp.	na	na	↓ Ω_{Ar} increases macrobioerosion, increasing by an order of magnitude with high DIN	c	na	DeCarlo et al., 2014
			<i>Acropora cervicornis</i>	N + P ↓ CO ₂ ↓ DIN/P + CO ₂ =	na	na	ex	Additive	Renegar and Riegl, 2005

				↓↓					
			<i>Acropora muricata</i>	CO ₂ + nutris = ↓calc	CO ₂ + nutris = ↑P _{net}	na	ex	na	Chauvin et al., 2011
CO₂	Nutr	Algae							
			<i>Halimeda opuntia</i>	No effect on growth	No effect on F _v /F _m	Enzyme activity affected by DIN/P addition.	(f)ex (2 x 2)	-	Hofmann et al., 2014
			<i>Chnoospora implexa</i>	na	T + CO ₂ = ↑prod F _v /F _m inconsistent effects	CO ₂ + T = ↓growth, but NOT with DIN/P	ex	na	Bender et al., 2014a
			<i>Halimeda opuntia</i> <i>Dictyota</i> sp.	CO ₂ : ns DIN/P = ↑growth in <i>Ho</i> DIN/P + CO ₂ = ↑ growth in <i>Dictyota</i>	DIN/P = Prod and resp↑ CO ₂ = ↓ETR in <i>Ho</i> CO ₂ + DIN/P = ↑ETR in both species	DIN/P influenced many responses	(f)ex (2 x 2)	-	Hofmann et al., 2015
			<i>Halimeda macroloba</i> , <i>H. opuntia</i>	<i>Ho</i> : pCO ₂ + DOC = ↓dark calc	DOC = ↓daily prod <i>H. opuntia</i> : +DOC = ↓Chla and F _v /F _m	Exposure to CO ₂ and DOC.	(f)ex (2 x 2)	Additive/ Synergistic	Meyer et al., 2015
CO₂	Nutr	Seagrass							
			<i>Halodule uninervis</i> <i>Thalassia hemprichii</i>	na	<i>H. uninervis</i> : CO ₂ = ↑prod and growth <i>T. hemprichii</i> : ns	<i>H. uninervis</i> : +NO ₃ ⁻ = ↓respiration NO ₃ ⁻ addition did not stimulate	(f)ex (3 x 2)	-	Ow et al., 2016b

						photosynthesis in either species			
CO₂	Nutr	Forams							
			<i>Marginopora rossi</i>	pCO ₂ ↓ distinct effect of DIN↓, P-	Prod reduced with OA, highest reduction under OA + DIN	Effect variable on other parameters (e.g. cell specific)	(f)ex (2 x 2)	-	Reymond et al., 2013
CO₂	Nutr	Others							
			na	na	na	na	na	na	na
CO₂	Light	Corals							
			<i>Acropora millepora</i>	CO ₂ + low IR↓ Bouyant weight and dark calc Light calc ns	-light = ↓prod and ↑resp	na	(f)ex (2 x 2)	Additive	Vogel et al., 2015
			<i>Acropora horrida</i> , <i>Porites cylindrica</i>	-light + CO ₂ = ↓light calc	High light + CO ₂ = ↑prod		(f)ex (2 x 2)	-	Suggett et al., 2013
			<i>Porites rus</i>	Light, CO ₂ and feeding ns	na	Feeding = ↑biomass	(f)ex (2 x 2)	-	Comeau et al., 2014
			<i>Acropora pulchra</i>	T + low IR ↓	na	Max biomass measured at 750 μatm pCO ₂ in 3 out of 4 combinations of	(f)ex (2 x 2)	-	Comeau et al., 2014

						light and temperature			
			<i>Acropora cervicornis</i>	+light = ↑linear extension, surface area and volume CO ₂ + low light = ↓buoyant weight	+light = ↓Fv/Fm CO ₂ ns		(f)ex (2 x 2)	-	Enochs et al., 2014
		Juveniles	<i>Pocillopora damicornis</i>	Mixed non-linear Calc responses: under ambient CO ₂ ↑calc at intermediate light. High CO ₂ opposite	na	Survivorship highest at intermediate light (no CO ₂ effect)	(f)ex (5 x 2)	-	Dufault et al., 2013
CO₂	Light	Algae							
			<i>Halimeda opuntia</i>	ns	-light = ↓prod and ↑resp	-light = ↑Chla	(f)ex (2 x 2)	-	Vogel et al., 2015
			<i>Hydrolithon reinboldii</i>	low IR ↓	na		(f)ex (2 x 2)	-	Comeau et al., 2014
			<i>Peyssonnelia</i> sp.	No CO ₂ or light effect	Na	low pH: cover ↓ No structural changes	(f)ex (2 x 2)	-	Dutra et al., 2015
CO₂	Light	Seagrass							
			<i>Cymodocea</i>	na	<i>C. serrulata</i> :	<i>C. serrulata</i> more	(f)ex	Additive	Ow et al.,

			<i>serrulata</i> <i>Halodule</i> <i>uninervis</i>		Light + CO ₂ = ↑growth and Pmax, +light = ↑prod, CO ₂ = ↓α <i>H. uninervis</i> : +light = ↑Prod and Pmax	sensitive to CO ₂ effects and light, while <i>H. uninervis</i> mostly responds to light. <i>C. serrulata</i> : DIC limitation under low light	(3 x 2)		2016a
CO ₂	Light	Forams							
			na	na	na	na	na	na	na
CO ₂	Light	Others							
			<i>Tridacna</i> <i>squamosa</i>	CO ₂ = ↓shell growth +light = ↑shell growth	na	CO ₂ = ↓survival and growth at mid-light levels. CO ₂ effect on survival absent at high-light	(f)ex (2 x 2)	(Antag.)	Watson, 2015
CO ₂	Pollut	Corals							
			<i>Stylophora</i> <i>pistillata</i> and <i>Acropora</i> <i>muricata</i>	CO ₂ ns Cobalt ↓ No interaction	Cobalt↓ CO ₂ not tested	Cobalt decreased growth by 28%, and stimulated photosystem II. [Zoox], Chla and F _v /F _m unaffected	(f)ex (2 x 2)	-	Biscéré et al., 2015
CO ₂	Pollut	Algae							
			na	na	na	na	na	na	na

CO₂	Pollut	Seagrass							
			na						
CO₂	Pollut	Forams							
			na						
CO₂	Pollut	Others							
			na						
CO₂	Salinity	Corals							
			na						
CO₂	Salinity	Algae							
			na						
CO₂	Salinity	Seagrass							
			na						
CO₂	Salinity	Forams							
			na						
CO₂	Salinity	Others							

			na	na	na	na	na	na	na
CO₂ + Temp		Corals							
			<i>Porites cylindrica</i> <i>Isopora cuneata</i>	na	na	T + CO ₂ = ↑skeletal bioerosion	ex	na	Reyes-Nivia et al., 2013
			<i>Stylophora pistillata</i>	T ↑, CO ₂ : n.s. T + CO ₂ ↓	T ↑ CO ₂ ↓	T: ↑Chl a Respiration: - CO ₂ = ↑cell specific density	(f)ex (2 x 2)	Synergistic	Reynaud et al., 2003
			<i>Acropora intermedia</i> <i>Porites lobata</i>	<i>Acropora</i> : Highest decrease under T + CO ₂ <i>Porites</i> : no T effect	<i>Acropora</i> : Highest decrease under T + CO ₂ <i>Porites</i> : complex pattern, elevated under medium pCO ₂	Bleaching: For Acropora and Porites highest under T + CO ₂	(f)ex (3 x 2)	-	Anthony et al., 2008
			<i>Pocillopora damicornis</i>	ns	T + CO ₂ = ↓Fv/Fm, O ₂ flux and P:R	T + CO ₂ = ↓larval size Larvae from parents under T + CO ₂ showed metabolic acclimation when subsequently re- exposed, unlike larvae from parents exposed	ex	na	Putnam and Gates, 2015

						to ambient conditions			
			<i>Pocillopora damicornis</i> larvae	na	na	T = ↑metabolism CO ₂ = ↓metabolism	(f)ex (2 x 2)	Additive	Rivest and Hofmann, 2014
			<i>Porites furcata</i>	T + sponge = ↓Calc	ns		(f)ex (3 x 2)	-	Stubler et al., 2015
			<i>Fungia fungites</i> <i>Lithophyllon repanda</i>	na	na	T = ↓survival of <i>L. repanda</i>	(f)ex (3 x 3)	-	Baria et al., 2015
			<i>Acropora digitifera</i>	na	na	T = ↓fertilisation	(f)ex (2 x 2)	-	Iguchi et al., 2015
			<i>Acropora millepora</i> <i>Seriatopora hystrix</i>	na	<i>S. hystrix</i> : O ₂ prod and Fv/Fm ↑with CO ₂ and ↓ with T <i>A. millepora</i> mostly ↓ with T	Bleaching: ↓ with CO ₂ and ↑ with T for <i>S. hystrix</i> , while ↑ with T in <i>A. millepora</i> .	(f)ex (2 x 2)	Additive	Noonan and Fabricius, 2015
			<i>Acropora millepora</i> , <i>Montipora monasteriata</i> , <i>Pocillopora damicornis</i> , <i>Turbinaria reniformis</i>	<i>A. millepora</i> : CO ₂ = ↓calc T ns for all species	na	T = ↓symbiont density in 2 species. No clear effects on Chla, symbiont densities, lipids and protein.	(f)ex (3 x 2)	-	Schoepf et al., 2013
			<i>Seriatopora caliendrum</i>	na	T = ↓Fv/Fm, ΔF/Fm' and P _{net}	T = ↓Chla and symbiont concentrations	f(ex) (2 x 2)	-	Wall et al., 2013

			Reef mesocosm study	CO ₂ + T = ↓calc	ns	CO ₂ + T = ↑coral bleaching, smaller sediment size and an increase in sediment microbe abundance	ex	na	Dove et al., 2013
			<i>Porites panamensis</i> (planula and juveniles)	CO ₂ + T = ↓juvenile skeletal mass	na	T = ↓zoox density CO ₂ + T = ↓biomass Survival ns	(f)ex (2 x 2)	Synergistic (labelled multiplicative)	Anlauf et al., 2011
			<i>Acropora millepora</i> gene expression	na	na	CO ₂ + T = ↓one gene (QCR2) down-regulated, while many unaffected	(f)ex (3 x 2)	-	Rocker et al., 2015
			<i>Pocillopora damicornis</i> larvae	na	na	Protein and zoox density ns T = ↑respiration CO ₂ and T = ↓survival	(f)ex (2 x 2)	-	Cumbo et al., 2013
			<i>Acropora cervicornis</i>	T + CO ₂ = ↓growth	na	T = ↓zoox density and Chla CO ₂ = ns zoox density or Chla	(f)ex (2 x 2)	-	Towle et al., 2015
			<i>Porites</i> spp.	T + CO ₂ = ↓calc	na	T = ↓zoox density	(f)ex (2 x 2)	-	Edmunds, 2011
			<i>Porites rus</i> <i>Porites</i> spp.	<i>P. rus</i> : high T + low CO ₂ = ↑ <i>Porites</i> spp.: ns	na	na	(f)ex (2 x 2)	-	Edmunds et al., 2012
			<i>Stylophora pistilata</i>	na	CO ₂ + T = ↓ T = ↓PSII efficiency	CO ₂ + T = ↓P and N uptake Very low pH used	(f)ex (3 x 3)	-	Godinot et al., 2011

						(7.5)			
			<i>Acropora tenuis</i> Early life history	na	na	CO ₂ + T = ↓fertilisation	(f)ex (2 x 2)	-	Albright and Mason, 2013
			Early life histories of <i>Acropora tenuis</i> , <i>Acropora millepora</i>	na	na	T = ↑development (but fert, survivorship and development = ns) +CO ₂ = ns	(f)ex (2 x 2)	-	Chua et al., 2013
			<i>Diploria</i> spp.	na	na	T = ↓surface mucus layer thickness No CO ₂ effects	(f)ex (2 x 2)	-	Pratte and Richardson, 2014
			<i>Galaxea fascicularis</i>	na	T = ↓P and respiration CO ₂ + T = same photosynthesis as controls	T = ↓ATP contents Microsensor study	(f)ex (2 x 2)	-	Agostini et al., 2013
			<i>Acropora millepora</i> <i>Turbinaria reniformis</i>	na	na	CO ₂ = ↓DOC flux (T ns) POC and TOC ns	(f)ex (2 x 2)	-	Levas et al., 2015
CO₂ + Temp		Algae							
			<i>Ostreobium</i> spp. (green alga)	na	na	T + CO ₂ = ↑abundance	ex	na	Reyes-Nivia et al., 2013
			<i>Porolithon onkodes</i> (CCA)	Highest decrease under T + CO ₂	Highest decrease under T + CO ₂		(f)ex (3 x 2)	Additive	Anthony et al., 2008

			<i>Porolithon onkodes</i> (CCA)	CO ₂ + T↓	na	T and CO ₂ negatively impact several parameters (e.g. partial mortality, tissue paleness)	(f)ex (3 x 2)	Synergistic	Diaz-Pulido et al., 2012
			<i>Porolithon onkodes</i> (CCA)	CO ₂ + T = ↑Dolomite conc Low CO ₂ + T = ↓aragonite	na	As oceans acidify and warm in the future, the relative abundance of dolomite in CCA will increase	(f)ex (3 x 2)	-	Diaz-Pulido et al., 2014
			<i>Hydrolithon onkodes</i> (CCA)	↑Calc at intermediate CO ₂	na	CO ₂ + T = ↑ <i>E. diadema</i> grazing	(f)ex (3 x 2)	Synergistic	Johnson and Carpenter, 2012
			Epilithic algal community (CCA and <i>Peyssonnelia</i> spp.)	CO ₂ = ↓calc	P _{net} lower at high T/present pCO ₂	CO ₂ + T = ↓community (although highest on intermediate T) and CCA cover, ↑ <i>Peyssonnelia</i>	(f)ex (4 x 4)	Additive	Vogel et al., 2016
			Turf algae community	na	No change in biomass	CO ₂ + T = ↑ <i>Lyngbya</i> spp. abundance	(f)ex (3 x 2)	-	Bender et al., 2014b
			<i>Neogoniolithon</i> sp. (CCA)	CO ₂ = ↓calc	na	T = ↑CCA disease CO ₂ = ↓disease	(f)ex/c (2 x 2)	Synergistic	Williams et al., 2014

			Turf algae community	na	T + CO ₂ = ↑biomass ↑O ₂ flux at intermediate temp and CO ₂		ex	na	Bender et al., 2015
			<i>Halimeda maculosa</i> <i>H. cylindraceae</i>	CO ₂ + T ↓	CO ₂ + T ↓	Practically no growth in 'controls' and negative in others suggest specimens compromised or system unsuitable	(f)ex (4 x 3)	Synergistic	Sinutok et al., 2011
			<i>Halimeda</i> spp.	T = ↑ CO ₂ = ↓	T = ↑ No CO ₂ effects	No effects on respiration	(f)ex (2 x 2)	-	Campbell et al., 2015
CO₂ + Temp		Seagrass							
			na	na	na	na	na	na	na
CO₂ + Temp		Forams							
			<i>Marginopora vertebralis</i> <i>Heterostegina depressa</i>	na	CO ₂ = ↓growth	T = negative effects on the physiology of both species.	(f)ex (2 x 2)	Synergistic	Schmidt et al., 2014
			7 species <i>Amphistegina lessonii</i> <i>Am. lobifera</i> <i>Am. radiata</i> <i>Calcarina defrancii</i> C.	na	na	80% retained normal symbiont colour where the temperature was approximately 40 degrees C and pH fluctuated between 5.9 and	ex	na	Engel et al., 2015

			<i>gaudichaudii</i> <i>Heterostegina</i> <i>depressa</i>			7.4 Extremely high T (up to 60°C) and low pH (5.9)			
			<i>Marginopora</i> <i>vertebralis</i>	CO ₂ + T↓	CO ₂ + T↓	Low yield and negative growth in 'control' conditions suggest specimens compromised or system unsuitable	(f)ex (4 x 3)	Synergistic	Sinutok et al., 2011
			<i>Marginopora</i> <i>vertebralis</i>	CO ₂ = ↓Calc T = ↑Calc	T = ↓Prod CO ₂ = ↓Chla CO ₂ + T = ↓Fv/Fm	T has more impact on photosynthesis and O ₂ flux than changes in CO ₂	(f)ex (2 x 2)	-	Sinutok et al., 2014
CO₂ + Temp		Others							
		Echinoids (adult)	<i>Echinometra</i> <i>sp.</i>	na	na	T + CO ₂ = ↓several metabolic parameters and gonad development	(f)ex (2 x 2)	Synergistic	Uthicke et al., 2014
		Microbial communities	Microbial communities on a variety of reef invertebrates	na	na	Temperature rise changes bacterial communities, but not mild pCO ₂ increase. No interactive effects	(f)ex (2 x 2)	-	Webster et al., 2016

		Sponge	<i>Cliona varians</i>	na	CO ₂ + T = ↑Fv/Fm CO ₂ = ↑Fv/Fm		(f)ex (2 x 3)	-	Stubler et al., 2015
		Sponge	<i>Aiolochoxia crassa Aplysina cauliformis Aplysina fistularis Ectyoplasia ferox Iotrochota birotulata Smenospongia conulosa</i>	na	na	Some T effects on attachment. Otherwise most ns results	(f)ex (2 x 2)	-	Duckworth et al., 2012
		Gastropod	<i>Gibberulus gibberulus gibbosus</i>	na	na	T = ↑Max O ₂ uptake No CO ₂ effects	(f)ex (2 x 2)	-	Lefevre et al., 2015
		Sponge	<i>Cliona orientalis</i>	na	↑P _{net} at intermediate CO ₂ + T, but declined at higher levels	Increased energy budget at intermediate increases in CO ₂ and T, but bleaching and negative energy budget at higher levels	ex	na	Fang et al., 2014

Abbreviation: ex: experiment, MQY: maximum quantum yield of photosystem II, Prod: Production/Photosynthesis, ns: not significant, m.s.: marginally significant (0.05<p<0.10). ↓: reducing effect on respective parameter, ↑: enhancing effect, - no effect. DIN: dissolved inorganic nitrogen, DIN/P: a mixture of dissolved inorganic nitrogen and phosphate. Light stands for the combined 'Light OR Irradiance OR Turbidity' search term, Temp = Temperature, Pollut=Pollution.

A.5 References

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APPENDIX B: CUMULATIVE IMPACT MODELS AND ANALYSES TO INFORM MANAGEMENT AND POLICY: A CASE STUDY OF CORAL REEFS

Kenneth R.N. Anthony

B.1 The need for cumulative impacts analyses in GBR management

Understanding cumulative impacts has become a priority for environmental policy, management and conservation globally (Xue et al., 2004; Halpern, Walbridge, et al., 2008; Yamasaki et al., 2008; Ma et al., 2009; Ban et al., 2010; GBRMPA, 2014a, 2014b; Kelly et al., 2014). In Australia, a fuller understanding of cumulative impacts from global and local stressors, and the ability to attribute those impacts to specific drivers and activities, are now a priority at both federal and state (Queensland) government levels, and have recently culminated in the Reef 2050 Long-Term Sustainability Plan (Commonwealth of Australia, 2015). Despite such prioritisation, however, reef managers currently rely largely on qualitative tools to assess risks from cumulative impacts associated with development proposals (GBRMPA, 2009). Without quantitative analytical tools for cumulative impact assessments, environmental decision-making may be biased by qualitative or subjective judgement, which can lead to suboptimal solutions (Hastie and Dawes, 2010).

A number of previous Marine and Tropical Sciences Research Facility and NERP projects, and separate projects commissioned by GBRMPA and the DoE to support the Strategic Assessment of the GBRWHA, have helped advance our understanding of cumulative impacts in complex systems and how that knowledge can support management and policy. Two examples are: (1) NERP project 5.2 investigating combined water quality and climate effects on coral reef organisms (<http://eatlas.org.au/nerp-te/gbr-aims-combined-water-quality-climate-effects-5-2>), and (2) the Cumulative Impacts and Structured Decision-Making (CISDM) approach for coral reefs and seagrass ecosystems (Anthony et al., 2013). While these projects provide insight into different aspects of the problem of cumulative impacts and their management application, they are not well integrated as decision support tools.

The purpose of this Appendix is twofold. Firstly, we briefly review a suite of models that can help researchers and managers analyse risks of cumulative impacts. We present these in the context of risk assessment and how they can inform environmental decision-making. Secondly, we present a new mechanistic model that links environmental drivers and pressures to biological stress responses in corals. Using a set of examples that focus on cumulative impacts from turbidity, nutrients and ocean warming in an inshore setting, we illustrate how the model works as a tool to predict cumulative impacts in space and time, and how model outputs can guide environmental management decisions to avoid, mitigate or offset risks.

B.2 A structured approach to guide decision-making around cumulative impacts

Managers and policy makers concerned with cumulative impacts are faced with a series of challenges, ranging from the formulation of the specific problem to the process by which data or models can inform decision-making. In the following, we offer a stepwise approach that builds on the concepts of structured decision-making (Gregory et al., 2012) and adaptive management (Schreiber et al., 2004; Rist et al., 2013), integrated with one or multiple cumulative impacts models. The steps in the approach are outlined in Figure B1 as an adaptive management cycle. Here, the two initial steps are the problem formulation and the definition of objectives. Both are critical for defining the scope of the project i.e. which ecosystems, habitats, populations or species should be the focus and which stressors should be prioritised for inclusion in the analyses?

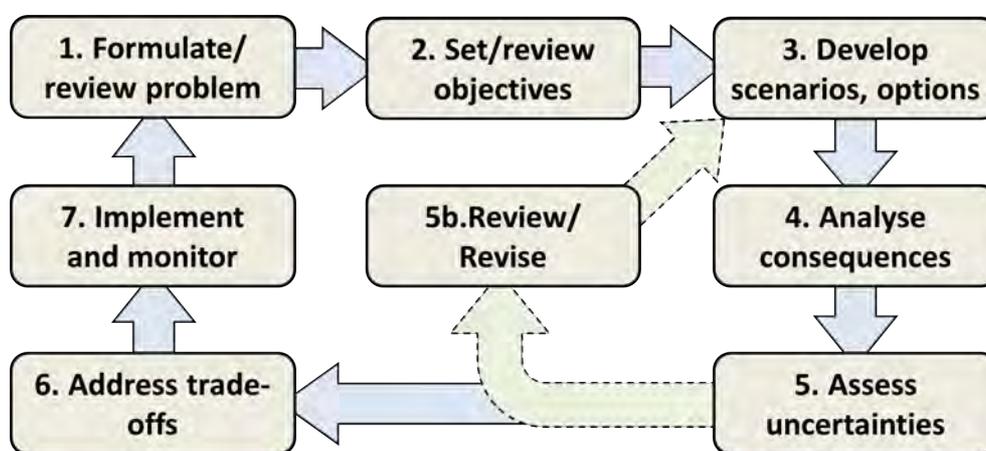


Figure B1: Overview of structured decision-making process as it integrates with the adaptive management cycle. Tradeoffs (Step 6) can here refer to the prioritisation of some objectives (e.g. habitats, locations or species) over others. Implement and monitor (Step 7) refers to decisions around management options (perhaps considering tradeoffs) and subsequent monitoring of the system's performance to evaluate the effectiveness of decisions. Modified from Gregory et al. (2012)

The development of scenarios (Figure B1, Step 3) includes exploration of environmental and development alternatives. This helps define which stressors are in scope and what the possible options for management interventions are. In Figure B1, Step 4 (analyse consequences) comprises the cumulative impacts analyses involving one or multiple models. The outputs here can be in the form of consequence tables that present estimated impacts on (or risks to) different objectives (e.g. increased mortality risk of one or more coral species) across different scenarios. Where spatial data are available, outputs can be in the form of risk maps.

For fully quantitative models, an assessment of uncertainty enables statistical comparisons of risks between different development proposals and between different options within a development proposal. Without estimates of uncertainty, the decision to choose one management option over another, or propose a costly proposal amendment in the case of

development projects, will not have a statistical basis. We touch briefly on the subject of uncertainty in decision-making under model analyses below.

Where reviews and revisions of development proposals or cumulative impacts management plans are part of an iterative process, we include a loop within the adaptive management cycle via a Step 5b (Figure B1). Here, the results of initial risk analyses can inform the review of development proposals or management strategies, and then be subjected to a second (or third) set of risk analyses. The value of this iterative process is that the environmental (and/or cost) benefits of the revisions can be analysed and demonstrated quantitatively, and where possible, uncertainties around environmental risks can be reduced.

We include the analysis of trade-offs as Step 6 (Figure B1) in the structured decision-making framework because different species, habitats or ecosystems might be affected differently by a given stress scenario. In addition, this prioritisation analysis is often influenced by economic and social drivers, e.g. the extent to which the protection of one species or habitat type should be prioritised over another and the consideration of other perhaps conflicting objectives, such as resource availability or socio-economic benefits of development. For assessments where all environmental objectives are considered priorities (e.g. matters of national environmental significance under the Environmental Protection of Biodiversity Conservation Act 1999 or Outstanding Universal Value of the GBRWHA) this step can be ignored.

The last Step (7) in the process is to implement [decided actions], monitor and review. We include this step because monitoring of, for example, compliance, responses, condition and trend is a key part of the performance evaluation of any development project or management strategy (Nichols and Williams, 2006). Further, a cumulative impacts management framework is proposed by GBRMPA as part of the Reef 2050 Long-Term Sustainability Plan (Commonwealth of Australia, 2015), as well as the establishment of an integrated monitoring and reporting program, which will be critical to assess whether cumulative impacts are being managed successfully (GBRMPA, 2015).

B.3 A framework for mapping impacts against likely causes and identifying management options

Managing for cumulative impacts requires insight into: (1) the drivers and activities that result in pressures on the system, (2) what scales they operate on (Halpern, McLeod, et al., 2008), and (3) in what ways these influences interact (Crain et al., 2008; Brown et al., 2013). Such insight helps identify impact pathways as well as management actions that can alleviate stress on the system, i.e. via effective management 'levers'.

A useful approach to assist in this process is the DPSIR framework (Atkins et al., 2011) combined with models of the linked social-ecological system (Schlüter et al., 2012; Anthony et al., 2013, 2015). This approach maps the pathways of pressures from sources to impacts on ecosystem goods and services and enables analysis of possible options for impact avoidance or mitigation by closing the loop back to pressures and drivers/activities via management responses (Figure B2). Essentially, the DPSIR framework as presented in Figure B2 is congruous with the structured decision-making approach as cumulative impacts on the state of values represent the environmental problem and objectives (Figure B1, Steps

1 and 2), and drivers and activities (and in some cases pressures) represent the sources of cumulative stress that management decisions need to act upon (Step 7).

By facilitating the exploration of: (1) possible scenarios that can lead to cumulative impacts at global and local scales (e.g. carbon emission paths, regional development trends, political and socio-economic changes), and (2) tangible alternatives for intervention (e.g. via the avoid/mitigate/offset principle of natural resource management), the DPSIR framework can guide problem formulation, the identification of primary and secondary objectives, and the development of operational models to assist in risk assessment/prediction and decision-making.

