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RESEARCH REVIEW

Identifying the interacting roles of stressors in driving the global loss of canopy-forming to mat-forming algae in marine ecosystems

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Abstract

Identifying the type and strength of interactions between local anthropogenic and other stressors can help to set achievable management targets for degraded marine ecosystems and support their resilience by identifying local actions. We undertook a meta-analysis, using data from 118 studies to test the hypothesis that ongoing global declines in the dominant habitat along temperate rocky coastlines, forests of canopy-forming algae and/or their replacement by mat-forming algae are driven by the nonadditive interactions between local anthropogenic stressors that can be addressed through management actions (fishing, heavy metal pollution, nutrient enrichment and high sediment loads) and other stressors (presence of competitors or grazers, removal of canopy algae, limiting or excessive light, low or high salinity, increasing temperature, high wave exposure and high UV or CO_2), not as easily amenable to management actions. In general, the cumulative effects of local anthropogenic and other stressors had negative effects on the growth and survival of canopy-forming algae. Conversely, the growth or survival of mat-forming algae was either unaffected or significantly enhanced by the same pairs of stressors. Contrary to our predictions, the majority of interactions between stressors were additive. There were however synergistic interactions between nutrient enrichment and heavy metals, the presence of competitors, low light and increasing temperature, leading to amplified negative effects on canopy-forming algae. There were also synergistic interactions between nutrient enrichment and increasing CO_2 and temperature leading to amplified positive effects on mat-forming algae. Our review of the current literature shows that management of nutrient levels, rather than fishing, heavy metal pollution or high sediment loads, would provide the greatest opportunity for preventing the shift from canopy to mat-forming algae, particularly in enclosed bays or estuaries because of the higher prevalence of synergistic interactions between nutrient enrichment with other local and global stressors, and as such it should be prioritized.

Keywords: anthropogenic stressors, canopy-forming algae, habitat shifts, management, mat-forming algae

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Introduction

Marine ecosystems are increasingly being subjected to multiple stressors (Halpern *et al*., 2007; Crain *et al*., 2009). The interactions between these stressors can have additive or nonadditive (i.e. antagonistic or synergistic) effects on marine ecosystems (Crain *et al*., 2008; Darling & Cote, 2008). Stressor interactions can alter food-web complexity, relationships between species, diversity within functional groups, the distribution, range and size of organisms or populations and the biogenic habitat structure (Vinebrooke *et al*., 2004; Adams, 2005; Crain *et al*., 2008). In some extreme cases, the nonadditive interactions between multiple stressors can result in shifts between alternative habitats (Scheffer *et al*., 2001; Folke *et al*., 2004; Petraitis & Dudgeon, 2004). These newly established habitats typically consist of species of lesser ecological, functional and human value than those that have been replaced, and can persist for decades without management, restoration or intervention actions (Suding *et al*., 2004; Jones & Schmitz, 2009).

Stressor interactions are driven by a range of processes which operate at different scales (Crain *et al*., 2008; Darling & Cote, 2008). In marine ecosystems, anthropogenic stressors (such as fishing, heavy metal pollution, nutrient enrichment and sedimentation) are predominantly driven by local processes (Knowlton & Jackson, 2008; Cote & Darling, 2010; Brown *et al*., 2013). These so called local anthropogenic stressors are more

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easily amendable to management and conservation actions than other types of stressors (i.e. biological, environmental or climatic), which can be driven by a complex suite of indirect triggers or processes (Russell & Connell, 2012; Brown *et al*., 2013). Thus, there is a growing interest in identifying the type and role of interactions between local anthropogenic and other stressors in driving habitat shifts in marine ecosystems (Carilli *et al*., 2012; Russell & Connell, 2012; Brown *et al*., 2013).

Canopy-forming algae or large brown seaweeds (defined as species from the orders Laminariales or Fucales) are the dominant organisms in many temperate rocky reefs in both intertidal and subtidal habitats (Steneck *et al*., 2002; Schiel & Foster, 2006; Smale *et al*., 2013). These species provide food, habitat, protection and structural complexity, and enhance biodiversity and productivity in coastal ecosystems (Dayton, 1985; Chapman, 1995). There is growing concern about the loss of canopy-forming algae, particularly in many urban areas across the world, e.g. Australia (Coleman *et al*., 2008; Connell *et al*., 2008; Smale & Wernberg, 2013), North America, (Steneck *et al*., 2002), Europe (Benedetti-Cecchi *et al*., 2001; Eriksson *et al*., 2002; Thibaut *et al*., 2005; Perkol-Finkel & Airoldi, 2010) and Japan (Okuda, 2008). Often these forests are being replaced by low lying, smaller and structurally less complex species of persistent turf-forming algae or ephemeral algae which are commonly defined as mat-forming algae (Gorman & Connell, 2009; Perkol-Finkel & Airoldi, 2010; Connell *et al*., 2013, 2014; Wernberg *et al*., 2013). Once established, these mat-forming algae can inhibit the recolonization of canopy-forming algae (Kennelly, 1987; Steen, 2004; Raberg *et al*., 2005; Gorman & Connell, 2009), thus forming an alternative stable state (Petraitis & Dudgeon, 2004; Connell, 2005). In many cases, these habitat shifts have been attributed to the effects on either canopy-forming algae, or mat-forming algae or both of nonadditive interactions between local anthropogenic and other stressors or the cumulative effects of multiple local anthropogenic stressors (Steneck *et al*., 2002; Petraitis & Dudgeon, 2004; Connell *et al*., 2008; Forster & Schiel, 2010; Wahl *et al*., 2011; Russell & Connell, 2012). The nonadditive interactions can result synergistic effects, a greater decrease or increase in growth or survival of the target taxa than the sum of the separate stressors, or antagonistic effects, a lesser decrease or increase in growth or survival than the sum of the separate stressors (Crain *et al*., 2008). Identifying the type of interaction has profound management implications, as synergies accelerate habitat shifts but also provide the greatest opportunity for remediation at the local scale, and therefore should be prioritized for management strategies (Brown *et al*., 2013).

