Identifying important species that amplify or mitigate the interactive effects of human impacts to marine food webs

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ABSTRACT

Some species may be more important in transferring the complex effects of multiple human stressors through marine food-webs. Here we show a novel approach to help inform conservation management in identifying such species. Simulating changes in biomass between species from the interaction effects of ocean warming and ocean acidification, and fisheries to year 2050 on the south-eastern Australian marine system, we constructed annual interaction effect networks (IEN's). Each IEN was composed of the species linked by either an additive (sum of the individual stressor response), synergistic (lower biomass compared with additive effects) or antagonistic (greater biomass compared with additive effects) response. Structurally, over the simulation period, the number of species and links in the synergistic IEN's increased and the network structure became more stable. The stability of the antagonistic IEN's decreased and became more vulnerable to the loss of species. In contrast, there was no change in the structural attributes of species linked by an additive response. Using indices of species importance common in food-web and network theory, we identified the most important species within each IEN for transferring the interaction stressor effect on changes in biomass via local, intermediate and global interaction pathways. Mid trophic level mesopelagic fish species were most often identified as the key species within the synergistic IEN's and phytoplankton or zooplankton within the antagonistic IEN's. For the additive response commonly assumed in conservation management demersal fish species were identified by all of the indices. Apart from identifying the most important species, we also identified other important species for transferring the different interaction effects. Knowing the most important species for transferring synergistic or antagonistic responses may help inform conservation strategies for conserving ecosystems under increasing multiple stressor impacts.

Keywords key species; marine food-webs; interaction effect networks; conservation management; climate change.

Introduction

Society's demand for sustainably managing and conserving marine diversity compels us to increase our understanding of the combined effects of stressors caused by human activities (Beaugrand et al. 2014). An important question in this context is whether we can identify species that are more important in transferring the effects of complex multiple stressor impacts through marine ecosystems. Knowing such species may help inform conservation strategies to conserve species with limited resources (McDonald-Madden et al. 2016).

Food-webs which are maps of trophic interactions between species can be a powerful guide to identify species of importance (Thompson et al. 2012). The complex interactions between species in food-webs are increasingly being simulated in ecosystem simulation models such as OSMOSE (Travers-Trolet et al. 2014, Ecopath with Ecosim (EwE) (Christensen & Walters 2004) and Atlantis (Fulton et al. 2007, 2011). They have proved useful as virtual laboratories to explore the impact of stressors at the species, community and ecosystem levels (Griffith et al. 2011, 2012; Nye et al. 2013; Fu et al. 2018).

The effect of the individual and combined effect of human activities on marine ecosystems from model simulations has been analyzed using a factorial meta-analysis approach where the response of each simulation such as the change in biomass between species is calculated using effect size as a common scale and as a measure of interaction strength (Gurevitch et al. 2000; Crain et al. 2008). The advantage of this approach is that it allows the complexity of combined stressor effects to be explored in a simple framework where the changes in effect size between pairs of species are classified as additive, synergistic or antagonistic. An additive response occurs where the combined effect of the stressors is equal to the sum of the individual effects. Most theoretical and

applied conservation research assume additivity as it underlies ANOVA models used in experimental studies on stressor effects and as the null hypothesis in multiple stressor studies. Other models exist such as multiplicative where the outcome is the product of the individual stress effects or comparative where a single dominant stressor drives the combined stressor effects (Darling & Côté, 2008). The additive approach has the advantage of being the most conservative in assigning and quantifying the negative effect of multiple stressors (Crain et al. 2008). If the additive model is assumed as the null hypothesis then any significant deviation greater than the additive effect can be classified as synergistic or less than the additive effect as antagonistic.

Here we extend this concept to identify the most important species at a local, intermediate and global scale in transferring either a synergistic (lower biomass compared with additive effects), additive or antagonistic (greater biomass compared with additive effects) response to the combined effects of ocean warming and ocean acidification, and fisheries on the south-eastern Australian marine system to year 2050.

