

The predictability of species contributions to ecosystem stability under multiple stressors

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1 **Abstract**

2 Simultaneous exposure to multiple stressors potentially complicates enormously the
3 challenge of predicting ecological responses to global environmental change. Here, we show
4 that, though the contributions of individual species and functional groups to ecosystem
5 stability may vary under different disturbance types, their contributions to stability under
6 combined stressors can nonetheless frequently be predicted from their contributions under
7 the individual disturbances acting in isolation. By disturbing natural rocky shore
8 communities experimentally with nutrients and sediments and simultaneously simulating
9 extinction of predatory whelks and grazing consumers both separately and in combination,
10 we found that trophic position does not, however, appear to be a useful general predictor
11 of species contributions to stability. We conclude that quantifying contributions of key
12 species and functional groups to stability across a range of environmental contexts may
13 provide a pathway towards predicting the multifaceted responses of ecosystems to distinct
14 combinations of stressors acting simultaneously.

Introduction

Humans are altering the biosphere in a variety of frequently interacting ways (Millennium Ecosystem Assessment, 2005; Halpern et al., 2008; Côté et al., 2016; Mottl et al., 2021). These actions are driving species to extinction at rates hundreds to thousands of times in excess of background (Pimm et al., 2014; De Vos et al., 2015; Humphreys et al., 2019) and compromise the capacity of ecosystems to reliably provide the goods and services upon which human societies depend (Millennium Ecosystem Assessment, 2005; Keyes et al., 2021; Ross et al., 2021). Compounding this complexity, ecological responses to disturbances are also highly multifaceted (Donohue et al., 2013; Garnier et al., 2017; Hillebrand et al., 2018; Radchuk et al., 2019; Polazzo & Rico, 2021), and the spatial extents, periods, durations, frequencies and intensities of disturbances all combine to affect ecosystems in distinct ways (García Molinos & Donohue, 2010, 2011; Miller et al., 2011; Macdougall et al., 2013; Mrowicki et al., 2016; Yang et al., 2019). Consequently, understanding and predicting ecological responses to multiple simultaneous disturbances is a key challenge facing ecologists trying to conserve ecosystems and manage their stability under global environmental change (Donohue et al., 2016; Kéfi et al., 2019).

Ecological stability is a multidimensional concept characterised by a family of measures that together capture the dynamics of the system and its response to perturbations (Pimm, 1984; Ives & Carpenter, 2007; Donohue et al., 2016; Kéfi et al., 2019). Often measured empirically as the inverse of variability in community properties, such as biomass or productivity, in time and/or space (*e.g.* Thebault & Loreau, 2005; Tilman et al., 2006; O’Gorman & Emmerson, 2009; Clark et al. 2021), stability can also be quantified as the capacity of communities to resist and recover from perturbations (that is, respectively, their resistance and resilience; Pimm, 1984; Donohue et al., 2016; Hillebrand et al., 2018;

White et al., 2020). Relationships between the various dimensions of ecological stability are, however, not fixed and vary both among communities and disturbance types (Donohue et al., 2013; Radchuk et al., 2019; Eagle et al., 2021; Polazzo & Rico, 2021). This means that assessment of ecological responses to disturbances always needs to be multidimensional, as one-dimensional characterisation of stability risks significantly underestimating the impacts of perturbations on ecosystems (Donohue et al., 2016).

One way of trying to understand and predict the stability of ecosystems is to quantify how the species they contain each contribute to the overall stability of the system (Donohue et al., 2016). Though it has recently been shown that individual species can simultaneously stabilise and destabilise ecosystems along different dimensions of stability (White et al., 2020), the extent to which individual species contributions to ecosystem stability remain consistent or, alternatively, are altered by different disturbance regimes is as yet unknown. Further, whether species contributions to stability act additively in response to cumulative stressors, or whether they behave in a less predictable manner is also unclear. Another open question is whether trophic position—a key determinant of the structural robustness of ecological networks (Borrvall et al., 2000; Borrvall & Ebenman, 2006, 2017; Sanders et al., 2013; Donohue et al., 2017)—might be a useful general predictor of species contributions to ecosystem stability. Through the removal of top-down control, loss of predator species can, for example, affect ecosystems very differently than loss of other consumers (Chen et al., 2020), increasing the vulnerability of key ecosystem processes (Estes et al. 2011; Ross et al., 2022) and destabilising the overall system (Donohue et al. 2013; 2017) in distinct ways. Thus, understanding the extent to which the contributions of individual species to stability may be determined by their trophic position would comprise a

significant step forward in our understanding and capacity to predict the overall stability of ecosystems.

Here, we test experimentally using natural communities in the field whether the simultaneous contributions of individual species and/or functional groups to multiple components of stability vary (1) under different types of disturbance or (2) with their trophic position (see Fig. 1 for a description of our experimental framework and Table 1 for the stability measures used and their derivation). We then examine (3) whether species contributions to stability under multiple stressors can be predicted from their contributions under individual stressors acting in isolation. We predict that species and functional groups will both contribute in different ways to the stability of the system under distinct disturbance types and, moreover, that predators will contribute to stability differently to consumers from other trophic levels. To address these questions, we simulated the loss of the predatory dog whelk, *Nucella lapillus*, and the functional group of gastropod grazers (comprising primarily *Littorina littorea*, the topshell *Steromphala umbilicalis* and the common limpet *Patella vulgata*) from a temperate rocky shore over 15 months and measured the subsequent response of macroalgal communities on the shore to chronic press disturbances of nutrient enrichment and elevated sedimentation, both separately and in combination (Fig. 1). In order to maximise the ecological realism of our results, our experiment was done on natural communities on the shore in an open experimental system that allowed immigration and recruitment of primary producers and many epibenthic consumers, including primary consumers and small predators (e.g. amphipods, polychaetes and Nemertea).

Nutrient enrichment and elevated sedimentation are among the most common stressors in coastal systems worldwide, with significant consequences for the structure and

functioning of biological communities (Thompson et al., 2002; Airoidi, 2003; Atalah & Crowe, 2010; O'Connor et al., 2015; Mrowicki et al., 2016). While both these stressors degrade water quality and reduce light penetration to underlying macroalgae, they tend to alter interactions among species in different ways. For example, nutrients tend to promote growth of opportunistic algae whereas sediments smother less robust species (Atalah & Crowe, 2010). Top-down pressure from grazers can buffer algal assemblages against (Atalah & Crowe, 2010; Rober et al. 2022), or even enhance, the impacts of both nutrient enrichment (O'Connor et al., 2015) and sedimentation (Mrowicki et al., 2016). There is, however, lack of understanding of how different functional groups contribute to resistance and recovery of communities from these stressors over longer time scales. On rocky shores, we expect to observe relatively stabilising and destabilising roles of predators and grazers, respectively, on algal communities as a consequence of their direct and indirect trophic and non-trophic interactions (Donohue et al., 2017).

The functional and compositional stability responses of communities to disturbance—that is, the responses of, respectively, total biomass and species composition (Table 1)—can be largely independent (Hillebrand et al., 2018; Hillebrand & Kunze, 2020; White et al., 2020). This is because environmental change often affects the density or biomass of populations before triggering compositional change (Gaston & Fuller, 2008; Hillebrand et al., 2008; Hull et al., 2015). Total biomass and productivity can also remain relatively constant despite considerable turnover in species composition, while fast recovery of biomass can occur in a community that has not yet recovered in terms of composition (Hillebrand & Kunze, 2020). We therefore quantified the contribution of whelks and gastropod grazers to multiple dimensions of both functional and compositional stability (Table 1), examined the

strength and nature of relationships between them, and tested our hypotheses independently for each.