Previous studies have suggested the key local anthropogenic stressors that could facilitate this habitat shift could include overfishing of higher trophic groups leading to outbreaks of grazers (Duffy & Hay, 2000; Tegner & Dayton, 2000; Steneck *et al*., 2002), eutrophication (Worm *et al*., 1999, 2001; Eriksson, 2002; Berger *et al*., 2004; Gorman & Connell, 2009), excess sediment loads (Devinny & Volse, 1978; Airoldi, 2003; Connell, 2003; Eriksson & Johansson, 2005; Irving *et al*., 2009), pollution from heavy metals (Andersson *et al*., 1992; Gledhill *et al*., 1997; Mayer-Pinto *et al*., 2010), other point source pollutants such as oil spills, detergents and antifouling paints (Chapman, 1995), and invasive species (Thomsen *et al*., 2009). These local anthropogenic stressors are thought to negatively interact with environmental stressors or global climatic stressors resulting in declines in canopy algae and increases in mat-forming algae (Connell *et al*., 2008; Russell & Connell, 2012). Although there have been meta-analyses conducted on the nature and type of interactions between local anthropogenic and other stressors on algal communities (Crain *et al*., 2008; Darling & Cote, 2008; Wahl *et al*., 2011), these studies have not specifically considered the effects on both canopy-forming algae and mat-forming algae. Other reviews on canopy-forming algae and mat-forming algae have largely been based on a qualitative rather than quantitative assessment of the literature (Dayton, 1985; Chapman, 1995; Coelho *et al*., 2000; Airoldi, 2003; Forster & Schiel, 2010). There is a pressing need for quantitative, comprehensive information on the cumulative effects of local anthropogenic stressors and the role of interactions between local anthropogenic and other stressors in driving the shifts between these two habitats.

In this study, we used a meta-analysis approach and a qualitative review to assess the nature and type of interactions between local anthropogenic stressors which are most frequently claimed to play a major role in the declines of canopy-forming algae (i.e. fishing, nutrient enrichment, heavy metal pollution and high sediment loads), and other stressors potentially interacting but less amenable to management (presence of competitors or grazers, low light or salinity, high light or salinity, increasing temperature, wave exposure or CO_2 and high UV). Specifically, we tested the hypothesis that nonadditive interactions (either synergistic or antagonistic) between fishing, nutrient enrichment, high sediment loads, and heavy metal pollution and other stressors and the cumulative effects of local anthropogenic stressors will have negative effects on the growth and/or survival of canopy-forming algae and/or positive effects on the growth and/or survival of mat-forming algae (Fig. 1 and references therein).

Materials and methods

We searched the literature using Google Scholar and Web of Science for fully factorial field and laboratory experimental studies in shallow marine systems (either intertidal or subtidal) that manipulated each of our target local anthropogenic stressors in combination with other stressors. We deemed this to be the best approach to evaluate the effects of and interactions between multiple stressors on the responses of canopy-forming and mat-forming algae (Crain *et al.*, 2008; Darling & Cote, 2008).

The search terms included ('effect* or impact*') of local anthropogenic stressors ('nutrient enrichment or eutrophication', 'heavy metal*', 'sediment*', 'fishing or trophic cascade*') and other stressors ('competitor*', 'grazer*', 'canopy*', 'light', 'salinity', 'CO_2', 'wave* or exposure', 'ultraviolet radiation') on canopy-forming algae ('canopy*, Fucales or Laminariales') or mat-forming algae ('ephemeral*, bloom*, Ulva, Cladophora, turf* or filamentous*').

We also searched the reference and citation lists of each article identified, using the same search terms. During the initial literature search, we also looked for articles on the effects of other pollutants, oil spills, disease, trampling, invasive species and habitat disturbance on encrusting red algae or nongeniculate coralline algae. However, these terms were excluded because there was insufficient literature for a meta-analysis.

We selected studies for the analyses that manipulated two or more stressors. We only included studies that were conducted between late spring and late summer, during the primary growth period of canopy-forming and mat-forming algae, because there were few experiments conducted in other seasons. The studies tested the effects of local anthropogenic and other stressors on population-level metrics (density and/or % survival) and individual metrics (growth: length, width and/or % cover and photosynthesis: maximum electron transport rate (ETR), maximal yield and/or gross P_{max}) on canopy-forming or mat-forming algae. We tested the effects of the stressors on the growth and survival of the two categories of algae, separately.

We found 167 multiple stressors studies and after various exclusions, (i.e. confounding with other factors, no control, data not shown in the article, experiments conducted between late autumn to winter) we extracted data from 118, using GetData Graph Digitizer version 2.25.0.32 (www.getdata-graph-digitizer.com). There were 65 studies on canopy-forming algae and 53 on mat-forming algae. We tested the effects of low and high levels of stressors, separately (e.g. low light vs. control and high light vs. control). We focused on extracting data from studies which tested the effects of stressors relative to ambient