Methods

Study area and model

Our study area was the south-eastern Australian marine ecosystem. The changes in biomass for 54 trophospecies or individual species from year 2010 to 2050 were simulated using the dynamic, largely deterministic end-to-end (E2E) Atlantis-SE Australian ecosystem model (Fulton et al. 2007; Fulton 2011) (Supporting Information). The trophospecies consist of groups of organisms sharing the same predators, prey and feeding links or represent individual species. For simplicity, we refer to species as either trophospecies or individual species. While there is ongoing and intense debate about E2E models (Griffith & Fulton 2014; Kaplan & Marshall

2016), Atlantis has proved useful for investigating the spectrum of potential community and ecosystem responses from global and regional human impacts (Griffith et al. 2011, 2012; Kaplan et al. 2012; Nye et al. 2013). We simulated the effects of ocean warming and ocean acidification, and commercial fisheries. The degree of ocean warming was simulated using oceanographic output from the CSIRO Mk 3.5 climate system model (Gordon et al. 2010), of the IPCC RCP 4.5 projections (IPCC, 2014). Fisheries include the groups and fishing methods of the current Australian quota management system (Fulton et al. 2007). Oceanic pH for the region is predicted to change from 8.07 in 2000 to 7.92 by year 2050 (IPCC, 2014). We modelled the effect of pH change as an additional mortality on the benthic invertebrate functional group of between 0.1% and 0.3% per day, based on observations (Griffith et al. 2012; Fay et al. 2017).

Classifying the interaction effect between species

We applied the following steps to classify the response of each pair of species to the interaction effect of the stressors as synergistic (lower biomass compared with additive effects), additive (equal to the sum of the individual stressors) or antagonistic (greater biomass compared with additive effects) (Fig. 1).

Step 1 – we ran four model simulations between years 2010 to 2050: control with no stressors (CT), the individual effect of fishing (F) and ocean warming with ocean acidification (OW), and the combined effect of ocean warming with ocean acidification, and with fisheries (FOW). Note that our individual simulation (OW) includes ocean acidification. We consider that this is the realistic simulation as it accounts for the interplay between ocean warming and ocean acidification. We tracked the daily difference in biomass between species using nitrogen ($\text{mg } N \text{ m}^3$) or silicon ($\text{mg } Si \text{ m}^3$)

for diatoms, then averaged to an annual biomass value for each species (Supplementary Information).

Step 2 – the annual difference in biomass between pairs of species (predator and prey) were composed into separate matrices for each simulation (CT, F, OW & FOW).

Step 3 – the interaction effect size (I) of the stressors between each pair of species was calculated applying the meta-analysis approach of Hedge's d , similar to an analysis of variance (ANOVA) (Gurevitch et al. 2000, Crain et al. 2008). Most multiple stressor models based on ANOVA assume additivity (Crain et al. 2008). In comparison, our hypothesis was to test how often the interaction effect of the multiple stressors deviated from the null model of additivity, consequently we applied Hedge's d . The interaction effect size (I) between each species pair was calculated as

$$Y_I = (Y_{FOW} - Y_{OW}) - (Y_F - Y_{CT}), \quad (1)$$

Step 4 – the individual effect size between each pair of species which represents the response in the presence of a stressor alone vs. the control was calculated as:

$$Y_f = (Y_F - Y_{CT}), Y_{ow} = (Y_{OW} - Y_{CT}), \quad (2)$$

Step 5 – we then classified the response between each pair of species in the interaction effect (I) matrices as either additive, synergistic or antagonistic using a classification scheme that considers both the direction (positive, neutral or negative) and magnitude of the effect sizes of the individual stressors (Y_f , Y_{ow}) and the interaction effect (Y_I) (Fig. 2). Considering both the direction and magnitude of the individual effects and the interaction effect rather than just the interaction effect alone has been shown to be more successful (Crain et al. 2008) in correctly identifying a synergistic or antagonistic response (Piggot et al. 2015). We then applied a simplified classification based on Fu et al. (2018) as follows:

- (i) antagonistic, $(Y_I) > (Y_f) + (Y_{ow})$,

- (ii) synergistic, $(Y_I) < (Y_f) + (Y_{ow})$,
- (iii) additive, $(Y_I) = (Y_f) + (Y_{ow})$.

Statistical significance tests of effect size using p -values as conventionally applied were not used for two reasons. First, our simulations produced very small p -values regardless of the effect size. Second, the null hypothesis of no difference between simulations is known *a priori* to be false (Wilson White et al. 2014).

Fig. 1. Schematic of the steps used to identify the most important species within the different interaction effect networks.

Fig. 2. Schematic of the classification scheme of the interaction effect of stressors between pairs of species. Effect sizes are calculated as the relative change in biomass between pairs of species. The 1:1 line represents the additive response. Effect size response between pairs of species below the 1:1 line are classified as synergistic and above the 1:1 line as antagonistic.