Methods

Experimental design

Eighty experimental plots were established on the mid-shore (*ca.* 2.0 m above Chart Datum; Table S1) at our experimental site, a moderately exposed rocky shore at Rush, Co. Dublin, on the east coast of Ireland (please see Supporting Information for a detailed description of the study site). Sixty plots were enclosed by cages (35 x 35 cm, 12 cm high) constructed from stainless steel mesh (0.9 mm wire diameter, 4.17 mm aperture, 67% open area) fixed to the substratum with screws and washers, enabling us to restrict the movement of our focal predator and grazer species in and out of our plots. This cage design has been used extensively and successfully to manipulate the presence of consumers on rocky shores with no consequences for the structure or stability of algal communities (O'Connor & Crowe, 2005; Donohue et al., 2013; O'Connor & Donohue, 2013; Mrowicki et al., 2015; 2016).

We established three treatments to quantify consumer contributions to stability: 'whelk removals', from which predatory whelks were excluded from plots; 'whelk and grazer removals' from which both consumer groups were removed; and 'no consumer removals', in which predatory whelks and gastropod grazers were present within plots. Experimental densities of grazers and predators used in the plots were within the range of natural densities recorded during preliminary surveys of the shore (Table S1). Consumer loss treatments were maintained at our experimental densities and adjusted accordingly where there were occasional escapees and/or invaders, though individuals were not replaced

where there was whelk-induced grazer mortality (identified by drill holes in grazer shells), to mimic natural community dynamics as closely as possible. No mortality of whelks was observed during the experiment.

Press perturbations of nutrient enrichment and elevated sedimentation were applied six months after the commencement of the experiment to allow sufficient time for our consumer manipulations to take effect and avoid transient dynamics (Donohue et al., 2013). The perturbations were maintained for six months (Fig. 1). Plots were then monitored for a further three-month 'recovery' phase after perturbations had ceased, resulting in a total experiment duration of 15 months. Our experimental design established two levels of both nutrient enrichment (ambient and enriched) and sedimentation (ambient and elevated). Nutrient enrichment was achieved by the addition of slow release fertiliser pellets (11N:11P:18K, Osmocote®) in plastic mesh cases (10 cm X 10 cm) to enriched treatments (following Worm et al., 2000; Atalah & Crowe, 2010; Vye et al., 2017). Empty mesh cases were added to non-enriched experimental plots to control for any experimental artefacts caused by the presence of the bag rather than the nutrients. One hundred and sixty grams of fertiliser was added to enriched plots and replaced every 8–12 weeks to sustain elevated concentrations of nutrients in appropriate treatments for the duration of the experiment (O'Connor & Donohue, 2013; O'Connor et al., 2015; Vye et al., 2017). After four weeks, samples were taken from the water column directly above each plot on an ebbing tide to test the effectiveness of this method. Water samples from plots with added fertiliser had significantly (Kruskal-Wallis test, $P < 0.001$) greater concentrations of dissolved inorganic nitrogen (mean \pm SE = $4.60 \pm 0.07 \mu\text{m L}^{-1}$) than ambient treatments ($2.53 \pm 0.28 \mu\text{m L}^{-1}$). This increase of approximately 70% is consistent with those in previous enrichment studies (Worm et al., 2000b; Sugden et al., 2008; White et al., 2018).

Elevated sedimentation was achieved by adding 800 g sediment, collected from an adjacent sandy shore, to plots weekly for six months. This sedimentation rate, equivalent to $\sim 800 \text{ g m}^{-2} \text{ d}^{-1}$, is almost twice the level considered the upper limit experienced by coastal habitats close to populated areas (Airoldi & Virgilio, 1998; Connell, 2005), though it is well below the levels recorded around harbours ($\sim 2000 \text{ g m}^{-2} \text{ day}^{-1}$; Irving & Connell, 2002). Weekly additions of sediment, therefore, mimicked the effects of storms with intermittent pulses in areas with considerable coastal infrastructure. Consumer loss, nutrient enrichment and sedimentation were all crossed fully in our experimental design, yielding a total of 12 caged treatment combinations, each replicated five times (Table S1).

Twenty open uncaged experimental plots were established on the shore, five of which were assigned randomly to each of the four perturbation treatment combinations (Table S1), to test for any experimental artefacts of cages. These plots were marked with screws and interspersed haphazardly amongst caged plots, enabling us to compare algal assemblage dynamics within caged plots to those on the natural shore. Algal cover and assemblage structure were similar in uncaged and caged plots with no consumer removals after six months of experimental perturbation (that is, we found no significant effects of cages or interactions between cages and disturbance treatments; Table S2).

The percent cover of individual macroalgal species was measured monthly using a 25x25 cm quadrat with 64 intersections, positioned centrally within cages to avoid sampling edge effects. Species found within the quadrat but not present underneath any of the intersections were assigned a cover value of 1% (O'Connor & Crowe, 2005). There were no differences in total macroalgal cover (ANOVA; $F_{15,64} = 0.51$, $P > 0.05$) or assemblage structure (PERMANOVA; Pseudo- $F_{15,64} = 0.84$, $P > 0.05$) between any caged or uncaged experimental treatments at the beginning of the experiment. Whelks consumed $11.5 \pm 2.1\%$

(mean \pm S.E.) of grazers over the duration of the experiment. Their consumption of grazers did not vary among perturbation treatments (ANOVA; $F_{3,16} = 0.18$, $P > 0.05$).

To determine whether percent cover served as a reliable proxy for macroalgal biomass, destructive samples of the central 25 x 25 cm area in each plot were taken on the final sampling date to estimate biomass of each macroalgal species, following drying to constant mass at 60°C. These analyses excluded crustose coralline species (*Hildenbrandia* spp. & *Lithothamnium* spp.), which grow as a thin crust (0.2–0.5 mm) on rock and adhere very strongly to the substratum. As such, they cannot be harvested or dried, unlike other erect algae. Dry biomass values for *Corallina officinalis* were multiplied by 0.2 to convert them to calcium carbonate-free estimates (Griffin et al., 2010). There was a significant linear relationship between total dry biomass and total cover of macroalgae [excluding crustose corallines; biomass (g m^{-2}) = $-1.481 + 0.323 \times \text{cover (\%)}^2$, $R^2 = 0.67$, $t = 24.27$, $P < 0.001$].

Data analyses

We quantified four components of both functional and compositional stability from macroalgal assemblages (Fig. 1, Table 1) based, respectively, on algal biomass (that is, using total cover as a proxy for total macroalgal biomass) and assemblage structure (Hillebrand et al., 2018). Our measurement of resilience (Table 1) was standardised such that positive values always corresponded with enhanced recovery towards unperturbed conditions and negative values to further deviations from unperturbed communities. For the few cases where perturbations increased biomass on plots or increased compositional similarity to unperturbed plots and, therefore, resulted in a positive resistance value, resilience was then multiplied by -1.