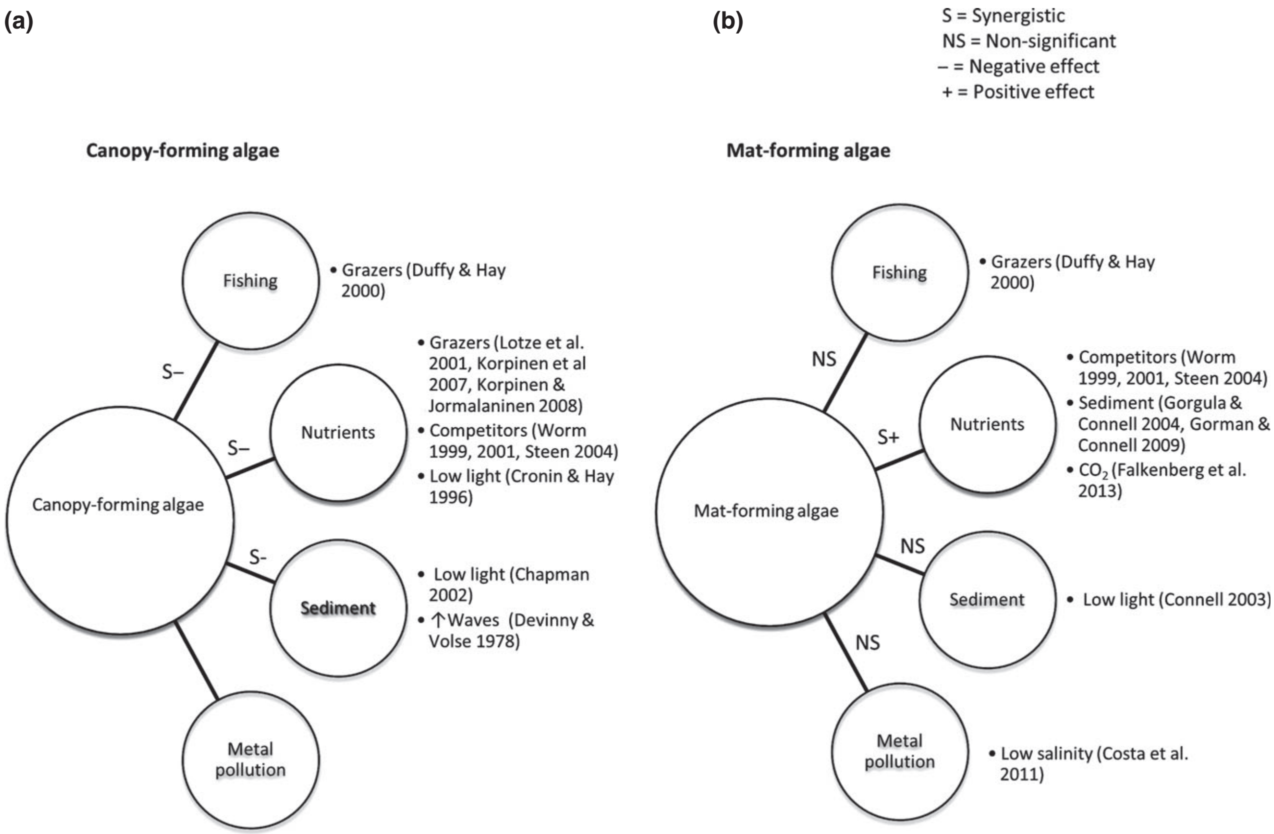

Fig. 1 Predicted effects of the interactions between key local anthropogenic and other stressors on (a) canopy-forming and (b) mat-forming algae based on factorial studies from the literature. Lines represent the type of interaction most commonly reported in the literature between the local stressor within the circle and the other stressors listed to its side. Unknown interaction types in the literature are not presented in the figure. Symbols are S = synergistic, NS = nonsignificant, – = negative effects and + = positive effects.

site levels. When studies used multiple levels for each treatment in the design or measured multiple responses of the algae to the same experiment (e.g. growth and photosynthesis or density and survival), we used the level or parameter that was most similar to other studies on the same topic. If the data were reported as a time series, we used data from the final sampling period. In cases where more than two stressors were manipulated in a study, the responses to each stressor pair were extracted at ambient levels of the third stressor. If data were reported on multiple species or at different sites in the same study, we recorded all information.

For the meta-analysis, we defined a study as the measured responses of an individual algal species or broader group, either canopy- or mat-forming algae to the stressors of interest. In some articles, the responses of multiple individual species or groups were measured in separate experiments or at multiple locations. For the purposes of the meta-analysis, these were treated as separate studies. We adjusted for the lack of independence of studies conducted at the same research centre when required (see analysis methods below). For each study, we recorded the means, standard deviations (where reported) and sample sizes for the treatment and the control. For canopy-forming algae, we recorded the life stage in two predefined categories: recruits to early juveniles (<1 year old) and juveniles to adults (≥ 1 year old), as previous work has suggested algae in these stages tend to be controlled by different factors (Schiel & Foster, 2006). For the mat-forming algae, we recorded their persistence in two predefined categories: ephemeral algae (e.g. Ulva spp.) and turf-forming algae (e.g. Feldmania spp.), as algae in these groups could be influenced differently by multiple stressors (Connell *et al*., 2013, 2014). For both canopy-forming and mat-forming algae, we recorded the geographical location of the study, and then we assigned each study a unique number.

The stressor interactions tested in the meta-analysis were:

1 nutrient enrichment and the presence of competitors (either canopy-forming or mat-forming algae), presence of grazers, removal of canopy algae, low light, low salinity, high light, high salinity, increasing temperature, increasing wave exposure, increasing CO_2 or high UV;
2 fishing and the presence of grazers
3 The studies on the effects of fishing and the presence of grazers selected for the meta-analysis focused on a combination of direct and indirect impacts. These studies tested the interaction between excluding predatory or omnivorous fishes or amphipods and the presence of grazers using a 2-factor approach. We used these studies to test whether the indirect effects of fishing (no predators with grazers) were stronger than the direct effects of the predatory or omnivorous fish or amphipods (predators, no grazers) or the grazers (predators with grazers);
4 heavy metal pollution and low light, low salinity, high light or high salinity;
5 high sediment loads and the presence of competitors (either canopy-forming or mat-forming), presence of grazers, low light, high light, increasing temperature, increasing wave exposure

In addition, we also explored possible interactions between multiple local anthropogenic stressors:

6 NO_3 enrichment and PO_4 enrichment;
7 nutrient enrichment and fishing, sedimentation or heavy metals;
8 heavy metal pollution (combined effect of two heavy metals)

Data analysis

The effect size of the local anthropogenic and other stressors on the growth and survival of the algae were measured as the Hedge's g standardized mean difference (SMD) (Hedges, 1981),

$$\mathrm{SMD} = \frac{\bar{Y}_{\mathrm{stressor(s)}} - \bar{Y}_{\mathrm{control}}}{S_{\mathrm{pooled}}}$$

We chose SMD as opposed to log response ratio, for the effect size of this meta-analysis because our data set contained both negative values (i.e. loss of biomass) and zeroes (i.e. no survival and/or no variance between replicates within the same treatment) (Borenstein *et al*., 2009). For the analysis, the effects of individual and combined stressors were tested against the control using a random effects model as there was significant heterogeneity between studies (determined by measuring heterogeneity via Cochran's Q, and testing it against a χ^2 distribution with n-1 degrees of freedom, where n is the number of studies). The model was fitted using the DerSimonian–Laird random effects estimator (DerSimonian & Laird, 1986). We compared the results from DerSimonian–Laird and the Hedges random effects models and found no detectable differences. For studies that tested the effects of the stressors on more than one species or at different locations, we treated each species/location as a different study. In this case, we tested whether results from the same article were more similar than from different article, by testing the effect of study identity as a moderator in the model (Tables S1, S2, S3 and S4). For canopy-forming algae, we also tested the effect of life stage (recruits to juveniles or juveniles to adults) and for mat-forming algae the effect of persistence (ephemeral or persistent turf-forming algae) as moderators (Tables S1, S2, S3 and S4). Where significant effects were found, we presented the results from the model that included the moderators. For studies that did not report the standard deviation, we substituted the maximum value of the standard deviation from the studies on the same pair of stressors (Furukawa *et al*., 2006). There were no detectable differences in effect sizes between the studies with and without standard deviations (based on overlapping 95% confidence intervals). We therefore presented results which included studies that did not publish standard deviations. The meta-analysis was only performed on pairs of stressors with three or more studies (see Tables S1–S4 for full details about the number of studies for each stressor pair). However, we also undertook a qualitative review on the effects of pairs of stressors with less than three studies to obtain a more holistic picture of the effects of multiple stressors on the responses of the algae. We checked whether there was a significant correlation between the effect size and sample size, as a measure of publication bias using qualitative tests (weighted frequency histogram, funnel plots and Q–Q normality plots of effect sizes). We also tested whether there were a high number of studies needed to overturn the results, using the Rosenthal's fail-safe number test (Tables S1, S2, S3 and S4).