B.4 Types of operational models for cumulative impact analyses

Attributing water quality impacts on inshore reefs to specific activities or sources can be difficult in an environment where, for example, sediment export from rivers is confounded with resuspension from dredging campaigns and from natural physical processes such as waves and tides (Fabricius et al., 2014, Fabricius et al., online). In situations where such attribution needs to inform decision-making associated with a proposed development project, cumulative risk assessments should be based on system models. For such models to be able to help managers and policy-makers solve issues around cumulative impacts, we suggest that they build on a set of general principles:

- Results should inform the assessments of risks – i.e. be presented in the language of likelihood and consequence.
- Uncertainty should be accounted for formally – both around input variables and outputs.
- Models should be grounded in theory, observations and experiments, and be able to be used to validate in field situations.
- The mechanics of the model, its assumptions, processes and results should be possible to communicate to, and be understood by, the lay user.
- The model should be able to accommodate new information as it becomes available and to explore alternative scenarios/hypotheses.

In the following, we first present an overview of different types of models that can add to the toolset of scientists and managers investigating or concerned with cumulative impacts. These are: (1) conceptual and qualitative models, (2) Bayesian Belief Networks, (3) statistical models, (4) mechanistic process models, and (5) the new SCIRA for corals. Depending on the problem and the management objectives, these models can be used individually or in combination.

B.4.1 Conceptual and qualitative models

These models produce a graphical layout of the targeted biological, ecological or linked social and ecological systems in the form of influence diagrams. They can include all identified drivers, stressor pathways, and impacts on goods and services within the DPSIR framework, and possible pathways for stress alleviation via actions on drivers or activities. Such a framework is amenable to qualitative analyses (Dambacher et al., 2003), which can provide first-order insight into the risks associated with cumulative stressors and impacts.

Qualitative analyses are largely based on the extent to which impact pathways converge on specific groups or processes, or are amplified by interacting factors. For example, pressures from multiple sources of sediment and nutrient pollution (land-use runoff, urban developments, dredging and resuspension) converge on corals by affecting the same suite of processes that underpin coral health (Figure B2). The strength of conceptual and qualitative models is that they can help identify: (1) drivers and scenarios that lead to impacts and (2) options for management actions on drivers and activities that can alleviate or prevent impacts. Weaknesses are that they are qualitative and do not account for effect sizes, shapes of response curves or spatial and temporal extents or behaviours (Anthony et al., 2013). Qualitative models effectively trade off precision for generality and descriptive clarity of system function (Levins, 1998).

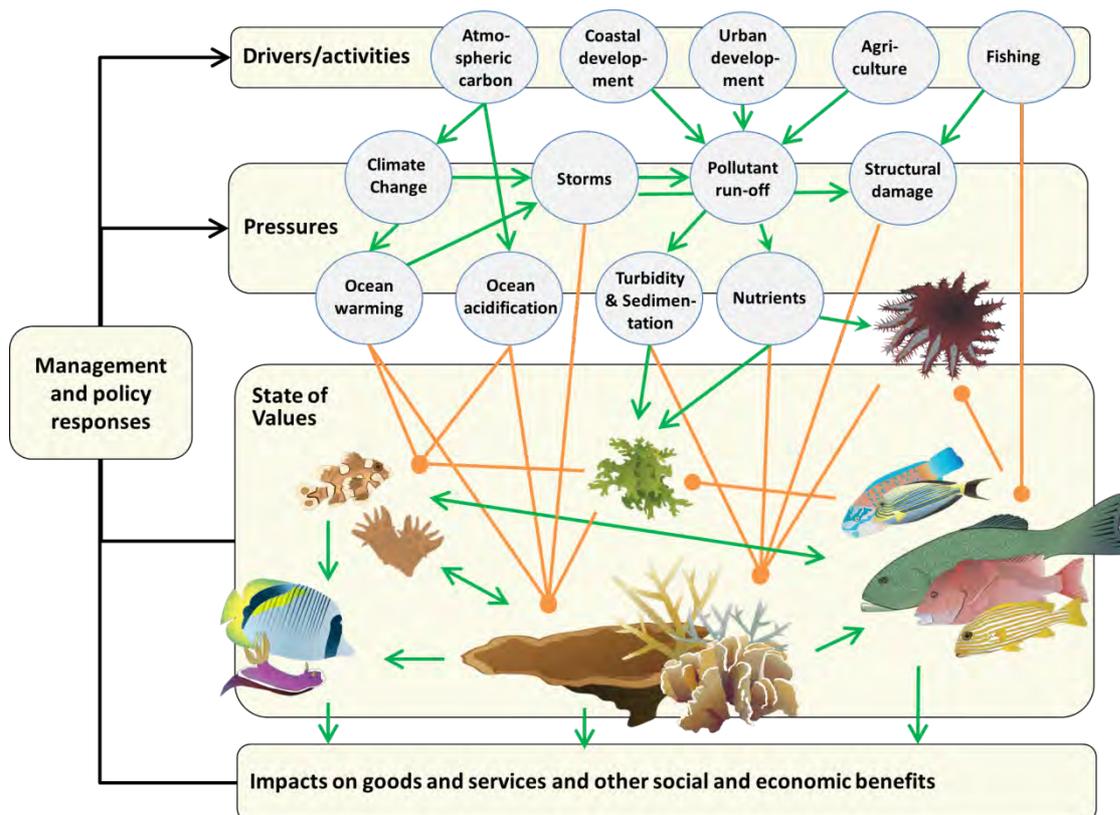


Figure B2: Conceptual model of global and local environmental influences on key functional groups on coral reefs. The model is structured within a DPSIR framework. Sharp (green) and blunt (orange) arrows indicate positive and negative influences, respectively. Specific examples of management and policy responses to changes in environmental values and societal impacts are discussed in the text. Fauna and flora images by T. Saxby, C. Collier and D. Tracey, Integration and Application Network, University of Maryland Center for Environmental Science (<http://www.ian.umces.edu/imagelibrary/>). Source: Anthony (in review).

B.4.2 Bayesian Belief Networks (BBNs)

BBNs are probabilistic models that can be constructed as extensions of conceptual or qualitative models – i.e. they can represent the network of linkages between drivers, pressures and impacts within a DPSIR framework (Anthony et al., 2013) (Figure B3). Results of BBNs can be communicated visually and can illustrate the uncertainty associated with stress scenarios and management outcomes. BBNs can be highly quantitative (Renken and Mumby, 2009; Young et al., 2011). However, in the context of management questions and

decision problems they are often constructed using combinations of data, theory and expert elicitation (Pitchforth and Mengersen, 2013; Ban et al., 2014). Some specific benefits of BBNs in the context of cumulative impact predictions and management decisions are that results can be directly translated to risk – i.e. as ‘likelihood (conditional probability) x consequence (impact severity or effect size)’. Also, dynamic updating as new evidence becomes available, state dependence and spatial processes can be captured in Bayesian models (Farmani et al., 2009; Mcdonald-Madden et al., 2010), but often at the expense of clarity.

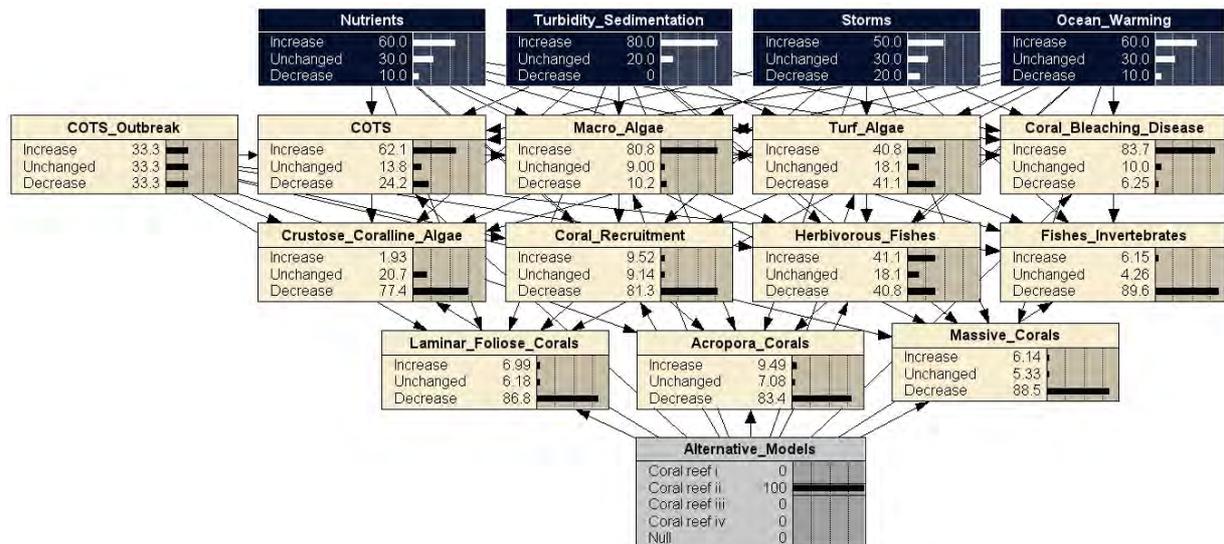


Figure B3: Example of a Bayesian Belief Network used to assess cumulative stress on inshore coral reefs under a complex scenario of nutrient enrichment, turbidity and sedimentation, storms and ocean warming. The box at the bottom is a switch that allows users to compare the ‘behaviours’ and results of four alternative models. Source: Anthony et al. (2013).

B.4.3 Statistical models

Appendix D reviews in detail the application of statistical models to the problem of cumulative effects, so mention of statistical models is only included here for the purpose of placing them in the context of the manager’s analytical toolbox. While conceptual, qualitative models and to some extent BBNs (as distinctive from the broader field of Bayesian statistics), rely to varying degrees on hard data to inform cumulative impacts problems, statistical models (frequentist or Bayesian) are applied exclusively to problems of data analysis – for example to understand the attribution of one or more stressors in a scenario to an observed effect, or the likely change in risk as a response to changed exposure to one or more stressors.

In the following we present a class of models where some statistical analytical capability is retained, but where the main purpose is that of response prediction under specific environmental scenarios and where time is a key factor.

Mechanistic process models

Where precision around impacts of specific stressors and the biological responses are a priority, mechanistic models can provide deeper insight into the processes that lead to cumulative stress and impacts. As the name implies, mechanistic models are based on the

mechanics, or processes, that make up the system using a mathematical approach (Craver, 2006; Buckley et al., 2010; Geritz and Kisdi, 2012). Mechanistic and mathematical models can encompass stochasticity and variation, and can also be subjected to statistical analysis (e.g. Reckhow et al., 1990; Anthony and Connolly, 2004; Bretó et al., 2009). A key strength of mechanistic models, however, is that they can accurately capture the shapes and characteristics of responses and interactions informed by a mixture of theory, experimental data and field observations. A potential weakness is that they are computationally complex and require investment into user interfaces.

In the following we present an example of a mechanistic cumulative stress model developed for reef corals. We first describe the model architecture, theoretical basis and assumptions, and then apply the model to a set of hypothetical scenarios and management problems for an inshore reef area of the GBR. When used as a risk assessment tool, it can inform management decisions around actions to mitigate or prevent stressor combinations that lead to cumulative effects and/or the exceedance of thresholds.

Cumulative Impacts Risk Analysis (CIRA) model for corals

Cumulative Impacts Risk Analysis links multiple environmental pressures and their drivers to risks of cumulative impacts via a set of coupled biological response functions derived from experimental or observational data and underpinned by theory (Anthony et al. in prep). Specifically, the model tracks mathematically how environmental variables affect coral photosynthesis, respiration, bleaching state, energy balance, energy reserves and consequently mortality risk. The model is structured within the DPSIR framework to facilitate scenario development and, on the basis of model outputs, helps compare cumulative risks among scenarios, and identify management options that are likely to represent reduced risk (Figure B4).

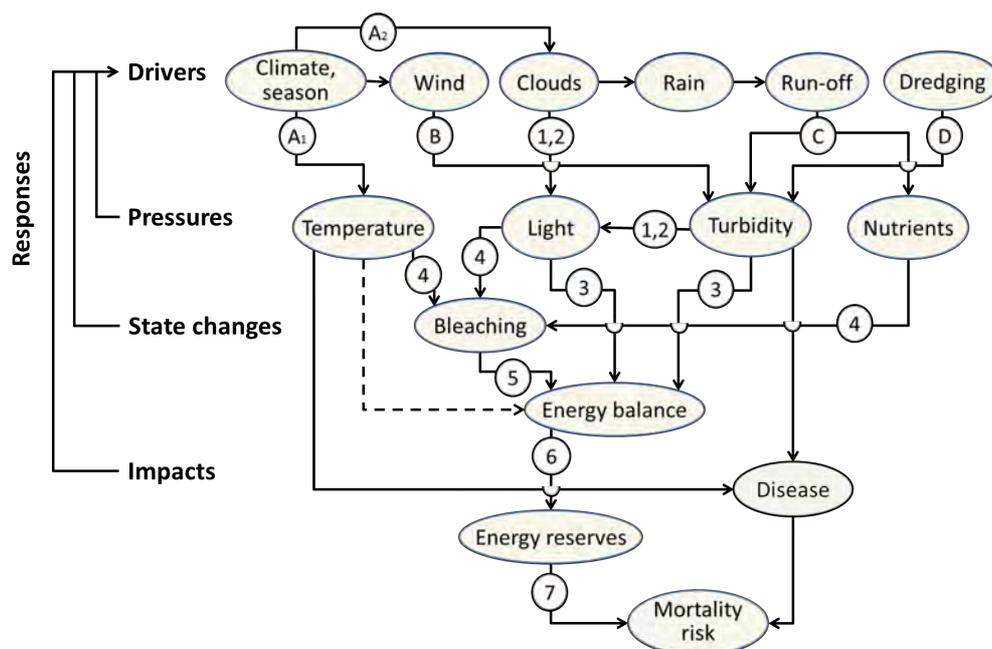


Figure B4: Conceptual representation of biological response model for corals embedded within a Drivers-Pressures-State-Impact-Response framework. Number tags refer to equations in Table B1. Mortality risk is here used as the end-point for cumulative impacts at the organism level. The model can be expanded to include population-level processes such as growth, reproduction and recruitment.

The linked biological response functions in the model build on the principles of dynamic energy budget theory (Muller and Nisbet, 2000; Nisbet et al., 2000, 2012; Anthony et al., 2009; Muller et al., 2009). Dynamic energy budget theory builds on the premise that vital biological functions such as maintenance, growth, immune function and reproductive output are energy-dependent (Nisbet et al., 2000). For reef-building corals, many environmental pressures impact directly on their energy budget (Anthony et al., 2009; Madin et al., 2012), which means it can be applied as a fundamental ecosystem response. For example, turbidity reduces benthic light availability and thereby photosynthesis (Anthony et al., 2004; Fabricius, 2005) and enhances respiration and excretion rates in corals (Telesnicki and Goldberg, 1995; Junjie et al., 2014). Bleaching, which is the loss of photosymbiotic algae, reduces photosynthetic capacity (Warner et al., 1996; Jones et al., 1998, 2000) and consequently leaves corals in a state of prolonged starvation (Grottoli et al., 2004; Rodrigues and Grottoli, 2007; Anthony et al., 2009). Compromised energetics increases mortality risk directly when energy reserves are depleted, and indirectly via the onset of disease via microbial infections (Ritchie, 2006; Haapkylä et al., 2011; Maynard et al., 2011; Pollock et al., 2014).

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CIRA application to cumulative impact scenario (example 1)

To illustrate the mechanics of the model, we first describe its behaviour schematically for corals exposed to a hypothetical cumulative impact scenario relevant for many reefs in the inner GBR lagoon. Specifically, we consider a situation where subtidal corals are exposed to a prolonged turbidity/nutrient event, for example due to resuspension of bottom sediments driven by a period of strong winds (Larcombe et al., 1995), and/or driven by sediment input from a river. Because the majority of dissolved nutrients are consumed and there is a shift state to particulates (Furnas et al., 2005), we use water column chlorophyll *a* as a proxy for nutrient enrichment. The turbidity/nutrient event is followed by a short recovery phase; then a prolonged warming event and a brief recovery phase (Figure B5 A). Thus, this is similar to the 'successive pressures' model in Figure B1 in section B.2. We use the model outputs to identify quantitative signs of cumulative stress over time as follows.

The increase in turbidity (event B on the timeline, Figure B5) reduces benthic light levels (e.g. at 4 m depth) to the extent that the coral energy balance (e.g. for acroporid corals) becomes negative (Figure B5 B). Consequently, energy stores (i.e. lipids) are gradually being drained. Towards the end of the turbidity event, disease risks are high due to elevated infection risk in turbid water (Pollock et al., 2014), and disease in combination with depleted energy reserves lead to high mortality risk (Figures B5 C and D). The drop in turbidity restores photosynthesis and energy balance, leading to a reprieve in disease risk, partly because some diseased corals suffered mortality (Figure B5 E). The onset of a subsequent warming event in combination with the now high light levels lead to increased bleaching risks (Figures B5 D and E). The drop in tissue chlorophyll levels (lost symbionts) reduces photosynthesis despite high light and hence, causes a shift to a negative energy balance followed by drains on energy stores (Figure B5 G). Increased disease risks are now driven by warming (Maynard et al., 2011), and the onset of disease in combination with low energy stores drives high mortality. Lastly, the slow return of normal (non-bleaching) temperatures lead to slow return of tissue chlorophyll (recovery from bleaching), subsequently a positive energy balance, and build-up of energy stores in surviving colonies (Figure B5 H).

The key message in this example is two-fold. Firstly, the impact on corals as mortality risk is a predictable, delayed function of stress responses to the environmental setting. Secondly, the sequential build-up of pressures and stress responses during the progression of the environmental scenario are captured and quantified by the mechanistic model, hence providing metrics for cumulative stress as early physiological indicators and cumulative impacts as mortality risk. Because the model integrates environmental and biological processes mechanistically through daily updating (today's physiological state is influenced by yesterday's physiological state and environmental conditions etc.), it can account for any level of scenario complexity temporally. In a later worked example, we will show that the model can capture effects both temporally and spatially.

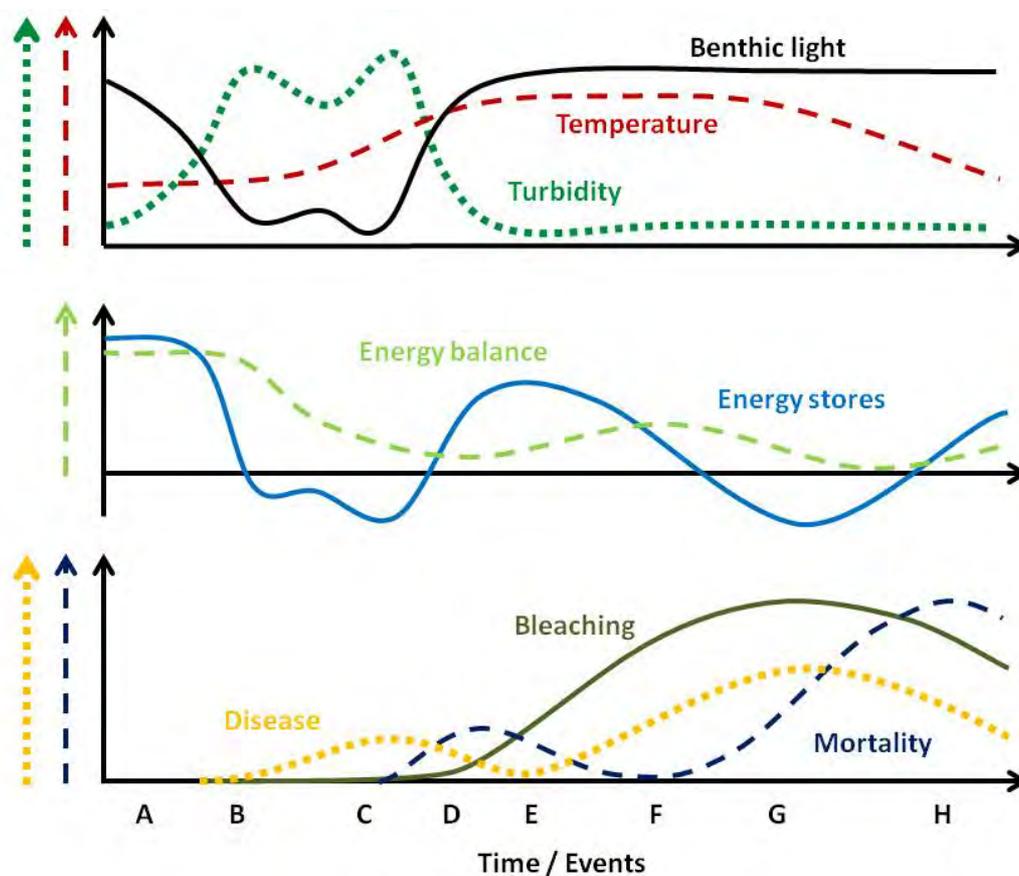


Figure B5: Schematic representation of the sequence of predicted biological responses of a coral species (e.g. *Acropora* sp.) to a hypothetical cumulative impact scenario. Letters on the time axis denote environmental conditions or events. **A:** baseline, **B:** start of turbidity event, **C:** onset of disease risk due to compromised energetics, **D:** elevated mortality risk from energy exhaustion and disease caused by turbidity event, **E:** recovery of energy balance following turbidity event, **F:** onset of bleaching event from warming and high light, **G:** elevated disease and mortality risks due to bleaching and low energy status, **H:** end of warming event and initial recovery of symbionts and energy balance. All axes are relative.

Quantitative assessment of cumulative impacts and model uncertainty (example 2)

To estimate the relative contributions from temperature, light, turbidity and nutrients (as chlorophyll *a*) on the risk profile over time for bleaching, energetics and mortality we systematically manipulated one pressure at a time while holding others constant. We

examined responses to 7 pressure combinations over a time span of 180 days for corals (*Acropora* sp.) at 4 m depth. The design is presented in Table B2. Disease risk is not included here due to the complexity and uncertainty around disease types and their environmental triggers.

Table B1: Summary of environmental settings used to examine the relative importance of turbidity, warming and surface and benthic irradiances at noon for bleaching and mortality risks of corals at moderate depth (4 m). Bleaching and mortality thresholds are here set arbitrarily to 50% of maximum values to allow comparison of results among scenarios. See Figure B6 for model predictions of the different settings.

Setting	SST (°C)	Surface irradiance ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	Suspended particulates (mg L^{-1})	Water column Chl <i>a</i> ($\mu\text{g L}^{-1}$)	Benthic irradiance ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	Bleaching threshold (days)	Mortality threshold (days)
Baseline	28.0	1500	0.5	0.1	786	na	na
A	28.0	1500	5.0	0.1	235	na	na
B	28.0	1500	5.0	0.5	235	na	na
C	32.0	1500	0.5	0.1	786	~60	~150
D	32.0	1500	0.5	0.5	786	~45	~120
E	32.0	1500	5.0	0.5	235	~90	>150
F	28.0	500	0.5	0.1	262	na	na
G	28.0	500	5.0	0.1	78	na	~100

In this model, uncertainties are propagated throughout the chain of processes from environmental drivers to responses using a Markov Chain Monte Carlo approach in which variance-covariance matrices are derived from response functions fitted to multivariate data. Specifically, confidence bands for projections are calculated using the routine *mvnormrnd* from the Markov Chain Monte Carlo library developed for MatLab (Shera, 1998). The sampling-projection procedure is repeated 1000 times for each model run and resulting confidence bands are represented by two standard deviations of the mean for the 1000 runs.

Results show that prolonged exposure to relatively high turbidity (5 mg L^{-1}) at non-bleaching temperatures ($28 \text{ }^\circ\text{C}$) and high surface irradiance ($1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$) leads to the build-up of coral tissue chlorophyll, a marginally negative energy balance and slow depletion of energy stores (Table B2, Figure B6 A). The increase in tissue chlorophyll is here driven by the low but potentially significant nutrient enrichment ($\sim 0.1 \mu\text{g chlorophyll L}^{-1}$) and temperature and light values below the bleaching threshold. The decline in energy balance is caused by a combination of reduced photosynthesis and elevated energetic costs from turbidity-enhanced respiration and excretion (Anthony and Connolly, 2004).

The combination of warming and low turbidity led to full bleaching after around 4 months followed by complete exhaustion of energy reserves and 100% predicted mortality after 5 months (Figure B6 C). Simulating slight nutrient enrichment to around $0.5 \mu\text{g chlorophyll L}^{-1}$ led to a marginally steeper slope of the bleaching response, and earlier onset of energy depletion and high mortalities (Figure B6 D). Adding high turbidity to Scenario D (warming and nutrients) to simulate combined run-off and resuspension, removed the light driver of

bleaching, thereby slowing the bleaching response by over 50%. Consequently, the energy balance was less negative and high mortalities based on resource constraints were delayed by around a month compared to Scenario D (Figure B6 E).

Simulating cloud cover by reducing surface noon irradiance to $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ under low turbidity led to a marginally reduced energy balance (Figure B6 F). The slight increase in energy balance over time is explained by photoacclimation, specifically the kinetics of the irradiance subsaturation parameter, I_k . Similar to Scenario A, low light in combination with low but significant baseline concentrations of suspended particulate matter and relative nutrient loads (Table B2) promoted the build-up of coral tissue chlorophyll over time. Energy stores declined less than 10% and mortality risk did not rise above the baseline hazard rate (Figure B6 F). Lastly, simulating a resuspension event under cloud cover by elevating turbidity without the concomitant nutrient enrichment resulted in a significantly negative energy balance and a precipitous drop in energy reserves (Figure B6 G). This scenario led to a rise in mortality risks after only two months, one to two months earlier than for any other scenario.

We draw the following general conclusions based on these results:

1. High prolonged (e.g. weeks to months) turbidity is a key mortality risk agent for subtidal corals by suppressing energy balance. Disease risk is a key secondary risk factor associated with turbidity (Pollock et al., 2014), but is not included here explicitly due to multiple disease types and lack of sufficient cause-effect data for model calibration. However, we implicitly account for some disease risks under compromised physiological state by using an elevated critical energy threshold for survival, specifically 20% as opposed to 10% of maximum energy stores (Anthony et al., 2009).
2. Bleaching risk can lead to the same mortality risk profile over the same time horizon, but based on different physiological processes. Bleaching risk is enhanced by high light under low cloud cover and/or shallow water and/or high water clarity. Interestingly, turbidity can reduce bleaching risk under warming by removing the light-induced part of the bleaching response (Scenario E). The extent to which turbidity offsets bleaching risk, and hence delays mortality risks, however, depends on the extent to which turbidity lowers the energy balance and elevates disease risk.
3. Cloud cover suppresses surface irradiance and consequently benthic irradiance and energy balance. The negative effect of cloud cover is strongly exacerbated by high turbidity, and can lead to a rapid rise in high mortality rates.