We calculated the contributions of consumers to stability as the inverse of the consequences of their loss (following White et al., 2020). That is, a strong destabilising effect of a disturbance in plots from which consumers were removed compared to when they were present implies that those consumers contribute strongly and positively to that component of ecological stability. Specifically, we calculated whelk contributions to stability as the log response ratio of stability in a plot from which whelk were removed relative to mean stability in the equivalent plots in which all focal consumers were present. As grazers constitute the dominant prey of whelk in our system, and our experimental design required whelk to persist under natural conditions for the duration of our experiment, we calculated grazer contributions as the log response ratio of stability in plots from which both grazers and whelk were removed relative to the equivalent stability measure in plots from which only whelk were removed. Thus, our method compared the individual effect of loss of consumers relative to the mean effects of their presence (White et al., 2020). We used two-tailed one-sample *t*-tests to test whether consumer contributions differed from zero (that is, to test whether they contributed significantly positively or negatively to a given measure of stability). *P*-values were adjusted for multiple comparisons (for two consumer groups), following Benjamini & Hochberg (1995), to control the false discovery rate. When significant contributions were identified, we ran two-sample *t*-tests between stressor treatment groups to identify differences in contributions between stressor groups, adjusting *P*-values for multiple comparisons (Benjamini & Hochberg, 1995). Variances were homogeneous.

We predicted the contribution of consumers to the various dimensions of stability in response to the combined effect of nutrient enrichment and sedimentation based upon the additive combination of their constituent contributions to the individual stressors (Griffin et al., 2009; White et al., 2020). To do this, we randomly selected consumer contributions to

stability in response to the individual constituent stressor treatments in isolation (that is, one measurement selected randomly from one of the plots belonging to each stressor treatment) and added these together, separately for each consumer group (that is, whelks and grazers), by bootstrapping (1,000 times). Bootstrapped predicted values were compared with our observed experimental results for combined stressors, after correcting for original sample size ($n = 5$, or $n = 7$ for spatial variability). We ran two-sample t -tests between predicted and observed contributions to stability, separately for each consumer group, to test whether observed responses to simultaneous combined stressors differed from those predicted from the sum of their observed responses to nutrient enrichment and sedimentation in isolation. P -values were adjusted for multiple comparisons (two comparisons per response variable; Benjamini & Hochberg, 1995). Variances were homogeneous.

Spearman correlations were used to test whether consumer contributions to stability components quantified in terms of function were correlated to the equivalent component measured for composition. All analyses were performed in R (Version 3.5.2; R Core Team, 2018). All multivariate tests involved 9,999 permutations of residuals under a reduced model and were based on Bray-Curtis dissimilarities calculated from $\log_{10}(x + 1)$ -transformed data to reduce the influence of dominant species (Clarke & Warwick, 2001) and satisfy assumptions of homogeneity of dispersions (Anderson, 2006).

Results

Not only did both predatory whelk and gastropod grazers contribute simultaneously positively and negatively to different stability components, but sediments and nutrients also modified their contributions to stability in distinct ways (Fig. 2). While grazers contributed

positively to the stability of the system by increasing the compositional spatial variability of algae across all perturbation treatments, increasing functional spatial variability under ambient conditions and increasing compositional resilience in response to nutrient enrichment, they also simultaneously destabilised the system by increasing functional temporal variability under ambient conditions (Fig. 2). This latter destabilising effect of grazers was, however, nullified when either sediments or nutrients were added experimentally to the system (Fig. 2a). The stabilising contribution of grazers to compositional spatial variability also varied significantly among each of our perturbation treatments ($P < 0.001$ for all pairwise comparisons), being greatest under ambient conditions and lowest under sedimentation (Fig. 2b).

Whelks contributed significantly to stability by increasing functional spatial variability, but only under sediment disturbance (Fig. 2a). However, whelks simultaneously destabilised the system by reducing compositional spatial variability (that is, homogenising community composition in space) under both ambient and nutrient enriched conditions, and significantly more so under the former (ambient vs. enriched, $P < 0.001$, Fig. 2b). This latter result contrasts markedly with the consistently stabilising effects of grazers on spatial compositional variability. There were, however, no other consistent differences in the stability contributions of whelk and grazers that might be attributable to their trophic position for any of the other stability dimensions we quantified (Fig. 2).

Stability responses to combined stressors could frequently be predicted from the sum of their observed responses to nutrient enrichment and sedimentation in isolation (that is, their observed responses to combined stressors were statistically similar to those predicted by the sum of the responses to sediments and nutrients in isolation; Fig. 3). In fact, this was the case for all stability–consumer combinations except for spatial variability

and grazer contributions to compositional resilience . Predictions of whelk contributions to spatial variability under combined nutrient enrichment and sedimentation were stabilising, whereas their observed contributions to the combined stressor treatment were neutral, and differed significantly from those predicted ($P = 0.003$, Fig. 3a). Grazer contributions to compositional spatial variability under combined nutrient enrichment and sedimentation were observed to be stabilising, but significantly less so than those predicted by the sum of responses to the individual stressors in isolation ($P = 0.002$). Similarly, grazer contributions to compositional resilience under combined nutrient enrichment and sedimentation were neutral, whereas predicted contributions were stabilising ($P = 0.008$). In terms of the overall macroalgal community, (that is, not consumer species contributions), observed stability responses to combined stressors were consistently less stable than those predicted by the additive combination of the individual constituent stressors for both functional and compositional spatial and temporal variability, and for compositional resilience (Fig. S1).

Across all of our experimental treatments, we found that consumer contributions to functional temporal variability correlated positively with those to compositional temporal variability ($\rho = 0.62$, $P < 0.001$, $n = 40$; Fig. 4a), while their contributions to functional resistance to disturbance also correlated positively with those to its compositional equivalent ($\rho = 0.64$, $P < 0.001$, $n = 30$; Fig. 4c). In other words, species that promoted, respectively, functional resistance and temporal variability also tended to promote compositional resistance and temporal variability. In contrast, species contributions to both functional spatial variability (Fig. 4b) and functional resilience (Fig. 4d) were statistically independent of their compositional counterparts.

Discussion

Our results show that species may contribute differently to ecological stability when ecosystems are disturbed in different ways. Moreover, our focal predator and grazers both stabilised and destabilised algal communities simultaneously along different dimensions of stability. *Whelks* stabilised communities in response to sediment but destabilised them in response to nutrients, via, respectively, increasing functional spatial variability and decreasing compositional spatial variability. Grazers promoted resilience to nutrients but destabilised communities by increasing functional temporal variability in the absence of stressors. It follows that the differing nature of the disturbances—both common stressors in coastal systems (Thompson et al., 2002)—can determine how they impact macroalgae and consumers, the interactions between them, and, ultimately, their contributions to the overall stability of the system (Polazzo & Rico, 2021; Simmons et al., 2021). Sediment physically smothers algae and reduces light availability for photosynthesis (Airoidi, 2003) but might physically hinder grazing activity (Airoidi & Hawkins, 2007), whereas nutrients have strong bottom-up effects stimulating algal growth that may be dampened by presence of grazers but accentuated via predator-induced grazer suppression (O'Connor & Donohue, 2013; Rober et al., 2022). Understanding whether there are generalities in how individual species or functional groups contribute to overall stability under different types of disturbances is essential to disentangle these complex interactions (Rezende et al., 2021).

Predatory *whelks* destabilised the system by homogenising community composition in space under both ambient and nutrient enriched conditions in contrast to the consistently stabilising effects of grazers on compositional spatial variability. Grazing limpets are known to increase spatial variability in benthic community composition and successional pathways via grazing of algal propagules (Kordas et al., 2017). This suggests, therefore, that the destabilising effect of predators on algal communities that we observed was likely an

indirect consequence of the effects of predators on their gastropod prey (Rober et al., 2022). These findings provide further evidence of the direct role played by grazers in increasing spatial heterogeneity of algal communities (Kordas et al., 2017), as well as the important indirect role of predators as compositional homogenisers, induced via grazer suppression (Ross et al., 2022). Nonetheless, the neutral contributions of consumers to functional spatial variability and lack of correlation between compositional and functional spatial variability suggests that the compositional homogenisation we observed had little impact on variability of total biomass in space in our study. Were compositional homogenisation accompanied by decreasing complementarity among functionally dissimilar communities (Villéger et al., 2014), however, consumers may drive subtle changes in other aspects of ecosystem functioning, such as metabolic rates and nutrient cycling, via this mechanism.