We tested whether the interactions between local anthropogenic and other stressors were antagonistic, additive or synergistic based on the methods proposed by Darling & Cote (2008). We focused on the additive model as this is a more conservative estimate of the predicted effect than the multiplicative model (Crain *et al.*, 2008; Darling & Cote, 2008). The formula has been modified from Darling & Cote, for use with the Hedge's g SMD effect size (Hedges, 1981).

$$\mathrm{SMD}_{\mathrm{additive}} = \frac{\bar{Y}_{\mathrm{stressorA}} - \bar{Y}_{\mathrm{control}} + \bar{Y}_{\mathrm{stressorB}} - \bar{Y}_{\mathrm{control}}}{S_{\mathrm{pooled}}}$$

We classified the interaction as antagonistic if the actual effect size of Stressor A × B was closer to zero than the predicted effect size and synergistic when the actual effect size of Stressor A × B was further away from zero than predict effect size. Interactions were nonadditive if the confidence intervals of the actual effect size did not overlap the predicted effect size and additive if the confidence intervals of actual effect size overlapped of the predicted effect size. All analyses were conducted using the *Rgui* library metafor (Viechtbauer, 2010) and all plots were produced using *Rgui* (Team RC, 2012).

Results

Of the 118 studies from which data were extracted, the local anthropogenic stressor with the greatest number of experiments was nutrient enrichment (60%), followed by heavy metal pollution (17%), sedimentation (14%) and fishing (8%). The studies were not evenly distributed around the globe, and most of the experiments were conducted in Europe (Fig. 2). We studied the effects of 22 pairs of stressors on the growth and survival of canopy-forming algae and the effects of 20 pairs of stressors on the growth and survival of mat-forming algae (see Tables S1, S2, S3, S4, S5 and S6 for full details). Contrary to our hypotheses (Fig. 1) across all the pairs of stressors, the majority of interactions were additive (81% growth of canopy-forming algae, 78.57% survival of canopy-forming algae, 68.75% growth of mat-forming algae and 85.72% survival of mat-forming algae) (Tables S5 and 6). There were notable exceptions in the synergistic interactions between nutrient enrichment and other stressors (Fig. 3).

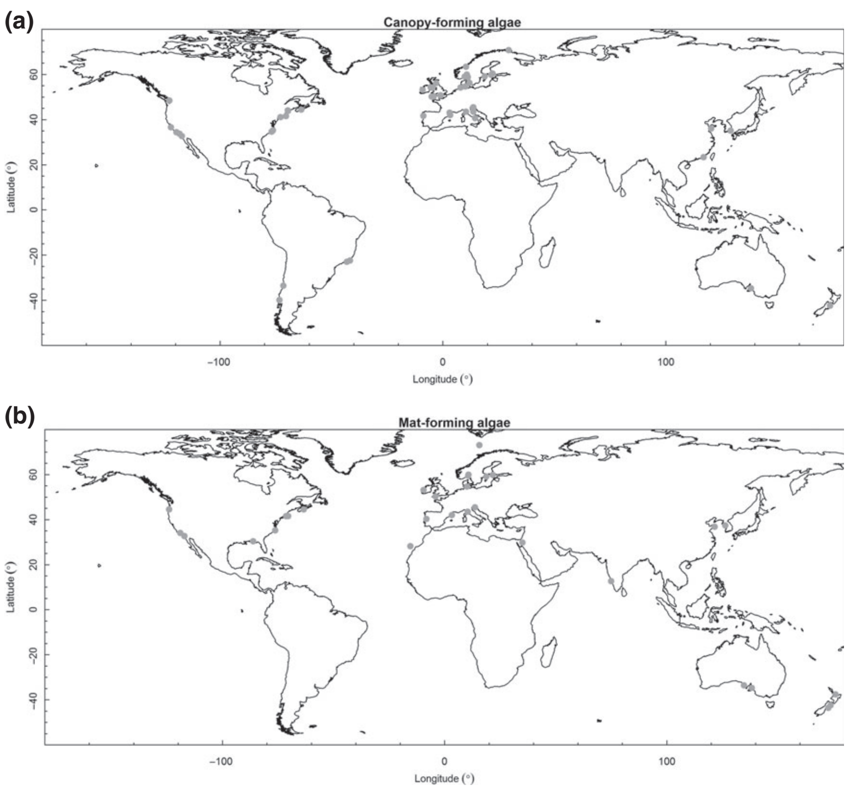

Fig. 2 Map showing the geographical location of the studies for (a) canopy-forming algae and (b) mat-forming algae.

Interactions between nutrient enrichment and other stressors

As we hypothesized (Fig. 1), nutrient enrichment had synergistic interactions with the presence of competitors and low light leading to amplified negative effects on the growth and survival of canopy-forming algae (Fig. 3, Tables S1 and S2). There were also synergistic interactions between nutrient enrichment and increasing temperature with negative effects on the growth of canopy-forming algae (Fig. 3, Tables S1 and S2). In general, the effects of the stressor pairs were consistent between both juveniles and adult life stages (Tables S1 and S2). Contrary to our expectations, there was an additive interaction between nutrient enrichment and the presence of grazers, which had a negative effect on the growth of juveniles to adults but no detectable effect on the growth of recruits to juveniles of canopy-forming algae (Fig. 3, Tables S1, S2 and S5).