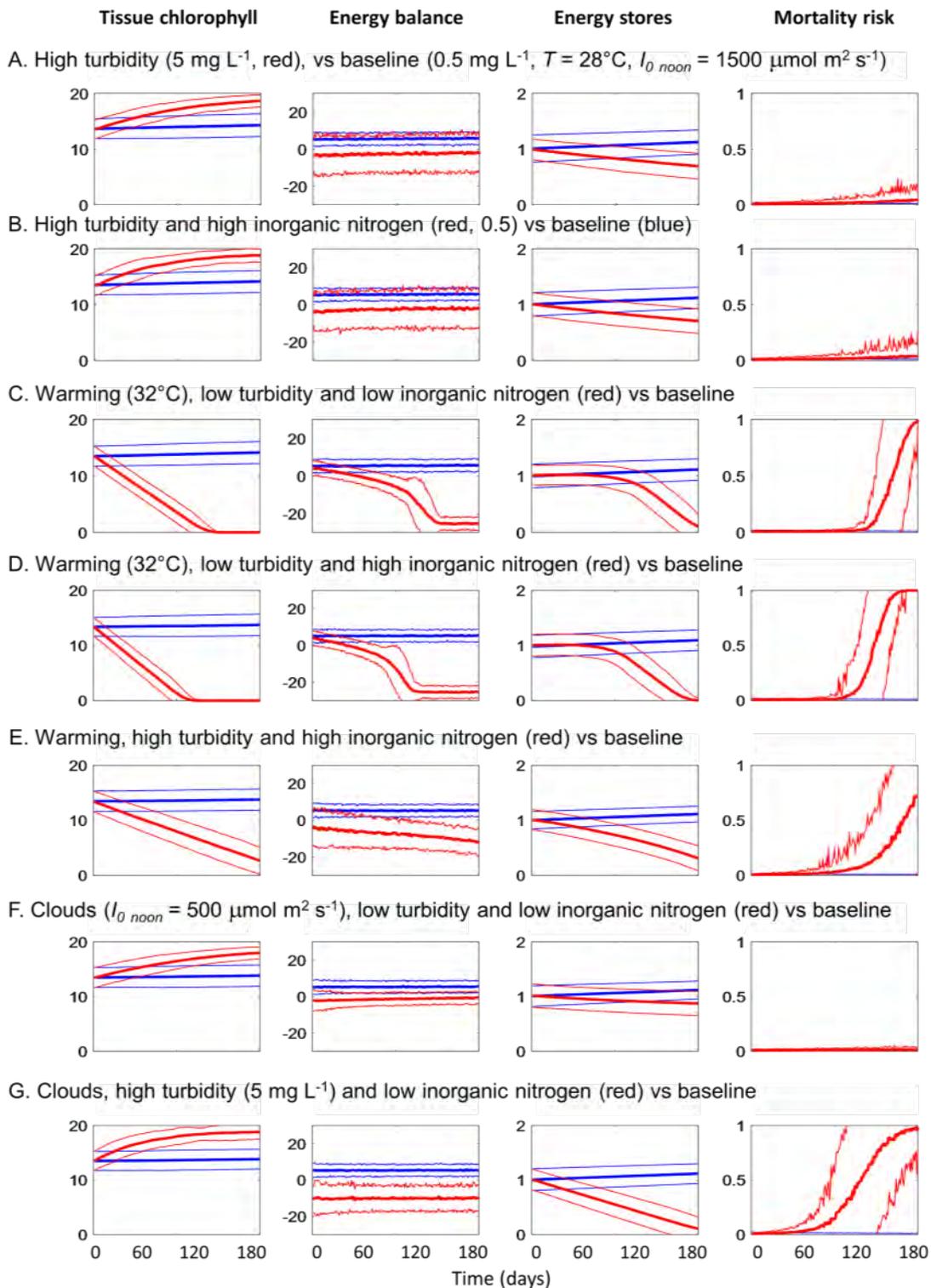


Figure B6: Impacts of turbidity, warming, surface irradiance and nutrients on bleaching (tissue chlorophyll), energetics and mortality risk in different static environmental settings over a 180-day period. Blue thick lines are mean projections for the baseline conditions and red thick lines are for experimental settings in Table B2. Thin lines indicate confidence bands as two standard deviations from the mean. Means and confidence bands are estimated using Markov Chain Monte Carlo analyses of means and variances from experimental and observational data (Table B2).

B.4.4 Spatial Cumulative Impacts Risk Analysis (SCIRA) model

Management problems around cumulative impacts are spatial and dynamic because environmental stressors and their drivers vary in time and space. Building on the principle of cumulative impact risk maps (Halpern et al., 2008b, 2015), we present a prototype of a dynamic and spatial predictive model of cumulative impacts that can be applied to specific management problems around: (1) CIRA, (2) stressor attribution, (3) risks of threshold exceedance and (4) identification of actions that can alleviate or reduce risks (Anthony et al. in prep).

The SCIRA described here uses environmental layers as input variables, and with bathymetry (depth contours), land and habitat (e.g. reef) masks as base layers. Computationally, SCIRA uses CIRA as its core, i.e. CIRA is implemented at the level a coral or a reef cell informed by environmental time series for that coral or reef cell. In SCIRA, the biological response functions (Table B3) of CIRA use the dynamic information from spatial environmental layers (covering multiple reef cells) as input variables and integrated as response layers in SCIRA. To fully inform the biological processes within SCIRA (and CIRA), the model uses daily time steps, but can produce weekly or monthly outputs (risk maps) for bleaching and mortality including maps of risk uncertainty. Disease predictions are not included here as analyses are in progress, but will be included in the next iteration of the model. As distinct from risk maps consisting of amalgamated exposure maps (Maynard et al., 2015), SCIRA integrates dynamic exposure layers informed by the interplay of biological processes. Outputs are hence more reflective of biological risks in space and time.

To illustrate the application of SCIRA to relevant management issues on the GBR, we present an example of stress scenarios for coral reefs around the Palm Islands (Figure B7). The Palm Islands are episodically exposed to sediment, turbidity and nutrients from two main sources: plumes from the Burdekin and Herbert Rivers (Thompson et al., 2012) and resuspension by waves during strong south-easterly trade winds (Anthony et al., 2004). Also, reefs around the Palm Islands were affected by coral bleaching during the 1998 and 2002 warming events on the GBR (Berkelmans et al., 2004). While dredging is not a relevant issue in the vicinity of reefs in the Palm Islands, dredging events can easily be accommodated in SCIRA using modelled or observed dredge plume layers (as time series) as additional input. The model uses water column concentrations chlorophyll *a* as a proxy for nutrients, consistent with water quality monitoring programs (Thompson et al., 2012; Devlin et al., 2013).

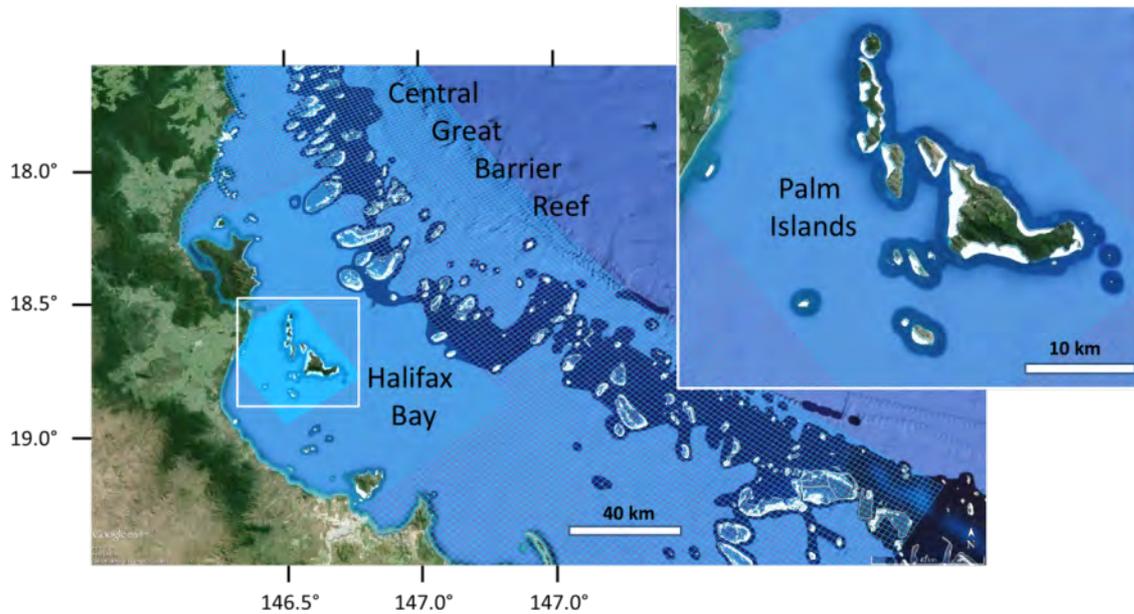


Figure B7: Focus area for case study (inset) in the central section of the Great Barrier Reef, Australia. White shapes in inset indicate reefs. Spatial resolution for the focus area is 200 m.

In this example, we set up a series of 12 environmental scenarios that we played out over a period of six months (180 days). We design these scenarios so that they include multiple systematic combinations of warming and water quality representing different influences from climate change and sediment and nutrient runoff from rivers (Table B3). In this way the effect of different management options can be identified directly from: (1) comparisons of resulting risk maps, or (2) by analyses of summary results of bleaching and mortality risks in consequence tables. By varying turbidity and nutrients orthogonally, analyses can take account of wave-driven resuspension, which is a partly consequential effect of sediment deposition from runoff and partly a natural consequence of proximity to coastlines. Each scenario is run as a mixture of events, i.e. as a 3–4 month warming event starting a month into the run and/or a 2–3 month turbidity/nutrient enrichment event, both with temporal behaviours consistent with those of historical events. For simplicity, we here run each scenario so that the thermal event and the water quality event have the same temporal behaviour across scenarios. In applications to real-life assessments, the temporal and spatial behaviour of environmental layers would be modelled as more stochastic processes.

Table B2: Set of example scenarios used as input conditions for the spatial cumulative impacts risk analysis (SCIRA) model. All scenarios start from a baseline temperature of 27.5 °C and then follow a 4-month warming profile characterised in Figure B6. Similarly, turbidity and nutrients start from a low baseline value and build and decline over a 3-month event that overlaps with the warming event. These scenarios are kept simple here for the purpose of illustration, but more complex temporal behaviours can be accounted for in the model.

Scenario	Climate	Water quality	Max T °C	Max SPM (mg L⁻¹)	Mean SPM (mg L⁻¹)	Chla (µg L⁻¹)
A1	Baseline	Low turbidity low nutrients	28.5	0.9	0.5	<0.1
A2		Low turbidity mod nutrients	28.5	0.9	0.5	~0.5
B1		Mod turbidity low nutrients	28.5	3.7	1.8	<0.1
B2		Mod turbidity mod nutrients	28.5	3.7	1.8	~0.5
C1		High turbidity low nutrients	28.5	9.3	4.4	<0.1
C2		High turbidity high nutrients	28.5	9.3	4.4	~1.0
D1	Warming	Low turbidity low nutrients	32.0	0.9	0.5	<0.1
D2		Low turbidity mod nutrients	32.0	0.9	0.5	~0.5
E1		Mod turbidity low nutrients	32.0	3.7	1.8	<0.1
E2		Mod turbidity mod nutrients	32.0	3.7	1.8	~0.5
F1		High turbidity low nutrients	32.0	9.3	4.4	<0.1
F2		High turbidity high nutrients	32.0	9.3	4.4	~1.0

Sea surface temperature (SST) data are partly from NOAA's Coral Reef Temperature Anomaly Database (CoRTAD, v.5) (Selig et al., 2010) and partly from eReef (provided by H. Tonin, AIMS). Weekly CoRTAD SST data with 4km resolution were downscaled to daily SST at 200m resolution using harmonic intrapolation (N. Wolff, The nature Conservancy). For simplicity, we used a generic 29 °C thermal bleaching threshold for the area (Berkelmans, 2002), potentially overestimating degree heating days at the innermost reefs. In the absence of complete water quality data layers as time series associated with major environmental events and observed coral bleaching and mortality events, we here use synthetic turbidity and chlorophyll gradients for the area for the purpose of illustration only (Figure B8). The amplitude and temporal behaviour of those gradients were then used to construct different water quality scenarios in conjunction with warming episodes.

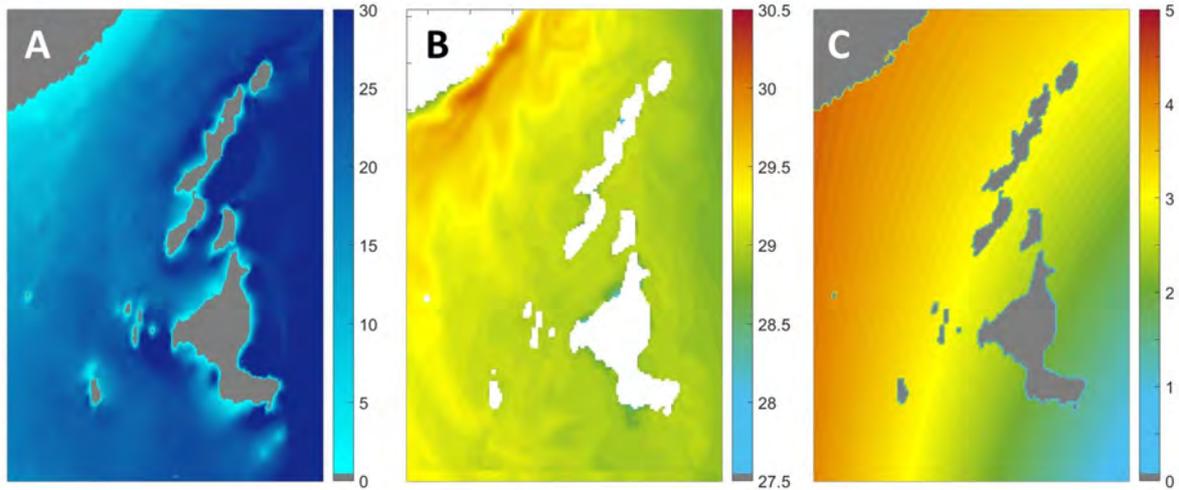


Figure B8: **A:** Bathymetry for the focus area (m below lowest astronomical tide), **B:** sea surface temperatures (°C) for late February 2015 (eReefs), and **C:** modelled gradient of suspended particulate matter (mg L^{-1}) used in scenario analyses. Additional dynamic environmental layers can be included to inform more comprehensive risk analyses of additional drivers, for example the dynamic behaviour of nutrients, chlorophyll *a*, dredge plumes and surface irradiance.

Dynamic risk maps using SCIRA

The spatial projections of bleaching and mortality risk in SCIRA integrate environmental information across two static and three dynamic layers: bathymetry and surface irradiance (static), and temperature, turbidity and nutrients (dynamic). Consequently, bleaching and mortality predictions are influenced by strong spatial and temporal effects. For example, in the warm and moderately turbid scenario for the Palm Islands (Scenario E2 in Table B3), bleaching was severe in shallow (2–4 m) reef areas, leading to significant mortality at the end of the period (Figures B9 and B10 blue lines). In deep water (7–9 m), however, corals bleached less but energy balance was compromised due to elevated turbidity in the first half of the period, leading to a drop in energy stores (Figure B10 red lines). The drop in energy stores led to a peak in mortality risk (but with high uncertainty) at the end of the turbidity event, followed by slow recovery.

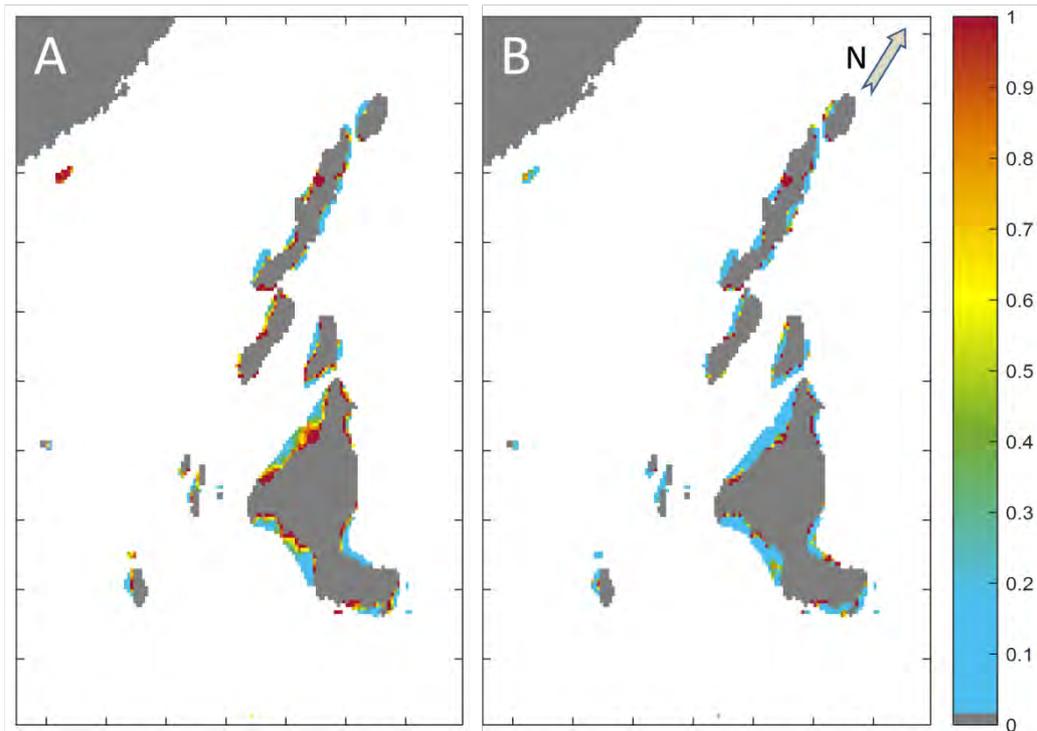


Figure B9: Result of bleaching (left panel) and mortality (right panel) risk predictions for example scenario at the end of a warming event (27.5 – 32.0 °C) under moderate turbidity (mean of 1.8 mg L⁻¹ at peak of the event) and elevated chlorophyll *a* (~0.5 µg L⁻¹)(Scenario E2 in Table B3). Note that bleaching is predominantly in shallow water and leads to some mortality. In deep water, mortality is driven by varying degrees of bleaching and light limitation.

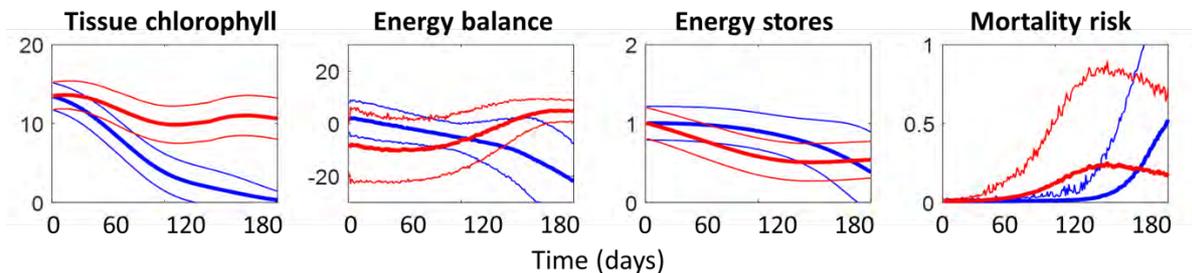


Figure B10: Temporal profile of bleaching, energetics and mortality responses of corals exposed to the E2 scenario in Table B3 and Figure B9. The blue lines are for corals in 2–4 m depth and the red lines are for corals at in 7–9 m. Thin lines indicate 2 standard deviations of the mean for 200 simulations.

Preliminary field validation of SCIRA

To partially validate bleaching predictions for SCIRA against field data, we compared model predictions with observed bleaching levels for *Acropora* sp. at seven sites in the Palm Islands group in early-mid April 1998 at the tail of the bleaching event. Specifically, coral bleaching status (bleached, partly bleached and not-bleached) were scored from 200 points along two 50-m long video transects per site (Fabricius, unpublished data). This dataset was complemented by bleaching and mortality observations from two additional surveys conducted in parallel at Orpheus Island west (Marshall and Baird, 2000; Willis and Anthony, pers obs).

For simplicity, we used a generic 29 °C thermal bleaching threshold for the area (Berkelmans, 2002), potentially overestimating degree heating days at the innermost reefs.

To mimic doldrum conditions, surface noon irradiances were set to $2,000 \mu\text{mol m}^{-2} \text{s}^{-1}$, maximum turbidity was set to 0.5 mg L^{-1} and water column chlorophyll to $\sim 0.1 \mu\text{g chl} \text{a L}^{-1}$. Predictions corresponded well with observations (Figure B10). Reduced levels of bleaching at Pandora Reef can potentially be explained by higher turbidity, acting as a light filter, thus lowering light pressure on symbiont photosystems. Reduced bleaching at the southernmost site on Great Palm Island could be due to: (1) increased influence from cooler mid-shelf waters, or (2) lower chlorophyll *a* concentrations in the water column and potentially a higher bleaching threshold (Wooldridge and Done, 2009).

Using SCIRA to inform management decisions

As outlined at the beginning of this Appendix and illustrated in Figure B1, analyses of cumulative risks and their associated uncertainties comprise Steps 4 and 5 of a structured process to guide environmental decision-making. Because analyses of bleaching and mortality risk for the Palm Island case are here structured into 12 combinations of warming and water quality (turbidity and chlorophyll *a*) scenarios, the effect of management interventions can be inferred directly from differences between the risks associated with different scenarios. For example, effects of managing cumulative risks from nutrient run-off under warming and moderate turbidity (for example from resuspension) can be assessed by comparing outcomes of Scenarios E1 and E2 (Table B3). Further, outcomes of managing sediments and nutrients under warming can be assessed by comparing results of Scenarios E versus D. Thus, because management options are captured implicitly by the design of the analysis, the loop from Step 5 back to Step 3 via mitigation options can be bypassed (Figure B1). Note that standard deviations in Table B4 represent the variation across all sites, and are only included here to indicate the model's capability to propagate uncertainty. For applications to risk assessments for specific sites or habitats of interest, estimates of uncertainty will have tighter confidence envelopes (e.g. see Figure B11).

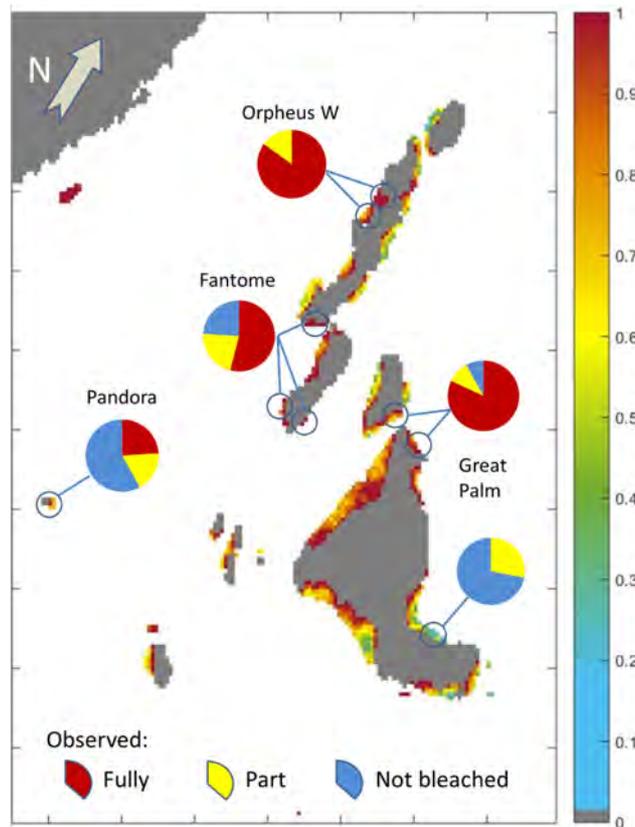


Figure B11: Coral bleaching estimates (as relative loss of tissue chlorophyll content, colour bar) for the late part of the December 1997 - April 1998 warming event. Results are means of 10 model runs (multivariate predictions using a Markov Chain Monte Carlo method) for each reef cell. Pie charts indicate results of bleaching surveys in early-mid April for *Acropora* sp. at 5–6 m depth for all sites except Orpheus Island west (Orpheus W; Fabricius et al. unpublished). Synoptic data for Orpheus Island are from Willis and Anthony (pers. obs.) and Marshall and Baird (2000). Source: Anthony et al. in prep.

Using mortality risk as the endpoint in focus for cumulative risk analysis, the following conclusions can be drawn from the results of Table B4 (for now ignoring confidence envelopes). Firstly, elevated nutrients (represented in analyses by elevated water-column concentrations of chlorophyll *a*) lead to increased bleaching risk, and especially so under low turbidity. Interestingly, however, nutrient loads do not lead to increased mortality, potentially because predictions of disease risk are not yet operational in the model. Secondly, turbidity is the strongest driver of mortality across scenarios and was in our analyses not significantly exacerbated by warming. The latter is potentially because we used a relatively benign warming scenario with 32 °C as a relatively brief temperature maximum. Thirdly, from a management perspective, while turbidity might lower bleaching risks under warming, elevated turbidity represents high mortality risk, which is exacerbated by warming.

Table B3: Summary of results of bleaching and mortality risk projections under six different warming and water quality scenarios. Surface irradiance at noon is set to 2000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. 'Low' and 'elevated' nutrients refer to water column chlorophyll *a* concentrations of 0.2 and 0.5 $\mu\text{g L}^{-1}$, respectively. The different light attenuation effects of different chlorophyll *a* and suspended sediment compositions are not accounted for here.

Scenarios	Bleaching		Mortality	
	max	SD	max	SD
A1. Cool, low turbidity, low nutrients	0.11	0.17	0.03	0.08
A2. Cool, low turbidity, elevated nutrients	0.25	0.28	0.04	0.06
B1. Cool, moderate turbidity and low nutrients	0.05	0.14	0.20	0.33
B2. Cool, moderate turbidity and elevated nutrients	0.13	0.23	0.18	0.29
C1. Cool, high turbidity and low nutrients	0.03	0.11	0.52	0.44
C2. Cool, high turbidity and elevated nutrients	0.06	0.18	0.49	0.44
D1. Warm, low turbidity, low nutrients	0.32	0.29	0.06	0.11
D2. Warm, low turbidity, high nutrients	0.40	0.31	0.09	0.17
E1. Warm, moderate turbidity, low nutrients	0.16	0.26	0.22	0.33
E2. Warm, moderate turbidity, mod nutrients	0.23	0.32	0.25	0.34
F1. Warm, high turbidity, low nutrients	0.08	0.20	0.53	0.44
F2. Warm, high turbidity, high nutrients	0.11	0.26	0.54	0.44

B.5 Conclusions

In this Appendix, we present a structured approach to the analysis of cumulative impacts, using corals on inshore reefs as a case study. We build on the DPSIR framework to formally link causes of stress to their consequences, and to help identify management options and strategies for stress mitigation and avoidance. In this and other chapters and appendices, we show that multiple analytical tools are available to support cumulative impacts assessments, ranging from conceptual and descriptive cognitive maps to highly quantitative statistical models. Because the problem of cumulative impacts on coral reef ecosystems is a complex challenge for research and management, one key purpose of cumulative impact models is to provide clarity around the problem and options for solutions, and transparency around management decisions. To achieve this, we recommend that a succession of model toolsets is used rather than individual tools. Specifically, conceptual models provide a canvas for researchers, managers and stakeholders to come to agreement around which drivers, activities, pressures and values must be included in the problem and what environmental, social and economic objectives need to be considered. Conceptual models can then function as structural templates for the development of analytical models. Where hard data is limiting, BBNs can estimate risks from cumulative impacts based on combinations of qualitative models, data and elicitation of expert opinion. Where decision-making needs to be based on quantitative environmental data or projections and formal analyses of risks, statistical and mechanistic model are the most appropriate tools. Again, for the purpose of communicating the problem and the development of the toolset that can help managers solve the problem, quantitative models are most effective when first developed based on conceptual models in partnership with managers and key stakeholders.