Contributions of our focal consumers to community stability were often highly context-dependent. For example, grazers promoted resilience of macroalgal assemblages after nutrient enrichment in isolation, yet had no effect on resilience when both nutrients and sediments were combined. Grazing can help maintain heterogeneous algal assemblages (Kordas et al. 2017; White et al. 2020), despite nutrient loading favouring opportunist species (O'Connor et al., 2015). Our results suggest that sediment interfered with this interaction and/or suppressed growth of a subset of algal species. Although predator-grazer-producer interactions responded consistently to constrain compositional spatial heterogeneity of algal assemblages in our experiment, likely as a consequence of the grazers enhancing small-scale spatial variability (Kordas et al. 2017; White et al. 2020), our results indicate that trophic position is nonetheless unlikely to be a useful general predictor of how consumers contribute to the overall multidimensional stability of ecosystems (Donohue et

al. 2013). In our experiment, nutrients and sediments were acting on multiple different components of the community, and hence their trophic and non-trophic interaction networks, simultaneously. Given the importance of non-trophic interactions in driving community dynamics and responses to disturbances (Kéfi et al. 2012; 2015; Donohue et al., 2017), coupled with their strong context-dependence (Wirsing et al., 2021), the relative influence of trophic interactions as a driver of stability may have been tempered by other interaction types at our experimental site. Developing theory and testing experimental frameworks in different ecological contexts are, therefore, needed both to examine the generality of these findings and identify other factors that might predict the contributions of individual species to stability.

Even though interactions between stressors can modify several stability dimensions (Polazzo & Rico, 2021), we found that species contributions to stability under combined stressors could frequently be predicted from their contributions under the individual disturbances acting in isolation (that is, the observed responses to nutrients and sediments in combination were statistically similar to those predicted by the sum of the responses to nutrients and sediments in isolation). This suggests that predicting species contributions to stability under multiple stressors may be a somewhat less complex problem than predicting stability responses of entire communities. For spatial variability and compositional resilience, however, stressors tended to behave antagonistically to reduce their cumulative effect on stability. That is to say that the relative role of consumers in stabilising the community was diminished when exposed to both stressors combined, although this varied among consumers. In contrast, species contributions to all other stability dimensions under multiple stressors could be predicted from the effects of individual stressors acting in isolation. Contributions of whelk to some dimensions of stability, such as resistance and

372 temporal variability, were, however, particularly variable, with large confidence intervals.
373 This constrains to some extent our capacity to robustly classify some of the observed
374 contributions under multiple stressors as predictable. Such high variability in species
375 contributions to stability is likely a consequence of a combination of intraspecific variation in
376 feeding behaviour and spatially variable behavioural responses of their prey species, driven
377 by heterogeneity in small-scale habitat structure and availability of refugia across our
378 experimental site (Donohue et al., 2017; Atkins et al., 2019; Gaynor et al., 2019). In spite of
379 these additional potential sources of variation, however, many of our predicted and
380 observed contributions to stability had relatively low variance and yet were statistically
381 indistinguishable. Future experiments are, therefore, needed both to tease out the relative
382 importance of these additional potential sources of variation across a broader range of
383 species and to test the generality of our findings in other systems exposed to a range of
384 different disturbance types.

385 Consumers that promoted functional resistance and temporal variability
386 simultaneously promoted the equivalent compositional dimensions of stability. This is
387 consistent with the findings of Hillebrand et al. (2018) and White et al. (2020), both of
388 whom found significant relationships between some functional stability dimensions and
389 their compositional counterparts. Fast recovery of biomass can occur in a community that
390 has not yet recovered in terms of composition (Hillebrand & Kunze, 2020), and pulse
391 perturbations may take longer to manifest as shifts in functional variability than
392 compositional changes (Ross et al., 2022), most likely as a consequence of compensatory
393 community dynamics. In contrast, resistance tends to depend on instantaneous responses
394 to disturbance regimes such that it is less affected by compensatory interactions among
395 species (Yang et al., 2019; Clark et al., 2021). This would explain the coupling between

functional and compositional counterparts observed here and in other studies (Hillebrand et al., 2018; White et al., 2020). Exploring individual algal species co-tolerance to multiple stressors (Vinebrook et al., 2004), taking in to consideration taxonomy, morphology and life history, would help to illuminate further differences in coupling between functional and compositional stability dimensions.

As with almost all field-based ecological experiments, our study is limited in scope by its spatial scale. Recently derived general statistical scaling rules of stability (Clark et al., 2021) may, however, be useful in exploring the generality and implications of our findings at larger scales in space and time. Even so, our results imply that, in biologically diverse systems such as rocky shores, stability varies with community structure, such that removing species or altering how species interact with one another has the potential to alter these scaling relationships (Jacquet et al., 2016; Arnoldi et al., 2018; Hillebrand et al., 2018; White et al., 2020). Further, due to logistical constraints, our experiment considered just two levels of each stressor treatment, which limited the kinds of interactions that could be identified. It is evident that the intensity (Vye et al., 2015), temporal pattern (García Molinos & Donohue, 2010, 2011; Mrowicki et al., 2016), and legacy effects (Jackson et al., 2021; Miller et al., 2021; Ross et al., 2022) of disturbances all regulate their impacts on communities. Considering multiple dimensions of disturbances within the context of ecological stability must, therefore, be a priority for future research (Donohue et al., 2016; Kéfi et al., 2019, Orr et al., 2022).

A key finding of our study is that consumers can, irrespective of their trophic position, contribute simultaneously positively and negatively to different dimensions of ecological stability and that their contributions to the stability of the system also depend on the nature of the stressor to which communities are exposed. Nonetheless, the

contributions of species to stability under combined stressors could be predicted from knowledge of how species contribute to stability under individual stressors acting in isolation. This knowledge may, therefore, provide a pathway towards predicting the multifaceted responses of ecosystems to distinct combinations of stressors acting simultaneously. We conclude that, though species contribute to the stability of ecosystems in multifaceted and frequently idiosyncratic ways, predicting those contributions is not necessarily made intractably complex by the simultaneous action of multiple stressors.

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Conflict of interests

The authors declare no competing interests.

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658

659 **Table 1. Components of ecological stability quantified in this study, their measurement and interpretation.** All stability components (see also
660 Fig. 1) were calculated at plot level, based largely upon Pimm (1984), Donohue et al. (2013), and Hillebrand et al. (2018), except for spatial
661 variability, which could only be calculated across plots within experimental treatments separately for each algal census (White et al. 2020).
662 Measures of functional and compositional stability were based upon, respectively, total macroalgal biomass and assemblage structure
663 (Hillebrand et al., 2018). Compositional stability metrics were based on Bray-Curtis dissimilarity matrices calculated from log-transformed algal
664 cover data.