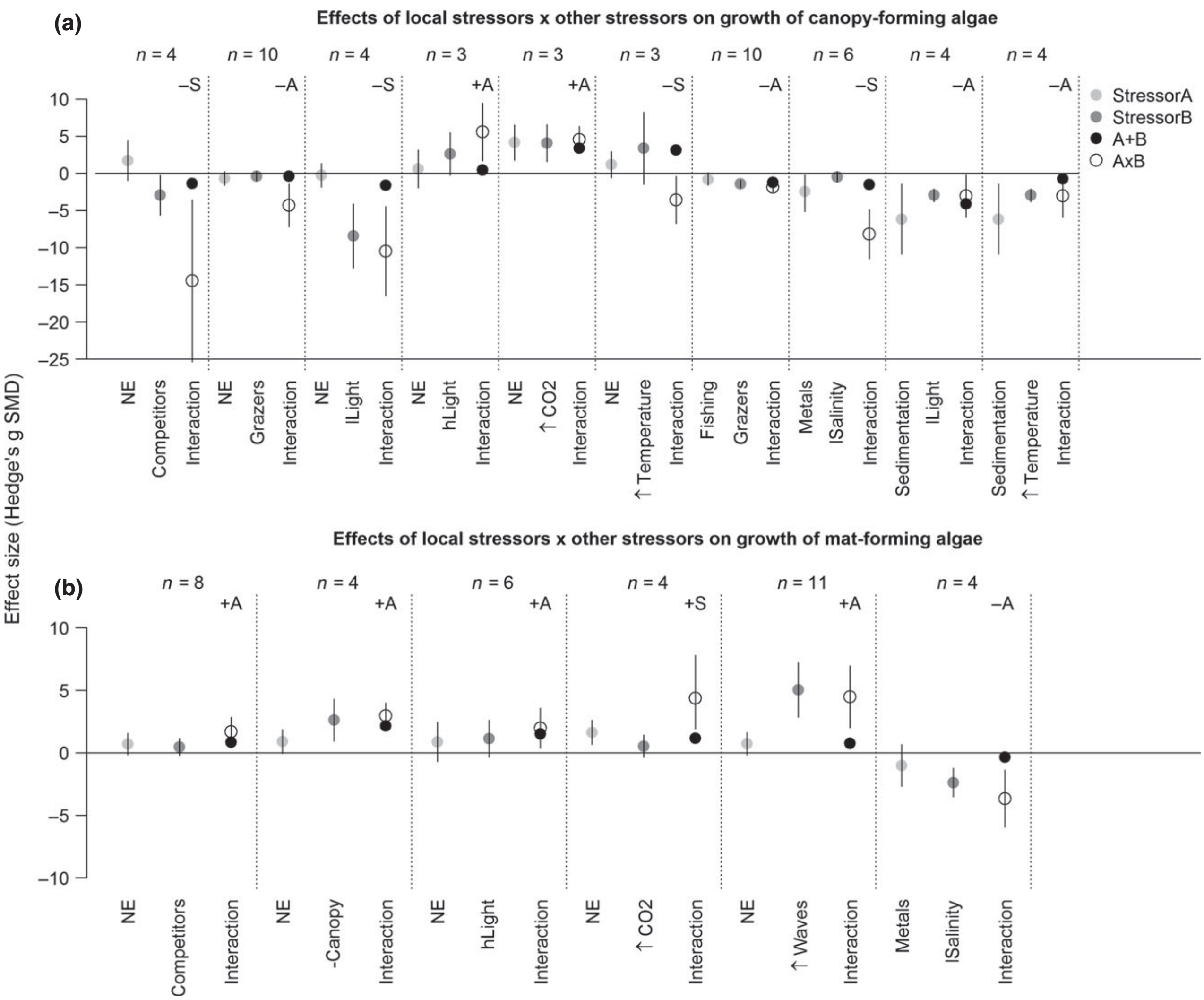

Fig. 3 Results of meta-analysis (Hedge's g standard mean difference effect size and 95% confidence intervals) on the effects of local anthropogenic stressors [nutrient enrichment (NE), fishing, heavy metal pollution (metals) and sedimentation] (Stressor A), other stressors (Stressor B), and their combined effect (A + B = predicted effect of the interaction see Eqn (2) and A × B = actual effect of the interaction) on the (a) growth of canopy-forming algae and (b) growth of mat-forming algae. Effects are significant if confidence intervals do not overlap zero. Only significant interactions are shown. Interactions are synergistic with negative effects (−S) if the upper 95% confidence interval of the observed interaction is lower than the predicted interaction, synergistic with positive effects (+S) if the observed interaction was less than the lower 95% confidence interval of the predicted interaction, additive with negative effects (−A) if the observed interaction is lower than zero and the 95% confidence interval overlaps the predicted interaction and additive with positive effects (+A) if the observed interaction is higher than zero and the 95% confidence interval overlaps the predicted interaction. Symbols are: l = low, h = high and ↑ = increasing. Note the differences in the *y*-axis between (a) and (b).

Contrary to our hypotheses (Fig. 1), nutrient enrichment had an additive interaction with the presence of grazers and the presence of competitors with positive effects on the growth and/or survival of mat-forming algae (Fig. 3, Tables S3, S4, S5 and S6). As we predicted (Fig. 1), there was a synergistic interaction between nutrient enrichment and high CO_2 with positive effects on the growth of mat-forming algae (Fig. 3, Tables S3 and S5). The qualitative review suggested there could be a synergistic interaction between nutrient enrichment and temperature with positive effects on the growth of mat-forming algae (Table S6). Interestingly most studies on mat-forming algae focused on the responses of ephemeral taxa (Tables S3 and S4).

Interactions between fishing and the presence of grazers

Contrary to our hypotheses (Fig. 1), there was an additive interaction between fishing and the presence of grazers with negative effects on the growth of adult canopy-forming algae (Fig. 3, Tables S1 and S5). As we expected (Fig. 1), there was no detectable effect of the interaction between fishing and the presence of grazers on the growth of mat-forming algae (Table S3).

Interactions between heavy metal pollution and other stressors

There was an additive interaction between heavy metal pollution and low light which resulted in declines in the survival of recruits to juveniles of canopy-forming algae (Fig. 3, Tables S1 and S2). The qualitative review also suggested there could be a synergistic interaction between heavy metal pollution and increasing temperature with negative effects on the survival of adult canopy-forming algae (Tables S6). Contrary to our hypotheses (Fig. 1), there was a synergistic interaction between the heavy metal pollution and low salinity with negative effects on the growth of mat-forming algae (Fig. 3, Table S6).

Interactions between sediment and other stressors

Contrary to our hypotheses (Fig. 1), there were additive interactions between high sediment loads and low light with negative effects on the growth of canopy-forming algae (Fig. 3, Tables S1 and S2). Similarly, there were additive interactions between high sediment loads and increasing wave exposure with negative effects on the survival of recruits to juveniles of canopy-forming algae (Tables S1 and S2).

Contrary to our hypotheses (Fig. 1), only high sediment loads affected the growth of mat-forming algae, and there were no detectable interactions with low light (Table S3).

Interactions between local anthropogenic stressors

There were no detectable effects of PO_4 and NO_3 combined, or nutrient enrichment and fishing combined on the growth or survival of canopy-forming algae (Tables S1 and S2). There was however, a synergistic interaction between nutrient enrichment and heavy metal pollution with negative effects on the growth of adult canopy-forming algae and an additive interaction between heavy metals (two heavy metals combined) with negative impacts on the growth of canopy-forming algae (Fig. 4, Tables S1 and S6). The qualitative review suggested there could also be a synergistic interaction between heavy metal pollution and excess sediment with negative effects on the growth of adult canopy-forming algae (Table S6).

There was an additive interaction between nutrient enrichment (PO_4 and NO_3 combined) and nutrient enrichment and excess sediment with positive effects on the growth of mat-forming algae (Fig. 4, Tables S2 and S6). There was also an additive interaction between nutrient enrichment heavy metals with negative effects on the growth of ephemeral algae (Fig. 4, Tables S3, S4 and S6). In contrast, there were no detectable effects of the interaction between nutrient enrichment and fishing on the growth of mat-forming algae (Table S3).