A key focus of this Appendix is the presentation of a prototype of a new CIRA model and its spatial extension (SCIRA). Cumulative Impacts Risk Analysis predicts time trajectories of

bleaching and mortality risk under complex environmental scenarios in time based on calibrated biological response functions. The advantage of CIRA is that it can produce forecasts of physiological risks under almost any set of turbidity, nutrients (chlorophyll) and ocean warming conditions with complex behaviours over time. For spatial and temporal problems of cumulative impacts, SCIRA mechanistically integrates a suite of environmental layers to produce dynamic projections of cumulative risks in complex settings. As distinct from risk mapping based on multiple exposure layers (e.g. Maynard et al., 2015), SCIRA integrates environmental information layers based on combinations of experimental and observational research and can be updated as new data and alternative hypotheses become available. While SCIRA is work in progress, it demonstrates potential as an analytical tool for cumulative impacts risk assessments and a support tool for decision-making in complex, multiple-stressor scenarios. Two priority areas are currently in focus for model calibration and validation: (1) disease risks and (2) the identification of environmental conditions that represent critical thresholds for resilience loss.

Managing successfully for cumulative impacts on key values in the GBRWHA is a high priority for GBRMPA, the DoE and the Queensland Government. Achieving this goal will require analytical tools that can guide effective decisions to avoid, mitigate and offset risks from cumulative impacts. The example in this report illustrates the application of a three-pronged toolset consisting of: (1) a conceptual model, (2) SCIRA and (3) a structured decision-making framework applied to inshore coral reefs, but the approach can be extended to coral reefs generally. Further development and validation of SCIRA and associated decision analyses could see it become a novel and timely tool to support resilience-based management of the GBR and inform the Reef 2050 long-term sustainability plan.

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APPENDIX C: ASSESSMENT OF CUMULATIVE IMPACTS FROM MULTIPLE PRESSURES: APPROACHES FROM ECOTOXICOLOGY

A. Negri, R. Smith, M. Warne

C.1 Introduction

Experimental studies under controlled conditions are valuable for investigating cause-effect pathways and the responses and thresholds of organisms to single and multiple pressures. Ecotoxicology, the study of how chemicals affect organisms, communities and ecosystems, has well-defined approaches for experimentally assessing effects of contaminants on organisms (Chapman, 2002). Typically, concentration-response curves are generated by exposing a single species to multiple (usually six or more) concentrations from which can be derived effect concentrations (EC) – the concentrations that cause a certain percentage of individuals or affect organisms by a certain percentage compared to the controls, either 10% (EC₁₀) or 50% (EC₅₀). Such experiments and the resulting estimates of toxicity are preferred over traditional point-measurements of stress to determine thresholds, such as the lowest observed effect concentration (LOEC), which is obtained statistically but can be highly dependent on the arbitrary choice of experimental conditions (Warne and van Dam, 2008; Warne et al., 2015). Water quality guidelines for pollutants are derived by combining the effect thresholds (typically the EC₁₀ or no observed effect concentration [NOEC] values) of multiple taxa across several trophic levels to generate species sensitivity distributions (SSDs) (Warne et al., 2015). Cumulative frequency distributions (e.g. logistic, normal and Burr Type III distributions) fitted to the multi-species threshold data can be used to estimate concentrations that are protective of any chosen percentage of species in a selected ecosystem. The levels of protection calculated frequently are 80%, 90%, 95% or 99% of species in an ecosystems (ANZECC and ARMCANZ, 2000).

The construction of SSDs for deriving water quality guidelines relies on the results of multiple studies with different species and the quality of the SSD is determined by the reliability of each of the studies contributing to the dataset. The procedures for deriving water quality guidelines in Australia have recently been revised (Warne et al., 2015) and recommended criteria for experiments include: (1) a preference for chronic over acute tests, (2) endpoints which are ecologically relevant (e.g. effects on mortality, growth or reproduction), (3) inclusion of local species, (4) modelled (e.g. EC₁₀) rather than hypothesis-based (NOEC) toxic threshold estimates and (5) use of appropriate controls. While these criteria have been developed with a view to ecotoxicological studies, they are equally applicable to problems focused on experimentally testing of the effects of multiple pressures, including climate effects on species and communities of the GBR. The purpose of this Appendix is to introduce ecotoxicological approaches to predict and assess the responses of organisms and ecosystems to cumulative pressures and to test these approaches on situations relevant to the GBR.

C.2 Testing the joint action of multiple pressures on single organisms

Most ecotoxicology studies have been conducted for single pressures (e.g. chemicals) but there is a series of well-established approaches (models) to explore the combined effects (joint action) of multiple chemicals (de Zwart and Posthuma, 2005; Tang et al., 2015). If the full scale of response (from 0% = no response to 100% = response) of each pressure is established for an organism, then these models can be used to predict how simultaneous exposure to both chemicals might affect the organism. The approach taken depends on whether the toxic mode of action (MoA) of the pressures is the same or different, and whether the pressures interact toxicologically (Plackett and Hewlett, 1952). Typically, ecotoxicologists would attempt to classify the type of joint action between multiple pressures in mixtures into one of four classes (Table C1). There are also types of joint action that are intermediate to the main four, as discussed in de Zwart and Posthuma (2005).

Table C1: Types of joint action for toxicant mixtures. Adapted from Plackett and Hewlett (1952). *While the four classes of joint action were originally developed for toxicants they can equally apply to non-chemical stressors.

	Similar Mode of Action	Dissimilar Mode of Action
Non-interactive (One pressure does not affect the action of another)	Chemicals* have similar MoAs and they do not interact. Concentration Addition Joint Action. Joint action can be predicted	Chemicals have different MoAs but do not interact. Response Addition Joint Action. Joint action can be predicted.
Interactive (One pressure can affect the toxic action of another)	Chemicals have similar MoAs but they interact. Complex Similar Joint Action. No predictive model – responses are derived from experimental observations	Chemicals have different MoAs and they interact. Dependent Joint Action. No predictive model – responses are derived from experimental observations

C.2.1 Concentration Addition (CA)

For chemicals with similar toxic mode of action and no toxicological interaction, the joint effect can be calculated using the Concentration Addition (CA) model (Loewe, 1953; de Zwart and Posthuma, 2005). This can be applied for pressures that act in exactly the same way (their concentration-response curves are parallel and their tolerance to each chemical is completely correlated) – e.g. organisms most vulnerable to chemical A will also be most vulnerable to chemical B. PSII herbicides have the same MoA and CA has been recently applied to demonstrate the non-interactive (additive) response of seagrass photosynthesis to the exposure of 10 PSII herbicides in complex mixtures (Wilkinson et al., 2015). Low concentrations of a mixture of PSII herbicides in the field can have a combined cumulative toxicity that is predictable from CA and this can be compared against water quality guidelines for individual toxicants (Lewis et al., 2012; Smith et al., 2012). The total response of an organism to the mixture of A and B can be predicted by summing the concentrations of each of the chemicals after potency of each is adjusted relative to a reference toxicant:

$$E_{\text{Mix}} = \sum (C_A/ECx_A + \dots C_n/ECx_n) \quad \text{Eq. 1}$$

where E_{Mix} = total effect (response) to the mixture of chemicals, C_A is the concentration of a chemical in the mixture and ECx_A is the concentration that causes $x\%$ effect and the subscripts denote the chemical.

C.2.2 Response Addition (RA)

For chemicals with different MoAs and no toxicological interaction (independent responses), the Response Addition (RA) model can be used to calculate the expected joint action of a mixture (Bliss, 1939; de Zwart and Posthuma, 2005). Using this model, the response to the chemical is scaled 0 – 1 (0% – 100%). The RA model accounts for the reality that the same response in an organism due to pressures A and B cannot occur twice: the total response has an upper limit of 1 (= 100%). This model does not assume there is a correlation between the responses of an organism to each of the components and is expressed as the sum of independent event probabilities:

$$E_{\text{Mix}} = E_A + E_B - E_A * E_B \quad \text{Eq. 2}$$

where E_{Mix} = total effect (response) to the mixture of chemical A and B ($0 \leq E_{\text{Mix}} \leq 1$), E_A = effect (response) to A and E_B = effect of B. E_A and E_B must have a value between zero and one.

RA has sometimes been described by the term ‘multiplicative’ response (Folt et al., 1999; Griffen et al., 2016) and can be alternatively expressed for a mixture of i toxicants as:

$$E_{\text{mix}} = 1 - (1-E_A).(1-E_B)....(1-E_n) \quad \text{Eq. 3}$$

where E_{Mix} = total effect (response) to the mixture of chemicals A to n ($0 \leq E_{\text{Mix}} \leq 1$).

However, this term should not be confused with statistical ‘multiplicative effects’ as used in Appendix D. A key limitation to the use of the RA model is that it requires the entire concentration-response relationship to be available for all of the mixtures components (Dyer et al., 2011), which is seldom the case in the scientific literature.

C.2.3 Mixed or two-step models in ecotoxicology

The total toxicity of mixtures containing groups of contaminants with both similar and different toxic MoAs can be assessed by a combination of the CA and RA models. Here, the responses to chemicals with the same MoA are assessed first using CA, then the total responses of each group with different MoA are combined using RA (Figure C1; Hamers et al., 1996; Altenburger et al., 2004; Junghans, 2004; de Zwart and Posthuma, 2005; Olmstead and LeBlanc, 2005).

an organism (sometimes with partially overlapping modes of action or on secondary processes) is likely to result in some form of interaction; therefore, also invalidating a key assumption of the RA model (Goldoni and Johansson, 2007). Despite the high probability that CA and RA models of additivity will not wholly explain an organism's response to simultaneous pressures, they are simple to apply and the size and direction of deviations from agreement with the models provides evidence of interactions at the observed scale of response. Further studies on identifying modes of action for non-chemical stressors will enable better selection of models and tools to evaluate interactions (Griffen et al., 2016).

A logical extension of the CA and RA models is to generate surfaces of non-interaction (predicted additivity) across all possible combinations, which for two stressors and a response can be represented in a three-dimension space (Goldoni and Johansson, 2007). By comparing the observed response versus the predicted response of non-interaction as calculated from CA or RA, the size and direction of interactions can be described. Three-dimensional surface models of experimental data can also be developed from general linear models and can be used to explore interactions (Appendix D) and the functions of these 3D response surfaces can be used to predict responses at any combination of pressures A and B.

C.2.5 Example of the application of the RA model to assess cumulative effects

To assess cumulative (joint) effects of multiple pressures we have explored one of the few datasets for tropical marine species that includes an entire pressure-response curves for a combination of water quality (copper) and ocean warming scenarios (Negri and Hoogenboom, 2011). In this experiment, coral larvae were simultaneously exposed to copper (Cu) and elevated temperatures for 6 h (10 x Cu and 6 x Temp. = 60 combinations). After this, they were induced to metamorphose into juvenile polyps and their metamorphosis success was assessed after 24 h (Negri and Hoogenboom, 2011). Both Cu and temperature inhibited metamorphosis and the responses were scaled to between 0% and 100% inhibition relative to the metamorphosis under control conditions of 28 °C and 0.37 µg L⁻¹ Cu. The responses were plotted as typical pressure-response curves (Figure C2 A and B). Logistic functions were fitted to the data, allowing the determination of Cu concentrations that affected metamorphosis by 50% (EC₅₀ = 26.2 µg L⁻¹ Cu) and temperatures that inhibited metamorphosis by 50% (ET₅₀ = 32.8 °C). The pressure-response curves for all 60 Cu and temperature combinations were plotted together (Figure C2 C). At 28 °C and 30 °C the slopes overlapped and were essentially parallel, indicating that only Cu negatively affected metamorphosis. At 31 °C the slope became steeper and this was more pronounced at 32°C, indicating a possible change in mechanism or an interaction between the two stressors. Effects on metamorphosis (~70%) were apparent at 33 °C in the absence of Cu toxicity and no metamorphosis was observed at 34 °C irrespective of the Cu concentration.

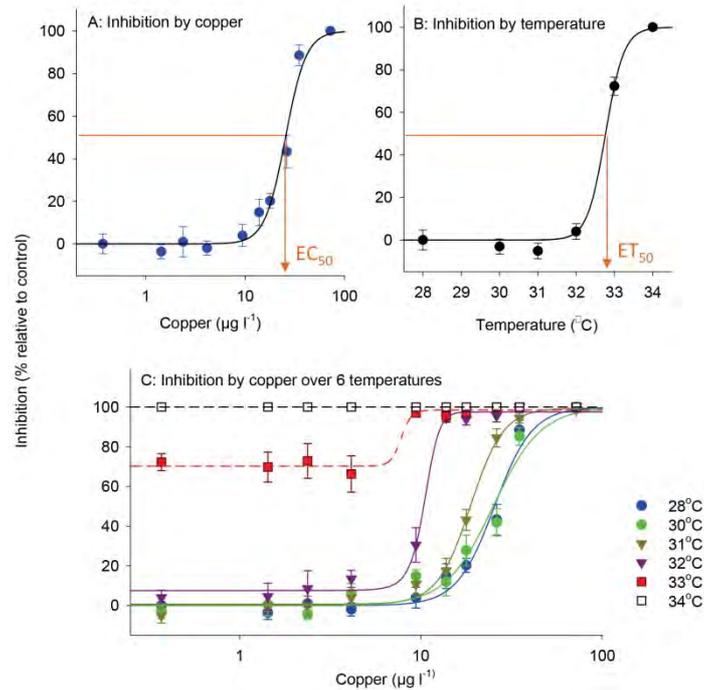


Figure C2: Pressure-response curves for coral larvae simultaneously pre-exposed to 10 copper (Cu) concentrations at 6 temperatures (60 combinations). **A:** concentration-response curve for Cu at the control temperature of 28 °C, **B:** temperature-response curve at the control Cu concentration of 0.37 $\mu\text{g L}^{-1}$ and **C:** a series of Cu concentration-response curves at six temperatures.

Copper and temperature are both likely to affect multiple biochemical and physiological pathways in coral larvae. While some of these may be the same, the dominant modes of action are unlikely to be identical and it could be considered more appropriate to calculate the expected response for additivity using the RA model of joint action. We plotted the expected inhibition of metamorphosis calculated using the RA model (Equation 2) against the experimentally observed inhibition (Figure C3). If the response of larvae to the two pressures was non-interactive (additive according to response addition) then the measured inhibition would be the same as the expected inhibition and intersect the 1:1 diagonal line (data for all control conditions of 28 °C and/or 0.37 $\mu\text{g L}^{-1}$ Cu were not plotted as by definition, these fall on the diagonal line). Responses below the diagonal line indicate sub-additivity or antagonism; and data points above the additivity line indicate synergism occurred.

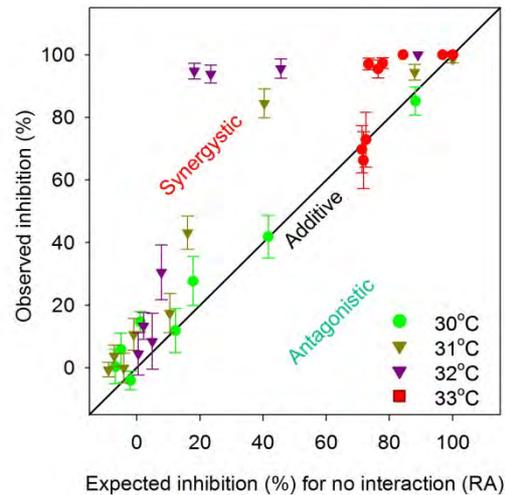


Figure C3: Plot of observed vs. expected toxicities calculated using the response addition model of joint action. Data points intersecting the zero-interaction (1:1) line indicate additivity (no interaction); points below this indicate sub-additivity or antagonism occurred; and data points above the line indicate synergism occurred. The 34 °C response curve was not plotted as inhibition was 100% in all cases.

The results indicate that combinations of Cu and temperature resulted in both additive and synergistic responses, depending on the levels of the two pressures. As expected, raising the temperature from 28 °C to 30 °C results in largely additive responses (many green data points intersect the diagonal, Figure C3); however, the temperatures that caused intermediate stress on their own (31 °C and 32 °C) combined with moderate Cu concentrations resulted in synergistic responses (purple and olive green points, above the diagonal, Figure C3). Diagrams such as Figure C3 that are plotted on the observed experimental scale can facilitate the development of hypotheses on potential toxicological/biochemical mechanisms that cause deviations from expected responses to multiple pressures. For example, the uptake or accumulation of Cu may increase with temperature as seen for a range of ectotherms (Sokolova and Lannig, 2008), possibly enhancing Cu toxicity to coral larvae over the 31 – 32 °C range. The current example demonstrates that the RA model predicts relatively well the responses expected for additivity (no interaction) on the observed scale of the experiment. Deviations from predicted response indicate interactions and provide clues to harmful mechanism that warrant further investigation. While modelling all the response from this balanced dataset provides a hierarchy of relationships to predict responses from all combinations of stressors (the same dataset was analysed in a complementary way using general linear models (see Appendix D) the RA and CA models provide options to predict responses in the absence of good experimental data (but where there is some information on the mechanisms involved).

C.3 Applying the SSD and multisubstance-potentially affected fraction (ms-PAF) methods to predict the interaction of multiple pressure impacts

While single-species toxicity tests are necessary for assessing the joint action of multiple pressures on organisms, they provide only a limited insight into how a whole ecosystem might respond. SSDs have been widely used in ecotoxicology and represent the next tier in complexity for predicting impacts of pressures (Warne et al., 2015). Some of the limitations can be overcome by using field-based ecotoxicity data (e.g. Leung et al., 2005; Kwok et al., 2008). Most typically used for chemicals, there are very few examples of SSDs developed for non-chemical stressors especially for temperate and tropical species, including SSDs for thermal stress (de Vries et al., 2008), acidification (de Vries et al., 2013; Azevedo et al., 2015) and sediments (Smit et al., 2008).

By combining data from multiple SSDs, the ms-PAF method can be used to predict the impacts of multiple chemicals on multiple species to represent community or ecosystem response (Traas et al., 2002). Here, we apply ms-PAF to assess the response of multiple GBR-relevant species to increased water temperatures, taking into account the additional risk to the community posed by contamination by the herbicide diuron. There is a high probability of these two pressures occurring simultaneously on the GBR with the advent of climate change impacts and agricultural runoff still considered a major risk factor for the Reef (Brodie et al., 2013). While there are currently a number of government initiatives in play to reduce diuron (along with many other agricultural herbicides) transported from agricultural lands to the GBR, it is still considered the highest risk pesticide to be detected in in-shore reef habitats of the GBR (Lewis et al., 2013; Davis et al., 2014; Negri et al., 2015).

C.3.1 Species Sensitivity Distributions

A marine SSD for diuron was developed as part of a revision of the Australian and New Zealand Water Quality Guidelines (Smith et al., in prep) and is being considered for the GBRMPA Marine Monitoring Program for reporting risk of PSII herbicides (Reef Plan, 2013). This SSD is currently under review, but has been used here for demonstrative purposes. A summary of the ecotoxicity data used to generate the diuron marine SSD is provided in Appendix A. Only data for phototrophic species were included, as diuron directly impacts photosynthesis and statistical analysis indicated a significant difference in sensitivity between phototrophic and non-phototrophic species (i.e. there was a bimodal distribution) (Smith et al., in prep). In such cases only the most sensitive group of species is used in the SSD (Warne et al., 2015). These species included a diverse range of taxa — green, red, and blue-green algae; diatoms; a phytoflagellate and a coccolithophore; as well as keystone reef species — seagrass and zooxanthellae. The data used in this SSD was selected based on the quality checking and screening processes outlined in (Warne et al., 2015).

An SSD to determine the proportion of GBR species likely to be affected by thermal stress was also generated using tropical species with a principal focus on phototrophic species. The rationale for selecting these types of species was:

1. species with higher acclimation temperatures have a lower tolerance to thermal stress (de Vries et al., 2008), hence only tropical species were included to avoid an underestimation of the percentage of adversely affected GBR species; and
2. joint action of diuron and temperature is likely to only occur for phototrophic species (at environmentally relevant diuron concentrations) (Negri et al., 2011).

It is expected that non-phototrophic GBR species can be sensitive to short-term temperature increases, for example fertilisation of coral gametes and metamorphosis of coral larvae were reportedly affected by a 4 °C increase in temperature (Negri et al., 2007; Negri and Hoogenboom, 2011); however, they are largely insensitive to diuron (NOEC >1000 µgL⁻¹; Negri et al., 2005).

The selection criterion used to determine the subset of temperature data were the same as for diuron, i.e. ecologically relevant test endpoints were preferentially selected, e.g. mortality, immobilisation, growth, development, population growth, and reproduction or the equivalent (Warne et al., 2015). To ensure there was suitable representation of GBR keystone species in the SSD the data selection criteria was extended to also include studies that used chlorophyll a fluorescence as an endpoint. Additional information on the selection criteria of data for the SSD can be found in Supplement B, along with a summary of species and temperature effect data used to generate the temperature SSD (Supplement C).

Thermal stress is influenced by the acclimation temperature of the organism (Urban, 1994; de Vries et al., 2008) and needs to be considered when determining the increase in temperature which will impact a species. For each species the number of °C, or temperature units (TUs), above the acclimation temperature that caused a measured effect on the organism was calculated. The TU is similar to the thermal tolerance interval (TTI) developed by Urban (Urban, 1994); the interval by which the temperature can increase above the acclimated temperature without killing more than 50% of the population. The TU provides more flexibility in that it is not restricted to a 50% effect on the population, instead it can be used to describe any effect on the population. Using a TU over a TTI will provide better alignment with the methods used to generate the diuron SSD, which is constructed from NOEC and EC₁₀ concentrations. Thus, the TU for a species is calculated according to Equation 4:

$$TU_x = T_x - T_a \quad \text{Eq. 4}$$

where TU_x is the temperature unit for a species that causes x% of the population to be affected, T_x is the temperature (°C) that affects x% of the population of a species and T_a is the acclimated temperature.

The SSDs for TUs (Figure C4 A) and diuron toxicity data (Figure C4 B) were plotted using SigmaPlot 13.0 (Systat Software, Inc.). Log-logistic cumulative distribution functions (CDFs) were fitted to the data according to Equation 5:

$$y = \frac{1}{1 + \left(\frac{x}{\alpha}\right)^{-\beta}} \quad \text{Eq. 5}$$

where x is the TU or diuron concentration on the x-axis, α is the value on the x-axis when $y = 0.5$ and β is the slope.

The resulting estimates of α and β (Table C2) were used to calculate the maximum TUs and concentrations of diuron which would protect $x\%$ of species, i.e. the protective TU (PT x) and protective concentration (PC x). The Australian and New Zealand water quality guidelines (ANZECC and ARMCANZ, 2000) recommend 99% species protection (PC99) should be applied to pristine and ecologically significant ecosystems such as the GBR Marine Park and Ramsar wetlands, and 95% species protection (PC95) should be applied to slightly to moderately disturbed areas such as coastal habitats of the GBR. The estimated PT99 and PT95 for temperature were 0.50 and 1.03 TUs ($^{\circ}\text{C}$), respectively, the estimated PC99 and 95 for diuron were 0.08 and 0.23 $\mu\text{g l}^{-1}$, respectively.

Figure C4: Species sensitivity distributions (SSD) of temperature unit increases (A) and diuron toxicity (B) to phototrophic species fitted with a log-logistic cumulative distribution function. Note temperature units are expressed as the temperature ($^{\circ}\text{C}$) above the acclimation temperature of each species.

Table C2: The coefficient of determination (R^2) values and parameters (α and β) of the fitted log-logistic cumulative distribution functions for the individual temperature and diuron hazard unit data.

	Temperature	Diuron
α	3.78	1.45
β	2.27	1.59
R^2	0.945	0.939

C.3.2 Application of the ms-PAF method to multiple-stressor interactions

A case study was carried out to estimate the combined effects of diuron and increased SST on Reef species using the ms-PAF approach, and to compare the results of the RA and CA models as reported by Traas et al. (2002). The SSDs generated for temperature and diuron presented above were used to estimate what fraction of GBR species would potentially be affected by the joint impact of temperature and diuron.

Response Addition

As discussed previously, the RA model is used for pressures that have different MoAs and that do not interact at the target site of toxic action. Traas et al. (2002) demonstrated how this model could be used to assess the potentially affected fraction due to two stressors (A and B) to multiple species based on the RA model of joint action (PAF_{RA}). In summary, the PAF (potentially affected fraction) for each of the two stressors is calculated from their SSD (e.g. Figure C4, Table C2) and then substituted into Equation 6 (Traas et al., 2002):

$$PAF_{RA} = PAF_A + PAF_B - (PAF_A \cdot PAF_B) \quad \text{Eq. 6}$$

where PAF_A is the potentially affected fraction of species from stressor A and PAF_B is the potentially affected fraction of species from stressor B.

Concentration Addition

The CA method (Traas et al., 2002) first normalises the stressor variables so they can be plotted on the same x-axis (independent of the units of measure, i.e. as dimensionless hazard units ([HUs]), by using Equation 7:

$$HU_j = \frac{EC_j}{\bar{X}} \quad \text{Eq. 7}$$

where HU_j is the HU for species j , EC_j = the effective concentration (or effective temperature (ET_j) in the case of temperature) of species j in the SSD, and \bar{X} is the median EC value of the SSD at which 50% of species are affected. Thus, the normalised data are distributed around $x=1$ (the concentration or TU at which 50% of species are affected) and the two stressors comparable.

The log-logistic CDFs are presented in Figure C5 A and B for the individual temperature and diuron HUs (respectively), and Figure C5 C for the combined temperature and diuron HUs. The CDF parameters and the R^2 values are reported in Table C3. The slopes (β) of the CDFs were comparable but not within $\pm 10\%$ of each other. According to Traas et al. (2002), SSDs have similar variance for compounds (or pressures in this case) with the same toxic mode of action, i.e. the standard deviation, and therefore β , of the HUs equal. However, Traas et al. (2002) also notes that if they do not differ, this does not necessarily prove concentration additivity, but may instead be a factor of small sample sizes.

Figure C5: Log-logistic cumulative frequency distributions of species sensitivity to (A) temperature and (B) diuron, scaled to dimensionless hazard units (HUs), and (C) the combined temperature (●) and diuron (○) HUs.

Table C3: The coefficient of determination (R^2) values and curve parameters (α and β) of the log-logistic cumulative distribution functions fitted to the individual temperature and diuron hazard unit (HU) data, and the combined temperature and diuron HU data.

	Temperature	Diuron	Combined
α	0.946	0.725	0.827
β (± 10 %)	2.27 (± 0.23)	1.59 (± 0.16)	1.79 (± 0.79)
R^2	0.945	0.939	0.907

C.3.3 Predicted ecosystem response from ms-PAF models

In this study, the tested diuron concentrations ranged up to $0.5 \mu\text{g L}^{-1}$, a concentration well within the range detected in coastal habitats of the GBR (freshwater and estuarine areas) (Lewis et al., 2009; Smith et al., 2012). As a reference, the reported maximum (monthly average) concentration detected in the GBR inshore marine area for 2015 was $0.027 \mu\text{g L}^{-1}$ (Gallen et al., 2013) and the estimated PC99 and PC95 for diuron (as reported above) were 0.08 and $0.23 \mu\text{g L}^{-1}$, respectively. The tested TUs ranged up to $2 \text{ }^\circ\text{C}$ above ambient conditions (i.e. 2 TUs) which is well within the SST increases predicted to occur by 2100 (Collins et al., 2013).