Stability component	Time window of quantification	Method of quantification: Functional stability	Method of quantification: Compositional stability	Interpretation
Temporal variability	Duration of perturbation phase (months 6 to 12)	<p>The coefficient of variance (CV) of total algal cover in each plot over time, detrended to remove potentially confounding effects of biomass change over the duration of the experiment (Tilman et al., 2006; Donohue et al., 2013).</p> $\mu_{t6-t12} / \sigma_{resid\ t6-t12}$ <p>where $\sigma_{resid\ t6-t12}$ = The standard deviation of residuals from regression</p>	<p>Mean Euclidean distance from each plot on every census, to their treatment centroid.</p> $\overline{ED_{t6-t12}}$ <p>where ED_{t6-t12} = Euclidian distance between a single plot in a given perturbed treatment and their own centroid on each census.</p>	High values correspond to greater variability over time and, thus, lower stability.

		of total algal cover in each unperturbed experimental plot over time, μ_{t6-t12} = mean total cover of a single plot over time.		
Spatial variability	Duration of perturbation phase (months 6 to 12)	<p>The CV of total algal cover among plots within each consumer treatment combination on each census, detrended to remove potentially confounding effects of biomass change over the duration of the experiment (Tilman et al., 2006; Donohue et al., 2013).</p> $\mu_{treat}/\sigma_{resid\ treat}$ <p>where $\sigma_{resid\ treat}$ = The standard deviation of residuals from regression of total algal cover in unperturbed experimental plot over time, for all plots within a given treatment on a given census, μ_{treat} = mean total cover in all plots within a treatment on a given census.</p>	<p>Mean Euclidean distance from experimental plots to their treatment centroid, calculated separately for each census.</p> $\overline{ED_{treat}}$ <p>where ED_{treat} = Euclidian distance between plots in a given perturbed treatment and their own centroid on a single census.</p>	<p>High values correspond to greater spatial variability and, in contrast to temporal variability, greater stability. This is because compositional spatial variability represents the spatial dissimilarity in community composition between plots, akin to beta diversity (Lande, 1996; Whittaker, 1972), which enhances the spatial asynchrony of ecosystem dynamics, and thus increases stability (France & Duffy, 2006; Olden et al., 2004). High spatial asynchrony of biomass can also stabilise communities by increasing temporal invariability (Wang et al., 2017) and providing spatial insurance effects (Gravel et al., 2016; Wang & Loreau, 2016).</p>

Resistance	End of perturbation phase (month 12)	<p>The log response ratio of total algal cover in perturbed relative to unperturbed plots (Garnier et al., 2017; Hillebrand et al., 2018).</p> $\ln\left(\frac{F_{pert}}{F_{con}}\right)$ <p>where F_{pert} = total cover in perturbed plot, F_{con} = mean total cover in unperturbed control plots in the corresponding consumer loss treatment.</p>	<p>The log response ratio of the mean Euclidian distance between all plots in a given perturbed treatment and their own centroid and that from a perturbed plot to the centroid of the unperturbed plots in the corresponding consumer loss treatment.</p> $\ln\left(\frac{\overline{ED}_{pert}}{ED_{pert-con}}\right)$ <p>where \overline{ED}_{pert} = mean Euclidian distance between all plots in a given perturbed treatment and their own centroid, $ED_{pert-con}$ = Euclidian distance from a perturbed plot to the centroid of the unperturbed control plots in the corresponding consumer loss treatment.</p>	<p>The extent of biomass loss (functional) or compositional change in algal communities in response to perturbations. Large negative values indicate large reductions in biomass or shifts in assemblage structure and, therefore, respectively, low functional and compositional resistance.</p>
Resilience	End of perturbation phase until end of experiment	<p>Slope of linear regression of functional log response ratio over time from the end of the perturbation phase until the end of the experiment.</p>	<p>Slope of linear regression of compositional log response ratio over time from the end of the perturbation phase until the end of the experiment.</p>	<p>Increasingly positive values correspond to higher resilience (and stability), increasingly negative values indicate further deviation from unperturbed plots (that is, low</p>

(months 12 to
15)

$$\ln\left(\frac{F_{pert}}{F_{con}}\right) = i + b * t$$

where i = intercept, t = time

$$\ln\left(\frac{\overline{ED}_{pert}}{ED_{pert-con}}\right) = i + b * t$$

where i = intercept, t = time

resilience and stability). Calculating the log difference is equivalent to calculating the rate of relative return, rather than the absolute rate, rendering resilience at least conceptually independent from resistance (Garnier et al., 2017; Hillebrand et al., 2018).

Figure legends

Fig. 1. Quantification of species contributions to multiple dimensions of ecological

stability. We quantified contributions of species to the various components of stability (see Table 1 for detailed description of stability measures and their quantification) by comparing stability properties in plots from which consumers were removed (lower red lines: predatory whelk removed; upper green lines: whelk and gastropod grazers removed) to those that experienced no species losses (middle blue lines). We measured stability responses to our experimentally-imposed press perturbations (that is, nutrient enrichment and sedimentation, both separately and together) by comparing perturbed (solid lines) to equivalent unperturbed (dotted lines) plots within species removal treatments. Where a dimension of stability was reduced (that is, the system was destabilised) in the absence of a species compared to when it was present, this implies that the species contributes positively to that dimension of stability, and *vice versa*. All stability measures were quantified separately from both total macroalgal biomass and assemblage structure as dimensions of, respectively, functional and compositional stability (Table 1).

Fig. 2. Consumer species contributions to multiple components of ecological stability

under different disturbance types. Mean (\pm 95% CI, $n = 5$ for all measures except spatial variability, for which $n = 7$) log response ratio, indicating contributions of predatory whelks (triangles) and gastropod grazers (squares) to multiple components of (a) functional and (b) compositional stability (see Fig. 1 and Table 1 for description of stability measures and their quantification). Data points above the dashed horizontal line indicate a stabilising contribution (that is, the presence of a consumer promoted resistance, resilience, or spatial

variability, or decreased temporal variability relative to the treatment from which it was removed) and those below the line indicate a destabilising contribution, whereby the presence of the consumer reduced stability. Asterisks (*) highlight where there was a significant ($P < 0.05$) stabilising or destabilising contribution of consumers (that is, where a consumer contribution was, respectively, significantly greater or less than zero), as identified by two-tailed t -tests (Table S3; P -values were adjusted for multiple groups to reduce detection rate of false positives).

Fig. 3. Comparison of observed consumer contributions to stability under combined disturbances to those predicted from the additive combination of the individual disturbances acting in isolation. Mean (\pm 95% CI, $n = 5$, for all measures except spatial variability, for which, $n = 7$) log response ratio indicating observed contributions of predatory whelks (triangles) and grazers (squares) in response to combined nutrient enrichment and sedimentation (pink closed symbols), and those predicted from the additive combination of the individual stressors (dark red open symbols) to multiple components of (a) functional and (b) compositional stability (see *Methods* for details on how predicted consumer contributions were calculated). Asterisks (*) indicate where observed stability contributions differed significantly ($P < 0.05$) from those predicted, via two-tailed two-sample t -tests (P -values were adjusted for multiple comparisons to reduce detection rate of false positives).

Fig. 4. Relationships between species contributions to functional and compositional stability components. Analyses were pooled across consumer treatments ($n = 40$ for temporal variability, $n = 56$ for spatial variability, $n = 30$ for both resistance and resilience),

714 with each point representing a consumer contribution measured from an individual plot.
715 Significant ($P < 0.05$, Spearman correlations) relationships are indicated by the presence of a
716 least-squares regression line.