Discussion

This meta-analysis represents the first systematic global assessment of the role of the interactions between local anthropogenic and other stressors in driving the ongoing global transitions from forests of canopy-forming algae to mat-forming algae in temperate rocky reef ecosystems. Our results indicate that the interactions between the four dominant local anthropogenic stressors in temperate rocky reef ecosystems (i.e. fishing and outbreaks of grazers, eutrophication, heavy metal pollution and high sediment loads) and other stressors can enhance declines in the growth and survival of canopy-forming algae, at both the recruit to juvenile and juvenile to adult life stages. In contrast, many of the same pairs of stressors had no detectable or positive effects on the growth or survival of mat-forming algae, irrespective of their persistence. These results provide strong evidence to suggest that increasing population growth and development of coastal areas and their associated human activities will have major impacts on the algal community (Coelho *et al.*, 2000; Airoldi & Beck, 2007; Coleman *et al.*, 2008; Mangialajo *et al.*, 2008; Gorman *et al.*, 2009). The information can be used to identify appropriate management actions at a local scale that can help to halt the global loss of canopy-forming algae and their replacement by mat-forming algae.

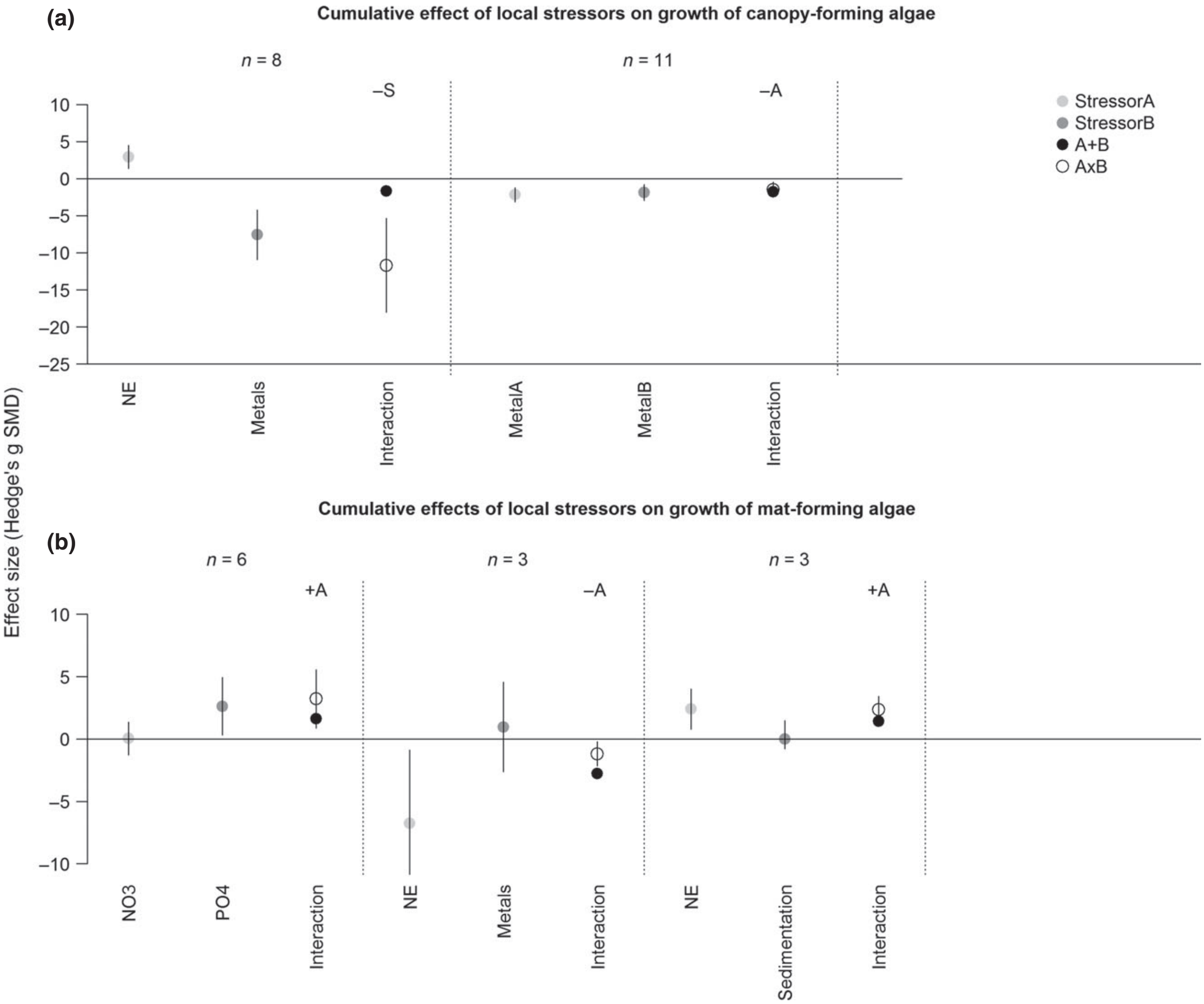

Fig. 4 Results of meta-analysis (Hedge's g standard mean difference effect size and 95% confidence intervals) on the cumulative effects of local anthropogenic stressors [NO_3, PO_4, heavy metal A (metal A), heavy metal B (metal B) and sedimentation], Stressor A or Stressor B, and their combined effect (A + B = predicted effect of the interaction see Eqn (2) and A × B = actual effect of the interaction) on the (a) growth of canopy-forming algae and (b) growth of mat-forming algae. Effects are significant if confidence intervals do not overlap zero. Only significant interactions are shown. Interactions are synergistic with negative effects (−S) if the upper 95% confidence interval of the observed interaction is lower than the predicted interaction, additive with negative effects (−A) if the observed interaction is lower than zero and the 95% confidence interval overlaps the predicted interaction and additive with positive effects (+A) if the observed interaction is higher than zero and the 95% confidence interval overlaps the predicted interaction. Note the differences in the *y*-axis between (a) and (b).