The results of ms-PAF analysis for this case study (Figure C6) demonstrate that conditions considered protective for the individual stressors, quickly exceed protection levels when they are combined. For example, a diuron concentration of $0.2 \mu\text{g L}^{-1}$ on its own is estimated to affect only 4.1% of phototrophic species and therefore would meet within the PC95. However, this protection level is exceeded when this concentration of diuron is combined with an increase in SST of just $0.25 \text{ }^\circ\text{C}$ when calculated using to the CA model (PAF = 5.13%) and $0.5 \text{ }^\circ\text{C}$ when calculated using the RA model (PAF = 5.05 %). It was estimated that an increase in SST of $2 \text{ }^\circ\text{C}$ would affect 19% of GBR phototrophic species, but when combined with diuron concentrations of just $0.5 \mu\text{g L}^{-1}$, the estimated PAFs increased to 32 and 45% of phototrophic species, according to the RA and CA models, respectively.

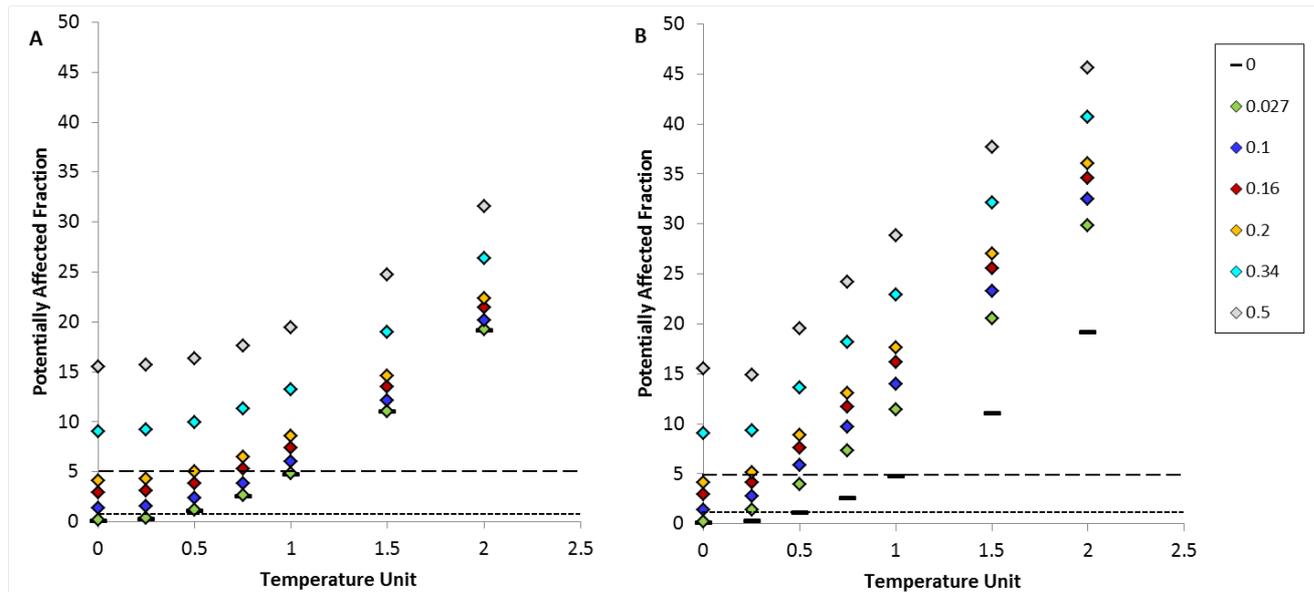


Figure C6: The potentially affected fraction of phototrophic reef species to the combined impact of diuron and increased sea surface temperature, predicted using the (A) response addition, and (B) concentration addition models of joint action. The colour coding of the diuron concentrations ($\mu\text{g L}^{-1}$) is presented in the legend. The dashed horizontal and dotted line indicate when 5% and 1% of species are affected, respectively.

These calculations demonstrate the importance of estimating the combined impacts to an ecosystem from multiple stressors. However, they also demonstrate how the choice of model to combine the SSDs (in this case RA or CA) can impact on the predicted community response (Figure C7). The CA model estimated a higher proportion of species affected compared to the RA model, as has been noted on many occasions previously (Faust et al., 1994; Backhaus et al., 2000a; Backhaus et al., 2000b; Dyer et al., 2000; Chèvre et al., 2006; Junghans et al., 2006), which becomes more apparent as the magnitude of the pressures increase (Figure C7). The choice between RA and CA is not clear in the case of diuron and temperature. A number of studies investigating the combined impact of diuron and temperature on reef species have found largely non-interactive (additive) responses according to RA (van Dam et al., 2012; van Dam et al., 2015). These studies measured chlorophyll *a* fluorescence as the endpoint, which is directly affected by the binding of diuron within PSII and thermal (oxidative) stress to PSII, so although the primary mechanisms are different some interactions between these pressures could occur. Thermal stress can also affect cellular mechanisms besides PSII, while the long-term effects of diuron include oxidative stress under high illumination and starvation under low light (Jones, 2005; Cantin et al., 2007). Thus, an endpoint that measures the response of the whole organism, e.g. growth or mortality, may demonstrate a different type of joint action. In addition to this, only phototrophic species were used in this case study. While diuron has a direct mode of action on phototrophic species, temperature is known to impact both phototrophic species (Supplement C) and non-phototrophic species (de Vries et al., 2008). Clearly, experimental validation of the community responses predicted by different models (CA, RA or other) employed by the ms-PAF technique is needed and this may differ among combinations of different pressures or stressors.

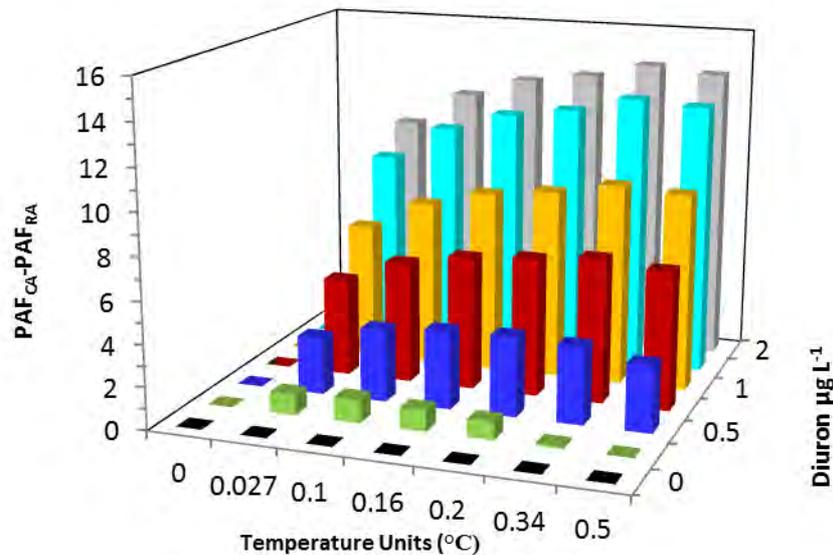


Figure C7: Differences between the predicted potentially affected fractions (PAFs) by the concentration addition (CA) and response addition (RA) models.

C.4 Challenges and opportunities for applying ecotoxicology principals and methods to address cumulative impacts on the GBR

Models of joint action, such as CA and RA that are commonly applied in ecotoxicology, provide straightforward methods to explore potential interactions between multiple pressures. The CA and RA models rely on the modes of action being either identical (CA) or completely independent (RA), which is possible for mixtures of pesticides (de Zwart and Posthuma, 2005), but is otherwise unlikely for other GBR-relevant pressures such as thermal stress, sediment, nutrients etc., which act in multiple ways on organisms and communities. Nevertheless, the CA and RA models can be used to assess deviations from additive responses caused by interactions and inform the choice of more complex statistical models. Data from multi-pressure ecotoxicology experiments are suitable for application in alternative statistical modelling that can be used to quantify interactions between pressures (Appendix D). These models can then be incorporated into risk maps (Appendix B).

CA models accurately predict the combined effects of PSII herbicides on GBR seagrass and algae (Magnusson et al., 2010; Wilkinson et al., 2015). Risks posed by multiple PSII herbicides in the GBR have already been assessed by combining CA models (to calculate total toxicity) with exposure maps (Lewis et al., 2012). The risks were informed by water quality guidelines developed from ecotoxicology studies on relevant taxa (GBRMPA, 2010) and the same protocols have been applied to pesticide monitoring in the Reef Plan (Reef Plan, 2013). While applicable to contaminants with the same modes of action, more work needs to be done to assess risks posed by combinations of a wider diversity of pressures and to factor in exposure durations (see below).

SSDs have been widely used in ecotoxicology and represent the next tier in complexity for predicting impacts of pressures on communities and ecosystems (Warne et al., 2015). SSDs have been developed for a range of chemicals including herbicides commonly detected in the GBR (Smith et al., in prep) and there is great potential for this approach to be used to quantify GBR-specific community thresholds to climate (thermal stress, ocean acidification) and flood plume pressures (nutrients and sediments). We have demonstrated how relevant SSDs in response to climate and pollution stress can be applied to predict community responses to multiple pressures using the ms-PAF method. One issue we faced was how to deal with chemicals which have a direct MoA on a subset of the species within an ecosystem (e.g. in this case, diuron has a direct MoA on phototrophic species only), whereas non-chemical stressors, such as temperature, irradiance, sediment etc., have less specific MoAs or multiple MoAs which may also vary depending on the organism type. In the case of diuron and temperature, phototrophic species would be directly impacted by both pressures, however, non-phototrophic species are unlikely to be affected by diuron at environmental concentrations (Negri et al., 2005). In this case we included both phototrophic and non-phototrophic species in the temperature SSD (but with a preference for phototrophic species), and therefore the RA model would be more appropriate to use in these circumstances. But if a CA model is a better estimate for a subset of the organisms where the known MoA is additive, then perhaps a combination of the CA and RA models would be required. Dealing with the MoA of different organism types for multi-stressor impacts needs to be considered and tested in greater detail (through careful experimental examination). The ms-PAF is a promising approach to understand community response(s) to multiple pressures, but more reliable stress threshold data on GBR-relevant pressures is required, along with multifactorial experiments to provide data that can be used to validate the choice of joint action models employed by this technique.

A current hurdle for applying non-chemical stressor data for predicting impacts to ecosystems is the quality and comparability of the available data. Standardised experimental methods, statistical analysis and data selection criteria are well established in the field of ecotoxicology to ensure toxicity data are both reliable and comparable. However, these formalised processes are not common in the experimental methods of non-chemical stressor impacts (see Supplement A). For example, fitting probability curves to concentration-response data and the calculation of EC/LCx concentrations is commonplace in ecotoxicity studies, and provides important parameters to compare between species and test conditions. It was found that in many of the studies that evaluated the impacts of increased surface sea temperature, that this type of statistical analysis was rarely conducted. In addition, care in the accuracy of the measurements and the type of endpoints that were applied in these studies varied considerably compared to current ecotoxicity studies. For example, the temperature treatment was reported but not necessarily measured which became an issue particularly when only NOET and lowest observed effect temperature (LOET) data could be extracted. Reporting whole units (°C) rather than the specific measured temperature, to 1 or 2 decimal places, resulted in a number of species with the same effect temperature included in the SSD. When the range of potential effect temperatures is so small (up to 9 units above the acclimated temperature), greater accuracy of the test temperatures is required. Using ET₁₀ (or TU₁₀) data helps resolve this problem; however, the accuracy of the reported TUs may not be reliable if temperatures were not directly measured and the intervals between temperatures large. Test standards consistent with those used in ecotoxicology should also

be applied to determine thresholds and response relationships for other GBR relevant non-chemical stressors such as acidification, elevated nutrients and turbidity.

C.5 Conclusions and Recommendations

Ecotoxicology offers a range of models and methods to predict organism (CA and RA) and community responses (ms-PAF) to cumulative pressures, and other valuable contributions to this issue will be: (1) formal approaches to generate reliable experimental data on organism stress; (2) identification of stress mechanisms; (3) establishment of thresholds for stress and (4) to generate multi-factorial data suitable for validating models discussed in Appendices B and D. Additional experimental work and validation is needed to maximise the utility of these approaches to predict the responses of GBR organisms and ecosystems to cumulative pressures under a wider range of scenarios. This includes improving experimental protocols for identifying thresholds for more non-chemical pressures and conducting more multi-factorial experiments with GBR-relevant pressures and organisms (see above). Simultaneous exposures explored here represent some of the most straightforward scenarios leading to cumulative and other potential scenarios remain largely untested in experiments (see Appendix B). For example, many current risk assessments and models explore responses after single exposures (acute or chronic), whereas at least in the near-shore of the GBR organisms are typically exposed throughout the year but with relatively short periods of relatively high concentrations (pulses associated with flood events). Exposure duration (including acclimation) represents an important variable that should be incorporated in statistical effect and risk models and therefore, future pressure-response experiments should supply data on responses over multiple exposure durations and examine the effects once exposure has terminated. These scenarios can be tested using a variety of toxicology models including the Threshold Damage Model, Time-Weighted Averages Model and Toxicokinetic-Toxicodynamic Model (Ashauer et al., 2007; Jager et al., 2011). In order to apply even the simplest of repeated pulse models requires appropriate experimental data (e.g. survival over time) (Jager et al., 2011) and additional relevant experiments are needed before these approaches can be confidently applied to cumulative pressures in the GBR.

Field data and ms-PAF datasets allow us to explore cumulative impacts on communities. However, field data may be confounded with unknown pressures and influences, which can complicate the identification of clear cause-effect pathways or the conclusive source and size of apparent interactions. The use of the adverse outcome pathway framework (e.g. Ankley et al., 2010) for a wide variety of stressors (or pressures) would facilitate the identification of the most appropriate joint action model to use and potentially facilitate deviations from the CA or RA predictions. A lack of appropriate threshold data for key GBR species to the wide range of relevant pressures is also a problem for the application of ms-PAF to cumulative GBR scenarios. Simulating community responses in microcosm and microcosm experiments offers further opportunities to investigate thresholds and cumulative responses of organisms and communities over time (including indirect effects such as predation and competition) in simplified ecosystems that better mimic real-world scenarios (Caquet et al. 2000). So far, the cost and complexity of conducting microcosms and microcosms has severely limited the testing of multiple stressors, but now such work is not only feasible in state-of-the-art experimental facilities such as Australia's National Sea Simulator, but should be a research priority.

C.6 References

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Supplement A: Summary of the effect data of phototrophic species to diuron used to generate a species sensitivity distribution for diuron in marine environments (Smith et al., in prep).

Species Scientific Name	Group	Media Type	Exposure period	Effect Value	Endpoint	Concentration ($\mu\text{g L}^{-1}$)
<i>Nephroselmis pyriformis</i>	Green algae	Estuarine	3 d (chronic)	EC10	Population growth rate	1.1
<i>Navicula sp.</i>	Diatom	Estuarine	3 d (chronic)	EC10	Population growth rate	0.5
<i>Chlorococcum sp.</i>	Green algae	Marine	10 d (chronic)	Converted NOEC/EC10 (from EC50)	Abundance	2
<i>Dunaliella tertiolecta</i>	Green algae	Marine	10 d (chronic)	Converted NOEC/EC10 (from EC50)	Abundance	4
<i>Synechococcus sp.</i>	Blue-Green algae	Marine	3 d (chronic)	NOEC	Abundance	0.21
<i>Pocillopora damicornis</i>	Zooxanthellae	Marine	4 d (chronic)	NOEC	Abundance	1
<i>Emiliania huxleyi</i>	Coccolithophorid	Marine	3 d (chronic)	NOEC	Abundance	0.54
<i>Isochrysis galbana</i>	Phytoplankton	Marine	10 d (chronic)	Converted NOEC/EC10 (from EC50)	Abundance	2
<i>Chaetoceros gracilis</i>	Diatom	Marine	3 d (chronic)	Converted NOEC/EC10 (from EC50)	Abundance	7.2
<i>Entomoneis punctulata</i>	Diatom	Marine	3 d (chronic)	NOEC	Population growth rate	2

<i>Nitzschia closterium</i>	Diatom	Marine	3 d (chronic)	NOEC	Population growth rate	2
<i>Phaeodactylum tricornutum</i>	Diatom	Marine	10 d (chronic)	Converted (from EC50)	NOEC/EC10 Abundance	2
<i>Ceramium tenuicorne</i>	Red algae	Marine	7 d (chronic)	Converted (from EC50)	NOEC/EC10 Population growth rate	0.68
<i>Zostera marina</i>	Seagrass	Marine	10 d (chronic)	NOEC	Biomass	2.5

Supplement B: Selection criteria for data to generate a temperature species sensitivity distribution

For some species multiple data records of temperature effects were available, as a result of different test endpoints, exposure periods and/or effect values. For example, *Neogoniolithon fosliei* has six data records of temperature effects from different endpoints and effect values (Supplement C). In these cases, a data selection process consistent with that used to derive one value per species for chemical stressor data was used (Warne et al., 2015). The selection process for temperature effect data was as follows:

1. the NOET and LT/ET₁₀ data were preferentially selected over LOET and LT/ET₅₀ data¹,
2. the geomean of TUs with the same endpoint but different literature sources, exposure periods, and/or effect values were calculated, and
3. the minimum TU of all endpoints tested was used to represent the TU for the species (Supplement C).

The selection process above varied from the process used for chemical stressor SSDs in one way; the preferential selection of chronic exposure periods over acute exposure periods was not included (Warne et al., 2015). In this case study we did not consider what constituted an acute and chronic exposure period for temperature, and instead treated all exposure periods equally. The thermal stress SSDs developed by (de Vries et al., 2008) used an opposing approach, i.e. they only used the acclimation and exposure periods of the studies to preferentially select from multiple data records for a species, and they preferred to use the longest exposure and acclimation periods. The exposure periods presented in Supplement C range from 96 hours to 10 weeks. In the GBR average seasonal temperatures range by 4 °C in the north and 6 °C in the south and differences in daily minimum and maximum temperatures can be over 9 °C (Lough, 2007). Coral bleaching events have been known to result from 3–6 day exposures to 1–3 °C temperature increases in summer (Berkelmans et al., 2004). Additionally, the coral bleaching threshold for some coral species was found to be 1 °C lower in winter compared to the summer threshold, indicating the likelihood of seasonal acclimation in corals and the potential capacity of some coral species for short-term temperature acclimation (Berkelmans and Willis, 1999). Thus, acute and chronic exposure periods need to be defined for thermal stress, which is likely to be dependent on the species and natural climatic conditions of the ecosystem in question. This is an important issue for the development of SSDs and ms-PAF for non-chemical pressures particularly for reef species, which needs to be explored more thoroughly.

¹ NOET is the maximum TU tested that elicits an effect that is not significantly different from the control; LT/ET₁₀ is the lethal/effective TU that affects 10% of the population; LOET is the minimum TU tested that elicits an effect that is significantly different from the control; and LT/ET₅₀ (as described by de Vries et al, 2008) is the lethal/effective TU that affects 50% of the population.

Supplement C: Summary of the effect data of phototrophic species to increased temperature that was used to generate a species sensitivity distribution for temperature in marine environments.

Species	Group	Endpoint	Exposure Period	Effect Value	Temperature (°C)			Preferential Selection ^a (Effect Value)	Geomean of TUs (per endpoint)	Minimum TU ^b (all endpoints)	Reference
					Acclimated	Effect	Effect Temperature Units (TUs)				
<i>Acropora millepora</i>	Coral	ΔF/F'm	7 d	NOEC	26	31	5	1	5	5	1
		ΔF/F'm	7 d	LOEC	26	32	6	2			
<i>Alphaproteobacterium</i>	<i>Symbiotic bacterium</i>	proportion of the culturable fraction	14 d	NOEC	27	31	4	1	4	4	2
<i>Alveolinella quoyi</i>	Foraminifera	ΔF/F'm	96 h	NOEC	26	30	4	1	4	4	3
<i>Calcarina mayorii</i>	Foraminifera	ΔF/F'm	96 h	EC12	26	34	8	1	8	8	3
<i>Heterostegina depressa</i>	Foraminifera	bleaching - Chl- <i>a</i> content	96 h	EC10	26	28	2	1	2	2	3
<i>Heterostegina depressa</i>	Foraminifera	ΔF/F'm	96 h	NOEC	26	30	4	1	4	4	3
<i>Marginopora vertebralis</i>	Foraminifera	bleaching - Chl- <i>a</i> content	96 h	EC30	26	28	2	1	2	2	3
<i>Marginopora vertebralis</i>	Foraminifera	ΔF/F'm	96 h	EC05	26	34	8	2	N.A.	2	3
<i>Marginopora vertebralis</i>	Foraminifera	ΔF/F'm	96 h	EC12	26	34	8	2	N.A.	2	3
<i>Mycedium elephantotus</i>	Coral gametes	pre-acclimation of gametes - fertilisation & abnormal development	4h	NOEC	28	32	4	1	4	4	5
<i>Neogoniolithon fosliei</i>	Crustose coralline algae	Fv/Fm	7 days	LOEC	27	31	4	2	N.A.	2	4
<i>Neogoniolithon fosliei</i>	Crustose coralline algae	visible CCA bleaching	7 days	LOEC	27	31	4	2	N.A.	2	4
<i>Neogoniolithon fosliei</i>	Crustose coralline algae	Fv/Fm	7 days	NOEC	27	29	2	1	2	2	4

Multiple and cumulative impacts on the GBR: assessment of current status and development of improved approaches for management

<i>Neogoniolithon fosliei</i>	Crustose coralline algae	visible CCA bleaching	7 days	NOEC	27	29	2	1	2		4
<i>Peneroplis planatus</i>	Foraminifera	$\Delta F/F'm$	96 h	NOEC	26	34	8	1	8	8	4
<i>Pocillopora darnicornis</i>	Coral	Chl- <i>a</i> content/zooxanthella cell	10 weeks	LOEC	27.9	31.68	3.78	2	N.A.		6
<i>Pocillopora darnicornis</i>	Coral	Chl- <i>a</i> concentration/no. of zooxanthellae	10 weeks	NOEC	27.9	28.4	0.5	1	0.5		6
<i>Pocillopora darnicornis</i>	Coral	Chl- <i>a</i> content/zooxanthella cell number of zooxanthellae/coral	10 weeks	NOEC	26.2	26.4	0.2	1	0.2		6
<i>Pocillopora darnicornis</i>	Coral	protein number of zooxanthellae/coral	10 weeks	NOEC	27.9	28.4	0.5	1	0.27	0.2	6
<i>Pocillopora darnicornis</i>	Coral	protein number of zooxanthellae/coral	10 weeks	NOEC	26.2	26.4	0.2	1	N.A.		6
<i>Pocillopora darnicornis</i>	Coral	protein number of zooxanthellae/coral	10 weeks	NOEC	26.2	26.4	0.2	1	N.A.		6
<i>Rhopaloeides odorabile</i>	Sponge	Mortality	4 days	LC100	27	32	5	2	N.A.	4	7
<i>Rhopaloeides odorabile</i>	Sponge	Necrosis	14 d	NOEC	27	31	4	1	4		3
<i>Symbiodinium C1 (A. tenuis)</i>	Symbiodinium clades	$\Delta F/F'm$	8 d	NOEC	26	30	4	1	4	4	8
<i>Symbiodinium D (A. millepora)</i>	Symbiodinium clades	$\Delta F/F'm$	8 d	NOEC	26	30	4	1	4.	4	8

^a NOEC and EC10 effect data were preferentially selected for use in the temperature SSD over other effect data

N.A. = not applicable, data were not used to calculate the TU for a species based on the Preferential Selection of Effect Data

^b Values used for temperature SSD.

^c References: 1 (Negri et al., 2011); 2 (Webster et al., 2008); 3 (van Dam et al., 2012); 4 (Webster et al., 2011), 5 (Negri et al., 2007); 6 (Glynn and D'Croz, 1990); 7 (Simister et al., 2012); 8 (van Dam et al., 2015)

APPENDIX D – STATISTICAL TOOLS TO DETECT CUMULATIVE TEMPORAL AND SPATIAL CHANGES IN ECOLOGICAL SYSTEMS

G. De'ath

D.1 Introduction

A crucial issue for both scientists and managers is to quantify the cumulative effects of temporal and spatial change in ecological systems, and to identify the drivers and mechanisms of such change. This is not a simple issue. Ecosystems are typically complex, difficult to observe and highly variable. Knowledge of the relationships between the individual components of ecosystems and their environments is also usually weak. Despite these difficulties, modern statistical methods are proving to be invaluable in the development of our understanding of these complex systems.

This Appendix focuses on the process of statistically modelling cumulative effects of temporal and spatial change – from design and implementation, through choice and application statistical analysis, to interpretation of models. We start with the basic ideas of model-based analysis and explain how to define the objectives of a statistical study for both laboratory experiments and field studies. We then explain the workings and use of linear, generalised linear and generalised additive models, and focus on the definitions and interpretations of interactions from both statistical and ecological perspectives.

The process of identifying and estimating interactions between model predictors is a primary focus of this work, since these interactions are the key to classifying environmental effects as synergistic, additive and antagonistic. The issue is that parameters of many statistical models are often not estimated on the scale of observations. For example, effects that are additive on the working scale of a logistic model with a simple linear predictor will manifest interactions as synergistic, additive and antagonistic on the observed scale.

The primary focus of this work is to resolve this issue. The only viable solution is to define the terms synergistic, additive and antagonistic on the scale of the model parameters, not the observed scale. The difficulties of defining them in terms of the observed data are also discussed.

Three detailed examples are presented including laboratory and field studies to illustrate the need for incorporating statistical models from the start of the experimental design of studies on cumulative impacts. These include:

1. Analysis of laboratory study of joint effects of drivers (copper and temperature) on coral larvae metamorphosis. This two-way laboratory survivorship trial analyses using generalised linear models (GLMs) and assesses the functional relationship between the response and predictors and their interactions.
2. Modelling the effects of cumulative temporal and environmental change in a field study. This analysis of a large complex environmental data set demonstrates

temporal change in coral cover on the GBR and the cumulative effects of three environmental drivers. We estimate growth rates, cumulative losses due to environmental drivers, and forecast future states of ecosystems under various scenarios.

3. Complementary analyses using boosted trees (BTs) and generalised additive models. Boosted trees are a machine learning (ML) approach to statistical analysis, and they can identify interactions between ecological drivers difficult to detect using traditional methods. The joint use of statistical models and modern ML is shown to be extremely effective for analysis of complex ecological and environmental data.

D.2 Model-based statistical analysis

D.2.1 Introduction

The starting point for any statistical analysis should be a concise statement of the objectives. The objectives define, through the modelling process, how the data are to be analysed. The objectives must be succinct enough to form a statistical model, and although the number of possible analysis objectives is unlimited, only four are commonly used:

1. Exploration of the relationships between the covariates and the response(s), and determining which – if any – are important. An example is determining if temperature change, due to climate change, affects the abundance of a particular species.
2. Prediction of values of a variable of ecological importance in locations or at times that do not have observed data. For example, predicting future fish species abundances after rezoning the GBR.
3. Quantifying the effect of predictors. For example the effects of CoTS and cyclones on coral cover of the GBR.
4. *A priori* testing of a hypothesis, e.g. testing if there is an effect on a coral community when they are subjected to changes in environmental conditions.

All of the above four objectives should always be addressed through a statistical model(s). The analyst must think in terms of statistical models and use them to represent the ecological processes. Analysis begins with data exploration, both graphical and quantitative. This should inform the analyst about: (1) the ranges and distribution of the response(s) and predictors, (2) the relationships between response(s) and predictors, and (3) outliers (unusual) values.

D.2.2 Laboratory experiments and field studies

Laboratory experiments and field studies involve different challenges from the statistical perspective. For each type of study, the key is to clearly define the objectives and priorities of the study, and then to implement a design that can achieve them efficiently and in a cost-effective manner. One of the most essential prerequisites is knowledge of the likely variability of the data to be collected. Without such knowledge, studies too small will be inconclusive and too large will be a waste of time and resources. Pilot studies are often useful, as are reviews of similar studies, in order to provide such information.