Building interaction effect networks (IEN's)

Step 6 – We then subdivided each annual interaction effect (I) matrix into additive, synergistic or antagonistic matrices based on the classification scheme (Fig. 1). The matrices were composed into networks we term as interaction effect networks (IEN's) (Supporting Information). The advantage of the network approach over just considering biomass changes between species lies in its ability to reveal the complex direct and indirect pathways of stressor response on food web structure and functioning (Thompson et al. 2012; Dale 2017). Each IEN was visualized using the software Network3D (Williams, 2010). The network nodes represented the species and the links the interaction affect (Y_I) between predator and prey.

Identifying important species

Step 7— Owing to the structural complexity of networks, there is no one network index for quantifying species importance (Lai et al. 2012). A single network index may not fully reflect the structural or ecological importance of a species requiring the application of multiple measures (Estrada 2017). In this study, we wanted to identify the most important species for transferring an interaction effect between species at different scales of interaction effect. Consequently, we chose indices commonly used in food web research to describe the level of interactions a species has within the network structure at a local, intermediate and global scale (Jordán et al. 2006; Dambacher et al. 2010; Opsahl et al 2010; Lai et al. 2012). Additionally, the indices we chose comprise a set of management indices applied to prioritizing strategies to identify the best combination of species to conserve with limited resources (McDonald-Madden et al. 2016). There are numerous other food web indices that have been applied to large ecosystem and food web models that can also be applied to our approach (e.g. Plaganyi & Essington, 2014). To identify the most important species for transferring the different interaction effects at a local scale we used two indices that originated in social network theory. First, degree centrality (D) that simply quantifies the number of predators and prey a species has (Jordán et al. 2006). Second, weighted betweenness centrality (B_i) that quantifies how frequently a species is part of the shortest path of between two species by weighting the interaction effect size between species (Opsahl et al. 2010). Species with the highest betweenness centrality (B) can be positionally very important as any change in a species interaction effect size can be rapidly spread to many other species and can represent a single point of failure in the food web (Borgatti & Everett, 2006). For interaction effects at the intermediate scale we used two variations of the keystone index for direct (K_{dir}) and indirect effects (K_{indir}) to assess the importance of

species in transferring stressor effects between trophic levels (Jordán et al. 2006). To identify the most important species for transferring stressor effects globally through the food web we used two indices. First, weighted closeness centrality (C_i), a global measure that quantifies the shortest pathways for a change in one species to impact all (Opsahl et al. 2010). Species with a high C_i are important because any effect of the stressors on their biomass can affect the biomass of others more quickly. Second, a modified Google PageRank (GPR) index, a global measure that classifies key species as those where any change in biomass can impact the most number of other species via both the direct and indirect predator and prey interactions (Allesina et al. 2009).

We also applied one index of species importance based on the functional role of species in the different food web structures. Many of the common functional indices often support the traditional view that either top predators or producers are of the highest importance (Hobday et al. 2015). Instead we used the functional keystone index (KS) (Libralato et al. 2006), that has the property of attributing high values of functional importance to species that have both low biomass proportion and high overall effect. Indices were calculated by using Network 3D (Williams, 2010) and Matlab R2017b.

Structural properties

To characterize the structural properties of each IEN, we applied four standard food web metrics to each IEN: Linkage Density (number of links per species), Generality (mean number of prey per predator), Vulnerability (mean number of predators per prey) and Robustness (minimum set of secondary extinctions that occurs in response to a particular perturbation such as species removal (Dunne et al. 2002; Williams, 2010;

Thompson et al. 2012). The attributes were calculated using the software Network3D (Williams, 2010).

Results

Structural attributes

The additive IEN's had an average of 13 links per species. The antagonistic IEN's averaged 6 links per species in year 2010 and 3 links per species by year 2050. The synergistic IEN's showed an increase in links per species from an average of 6 in year 2010 to 10 by year 2050 (Fig. 3a). The mean number of prey per predator (Generality) by year 2050 was 47% greater in the antagonistic and 10% greater in the synergistic IEN's when both were compared with the additive IEN's (Fig. 3b). In the additive and antagonistic IEN's, Generality remained constant between years 2010 and 2050, but it fell 13% between year 2030 and 2050 in the synergistic IEN's. The number of predators per prey (Vulnerability) in the antagonistic IEN's fell by 12 % between year 2010 and 2020 and then increased 25 % by year 2050 (Fig. 3c). By year 2050 there were 40 % greater predators per prey in the antagonistic IEN's compared to the synergistic IEN's. In the synergistic IEN's the mean number of predators per prey was relatively constant between year 2010 and 2050. Analysis of the robustness of each structure by randomly deleting species to test for secondary extinctions (Dunne et al., 2002) showed increasing robustness by 95% at year 2050 for the synergistic IEN's (Fig. 3d). The antagonistic IEN's showed decreased robustness of 34 % by year 2040. The additive IEN's showed a negligible (< 1%) change in robustness between years 2010 and 2050.