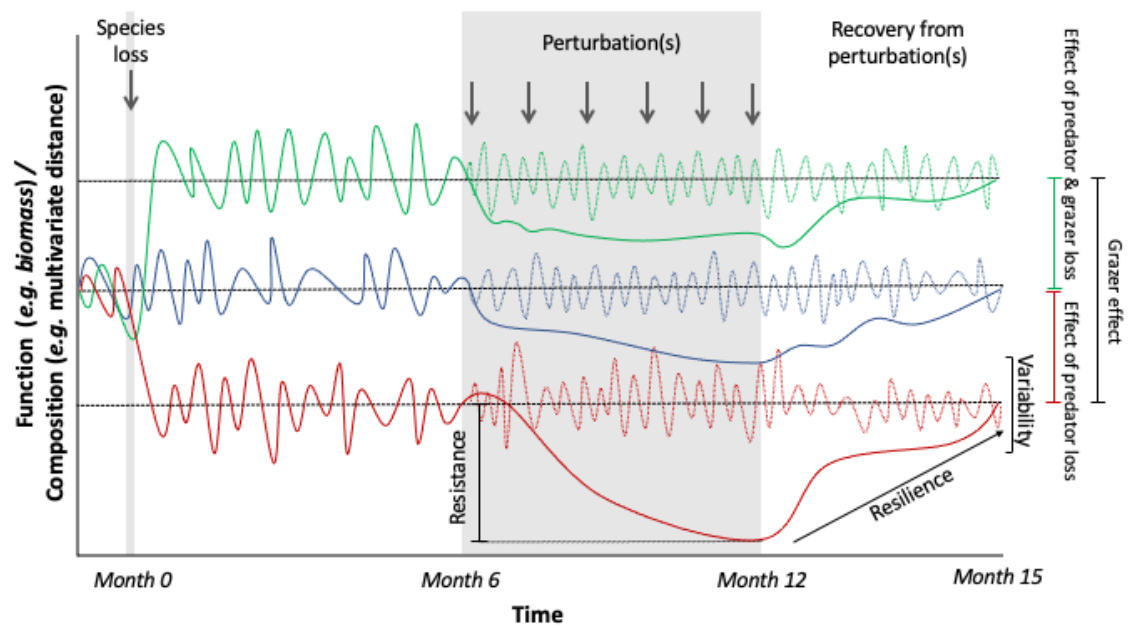


Fig. 1. White *et al.*

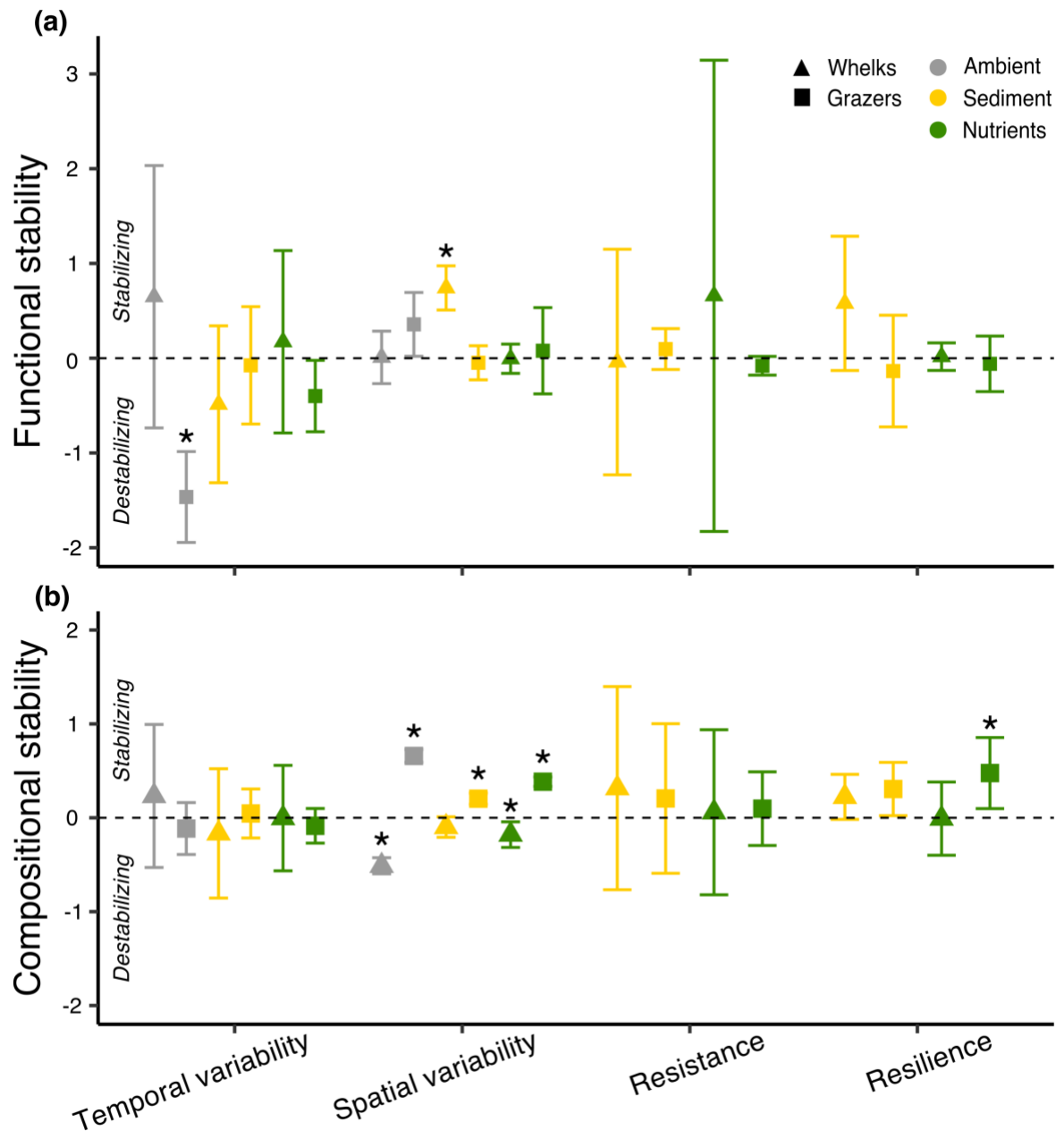


Fig. 2. White *et al.*

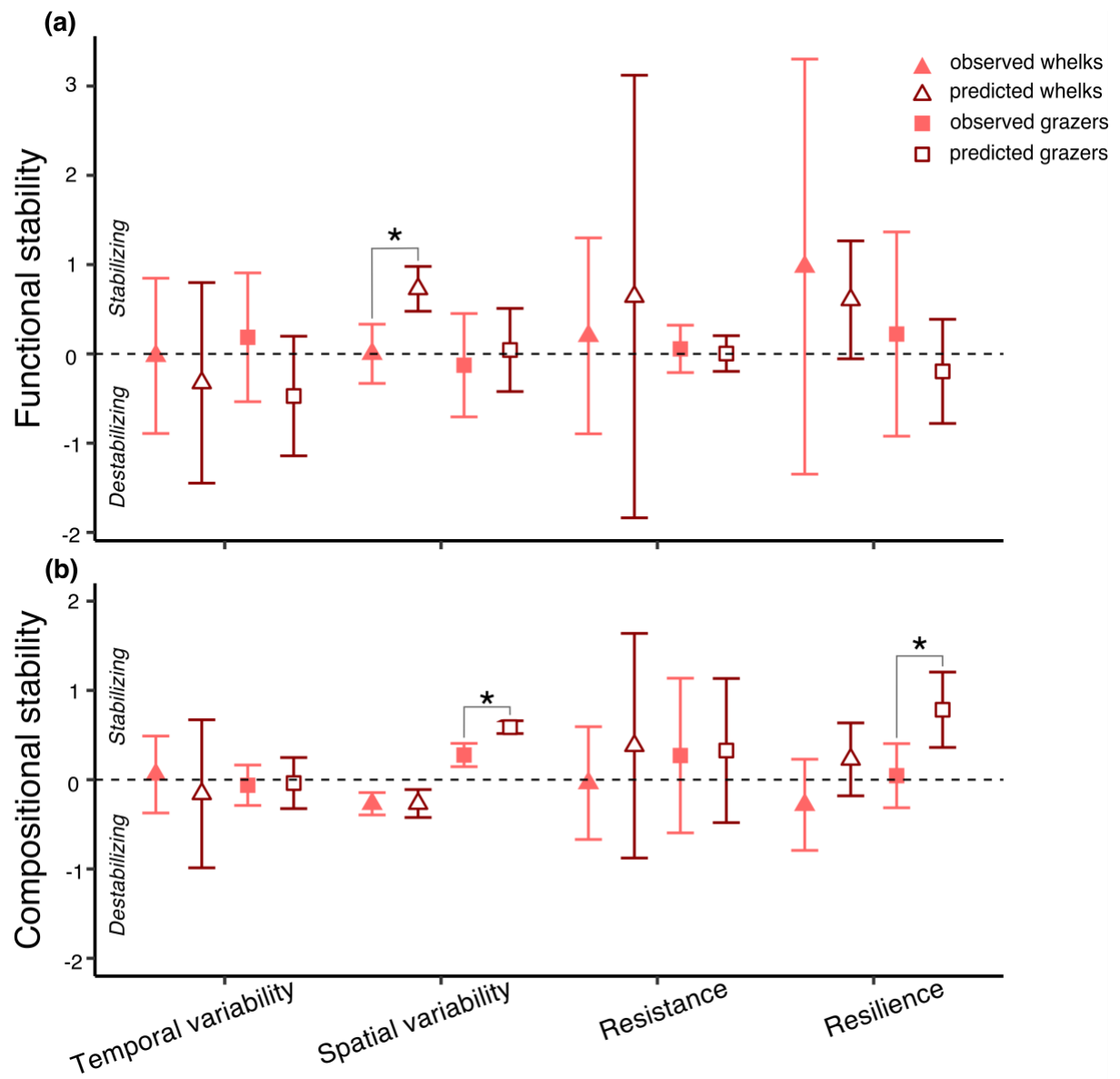


Fig. 3. White *et al.*

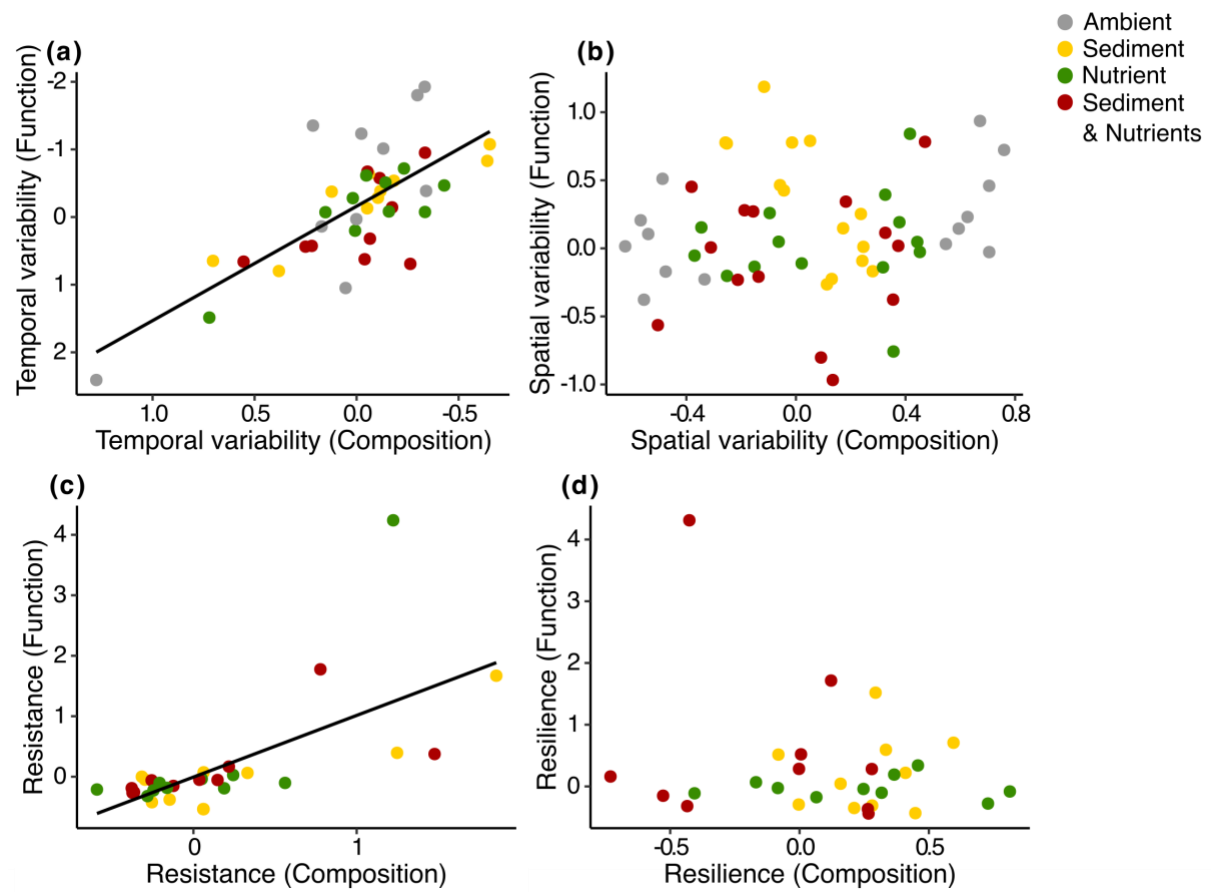


Fig. 4. White *et al.*

Supplementary information

Study site

Our experiment was conducted on a moderately exposed rocky shore at Rush, Co. Dublin, on the east coast of Ireland (53.524° N, 6.078° W), for 15 months from August 2015. The shore comprised a network of macroalgal canopies and turfs, bare emergent substratum and rare interspersed mussels (*Mytilus edulis*) and barnacles (predominantly *Austrominius modestus*). Macroalgal assemblages comprised mostly red algal turfs (*Chondrus crispus*, *Osmundea pinatiffida* and *Dumontia cortorta*) interspersed with green filamentous species (*Cladophora rupestris*, *Ulva* spp. and *Rhizoclonium riparium*), overlain by canopies of brown macrophytic algae (*Fucus vesiculosus* and *Fucus serratus*). Encrusting macroalgae (*Lithothamnium* spp. and *Hildenbrandia rubra*) were common on bare rock and barnacles.

Common gastropod grazers on the mid-shore included *Littorina littorea* ($201.2 \pm 14.6 \text{ m}^{-2}$ [mean \pm SE]; $n = 30$), the topshell *Steromphala umbilicalis* ($13.6 \pm 2.0 \text{ m}^{-2}$), and the common limpet *Patella vulgata* ($12.0 \pm 2.1 \text{ m}^{-2}$), together with other littorinids at lower densities, including *L. saxatilis* and *L. obtusata*. The most abundant predator on the shore by some distance was the dog whelk, *Nucella lapillus* ($20.8 \pm 2.9 \text{ m}^{-2}$).

Table S1. Our experimental treatment combinations. Consumer loss, nutrient enrichment and sedimentation were all crossed fully in our experimental design, yielding twelve caged and four uncaged treatment combinations, each replicated five times, resulting in a total of 80 plots.