For laboratory experiments involving several treatments, it is essential to prioritise them, and to design the experiment in such a way that the contrasts within treatments of highest priorities are estimated with maximum precision. A common example is nested plots within blocks design. Comparisons between plots within blocks will be more precisely estimated than those between blocks, since the former only depends on variation with plots, whereas the latter depends on both block and plot variation.

It is also essential to replicate to the level such that if one or two experimental units fail, then sufficient information still results from the study. Using a balanced design (i.e. the same number of replicates in each sampling unit) is advisable otherwise information is lost due to confounding of treatments, which will likely lead to less precise and possibly biased parameter estimates. However, there can be exceptions to the exclusive use of balanced designs. For example:

1. Suppose one wants to compare many treatments with the control group only. In that instance, increasing the number of replicates of the control group, and slightly reducing the number of replicates in each of the treatment groups, will increase the precision of control-treatment comparisons for a similar effort.
2. If there are contrasts between treatments that are not of interest, then they can be confounded within the blocks of the design, and the efficiency of the estimates will be enhanced.

For field studies, the challenges of good design are often greater than their laboratory counterparts, due to the lack of control in both space and time. For example, the objectives of field studies are often less well defined than their experimental counterparts, and they are invariably more costly to undertake. Also, a broad spectrum of measurements is likely to be made on each visit to a site, and the suite of measures is likely to vary in terms of the number, cost, precision and difficulty of measurement. Thus, determining optimum sampling intensities in space and time will always involve many trade-offs, and the objectives of the sampling program will often be modified over time due to changing technologies and objectives. For example, interest may shift towards a greater spatial spread of sites and less frequent visits – or vice-versa. Also, the measurement technologies are also likely to change over time, and cross-calibration of the different methods will be required.

In recent times, our capacity to collect data through automated observation systems has increased exponentially. Analysis of the resulting massive data sets can be difficult and size can be a major impediment for the ensuing statistical analysis. This, in turn, has not only resulted in the need for greater computational power, but also for statistical methods that scale more efficiently with size. Machine learning is filling this need and is playing an increasingly greater role in the analysis of ecological and environmental data, and in this work we contrast its use with traditional statistical methods.

In summary, irrespective of the data sources, be it laboratory experiments, field monitoring data or remote sensing, statistical design and analysis should be involved from the first thoughts to the final interpretation and application of the data.

D.2.3 Overview of statistical models

This overview presents a hierarchy of statistical models most useful for the analysis of cumulative change in ecological systems. It includes the most basic – i.e. linear models – through to the most modern – i.e. ML.

Linear Models

Linear regression and analysis of variance models are effective and broadly used since many responses behave linearly (at least over small ranges) and have normally distributed (Gaussian) errors. The linear model (LM) can be expressed as $Y = X\beta + \epsilon$ where Y is the response, X is the design matrix (the values of the predictors, also called covariates), β is the vector of parameters that express Y as a linear function of X , and thus $X\beta$ is the mean of Y . Finally, ϵ is the error, assumed to be normally and independently distributed with constant variance. Thus we say that Y is distributed normally with mean $X\beta$ and variance.

For non-linear responses and/or responses with non-constant variance, transformations are often used to approximate linearity, but this leads to complications when interpreting the parameter estimates and fitted values of the response, and thus GLMs should be used instead.

Generalised Linear Models

The advent of GLMs enables us to deal with a much greater range of models in terms of both the types of error (e.g. binomial, poisson) and also the types of response data. Such data that can now be modelled without the use of adhoc transformations of the response, and the linear model is now seen as just one of the many forms of GLM, albeit the most widely used one.

Generalised linear models (and generalised additive models [GAMs]) are extensions of traditional linear models that enable us to model ecological responses (Y) that do not have constant Gaussian variance, and/or may have restricted ranges of their responses, e.g. count or proportions data. They can model count data for which the variance typically increases with the mean (e.g. log-linear models), or binomial data for which there are both upper and lower bounds to the response, and the variance of the response is also greatest in the middle of the range of Y .

Table D1: Generalised linear models: distributions, link functions and variance functions.

Distribution	Link Function	Variance Function
Gaussian	μ	1
Binomial	$\log(\mu/(1-\mu))$	$\mu/(1-\mu)/n$
Poisson	$\log(\mu)$	μ

Generalised linear models cater for non-normally distributed data by introducing two functions that deal with the non-linearity and heterogeneous variance of the response. First, we generalise the linear model, $Y = X\beta$, to $Y = f(X\beta)$ the transformation controls the range of values that Y can take. For example, if f is the exponential function, then Y is constrained to

values ≥ 0 . Second, we then generalise its distribution to include addition forms such as binomial and poisson. These so called families include logistic and log-linear models that are now routinely used for analysis of ecological data. These models are defined by their statistical distribution, and link and variance functions (Table D 1).

Note that the estimates of parameters are on the scale of the link function, not the response scale (i.e. the scale on which observations are made). Thus we use the inverse of the link function to get parameter values or predicted values back to the response scale. This is extremely important and is not well understood by many users of these methods. This in turn can lead to serious miss-interpretation, particularly so when estimating effect sizes – e.g. how much does the response change given a certain change in X? – and when detecting, classifying (e.g. synergistic, additive, antagonistic) or interpreting interactions.

Generalised Additive Models

Generalised linear models are linear in the $X\beta$ component of the model which is then linked to Y as described above. Generalised additive models (GAMs) are an extension of GLMs that include more complex forms of the quantitative predict. For example, if we had a polynomial term in a GLM we have to specify how flexible by its degrees of freedom. Generalised additive models enable us to estimate the amount of flexibility for 'smooth' predictors as part of the model fitting process. This is particularly useful when we have many quantitative predictors and the functional form of the relationships with the response is unknown.

A crucial aspect is that GLMs and GAMs involve two scales – one is the scale on which our observations are made and the other is the scale of the model calculations. For all GLMs and GAMs, the fitting of the model (i.e. the estimation of the model parameters), together with their standard errors and the overall measure of model fit (the deviance), takes place on the scale of the link function. Thus, for the log-linear model the 'working scale' is the log of the response, and for the logit model the log-odds (lods) is used. Parameters are estimated on this scale and fitted-values are calculated by back-transforming to the observed scale. We shall later see that this can be confusing to some, and care needs to be taken in how we describe and discuss results of GLMs and GAMs data analyses.

Machine learning

Machine learning (ML) is a relatively new branch of statistics that challenges traditional approaches to both explanation and prediction. From its beginnings in the early 1980's, it has expanded at an extraordinary rate due to its capacity to (1) accurately predict and (2) to deal with massive complex data sets. Machine learning is now widely accepted and used across many disciplines. It was originally seen as a 'black box' methodology with the inputs (predictors) going into one end of the box and the outputs (predictions) coming out the other end of the box. However, as ML methods have developed, many of these methods are interpretable in similar ways to statistical models – e.g. through effect sizes and proportions of variation accounted for by their predictors.

Machine learning differs from classical frequentist and Bayesian statistics, and it takes many forms. In the case of BTs, ML is not model-based since parameters are not used to describe the link between the response and the predictors. Boosted trees do however cater for many

types of random variation through a loss function (e.g. Gaussian, poisson, binomial). Machine learning also emphasises prediction, and the best model is selected by minimising prediction error. It is widely used for analysis of big-data since its computational efficiency scales far better than traditional parametric models. Overall, its presence has greatly expanded the toolbox available to data analysts for all sizes and types of data. One focus of this work is the detection and estimation of interactions between predictors, and BTs are particularly adept at identifying and quantifying such effects.

Boosted trees

Boosted trees (BTs: Friedman et al., 2000) are a machine learning technique based on stochastic gradient boosting of classifications and regression trees (Breiman et al 1984). Boosted trees are a collection of trees that are grown sequentially with each tree fitted to the 'residuals' of its predecessor. The loss function of BTs can take many forms: e.g. Gaussian, Laplace, Bernoulli, Poisson, Coxph, quantile, and thus many types of data are amenable to BT analysis. The individual trees are small and the number of splits defines the level of interactions of the overall model, e.g. a single split for each tree produces a tree with only main effects, two splits caters for 1st order interaction, etc. Boosted trees are grown slowly to avoid over-learning and to minimise prediction error that is estimated by cross-validation. The dependencies of the response on the predictors can be both quantified and plotted.

Many ML methods have proven to be good predictors, however it was not always understood why they were so effective. However, the theoretical understanding of BTs has increased, and this has led to refinements that makes them one of the best statistical predictive and modelling methods.

Boosted trees have many desirable properties:

1. They can be used for exploration, description and prediction of data.
2. They can automatically handle non-linear (smooth and discontinuous) effects and interactions.
3. The level and strengths of interactions is easily quantified.
4. The effects of predictors are invariant to their scaling.
5. The importance of each predictor can be quantified.
6. Data sets can be very large with many predictors and/or cases.
7. Partial dependency plots are used for interpretation.
8. Loss functions include Gaussian, Laplace, Bernoulli, Poisson and quantile models.

The capacity of BTs to easily identify the levels and strengths of interactions is important to this work. This is particularly the case for field studies where the number of predictors is substantially larger than in designed experiments and there is often a degree of confounding of effects.

D.2.4 Statistical modelling

Statistical modelling starts with the data – it is the core of statistical analysis. We begin by classifying the data using a two-stage process. First, we classify according to the type e.g. numeric or categorical, and then, within each type, according to their ranges of values e.g. $(-\infty, +\infty)$, $[0, \infty)$, $[0, 1]$ for numeric data, and as list of values [A, B, C...] for categorical data that maybe ordered or unordered.

In this study we are mainly interested in numeric responses, and thus henceforth we will focus exclusively on them. Observations of quantifiable phenomena show us that variation of a numeric response jointly depends on its range of values and the limits of those values:

1. Unbounded data $(-\infty, +\infty)$ is likely to have relatively constant variation.
2. For data bounded below $[0, \infty)$, variation is likely to increase with mean.
3. For data bounded both below and above e.g. $[0, 1]$, variation is likely to smallest at the limits of its range and greatest towards the middle of the range.

The development of statistical models has been greatly influenced by these simple observations. Prior to the invention of generalised models we only had models for unbounded responses with constant variation. These are the so-called linear models – e.g. linear regression and analysis of variance (ANOVA) and covariance. Data that were bounded either below, or bounded above and below, were typically transformed, analysed using linear models, and then the results (e.g. estimates of fitted values, predictions or parameters) were back-transformed to the observed scale. This was very unsatisfactory.

Generalised linear models (GLMs) overcame these limitations by building the range constraints and the relationship between the variation and the mean into the estimation process. This is done through the link function and the specification of the random variation of the model. For data bounded below $[0, \infty)$ the link function is usually logarithmic – this maps $[0, \infty)$ onto $(-\infty, +\infty)$ – and the mean-variance relationship is modified so that the variance increases with the mean. For data bounded below and above, e.g. $[0, 1]$ the link function is usually the logit function that maps $[0, 1]$ onto $(-\infty, +\infty)$, and the mean-variance relationship is modified so that the variance is proportional to $Y(1 - Y)$ assuming $0 \leq Y \leq 1$.

So how does the above description of how GLMs and GAMs work? The answer is simple. When we estimate vales using a GLM or GAM, the estimates are made on the working scale of the model – NOT on the scale of observations. Thus, judgements about parameter estimates and/or predicted values may not correspond to what we ‘see’ in the observed data.

From the ecological perspective, this issue of scale can be problematic since the ecologist typically ‘sees the interaction’ on the observed scale, not the ‘working scale of the model’ – the scale on which estimation and classification of interactions take place. For example, consider the case of exponential growth. If the growth is large compared to the size of the organism(s), then we may ‘see it’ as exponential (e.g. in terms of doubling times), however, if the growth is small compared to size then we may ‘see it’ as linear.

Some important points about the statistical modelling process, irrespective of the method e.g. LM, GLM, GAM or BT, include:

1. Statistical analysis begins with graphical and quantitative data exploration. This provides information about:
 - (a) the ranges and distribution of the response(s) and predictors,
 - (b) the relationships between response(s) and predictors, and
 - (c) outliers (unusual) values.
2. When selecting the response, we classify it according to:
 - (a) the type, e.g. numeric or categorical, and
 - (b) the range of values e.g. $(-\infty, +\infty)$, $[0, \infty)$, $[0, 1]$ for numeric data and $[A,B,C,\dots,]$ for categorical data.

This classification is most important when selecting the type of model used; e.g. if the range of the response is restricted, then we would be more likely to use a GLM or GAM than a LM, since the range of predictions of the latter is unconstrained, and model predictions values beyond this range may occur. Data constrained to the ranges $[0, \infty)$ and $[0, 1]$ are obvious examples.

3. The predictors may be well defined *a priori*, or we may wish to consider alternate forms of any given predictors, e.g. if it is a discrete numeric variable we could treat it as either categorical or quantitative.
4. The functional relationship that links the response to the predictors depends on its type and range of values, e.g. if the response is count data then it is bounded by $[0, \infty)$ whereas proportions data are bounded by $[0, 1]$. The log and logit link functions are most often used for such data, although there are many alternatives for the latter, including the log-log link and the complimentary log-log link.
5. Data should not be transformed, e.g. to the '4th root to make it normally distributed'. Such transformations are often ineffective and they introduce all sorts of unnecessary complications, e.g. difficulties in interpretation of models and the need to back-transform estimated values and confidence intervals. The availability of GLMs enables us to model responses on the observed scale, without the use of such transformations.

Model estimation and selection

Fitting the model and assessing the fit of the model:

1. The initial model fitting should include all of the 'potential' predictors, and also any interactions of interest.
2. The fit of the model should be assessed by examination of the residuals. Do they satisfy the model assumptions? Plots of the residuals against the fitted values and absolute fitted values, and distribution plots e.g. QQ-plots.
3. Outliers should also be detected at this stage and the decision of how to treat them has to be made e.g. should they be discarded or should the model be modified to accommodate them?

Selecting the 'best' model:

1. There are many alternative methods for model selection, and the chosen method should reflect the future use of the model, e.g. if prediction is the objective then we should base the selection on some form of cross-validation.
2. If information criteria such as Akaike information criterion (AIC), Bayesian information criterion (BIC) and their many variants are to be used, then the user should be careful not to be over judgemental about a particular model(s), since the selection process is likely to be unstable.
3. Determining a best model can also be an unstable process when there are many predictors, and when we also wish to retain interaction terms.
4. Model averaging and/or cross-validation are useful approaches if good predictive performance is the prime objective.
5. The fit of the final model should be assessed again to check that it satisfies the model assumptions.

Modelling and interpreting statistical interactions

The notion of interactions in ecological studies is often either not clearly defined or not understood. This is an important issue since it can lead to misinterpretation of studies and erroneous conclusions.

From the statistical perspective, interactions are clearly defined in terms of the parameters of a statistical model. The magnitude of interactions can be assessed by examination of parameter estimates, or comparison of statistical models – one with only main effects and one with interaction term(s).

The simplest example of modelling an interaction is the case of two predictors (A and B) each with two levels (1 and 2), as was used in many experiments on cumulative pressures (see Appendix A). Thus, we have a response variable (Y) and observations of Y for all combinations of the levels of A and B – i.e. A1.B1, A1.B2, A2.B1 and A2.B2. For the LM, the presence of an interaction for such data is traditionally assessed by a statistical test (F or t-test) in a two-way analysis of variance.

This is typically done in one of two ways, either:

1. Fit the full model (i.e. main effects and interaction) and from the parameter estimates determine the significance of the interaction, or,
2. Fit two models, one with just main effects for A and B, and one that also includes the interaction effect A.B. Then test – e.g. using an analysis of variance (or deviance) – to see if the interaction term improves the model fit significantly.

So how does the above description of how GLMs and GAMs work? The answer is simple. When we estimate values using a GLM or GAM, the estimates are made on the working scale of the model – NOT on the scale of observations. Thus judgements about parameter estimates and/or predicted values may not correspond to what we 'see' in the observed data.

The analysis of the simple data set below (Table D2) can illustrate this apparent dilemma. If we analyse the data using a linear model 2-way ANOVA the Control-Treatment effect is 1, the X1-X2 effect is 0, and interaction effect size is 0 – i.e there is no interaction. The main effects only model would fit the data exactly.

Table D2: Two-way Analysis of Variance.

		Y		log(Y)	
		X2		X2	
		A	B	A	B
X1	A	1	2	0	0.693
	B	2	6	0.693	1.792

If, however, we used a GLM (log-linear) model for the analysis of these data, then the interaction term would be non-zero and the interaction term would be required for a perfect fit. This is because, in essence, the log-linear model is akin to fitting a linear data to the log-transformed response (Table D 2) which are no longer additive. So how does this affect our notion of additive and interactive effects in the ecological domain? Given many ecological data are non-Gaussian and log-linear models (or other GLMs) are now widely used to deal with such data, on what basis should the descriptions of additive, synergistic and antagonistic be applied?

For all linear models, the scale of observation of data and the working scale for calculations are identical, and hence classifying the interaction according to the size and sign of the parameter estimate that represents the interaction will always give the same conclusion as the ‘traditional method’ of basing it directly on the data. This will not be the case for all generalised linear models that have a non-identity link function such as log and logit models.

For non-Gaussian data, such as count data, a GLM (log-linear) analysis will typically provide a better model fit than a linear model since the variance of count data does typically increase with the mean. For the log-linear model, if data are additive on the modeled scale then they will be so on the observed scale and the interaction term will be negative, thereby suggesting an antagonistic interaction. Conversely, if data are additive on the observed scale then they will NOT be so on the log-scale and the interaction term will be negative, thereby suggesting an antagonistic interaction.

The three Figures (D1–3) below and their legends, display a variety of interactions and main effects only models. These include both LMs and GLMs.

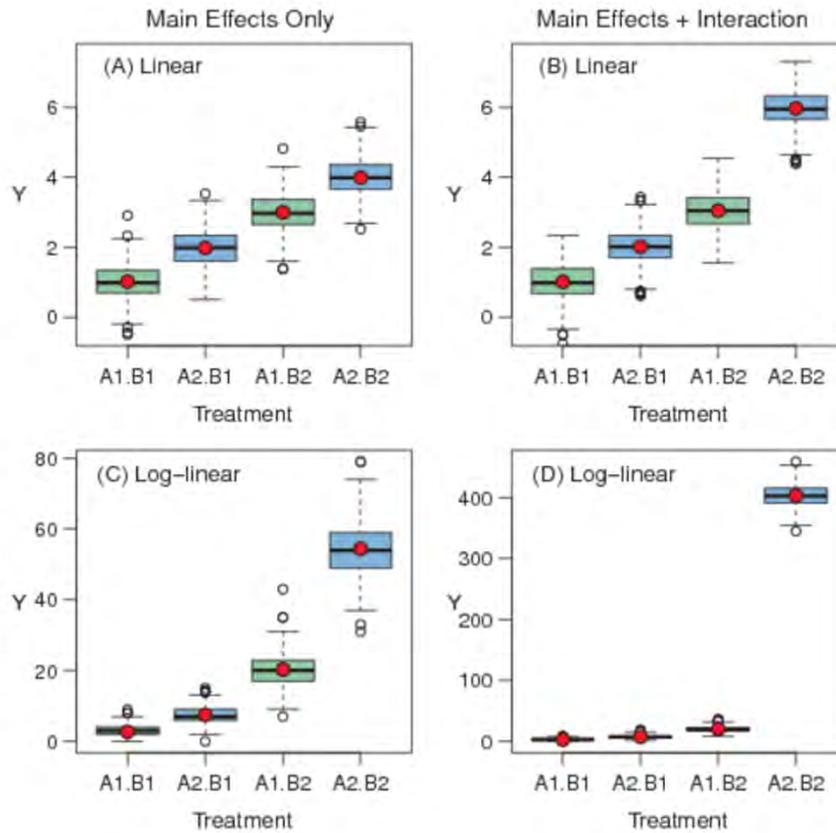


Figure D1: Analysis of simulated data illustrating the main and interaction effects in a 2-way factorial design for linear and log-linear models. The red points indicate the estimated mean values for each of the four treatment groups, and the boxplots show the distributions of the data about the means (solid bars indicate the median and the box contains the central 50% of the data). Models for rows 1–2 are linear (A, B) and log-linear (C, D) respectively, and the effects for columns 1–2 are additive and interactive respectively. For all models, the effect sizes are +1 for the constant, +1 for A, +2 for B, and for columns 1 and 2, are +0 and +2 respectively for the interaction AB. Thus, for the linear model (A), the mean for the group A2.B2 = $1(\text{const}) + 1(A) + 2(B) + 0(AB) = 4$, whereas for linear model (B), the mean for A2.B2 = $1(\text{const}) + 1(A) + 2(B) + 2(AB) = 6$. The means of other cells of the design can be similarly calculated. For example the mean of the 4 groups in Figure D2 A are 2.72, 7.39, 20.09 and 54.60, and for Figure D2 B are 2.72, 7.39, 20.09 and 403.4. This can be confusing since on the scale of the parameters the effects are additive, but they are multiplicative when transformed back to the observed scale.

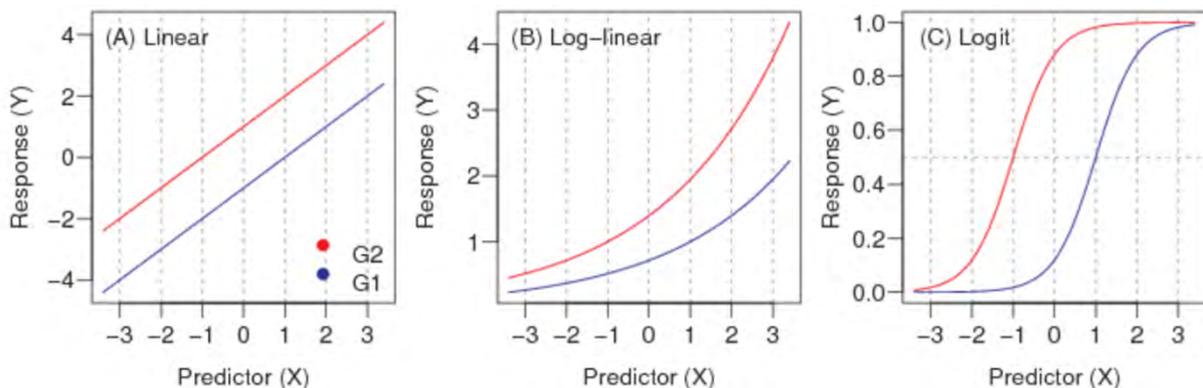


Figure D2: Illustration of the response curves for linear, log-linear and logistic models. The linear predictors for the 3 models are the same: $y = 2x - 1$ and $y = 2x + 1$ for the groups G1 and G2 respectively. Only the link function varies, being linear, log-linear and logistic respectively. Although the effect-size of G is constant ($= 2$) on the link scale, it is only constant on the observed scale for the linear model (A). For the log-linear model the effect on the observed scale increases exponentially with X, and for the logistic model we have maximum effect size at the point of inflection when $P = 0.5$, and as $P \geq 0$ or $P \leq 1$ the difference between the two curves $\rightarrow 0$. Thus, in ecological terms, this might be interpreted as synergistic for $P < 0.5$, additive when $P = 0.5$, and then antagonistic for $P > 0.5$.

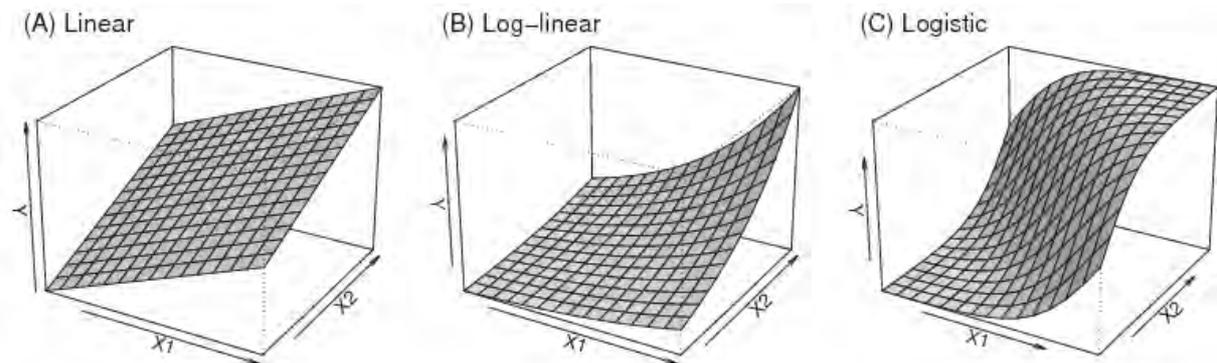


Figure D3: Additive effects (i.e. no interaction) of two quantitative predictors, X1 and X2, on the response Y for the linear, log-linear and logistic models. In a similar way to the example with one numeric and one categorical predictor we see the log-linear and logistic models express non-linear behaviour on the observed scale.

D.3 Metamorphosis of coral larvae simultaneously exposed to copper and elevated temperatures

D.3.1 Data

The data in this section are from a design experiment undertaken to assess the effects of exposure to copper and elevated temperatures (Negri and Hoogenboom, 2001). Experiments such as these can be used, to assess the risk of potentially harmful agents in the environment, and describe and quantify the cumulative effects of two pressures. This is the same dataset as used to illustrate ecotoxicology tools for data analysis in Appendix C. It should also be pointed out that this study is the one using the highest number of treatment levels for coral reef studies identified in Appendix A. Risk can be estimated across a series of levels for each agent, together with any interactions.

Coral larvae were exposed to combinations of two treatments – namely copper and temperature. There were ten copper levels varying from 0.37 to 72 $\mu\text{g L}^{-1}$ at roughly logarithmic intervals, and six levels of temperature namely 28, 30, 31, 32, 33 and 34°C. For each combination of treatments there were six replicates. Since we could not assume independence of samples within each treatment combination, all data were averaged across each combination of treatments – thus giving 60 values of the proportional metamorphosis, P. Since the number of replicates was identical for each treatment combination, there was no requirement to weight the means differently from each other in subsequent analyses. Metamorphosis of larvae varied between 0% and 100% with mean 40.6%, and exploratory analyses suggested strong dependencies of larval metamorphosis on both copper and temperature.

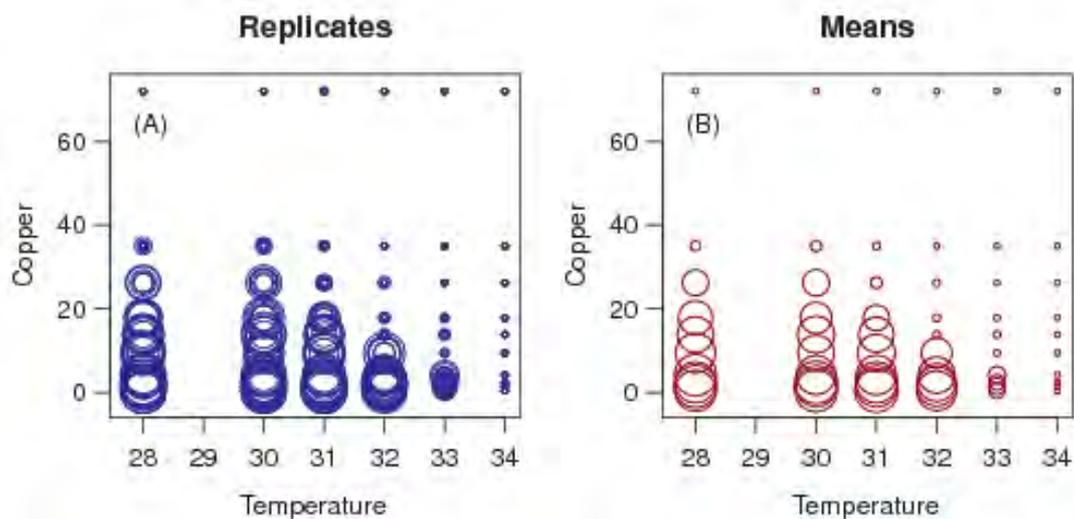


Figure D4: Plots of individual observations (A) and means of proportional metamorphosis (B) for each combination of copper and temperature. At the highest levels of both copper and temperature there is total metamorphosis and the metamorphosis gradients along copper and temperature are steep. The variation of the replicates within each treatment group is relatively small (A), and the variation of metamorphosis across the treatments is clearly systematic.