(a)

(b)

(c)

(d)

Fig 3. Changes in structural attributes for each of the interaction effect networks (IEN's). (a) Linkage Density ($=L/S$, L = number of links, S = number of species, (b) Generality (number of prey per predator), (c) Vulnerability (number of predators per prey), and d) Robustness (minimum level of secondary species extinctions that occur with species removal). Synergistic (lower biomass compared to additive effects). Antagonistic (greater biomass compared to additive effects).

Additive interaction effects

All indices except the keystone index (K_{dir}) identified either mesopelagic fish or demersal fish as the most important species for transferring additive effects (Table 1). Apart from the keystone index (K_{dir}), each index identified the same species over the simulation period. Degree (D), the simplest structural index identified mesopelagic fish (mid-trophic level species) as the species with the highest number of links with other species. Closeness centrality (C_i), identified mesopelagic fish as the species most important in effecting biomass changes via the shortest pathway to other species. The Google PageRank algorithm (GPR) identified demersal fish as the key species for global interaction effects. The functional importance index (KS) identified demersal fish species with the highest keystoneity. Orcas and pelagic sharks were the most important direct keystone species (K_{dir}) with additive effects.

Synergistic interaction effects

In comparison to the additive IEN's, the most important species identified by each index for transferring synergistic effects altered between years 2020 and 2030. At the local scale, demersal sharks were replaced by mesopelagic fish by year 2030 as the species with the most direct links (D). Mesopelagic fish replaced demersal fish by year 2020 as the most important species for transmitting locally indirect synergistic effects (B_i). At the mesoscale, by year 2020 pelagic sharks replaced orcas (K_{dir}) and demersal fish replaced small pelagic fish (K_{indir}). Globally, both the closeness centrality (C_i) index and Google PageRank algorithm (GPR), showed that by year 2030, mesopelagic fish became the most important species, where a reduction in their biomass from the interaction effect of the stressors would negatively affect the highest number of other species most quickly and the most number of other species via direct and indirect predator-prey interactions. While the structural indices showed the change to mesopelagic fish as important species, the functional keystone index (KS) showed a shift by 2020 to demersal fish species.

Antagonistic interaction effects

Within the antagonistic IEN's, represented by the species linked by a stressor interaction effect that resulted in a greater biomass for each species, the indices identified the greatest variation and changes in important species. With local interaction effects, small pelagic fish replaced shark species (D). The betweenness index (B_i) identified a change in most important species from piscivorous fish to the very important commercial benthic blue grenadier (*Macruronus novaezelandiae*) fish by year 2030, then replaced by seal species to year 2050. At the mesoscale, top predator species such as the sharks and orcas were replaced by cephalopods (K_{dir}) and

carnivorous infauna (K_{indir}). At the global scale, antagonistic interactions resulted in no change with zooplankton species identified as the most important species (C_i , GPR). The functional index (KS) identified different most important species in each decade until year 2040. After 2040, demersal fish species were identified by all the indices as the most important species responding to antagonistic effects.

Table 1

The most important species within the SE Australian marine food web identified at decadal intervals (2010-2050) by the network indices within each interaction effect network (IEN). A= additive, AN= antagonistic (greater biomass compared with additive effects), and S= synergistic (lower biomass compared with additive effects).