The identity of the local anthropogenic stressor had a major influence on the nature and type of the interaction and clearly demonstrated the importance of understanding the effects of individual stressors rather than groups or categories of stressors (Claudet & Fraschetti, 2010; Fraschetti *et al*., 2011). Contrary to our predictions, the majority of the interactions between local anthropogenic and other stressors were additive, with the notable exception of those interactions involving nutrient enrichment. Nutrient enrichment had synergistic interactions with the presence of competitors, presence of grazers, increasing temperature and heavy metal pollution, leading to much greater negative effects on the growth and/or survival of canopy-forming algae than predicted by the additive model. Conversely, there were synergistic interactions between nutrient enrichment and CO_2 which enhanced the growth and/or survival of mat-forming algae. These results confirm previous suggestions that mat-forming algae are more tolerant or actively benefit from the cumulative anthropogenic stressors that negatively affect the growth and/or survival of canopy-forming algae (Pedersen & Borum, 1996; Amado Filho *et al.*, 1997; Benedetti-Cecchi *et al.*, 2001; Steen, 2004; Eriksson & Johansson, 2005; Gorman & Connell, 2009; Costa *et al.*, 2011). The implications are that management strategies designed to reduce the levels of these four key local anthropogenic stressors, nutrient enrichment, excess sediment loads and heavy metal pollution could help to improve the resilience of canopy-forming algae to other stressors less amendable to local actions, and thereby prevent the shift to mat-forming algae.

Nutrient enrichment was the local anthropogenic stressor with the most frequent nonadditive interactions with other stressors. The input of excess nutrients (primarily nitrate and phosphate) to the marine environment is a global problem associated with a range of human activities. Nutrient enrichment can interact with heavy metals to block carbon storage in canopy-forming algae (Munda & Veber, 1996, 2004). It also increases the palatability of canopy-forming algae to grazers (Worm *et al.*, 1999; Korpinen *et al.*, 2007; Lotze *et al.*, 2001; Korpinen & Jormalainen, 2008), reduces the availability of light or increases turbidity by promoting the growth of epiphytes and algal blooms (Hoffman & Santelices, 1982; Cronin & Hay, 1996; Shivji, 1985), and becomes toxic at high temperatures (Yarish *et al.*, 1990). In contrast, the same synergistic interactions tend to have no detectable or positive effects on the growth of mat-forming algae because of their opportunistic traits which include higher nutrients requirements (Pedersen & Borum, 1996), the ability to assimilate high levels of CO_2 (Gordillo *et al.*, 2001), rapid growth at increased temperatures (Riccardi & Solidoro, 1996) and their positive associations with sediment (Airoldi & Virgilio, 1998; Gorgula & Connell, 2004). These findings suggest a much stronger potential for shifts in rocky coastal systems with poor water quality, particularly under future scenarios of climate change (Lotze & Worm, 2002; Falkenberg *et al.*, 2012, 2013; Steen, 2004).

The nature of the interactions between nutrient enrichment and other stressors might be also influenced by other factors not covered by the studies identified in this meta-analysis. Experimental tests on multiple stressors, which were the target of this review, are difficult to undertake, and most of the work was carried out in laboratories (85.47% of studies on canopy-forming algae and 54% of studies on mat-forming algae) or *in situ* in enclosed seas or estuaries (9% of studies on canopy-forming algae and 30.4% of studies on mat-forming algae). This could have enhanced the negative or positive effects of nutrient enrichment because there is very little or no mixing through ocean currents compared with areas along exposed coastlines where algal populations often experience long periods of nutrient depletion or oligotrophic conditions (Russell & Connell, 2012). Some interactions could also vary between seasons. For example, while nutrient enrichment and strong warming can worsen the decline of canopy-forming algae by synergistically promoting the growth of epiphytes or increasing their susceptibility to diseases during the late spring and summer (Kremer & Munda, 1982; Yarish *et al.*, 1990; da Costa & Valentin, 1994), such effects could be dampened or reversed with moderate warming in the winter and early spring (Yarish *et al.*, 1990). However, there were insufficient experiments to test for seasonal differences in the interaction between nutrient enrichment and increasing temperature in the meta-analysis. There was sometimes also high variability in the responses of different species of canopy-forming and mat-forming algae to the interactions between nutrients and other stressors within the same study (Yarish *et al.*, 1990; Worm *et al.*, 1999, 2001; Steen & Rueness, 2004; Steen & Scrosati, 2004). In the light of these gaps in the literature, a conservative management approach must assume that the interactions between nutrient enrichment and other stressors will have a negative effect on the growth and survival of canopy-forming algae.

Long-term sustainability requires the identification of the causes and interplay between multiple stressors, and the development of stakeholder support for management actions. However, we found significant and striking gaps in research between multiple stressors. The majority of the four local anthropogenic stressors have not been experimentally studied in combination with each other in controlled factorial experiments. There were also very few experiments testing the combined effects of fishing and other stressors on either canopy-forming or mat-forming algae. These gaps were particularly surprising given the large body of literature that suggested that global declines in canopy-forming algae are driven by the combined effects of local anthropogenic stressors (Walker & Kendrick, 1998; Coelho *et al.*, 2000; Connell *et al.*, 2008) or the effects of fishing and other stressors, including rising sea surface temperatures and increasing wave exposure (Tegner & Dayton, 2000; Halpern *et al.*, 2007). For some pairs of stressors, there were no replicate experiments to test the generality of our conclusions in a meta-analysis. The stressors examined in our review have been shown to commonly co-occur in increasingly human-dominated marine systems (Crain *et al.*, 2008, 2009; Darling & Cote, 2008; Cote & Darling, 2010) and research on their cumulative effects is needed for prioritizing management actions (Coelho *et al.*, 2000; Wahl *et al.*, 2011; Harley *et al.*, 2012). There is a particularly urgent need for research on three or more stressors, for which only a hand full of studies could be found (13 studies for canopy-forming algae and 10 studies for mat-forming algae) because of the increased probability of nonadditive interactions (Crain *et al*., 2008; Wernberg *et al*., 2012).

While the links between local anthropogenic stressor interactions and habitat shifts in algal communities are slowly becoming clearer, there is relatively little empirical evidence about whether reducing or managing these same stressors would be effective for disrupting nonadditive interactions, reversing the spread of alternative habitats, and promoting the recovery of more desirable configurations or species (Russell & Connell, 2012; Brown *et al*., 2013). Recent experimental research has shown that management of nutrients can suppress the growth of turf-forming algae under future scenarios of increased CO_2 (Russell *et al*., 2009; Falkenberg *et al*., 2012, 2013). Similar experimental work is urgently needed to test whether management of water quality can significantly enhance the resilience of canopy-forming algae in areas experiencing rapid increases in sea surface temperature by disrupting the negative synergies between these two stressors. Prioritization of conservation strategies would enormously benefit from experimental manipulations mimicking management actions geared towards recovery in a variety of degraded ecosystems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Effects (Hedges g standard mean difference) of (a) local anthropogenic [fishing, nutrient enrichment (NE), heavy metal pollution (Metal) and high sediment loads (Sediment)] and other stressors (presence of competitors, and grazers, removal of canopy algae, low light and salinity, high light and salinity, and increasing temperature, wave exposure and CO_2) and (b) multiple local anthropogenic stressors [NO_3 and PO_4 enrichment, heavy metals A and B, nutrient enrichment (NE), heavy metal pollution (metals)] on the growth of canopy-forming algae. Results are the overall estimate of effect size (overall estimate, 95% lower confidence interval (LC), higher confidence interval (HC), Q_E *P*-value (the test of the residual heterogeneity), and the effects of the moderators, study identity [estimate, 95% lower confidence interval (LC), higher confidence interval (HC)], and life stage (estimate, 95% lower confidence interval (LC), higher confidence interval (HC). The number of experiments with standard deviations reported (N with SD), without standard deviations reported (N no SD), the number of experiments at each life stage (Stage 1 = recruits to juveniles and Stage 2 = juveniles to adults) and the Rosenberg fail-safe number of experiments required to overturn the results (Fail safe no). Effects are significant if confidence intervals do not overlap zero. Significant effects are shown in bold print.