D.3.2 Analysis

Since the data were scaled to 0–100, we do not have access to the number of individuals that survived. That is somewhat unfortunate since it severely limits the analysis – particularly in terms of the choice of statistical model to be used for the analyses that may follow. For example, we are unable to use information-based measures of model-fit such as AIC and BIC, and approximate F-ratio tests are needed to determine a 'best' model. Thus, the information loss compared to knowing the number of coral larvae in each treatment and number of survivors is considerable and unnecessary. For example, if we have one survivor from two larvae, or 50 from 100, then the information in the latter is likely about 5 times as valuable since precision is proportional to the square root of N, the number of samples.

Preliminary inspection of the data

As we have suggested elsewhere in this document, careful inspection of the data – i.e. exploratory analysis – before any model-based analysis is vital to: (a) increase our understanding of the data and (b) determine the correct choice(s) of statistical model. This is particularly the case in this example. What does inspection of the Figure D4 tell you?

Two things should be obvious – there is a strong negative effect of copper at $< 30\text{ }^{\circ}\text{C}$, but no effect of temperature; but at $> 30\text{ }^{\circ}\text{C}$, there is a negative additive effect of temperature additional to the continuing negative effect of copper.

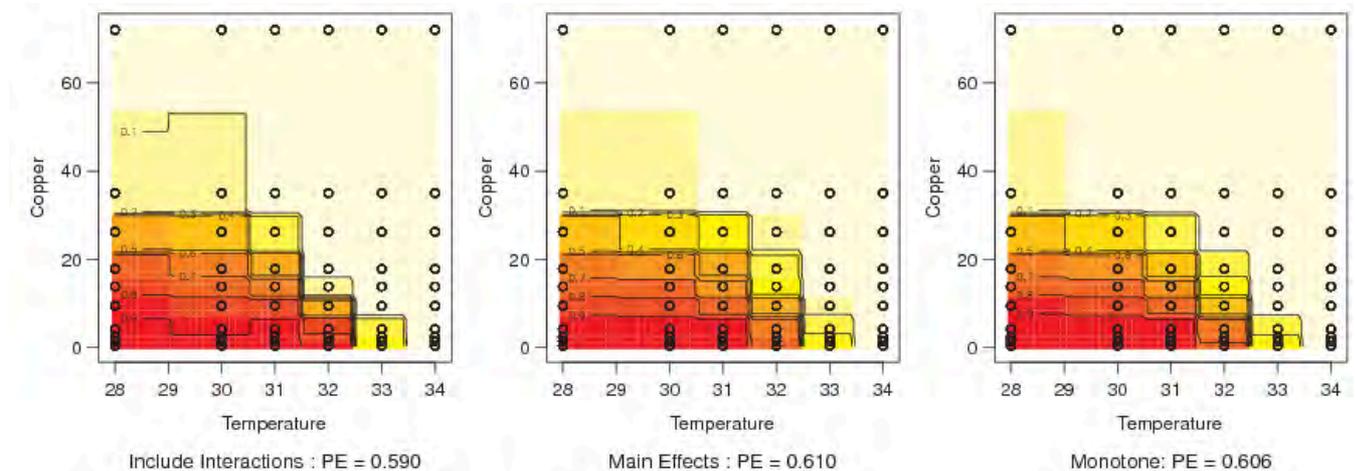


Figure D5: Boosted tree plots showing the predicted values of coral larvae for three models: (Left) main effects and 1st order interactions, (Middle) main effects only, and (Right) main effects only with monotonic constraints. The predicted errors of 0.590, 0.610 and 0.606 show the dominance of the main effects and the weak interaction.

We now use BT models, but only rather as part of the exploratory analysis. They are quick and effective to use, and in this instance, provide a wealth of information on the relationships between response and predictors. The BT analyses show strong main effects relative to the weak interactions (A) vs. (B, C) (Figure D5). Performance of BTs is assessed by how well models predict as opposed to how well they explain the data – the former being a more demanding test of any model. The main effects model showed only a small degradation in predictive ability, and further constraining the effects to be monotonic resulted in improved

predictions by 2–3%. The BT model analysis can inform the subsequent GLM models (Figure D6).

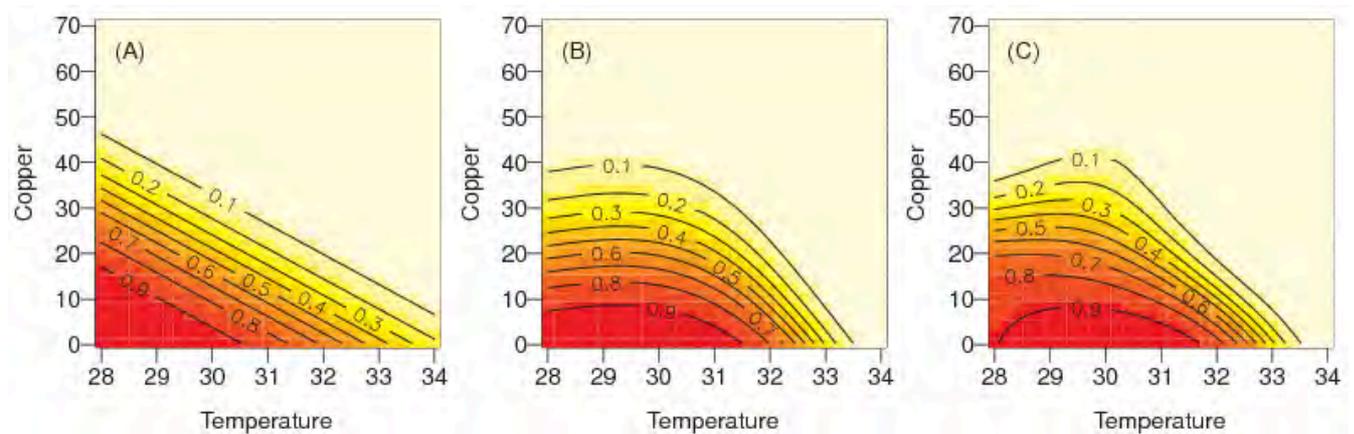


Figure D6: Generalised linear model (logistic regression) showing the estimated values of coral larvae for three models: (A) additive linear effects of copper and temperature, (B) additive quadratic effects of copper and temperature, and (C) additive quadratic effects of copper and temperature and interactions between the copper and temperature effects. In (C) the image plot shows a strong negative effect of copper at < 30°C, but no effect of temperature, but at > 30 °C, there is an additional negative additive effect of temperature.

Analysis of the trial data

As advocated earlier in this work, we adopt a model-based approach to dealing with these data – in this case a GLM analysis for the metamorphosis trials is highly recommended. Generalised linear models jointly model the response – predictors relationships, but do so in such a way that: (1) estimated response values and predictions always fall in the appropriate range, in this case [0, 1], and (2) the variation in predicted values conforms with that of the observations; in this case the variance is proportional to $p(1-p)$, where p is the metamorphosis probability. The chosen GLM model thus uses a logit link to constrain the range and models the variance as so-called ‘quasibinomial’.

We explore the dependency of metamorphosis on copper and temperature using a series of nested models. By nested models we mean that for two models A and B, model B is nested in A if the predictors (explanatory variables) of B are a subset of those in A. This gives us a framework to easily compare models, using e.g. residual variance or predictive ability. This gives us an optimal model according that measure of ‘bes’ model. For these data we use the traditional hierarchy of significance tests, based on F-ratios rather than Chi-squared test as would be the case if the counts were provided rather than the calculated proportions.

In choosing the form of predictors, both copper and temperature can be used in the model as categorical ordered or unordered classes, or as numeric variables. If we treat them as numeric predictors then we could use simple linear or smooth trends, or as ordered or unordered categories. We can also include interactions between the two predictors that can take many forms. For the sake of simplicity in this pedagogical example, we use a simple approach using a simple hierarchy of significance tests, and treat the predictors as both

quantitative and categorical. The strength of different forms of interactions between copper and temperature are also included in the model hierarchy.

Results of the GLM analysis

The chosen hierarchy of tests included quantitative linear effects of copper and temperature, then added quadratic and/or effects, both with and without interactions. This gives us a hierarchy of models and we simply select our best model. The results are presented for a subset of these models and include a detailed presentation and interpretation in both graphical and numeric formats (Table D3).

Table D3: Analysis of deviance for a series of nested models of larval metamorphosis. In the table ‘Temp’ and ‘Cu’ indicate linear effects of temperature and copper, ‘factor(Temp)’ indicates a factor representing a parameter for each level of temperature, and ‘Cu*factor(Temp)’ represents the interaction between temperature and copper. The final model represents, on the working scale, linear effects of copper for each level of temperature, the slopes and intercepts of which vary. On the observed scale this translates into a series of logistic curves.

Model	Predictors	Residual deviance	DF	Deviance	F	P
1	1	47.1	1			
2	1 + Temp	32.02	1	15.10	430.3	< 0.001
3	1 + Cu + Temp	7.95	1	24.07	686.1	< 0.001
4	1 + Cu + factor(Temp)	2.05	4	5.92	42.2	< 0.001
5	1 + Cu + Cu*factor(Temp)	1.07	5	0.96	5.4	< 0.001

The model assumptions of the chosen ‘best’ model should always be checked prior to any interpretation or application of it. This is usually done through a series of graphical assessments (Figure D7). In this case, all the diagnostics are satisfactory, although the large numbers of zeros in the data are reflected by the long tails in some of the residual plots. Since there was total metamorphosis for the highest level of copper these could possibly be discarded, resulting in likely better model diagnostics.

The results of the GLM analysis (Table D3) show the sequential fitting of models and the final model (i.e. the one selected as the ‘best’ model – model 5 in Table D3 represents, on the logit scale, linear trends in copper with varying slopes for each level of temperature. It is noteworthy that the interaction term that enables these substantially differing slopes for the copper profiles only accounts for about 2% of the explained deviance (Figures D8 A and B). Thus, seemingly small changes in the measures of overall fit due to changes to the set of predictors can result major changes in the model structure, and hence in its interpretation. The quality of the fit of the model is satisfactory as it meets the model assumptions (Figure D7) – details of which are presented in the figure legend.

The ‘best’ fitted model translates to a series of non-parallel curves on the observed scale (Figure D8). The slopes and spacing of the profiles vary systematically with increasing temperature, and differ substantially from the ‘parallel’ profiles model. When the interactions are dropped from the model – i.e. the model is additive – then the trends in copper are

parallel on the logit scale, and the relative spacing between the adjacent profiles match the differences in temperature (Figure D8). The latter is simply due to additive nature of that model.

Finally we can compare the fits of ‘parallel’ and ‘varying’ trends models (Figure D9). The quality of the fit of the two models is examined by plotting the observed and fitted values for each model.

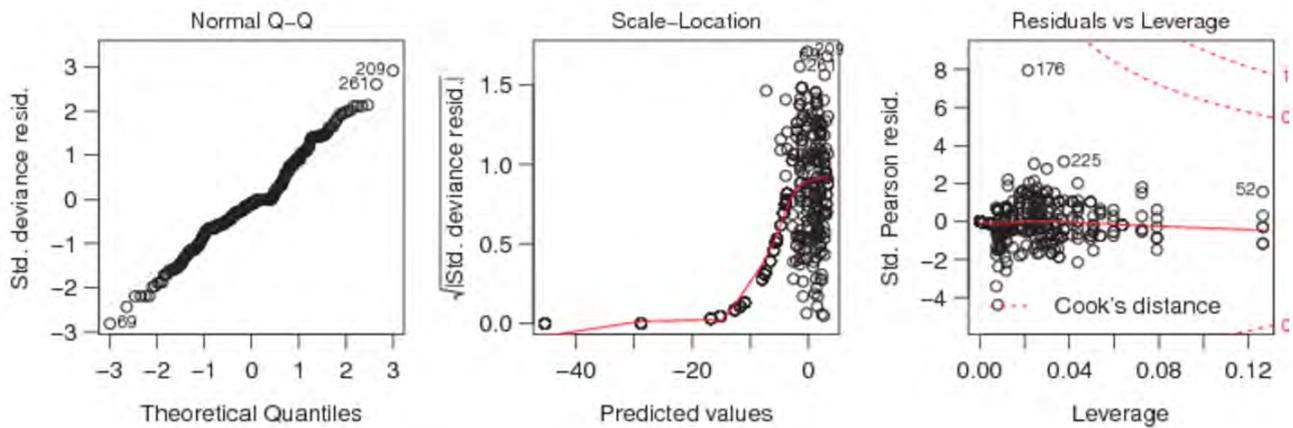


Figure D7: Residual plots for diagnosing the quality of the model fit. All three plots show good fit to the model assumptions. In the ‘normal-QQ’ plot, the points should be close the line and distant points indicates outliers. The numbered points are well within bounds expected under the model. In the ‘scale-location’ plot we are looking for an even distribution of residuals. Aside of the long tail where the model is over-fitting due to the large number of zeros, the fit is good. Finally, in the ‘residuals v leverage’ plot we are looking for outliers beyond the red dashed lines, and there are none. Overall the model fit is satisfactory.

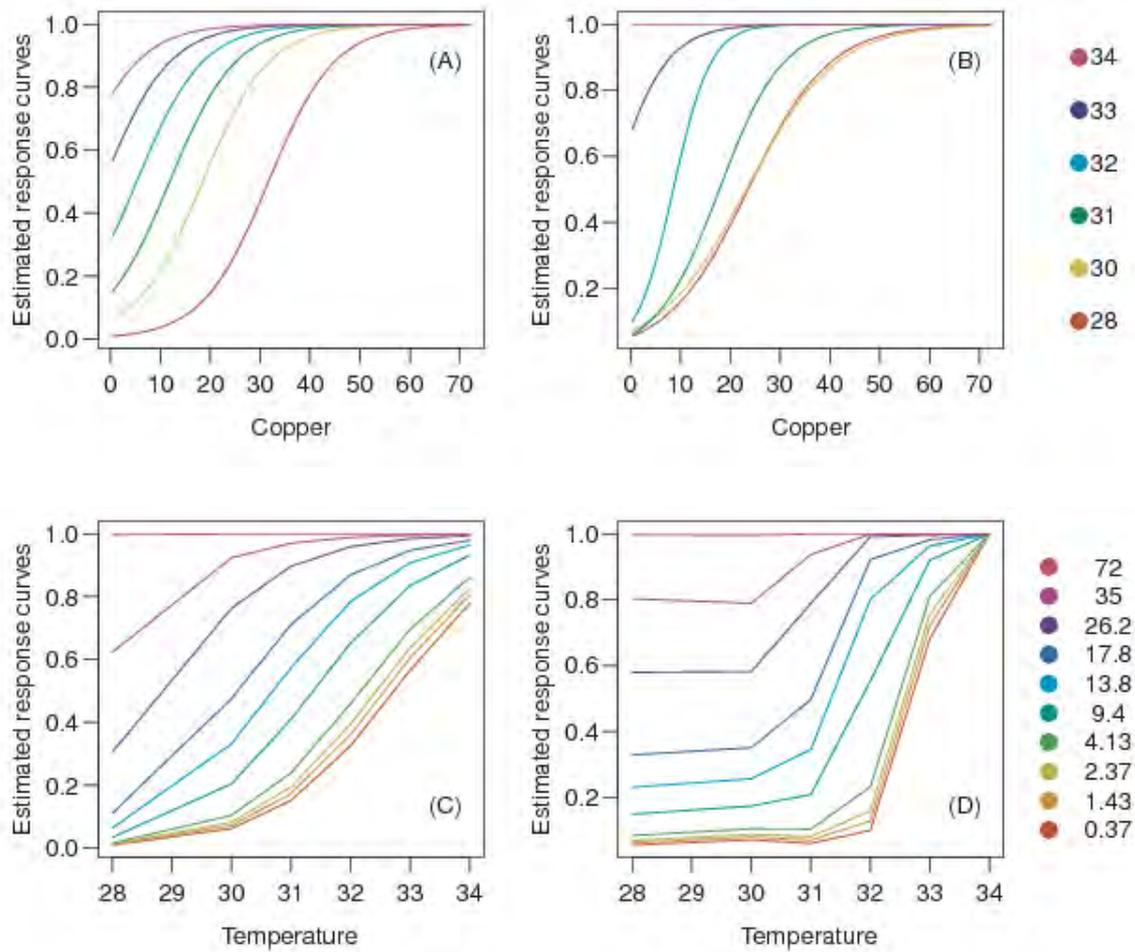


Figure D8: Estimated larval metamorphosis rates as functions of copper concentration and temperature (Appendix C). In (A) we have the additive model with linear 'parallel' trends in copper for each level of temperature (model 4 from Table D3). In (B) we have the model including 'varying' profiles in copper (model 5 from Table D3). In (C) and (D) we have the effects of temperature broken down by the levels of copper. The interaction model (B) and (D) is the preferred model and shows for copper: (1) the closeness of the two profiles for 28°C and 30 °C, (2) how the profiles then steepen with increasing temperature, apart from (3) the last two profiles that are dominated by total metamorphosis.

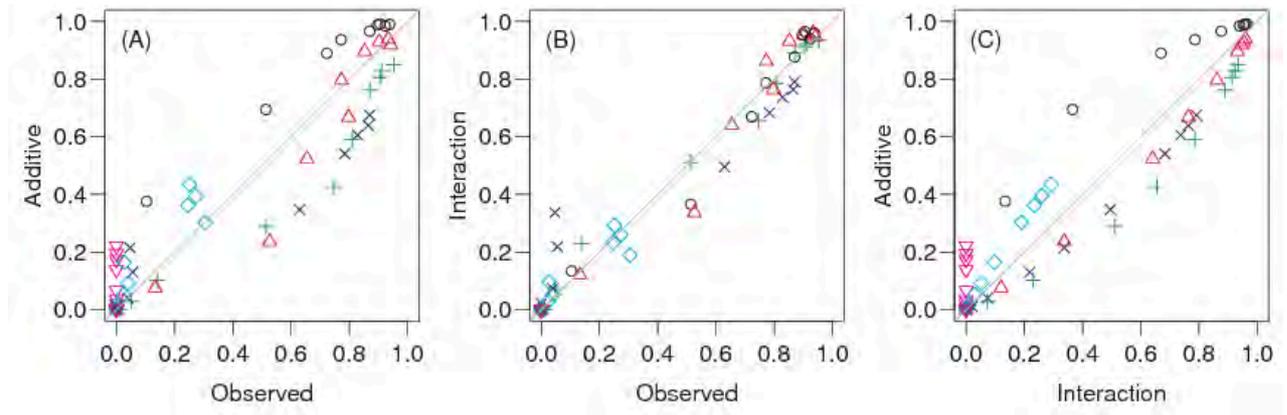


Figure D9: Comparison of fits of ‘parallel’ and ‘varying’ trends models. In plots (A) and (B) we diagnose the fit of the two models by plotting the observed and fitted values for each model. In (A) and (B) we see that (1) the fit is poorer and the points for each temperature are largely either above and below the line, and (2) the better fit with points for each temperature scattered either side of the line, thereby suggesting a better fit. In (C) we see a similar pattern to (B) due to the closeness of fit of the varying trends model.

The method of analysis for metamorphosis trials, as outlined above, can be highly efficient, effective and informative. It enables the researcher to comprehensively assess the effects of the two predictors – in this case copper and temperature – and present simple graphical and numerical summaries. The linearity of effects, or otherwise can be assessed, as can interactions between predictors. Results can be presented both numerically and graphically.

The model-based statistical approach is better than the non-statistical methods often used in such trials. Of major importance in the context of this work, model-based statistical analysis detected and estimated the interaction between the two predictors – copper and temperature – that would not (ever) be possible with two stage analyses.

As a final conclusion and summary, it is very clear that statistical model-based design and analysis could lead to substantial improvement in the conduct of metamorphosis trials, especially those with multiple drivers.

D.4 Modelling cumulative temporal environmental change

In this section we show the power and flexibility of statistical models to provide a comprehensive analysis of the cumulative temporal change in coral cover on the GBR, and how we can quantify the changes in coral cover due to the growth of coral, and estimate the losses due to environmental impacts from cyclones, crown-of-thorns starfish. From these estimates we can forecast future trends in coral cover under various scenarios, including the recent years of high levels of environmental disturbance, or for any other combinations of disturbances. Thus, for example, we can forecast future coral cover under scenarios such as absence of starfish or reduced levels of cyclonic activity. The data in this study were used in De’ath et al. (2012).

D.4.1 Estimating cumulative impacts of environmental pressures on coral cover of the GBR

This study investigates the temporal dynamics of coral cover, the main drivers of coral mortality, and rates of potential recovery of the GBR. Based on the world's most extensive time series data on reef condition (2258 surveys of 214 reefs from 1985–2012), we show a major decline in coral cover from 28.0% to 13.8% ($0.53\% \text{ yr}^{-1}$); a loss of 50.7% of initial coral cover. Tropical cyclones, coral predation by CoTS, and coral bleaching accounted for 48%, 42% and 10% of the respective estimated losses, amounting to $3.38\% \text{ yr}^{-1}$ mortality. The estimated rate of increase in coral cover in the absence of cyclones, CoTS and bleaching was $2.93\% \text{ yr}^{-1}$, demonstrating substantial capacity for recovery of reefs. However, at the current rate of decline, coral cover will fall to 5.2% (CI = 2.9%, 8.7%) by 2025. In the absence of CoTS, coral cover would have increased from 28% in 1985 to 53.5% in 2011, despite ongoing losses due to cyclones and bleaching. Coral cover averaged 22.9% over the 214 reefs and 27 years, and the cover on individual reefs ranged from 1.50% to 79.7% across space and time (Figure D10 B).

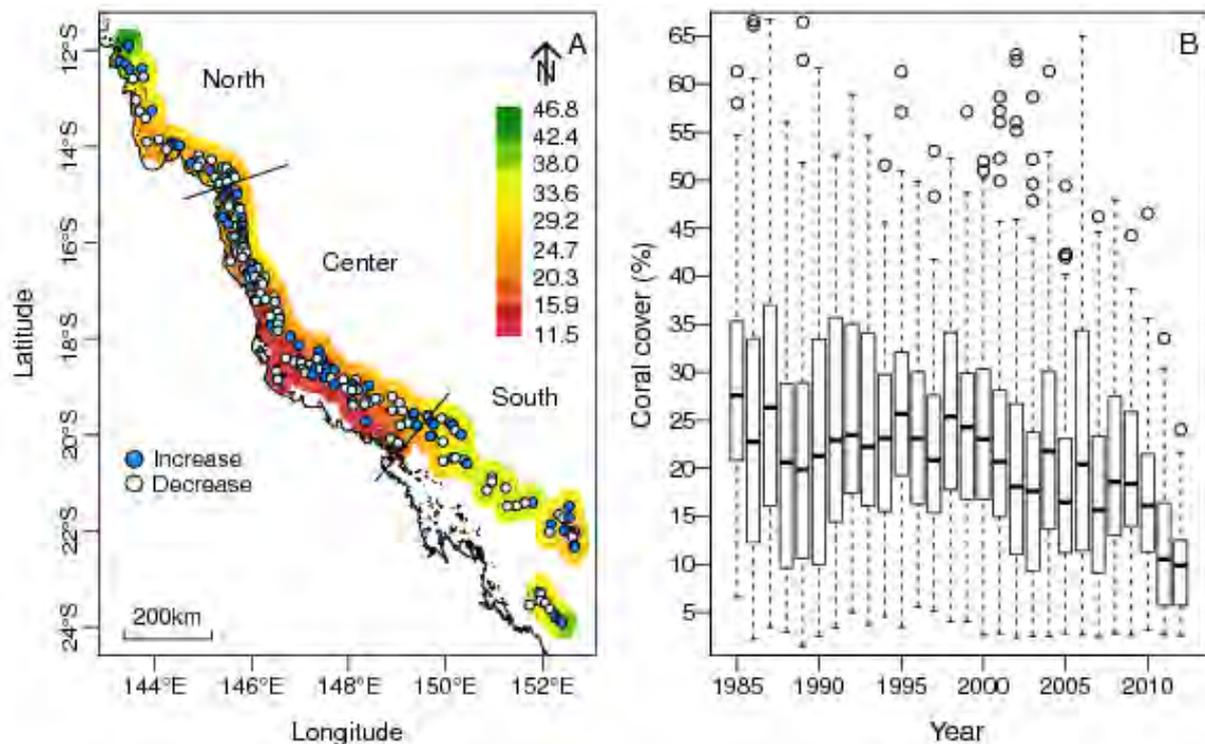


Figure D10: Coral cover on the Great Barrier Reef (GBR). A: Map of the GBR with colour shading indicating mean coral cover averaged over 1985–2012. Points show the locations of the 214 survey reefs in the northern, central and southern regions, and their colour indicates the direction of change in cover over time. B: Boxplots indicate the percentiles (25%, 50% and 75%) of the coral cover distributions within each year and suggest a substantial decline in coral cover over the 27 years.

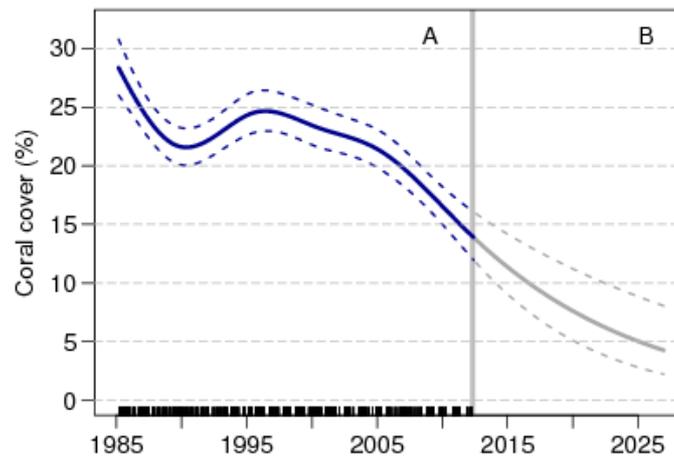


Figure D11: (A) Estimated trend in coral cover from 1985–2012 with 95% CIs. (B) Future prediction of coral cover from 2012–2026 given cover continues to decline at the 2012 rate of $1.51\% \text{ yr}^{-1}$.