Consumer loss	Nutrients	Sediment
No consumer removals		
Contained predators (two whelks), grazers (25 <i>L. littorea</i> , two <i>G. umbilicalis</i> , one <i>P. vulgata</i>) and a naturally occurring macroalgal community	Ambient	Ambient
		Elevated
	Enriched	Ambient
		Elevated
Whelk removals		
Contained grazers (25 <i>L. littorea</i> , two <i>G. umbilicalis</i> , one <i>P. vulgata</i>) and a naturally occurring macroalgal community	Ambient	Ambient
		Elevated
	Enriched	Ambient
		Elevated
Whelk and grazer removal		
Excluded all focal consumers from accessing a naturally occurring algal community	Ambient	Ambient
		Elevated
	Enriched	Ambient
		Elevated
Open uncaged plots		
Naturally occurring algal community open to ambient densities of all focal consumers and other mobile organisms.	Ambient	Ambient
		Elevated
	Enriched	Ambient
		Elevated

Table S2. The effects of cages (caged plots with no consumer removals vs. equivalent uncaged procedural control plots) on total cover and composition of macroalgal communities after six months of experimental perturbations (sedimentation and nutrient enrichment). Analysis of variance (ANOVA) and permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001; McArdle & Anderson, 2001; using 9,999 permutations of residuals under a reduced model and based on Bray-Curtis dissimilarities) were used to test for cage effects on, respectively, total algal cover and assemblage composition at the end of the disturbance period. Models incorporated individual and interactive combinations of cages (two levels: uncaged control & caged no consumer removal) and disturbance (four levels: ambient, nutrient enriched, added sediment, nutrients & sediment).

Source of Var	Total cover				Composition		
	DF	MS	<i>F</i>	<i>P</i>	MS	<i>Pseudo-F</i>	<i>P</i>
Cage (C)	1	0.180	0.444	0.512	0.152	1.624	0.139
C X Perturbation	4	0.480	1.183	0.344	0.113	1.205	0.239
Residual	24	0.406			0.093		

Table S3. Results of two-tailed one-sample *t*-tests on all consumer contributions testing whether they contributed positively or negatively to a given measure of stability (that is, testing whether they differed significantly from zero). *P*-values were adjusted for multiple comparisons following the Benjamini & Hochberg (1995) method to control the false discovery rate. Significant ($P < 0.05$) values in bold.

Metric	Treatment	Functional		Compositional	
		<i>t</i> -value	Adjusted <i>P</i> -value	<i>t</i> -value	Adjusted <i>P</i> -value
Temporal variability	Whelks ambient	1.301	0.263	0.847	0.445
	Grazers ambient	-8.478	0.002	-1.150	0.445
	Whelks sediment	-1.632	0.356	-0.645	0.643
	Grazers sediment	-0.338	0.752	0.500	0.643
	Whelks nutrients	0.500	0.643	-0.017	0.987
	Grazers nutrients	-2.944	0.084	-1.287	0.535
Spatial variability	Whelks ambient	0.077	0.941	-14.571	< 0.001
	Grazers ambient	2.596	0.081	23.716	< 0.001
	Whelks sediment	7.787	< 0.001	-2.213	0.068
	Grazers sediment	-0.659	0.534	8.360	< 0.001
	Whelks nutrients	-0.091	0.930	-3.305	0.016
	Grazers nutrients	0.422	0.930	18.704	< 0.001
Resistance	Whelks sediment	-0.094	0.929	0.810	0.513
	Grazers sediment	1.239	0.566	0.717	0.513
	Whelks nutrients	0.735	0.503	0.015	0.988
	Grazers nutrients	-2.240	0.177	0.688	0.988
Resilience	Whelks sediment	2.267	0.172	2.580	0.061
	Grazers sediment	-0.639	0.557	2.997	0.061
	Whelks nutrients	0.307	0.774	-0.210	0.843
	Grazers nutrients	-0.563	0.774	3.513	0.049

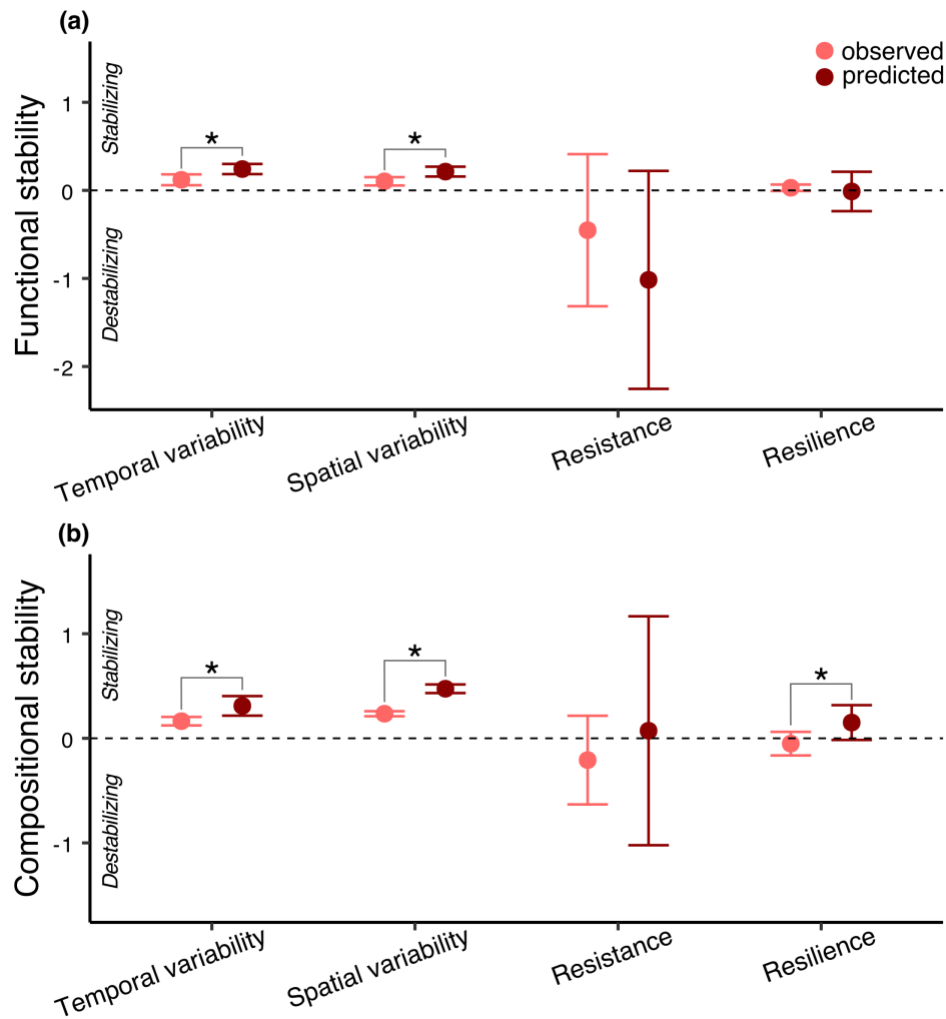


Fig. S1. Observed stability of the entire community in intact plots with no consumer removals under combined disturbances and those predicted from the additive combination of the individual disturbances acting in isolation. Mean (\pm 95% CI, $n = 5$, for all measures except spatial variability, for which, $n = 7$) stability in plots subject to combined nutrient enrichment and sedimentation (pink symbols), and those predicted from the additive combination of the individual stressors (dark red symbols) to multiple components of (a) functional and (b) compositional stability. Asterisks (*) indicate where observed stability differed significantly ($P < 0.05$) from those predicted, via two-tailed two-sample t -tests.