Year	IEN	Degree (D)	Closeness (C_i)	Betweenness (B_i)	Keystone 1 (K_{dir})	Keystone 2 (K_{indir})	Google PageRank (GPR)	Keystoneness (KS)
2010	A	mesopelagic fish	mesopelagic fish	demersal fish	orcas	demersal fish	demersal fish	demersal fish
	AN	demersal sharks	gelatinous zooplankton	piscivorous fish	pelagic sharks	demersal sharks	large zooplankton	orange roughy
	S	demersal sharks	small phytoplankton	demersal fish	orcas	small pelagic fish	small phytoplankton	small phytoplankton
2020	A	mesopelagic fish	mesopelagic fish	demersal fish	pelagic sharks	demersal fish	demersal fish	demersal fish
	AN	gulper sharks	large zooplankton	blue grenadier	orcas	carnivorous infauna	large zooplankton	macroalgae
	S	demersal sharks	small phytoplankton	mesopelagic fish	pelagic sharks	demersal fish	mesopelagic fish	demersal fish
2030	A	mesopelagic fish	mesopelagic fish	demersal fish	orcas	demersal fish	demersal fish	demersal fish
	AN	small pelagic fish	large zooplankton	blue grenadier	cephalopods	school whiting	large zooplankton	megazoobenthos
	S	mesopelagic fish	mesopelagic fish	mesopelagic fish	pelagic sharks	demersal fish	mesopelagic fish	demersal fish
2040	A	mesopelagic fish	mesopelagic fish	demersal fish	orcas	demersal fish	demersal fish	demersal fish
	AN	small pelagic fish	gelatinous zooplankton	seals	cephalopods	carnivorous infauna	large zooplankton	demersal fish
	S	mesopelagic fish	mesopelagic fish	mesopelagic fish	pelagic sharks	demersal fish	mesopelagic fish	demersal fish
2050	A	mesopelagic fish	mesopelagic fish	demersal fish	orcas	demersal fish	demersal fish	demersal fish
	AN	small pelagic fish	gelatinous zooplankton	seals	cephalopods	carnivorous infauna	large zooplankton	demersal fish
	S	mesopelagic fish	mesopelagic fish	mesopelagic fish	pelagic sharks	demersal fish	mesopelagic fish	demersal fish

Discussion

Decisions about the allocation of scarce conservation resources often focus on individual species without considering how that species is linked to other species within the ecosystem. Considering species in isolation may not only be detrimental to the species we wish to conserve but also to other non-focal species (McDonald-Madden et al. 2016). We have shown an approach to identify the most important species within networks of species linked by either an additive, antagonistic or synergistic interaction effect response to stressor effects on biomass changes within a large marine ecosystem.

The importance of considering a range of network theory indices is underscored by our finding that each index identified different important species between and within each annual IEN. That different indices should identify different species within each annual IEN is not surprising given that each index identifies important species depending on the type of interactions (local, global or mesoscale). Recent approaches using Bayesian belief networks (BBN's) as a framework for food-webs showed that no single network theory index provided a reliable guide to optimal management strategies for all food-webs (McDonald-Madden et al. 2016). The indices were applied to a range of terrestrial and marine food webs to reveal which index identified the best species to conserve that would also conserve the maximum number of species compared to an optimal strategy. In this case, the optimal strategy was based on the cost of species management and a fixed budget. In food-webs of low connectivity Degree (D) a local measure performed best. For analysis of real food-webs approaching our level of complexity but without capturing all the dynamics, the modified version of the Google PageRank (GPR) global measure performed best, minimizing the chance and severity of negative management outcomes.

Demersal fish were most often identified as important species within the additive IEN's and also as prey species (*Keystone 2*) within the synergistic IEN's. Recent work using changes in species distributional overlap since 1992 of 61 species including demersal species showed that demersal species have become more important as a structural keystone species to maintaining ecosystem stability (Griffith et al. 2018). The changes in species overlap strongly correlated with regional oceanographic changes from increasing southward transport of warmer and saltier water with the East Australian current. This study however, showed no correlation between changes in demersal species abundances and the oceanographic changes.

We found that mesopelagic fish species were important species within the synergistic IEN's at all three scales of interaction effect (local, mesoscale, global). This suggests that any reduction of the biomass of this species will have a greater than expected effect in reducing the biomass of other species that also responded synergistically to the combined effect of the stressors. Our results agree with growing evidence on the important linkage role of mid trophic level species such as mesopelagics in relaying trophic flow from basal species to top predators (Cury et al. 2000; Livi et al. 2011; Lai et al. 2012; Nye et al. 2013). Mesopelagic species are an important prey species of the SE Australian marine system (Smith et al. 2011) and dominate the neustonic layers not only of this region but also the Atlantic, Indian and Pacific Oceans (Olivar et al. 2016). Mesopelagic fish abundance could be underestimated by one order of magnitude suggesting that the role of these species in the ocean might need to be revised (Kaartvedt et al. 2012). Until recently, mesopelagics have received little fisheries or ocean management attention, although the productivity of these short-lived high biomass species would make them prime fisheries targets should a market develop. Given the potentially important structural role of mesopelagic species with multiple stressor

effects, our results suggest the importance to further research, conserve or carefully manage any direct targeting of these species.