Coral cover data were analysed using logistic regression mixed effects models. All models included random effects of reefs and a continuous auto-regressive structure over time for each reef. The first analysis consisted of a purely temporal model comprising a smoothed trend for the whole GBR. This showed that from 1985 to 2012, mean coral cover declined non-linearly from 28.0% (95% CI = (26.6, 29.4)) to 13.8% (12.4, 15.3) (Figure D11 A); a total decline of 14.2% ($0.53\% \text{ yr}^{-1}$). This is equivalent to a loss of 50.7% of the initial cover. Two thirds of that decline has occurred since 1998, and the current rate of decline is $1.51\% \text{ yr}^{-1}$. That rate of decline has been consistent from 2006–2012, and if maintained, predicted coral cover will be 5.2% (2.9, 8.7) by 2025 (Figure D11 B).

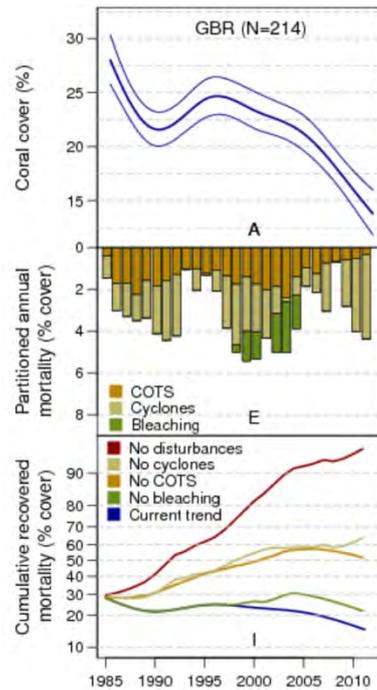


Figure D12: Temporal trends in coral cover (A), annual mortality due to CoTS, cyclones and bleaching (E), and cumulative recoveries (I) for the GBR over the period 1985–2012 (N = number of reefs). Panel A shows the trends in coral cover, with blue lines indicating estimated means (± 2 SEs) of each trend. In panel E the composite bars indicate the estimated mean coral mortality for each year, and the sub-bars indicate the relative mortality due to CoTS, cyclones and bleaching. The periods of decline of coral cover in A reflect the high losses shown in E. Panel I shows predicted cumulative change in coral cover on the whole GBR in the absence of estimated mortality from bleaching, cyclones or CoTS separately and in combination.

The temporal logistic model was expanded by adding the effects of the three main forms of acute disturbances, namely observed CoTS densities, modelled maximum wind speeds of 34 tropical cyclones, and mass coral bleaching in 1998 and 2002. These analyses were conducted for the whole GBR (Figure D10). Disturbances due to CoTS, cyclones and bleaching occurred frequently from 1985 to 2012, with only 3 of the 214 reefs remaining impact-free. CoTS were observed on 31.8% of reef visits, cyclones had affected reefs in the 18-month window before 46.0% of visits, and the two mass bleaching events had affected reefs in the 2-year window before 9.2% of visits. There were cyclical effects due to CoTS, but no evidence of increasing levels of mortality from disturbance across years (Figure D12 E). The presence of CoTS at a density of one CoT per 200 metre manta tow gave an estimated coral mortality of $5.48\% \text{ yr}^{-1}$ (SE = 0.66%) for a reef with 20% coral cover. Cyclonic winds of 40 ms resulted in a mean mortality of 7.36% (0.78%) cover, and bleaching lead to a mean mortality of 3.11% (0.55%) cover at 20% coral cover.

The mean annual reef cumulative mortality was estimated for each of the three forms of disturbance (Figures D12, Table D4 for 1985–2011; the 2012 disturbance data being incomplete. For the whole GBR, CoTS, cyclones and bleaching accounted for mortality of 1.42, 1.62 and 0.34% yr^{-1} (42%, 48% and 10%), respectively, giving a mean total mortality of 3.38% yr^{-1} . Given the estimated rate of decline of 0.45% yr^{-1} for 1985–2011, the estimated

net growth of coral cover was 2.93% yr⁻¹ for coral cover of 20%. Since this does not take into account any losses due to other agents (e.g. reduced calcification, diseases), this estimate can be interpreted as a lower bound of the increase in coral cover for the period 1985–2012.

Table D4: A: Estimated rates (% yr⁻¹) and standard errors (SE) of decline, growth and total mortality of coral cover. B: Total coral mortality partitioned between CoTS, cyclones and bleaching. All rates are based on 20% coral cover and are estimated for the whole GBR.

	Source	Mean (SE)
A	Decline	0.45 (0.08)
	Growth	2.93 (0.26)
	Total mortality	3.38 (0.19)
B	CoTS mortality	1.42 (0.17)
	Cyclone mortality	1.62 (0.22)
	Bleaching mortality	0.34 (0.08)

Based on the estimated cumulative mortality due to the three environmental drivers, we estimated change in coral cover had CoTS, bleaching and cyclone mortality not occurred (Figure D12 I). Without CoTS, GBR coral cover would have increased from 27.8% to 53.5% (95% CI = 43.8, 64.4) from 1985 to 2011, despite cyclone and bleaching mortality. Without cyclones, coral cover would have been 65.9% (52.1, 74.7) and without coral bleaching, coral cover would have declined to 24.0% (20.3, 27.2). In the absence of all three disturbances, coral cover would have effectively occupied all available space (Figure D12 I).

D.4.2 Discussion

The above analysis of temporal change of coral cover and the successive cumulative effects of cyclones, CoTS and bleaching (see Figure 1 in Chapter 1) illustrate the capacity of modern statistical models to precisely quantify change and to accurately attribute it to specific drivers of the system.

Additionally, we can estimate lower bounds on growth rates of corals, and other system parameters. We can predict future levels of coral cover under various scenarios; e.g. removal or reduction of any combination of the three environmental drivers.

The a major decline in coral cover from 28.0% to 13.8% over the period 1985–2012 was due to unusually high levels of cyclones and CoTS – in particular from 1998–2012. Since the end of the study, there have been few cyclones and storms. As a result, and conforming to this study, coral cover has recovered to a moderate degree (Australian Institute of Marine Science, unpublished data).

D.5 Complementary analyses using Boosted Trees and Generalised Additive Models

D.5.1 Introduction

In this section we use BTs and GAMs and show how these two forms of statistical analysis have different yet complementary properties. For example, BT analyses can easily identify interactions between predictors and highly non-linear relationship between the response and predictors, both being difficult tasks for GLMs and GAMs and more traditional techniques. On the other hand, due to their parametric structure, GLMs and GAMs can more easily describe the functional relationship between the response and its predictors. An example data analysis illustrates the use of BTs and its advantages over traditional statistical model-based analysis.

Data on richness of soft coral genera were collected during surveys of 150 reefs on the Great Barrier Reef (Figure D13). The response variable for these data is the richness of soft corals and the predictors are transect, across, along, visibility, waves and slope. There are 150 cases in total. The across-along variables are relative measures of each site across the GBR (Coast = 0; Outer shelf = 1) and along (Southern end = 0; Northern end = 1) provide a system of locally orthogonal spatial coordinates. There are clear relationships between richness and the six predictors, though some of them appear to be weak and non-linear.

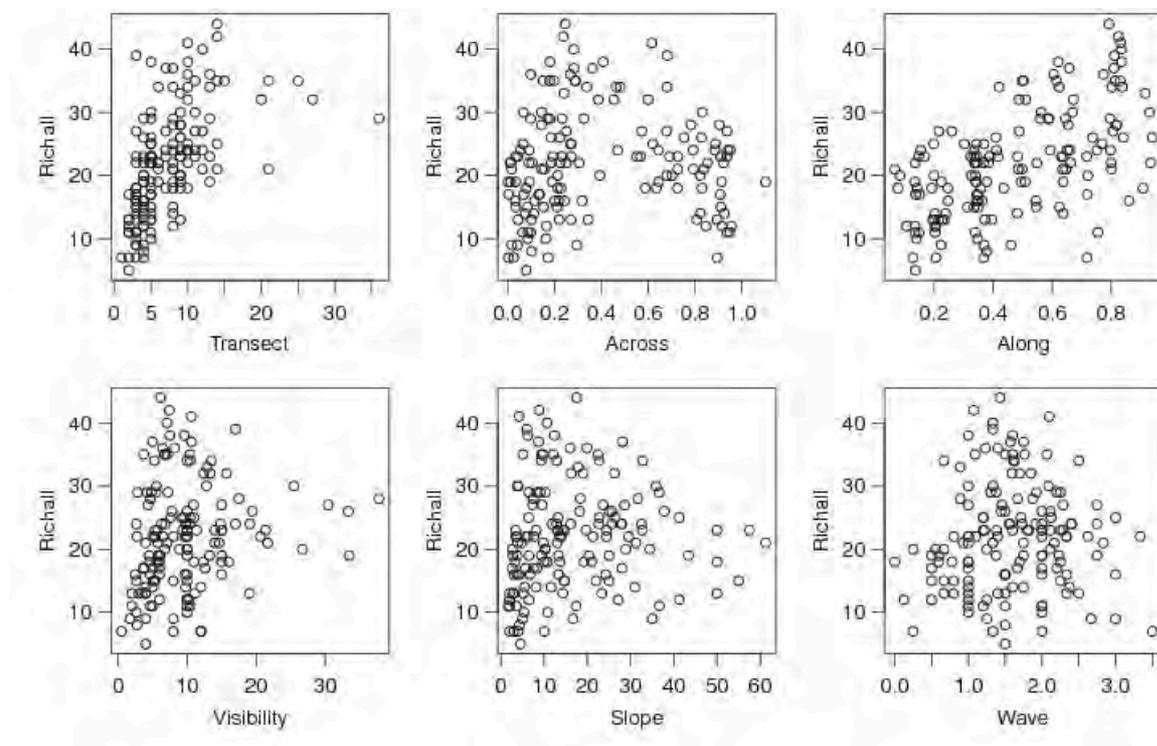


Figure D13: The site locations and richness of soft corals on the Great Barrier Reef.

Generalised Additive Model analysis of soft coral data

By way of comparison, the soft coral data were analysed using GAMs. Gaussian error was used to match the BT analysis, and smooth trends in the six predictors were used to capture the non-linearity in the relationships between richness and the predictors (Fig. D 14).

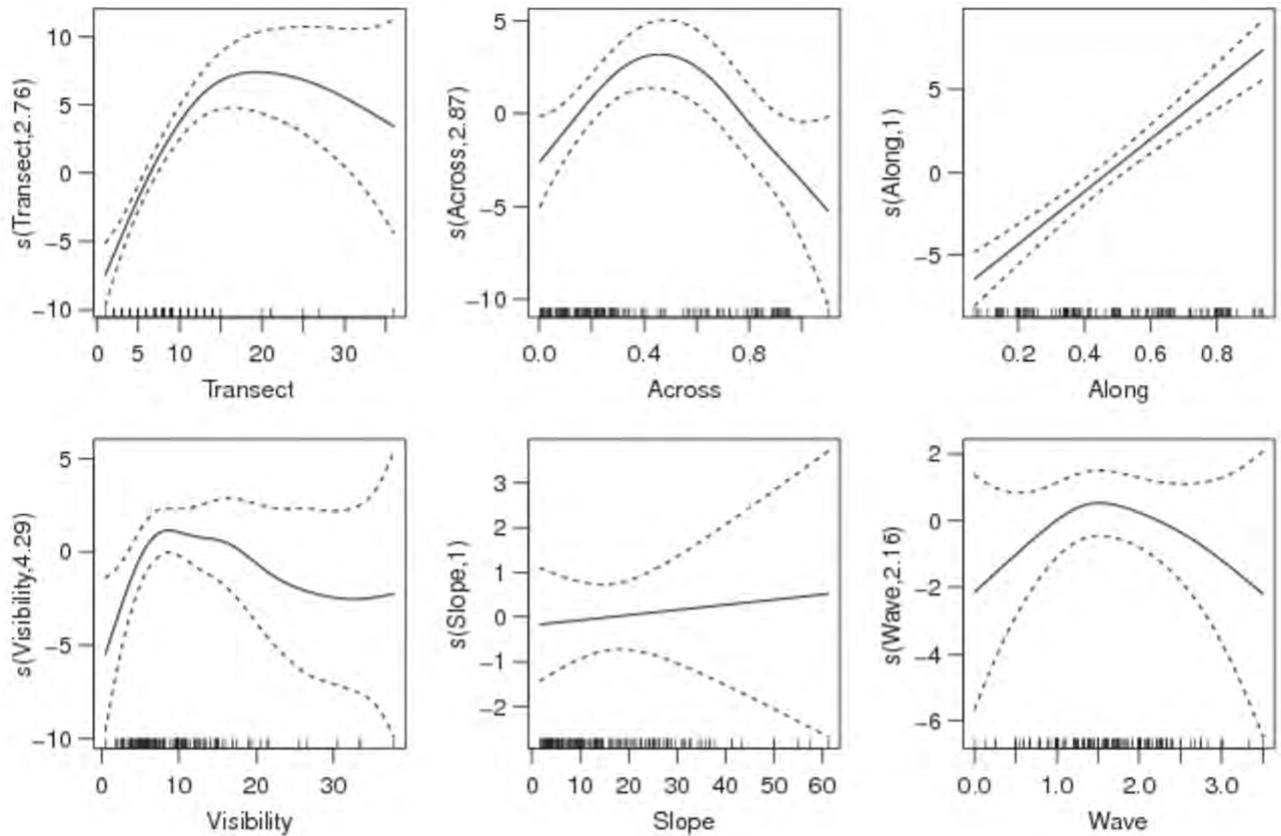


Figure D14: Partial effects showing the relationships between richness and the predictors. The solid lines represent the estimated effects and the dashed lines approximate 95% confidence intervals. Smoothness of response curves is based on cross-validation.

The additive GAM model (i.e. including no interactions) explained 74.2% of the total variance, only moderately higher than the 71.4% *predicted* by the BT analysis. For comparability, the cross-validated GAM model predicted 65.4% – a substantially less than the BT analysis. Based on the BT analysis, interactions involving smooth terms in across, along and waves, were added to the GAM model. This improved the cross-validated GAM model predictions to account for 69.3% of the richness variance.

D.5.2 Boosted Trees analysis of soft coral richness

Boosted trees are an example of ML – a relatively new approach to data analysis that is proving to be an effective alternative to classical statistical models. They can be used for exploratory, descriptive and predictive analysis of ecological and environmental systems, and as we will show, they complement traditional linear and generalised linear models.

Boosted trees and GAMs have very different strengths and weakness, and thus are very useful complimentary tools for statistical analysis of complex data. Both BTs and GAMs can be used to model data with diverse types of responses and loss functions. Boosted trees can discover complex structure in the forms of and relationships between predictors, and this makes them very useful for data exploration. In particular they deal with highly non-linear relationships, data outliers, large data sets that have many predictors and/or cases. Boosted trees are also very good predictors. Generalised additive models have the advantage of being parametric and thus the parameter estimates together with SEs can provide confidence, whereas BTs are non-parametric and thus only estimates of the response variable (and SEs) are available. It should be noted however, that this is not the case for all machine learning methods.

Many statistical models are evaluated by how well they explain the data, e.g. by the % of variance accounted for by the model. However for boosted trees and most ML techniques, cross-validated prediction error is was used as a measure of model performance. This has the advantage that, unlike the percentage of variance, the prediction error cannot be improved by simply adding more predictors to a model. Prediction error is widely used as the preferable measure of model performance in ML.

A BT analysis of richness was performed based on all six predictors and including all possible interactions up to the third order (Figure D 15). The loss function, i.e. the measure of lack of fit that we wish to minimise, was Gaussian. The link between the response and predictions was the identity function, and neither the response nor any of the predictors were transformed. The results of fitting this model quantify: (1) the partial dependency of richness on each of the six predictors, and (2) various 'measures of fit' of the model.

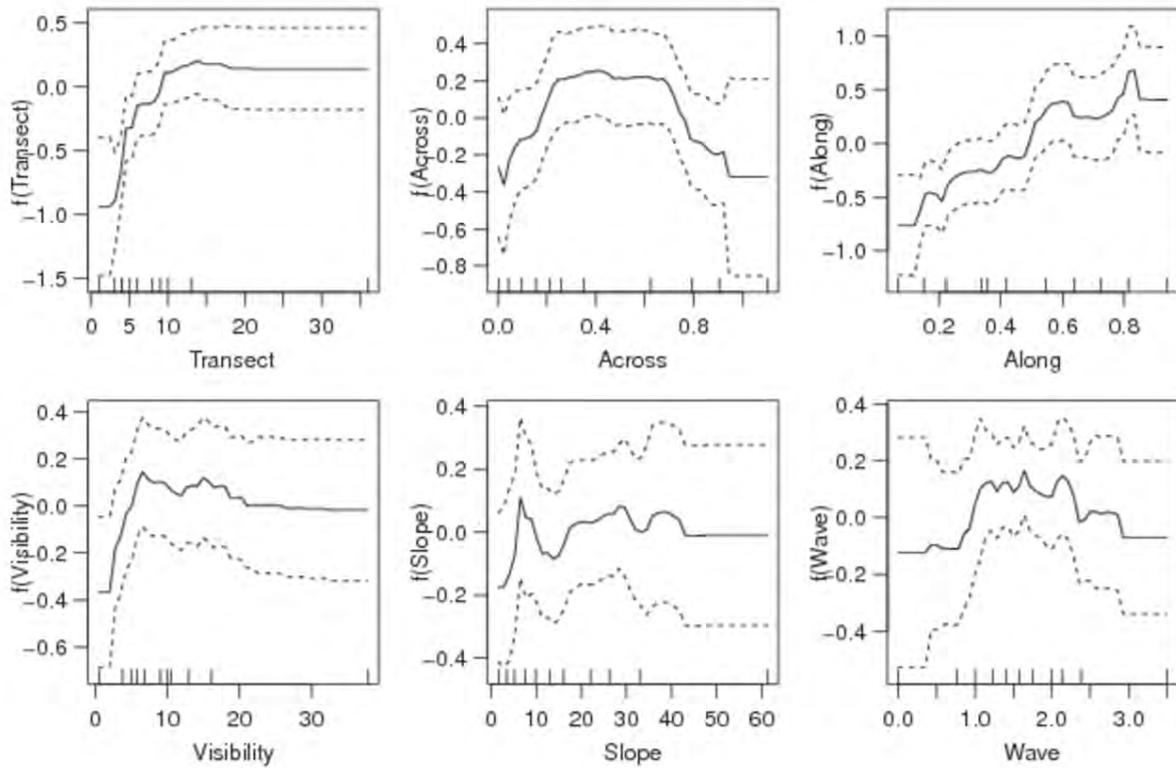


Figure D15: Partial dependency plots showing the effects of each of the six predictors. The solid lines represent the estimated effects and the dashed lines are 95% confidence intervals. The small dashes on the horizontal lower axis indicate the deciles of the distribution of six predictors, and in the case of transects and visibility show high skewness. The response plots are monotonically increasing for transects, visibility and distance along the Reef (S-N), and positively modal for distance across the Reef (Coast - Offshore).

Influence, partial effects and predictors correlations

Table D5: Summary table for the six predictors of richness. The spatial predictors, across and along, together with the number of transects predict 76% of variation, with smaller but systematic effects shown by visibility, waves and slope. The patterns of effects are consistent with our knowledge of soft corals.

Predictor	Influence	Partial	Correlation
Along	34.5	49.2	0.15
Transect	28.2	38.3	0.09
Across	13.9	6.9	0.10
Visibility	8.9	2.5	0.06
Wave	8.2	1.7	0.11
Slope	6.3	1.3	0.0

The total variance of richness was 71.5 of which the best model, based on cross validation, predicted 60.0 (71.4%). The relative contributions of each of the six predictors, and the form of those contributions, was estimated in three ways: (1) the percentage of variation accounted for (Influence), (2) the comparative strength of each predictor on its own (Partial), and (3) the aggregated strength of interactions with the other predictors (Correlation) (Table D5). The spatial variables, together with the number of transects, predicted 75.5% of the explained variation of richness with the remaining 24.5% being accounted for by the three environmental measures.

Pairwise correlations

Table D6: The effect size of pairwise interactions from the boosted trees. Three of the fifteen pairwise interactions are modestly strong and are limited to spatial (across – along) locations and wave action.

	Across	Along	Visibility	Slope	Wave
Transect	0.05	0.04	0.06	0.04	0.08
Across		0.12	0.04	0.07	0.12
Along			0.05	0.03	0.13
Visibility				0.07	0.09
Slope					0.10

The partial correlations between predictors indicate interactive effects (Table D6). The largest effects were waves associated with relative distance across and along the GBR. The effects of these interactions between waves, across and along, shown clear but modest effects (Figures D 16 and D 17), the clearest of which was the weaker variation in richness across the shelf in the Southern GBR.

Interactions between waves, across and along

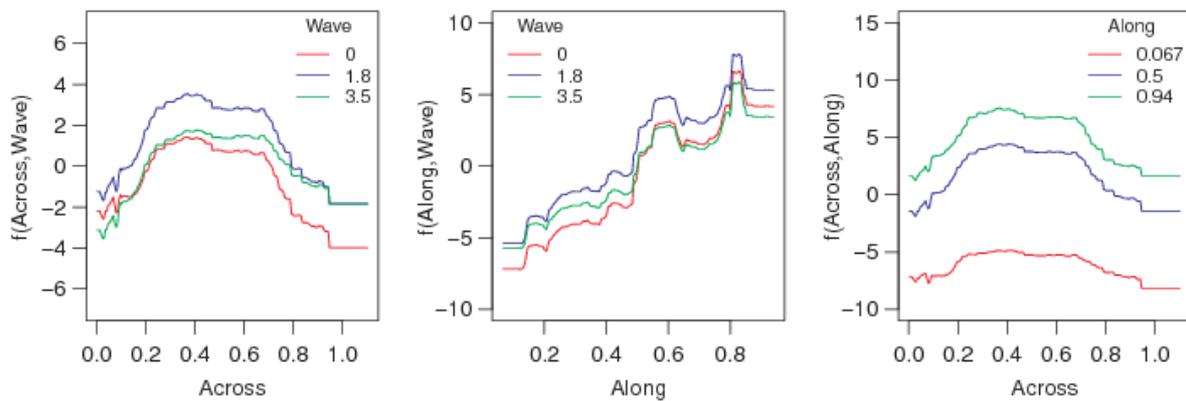


Figure D16: Illustration of the three largest interactions that were limited to spatial (across – along) locations and wave action. The non-parallel profiles of the grouped data indicate the directions and strengths of the interactions.

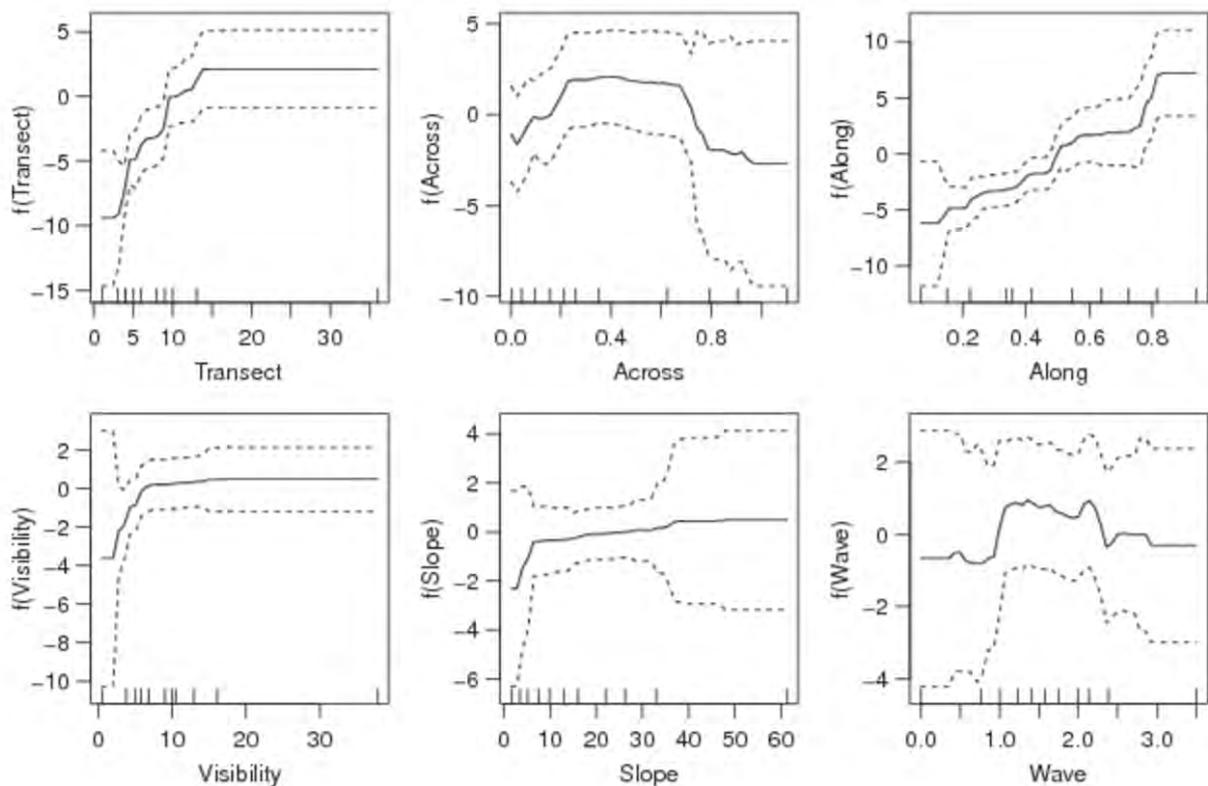


Figure D17: Monotonic constraints applied to transects, along, visibility and slope only increase the lack of fit from 23.6 to 23.7.

Interactions can be easily discovered and assessed by fitting a hierarchy of BTs with different sizes of trees. For example, if we fit a boosted tree that is based on a sequence of trees each of which only comprises a single tree, then that BT will not account for any interactive effects. Similarly, a tree with two splits can only include sub-trees that have first-order interactions –

and so on. Thus we can use a hierarchy of BTs of size 1, 2, 3, etc to detect main effects only, first order, and finally, second order interactions.

D.5.3 Summary

This small data example has provided some insights into the relative strengths of these two very different statistical methods. The strengths and weaknesses of the two methods are complementary: e.g. (1) BTs can better identify interactions between predictors and identify highly non-linear relationships between the response and predictors, whereas (2) GLMs and GAMs can better estimate effect sizes together with confidence intervals, and can better handle more complex experimental and survey designs. In summary, both methods should be part of every statistician and numerical ecologist's data analysis toolbox.

D.6 Conclusions

This Appendix reviews available statistical tools to identify and estimate the effects of multiple pressures on marine organisms and communities using both laboratory and field data. It focuses on the definitions and interpretations of interactions from a statistical and ecological perspective. It outlines pitfalls in past classifications of environmental effects as synergistic, additive and antagonistic, and resolves this issue by defining these terms in a statistical sense.

Examples of one experimental dataset and two field studies are used in this Appendix to illustrate how these techniques can help to: (1) choose the appropriate models for analysis, (2) tease out the most important pressures influencing communities in field data, and (3) quantify the effects of multiple pressures in a context of investigating cumulative pressures.

Learning to think in terms of model-based statistical analysis can be the first step towards more informative, efficient and robust scientific research. Empirical science is dominated by the formulation of models that attempt to both explain and predict the world. Many of these models are stochastic due to the need to account for the uncertainty of measurement and the influence of uncontrollable factors. Thus, model-based statistical analysis is well suited to the empirical science in the presence of uncertain measurement.

The three examples given in this Appendix in combination demonstrate that the joint use of classical statistical models and modern machine learning methods can be extremely effective for analysis of ecological and environmental data to identify and quantify the cumulative impacts of multiple pressures at the ecosystem level.

D.7 References

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