Table S2. Effects (Hedge g standard mean difference) of local anthropogenic [nutrient enrichment (NE), heavy metal pollution (Metal) and high sediment loads (Sediment)] × other stressors (presence of competitors and grazers, removal of canopy algae, low light and salinity, high light and salinity, and increasing temperature, wave exposure and CO_2) on the survival of canopy-forming algae. Results are overall estimate of effect size [overall estimate, 95% lower confidence interval (LC), higher confidence interval (HC), Q_E the test of the residual heterogeneity], and the moderators, study identity [overall estimate, 95% lower confidence interval (LC), higher confidence interval (HC)], and life stage [life stage estimate, 95% lower confidence interval (LC), higher confidence interval (HC)]. The number of experiments with standard deviations reported (N with SD), without standard deviations reported (N no SD), and the Rosenberg fail-safe number of experiments required to overturn the results (Fail safe no) on the density and survival of canopy-forming algae. Effects are significant if confidence intervals do not overlap zero. Significant effects are shown in bold print.

Table S3. Effects (Hedges g standard mean difference) of (a) local anthropogenic [fishing, nutrient enrichment (NE), heavy metal pollution (Metal) and high sediment loads (Sediment)] × other stressors (presence of competitors and grazers, removal of canopy algae, low light or salinity, high light or salinity, and increasing CO_2, temperature or wave exposure) and (b) multiple local anthropogenic stressors [NO_3 and PO_4 enrichment, nutrient enrichment (NE), fishing, heavy metal A and B, heavy metal pollution (Metal) and high sediment loads (sediment)] on the growth of mat-forming algae. Results are the overall estimate of effect size using the standard mean difference [overall estimate, 95% lower confidence interval (LC), higher confidence interval (HC), Q_E p-value (the test of the residual heterogeneity)], and the effects of the moderators, study identity [estimate, 95% lower confidence interval (LC), higher confidence interval (HC)], and persistence [estimate, 95% lower confidence interval (LC), higher confidence interval (HC)], the number of experiments with standard deviations reported (N with SD), without standard deviations reported (N no SD), the number of experiments for each functional group (ephemeral or turf-forming algae) and the Rosenberg fail-safe number of experiments required to overturn the results (Fail safe no). Effects are significant if confidence intervals do not overlap zero. Significant effects are shown in bold print.

Table S4. Effects (Hedges g standard mean difference) of (a) local anthropogenic [fishing, nutrient enrichment (NE), heavy metal pollution (Metal) and high sediment loads (Sediment)] × other stressors (presence of competitors and grazers, removal of canopy algae, low light and salinity, high light and salinity, increasing temperature, wave exposure, CO_2 and high UV) and (b) multiple local anthropogenic stressors [fishing and nutrient enrichment (NE)] on the survival of mat-forming algae. Results are the overall estimate of effect size using the standard mean difference [overall estimate, 95% lower confidence interval (LC), higher confidence interval (HC), Q_E the test of the residual heterogeneity], and the moderators, study identity [overall estimate, 95% lower confidence interval (LC), higher confidence interval (HC)], and persistence [life stage estimate, 95% lower confidence interval (LC), higher confidence interval (HC)], the number of experiments with standard deviations reported (N with SD), without standard deviations reported (N no SD), the number of experiments of each functional group (ephemeral or turf-forming algae) and the Rosenberg fail-safe number of experiments required to overturn the results (Fail safe no). Effects are significant if confidence intervals do not overlap zero. Significant effects are shown in bold print.

Table S5. Predicted effect (PE) and actual effect (AE) (Hedge g standard mean difference) of the interactions between (a) local anthropogenic [fishing, nutrient enrichment (NE), a heavy metal pollution (Metals) and high sediment loads (Sediment)] × other stressors (presence of competitors or grazers, removal of canopy algae, low light or salinity, high light or salinity, and increasing CO_2, temperature or wave exposure and high UV) and (b) multiple local anthropogenic stressors [NO_3 and PO_4, fishing, heavy metal A and B, nutrient enrichment (NE), heavy metal pollution (Metals) and high sediment loads (Sediment)] on the growth of canopy-forming algae and mat-forming algae and survival of canopy-forming algae and mat-forming algae. Results are the overall estimate of effect size using the standard mean difference [overall estimate, 95% lower confidence interval (LC), higher confidence interval (HC)]. Effects are antagonistic if the actual effect size of Stressor A × B was closer to zero than the predicted effect size and synergistic when the actual effect size of Stressor A × B was further away from zero than predict effect size. Interactions were non-additive if the confidence intervals of the actual effect size did not overlap the predicted effect size and additive if the confidence intervals of actual effect size overlapped of the predicted effect size. Antagonistic and synergistic interactions are shown in bold print.

Table S6. Qualitative review of nature of interactions between multiple local anthropogenic stressors [fishing, nutrient enrichment (NE), heavy metal pollution (M) and high sediment loads (Sed)] and local anthropogenic and other stressors (presence of competitors and grazers, removal of canopy algae, low light and salinity, high light and salinity, increasing CO_2, temperature, and waves and high UV) on the (i) growth of canopy-forming algae (ii) growth of mat-forming algae (iii) survival of canopy-forming algae and (iv) survival of mat-forming algae. Effects are additive (Add) if the actual effect size overlaps with the predicted effect size, antagonistic (A) if the actual effect size of Stressor A $\times$ B were closer to zero than the predicted effect size, synergistic (S) if the actual effect size was further away from zero than the predicted effect size and not significant (NS) if the actual effect overlaps zero. The numbers of experiments for each interaction type are indicated in brackets. Pairs of stressors in which the majority of experiments show antagonistic interactions are shaded in light grey and synergistic interactions are shaded in dark grey.