The greatest variation in important species occurred within the antagonistic IEN's. In one sense this may be good news for ocean management suggesting redundancy in the antagonistic interactions if an important species is removed. However, in some cases such as zooplankton, these species have short life histories with limited buffer capacity and vulnerable to increasing ocean acidification (Griffith et al., 2011). Thus it is possible that under extreme global and increasing regional human impacts, these species may drop to very low biomass levels, leaving marine ecosystem structures composed of a smaller number of species with key roles in transferring an antagonistic response.

Structural importance of a species does not imply that the species may also be the most important functional species. We found a lack of correlation between the six structural indices and the one functional index for the synergistic and antagonistic IEN's. Previous comparisons of structural and functional indices show the best correlation occurs when links were weighted (e.g. combined effect size) and for local structural indices such as betweenness (B_i) that included indirect interactions (Jordán et al. 2008; Scotti & Jordán, 2010). In our case, only the structural local index betweenness (B_i) and the global structural index Google Page Rank (GPR) applied to the additive IEN's, identified the same important species as the functional index keystoneity (KS).

Management implications

We argue that our approach is important as it shows the species that are linked by each type of interaction stressor effect dynamically and how the composition and strength of interaction effect changes with the ongoing impact of the multiple stressors.

Deconstructing multiple stressor effects in this way identified important structural changes with on-going stressor effects. Our results showed that the majority of species were linked by an additive response. This would seem to support the view that the majority of structural links could be maintained using management efforts based on additive expectations. In both theoretical and applied research, the effect of multiple stressors is commonly assumed to be the additive accumulation of effects associated with single stressors. This view has proved useful for identifying large-scale impacts of human stressors on ecosystem (Klein et al. 2010; Brown et al. 2013). Assuming additive interactions is considered an appropriate middle ground in estimating the potential impact of stressors at an ecosystem level (Brown et al. 2013). From a management perspective an additive effect allows for a straight-forward expectation of response predictable from the response of the individual stressors (Crain et al. 2008; Halpern et al. 2008; Brown et al. 2013). Managing any of the stressors and in particular the largest stressor will have the greatest benefit.

Our approach however, also showed the importance of considering the structure and robustness of the synergistic and antagonistic IEN's. The architecture of interactions affects the stability properties of dynamic networks (Qattin et al. 2004; Dunne 2006). The alteration of interaction structures may explain the loss of ecosystem robustness that can trigger rapid ecosystem state changes (Carpenter & Brock, 2006; Carpenter et al. 2011). We noted an increase in the size and robustness of the synergistic IEN's (Fig. 3d) with a concurrent decrease in the size and robustness of the antagonistic IEN's. Synergistic responses are of significant concern as predicting effects from individual stressors or by assuming an additive response will underestimate the actual negative stressor effects (Brown et al. 2013). In traditional food-web studies robustness is considered a positive attribute, measuring a system's ability to recover or maintain its

functions in the face of stressor effects (Dunne et al. 2006). In our case, the strengthening robustness of synergistic links with combined stressor effects may be a negative attribute. The sobering finding in this case is that any conservation efforts such as maintaining the biomass of key species we identified within the synergistic IEN's such as mesopelagic fish may have a less than expected benefit. We found that antagonistic interaction pathways comprised 24% of all interactions at year 2010, decreasing to 14% by year 2050. The decrease in the robustness of species linked by an antagonistic response also has potential management implications. Increasing the biomass of key species such as zooplankton may again not have the expected outcome as the number of species linked by an antagonistic interaction effect response decreases with on-going stressor effects.

We are not suggesting that management of the species we have identified as most important within synergistic or antagonistic IEN's is practical and would have a greater-than-expected conservation benefit. In considering the allocation of scarce resources to the global biodiversity crisis, our framework highlights three important considerations. First, the need to consider the subsets of species linked by different interaction effects from the impact of multiple stressors. Second, that important species to conserve based on straightforward assumptions of an additive response may not be the optimal species to manage. Third, that the most important species to conserve may change with the ongoing complex interaction effects of multiple stressors.

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Supporting Information

Supplementary information associated with the article will be made available on line.

Data, programs and analysis are available from the corresponding author or at the IMAS Data Portal (<http://data.imas.utas.edu.au>). The authors are solely responsible for the content and functionality of these materials. Queries should be directed to the corresponding author.