

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.

15 **Introduction**

16 Humans are altering the biosphere in a variety of frequently interacting ways
17 (Millennium Ecosystem Assessment, 2005; Halpern et al., 2008; Côté et al., 2016; Mottl et
18 al., 2021). These actions are driving species to extinction at rates hundreds to thousands of
19 times in excess of background (Pimm et al., 2014; De Vos et al., 2015; Humphreys et al.,
20 2019) and compromise the capacity of ecosystems to reliably provide the goods and
21 services upon which human societies depend (Millennium Ecosystem Assessment, 2005;
22 Keyes et al., 2021; Ross et al., 2021). Compounding this complexity, ecological responses to
23 disturbances are also highly multifaceted (Donohue et al., 2013; Garnier et al. , 2017;
24 Hillebrand et al., 2018; Radchuk et al., 2019; Polazzo & Rico, 2021), and the spatial extents,
25 periods, durations, frequencies and intensities of disturbances all combine to affect
26 ecosystems in distinct ways (García Molinos & Donohue, 2010, 2011; Miller et al., 2011;
27 Macdougall et al., 2013; Mrowicki et al., 2016; Yang et al., 2019). Consequently,
28 understanding and predicting ecological responses to multiple simultaneous disturbances is
29 a key challenge facing ecologists trying to conserve ecosystems and manage their stability
30 under global environmental change (Donohue et al., 2016; Kéfi et al., 2019).

31 Ecological stability is a multidimensional concept characterised by a family of
32 measures that together capture the dynamics of the system and its response to
33 perturbations (Pimm, 1984; Ives & Carpenter, 2007; Donohue et al., 2016; Kéfi et al., 2019).
34 Often measured empirically as the inverse of variability in community properties, such as
35 biomass or productivity, in time and/or space (*e.g.* Thebault & Loreau, 2005; Tilman et al.,
36 2006; O’Gorman & Emmerson, 2009; Clark et al. 2021), stability can also be quantified as
37 the capacity of communities to resist and recover from perturbations (that is, respectively,
38 their resistance and resilience; Pimm, 1984; Donohue et al., 2016; Hillebrand et al., 2018;

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

45 One way of trying to understand and predict the stability of ecosystems is to
46 quantify how the species they contain each contribute to the overall stability of the system
47 (Donohue et al., 2016). Though it has recently been shown that individual species can
48 simultaneously stabilise and destabilise ecosystems along different dimensions of stability
49 (White et al., 2020), the extent to which individual species contributions to ecosystem
50 stability remain consistent or, alternatively, are altered by different disturbance regimes is
51 as yet unknown. Further, whether species contributions to stability act additively in
52 response to cumulative stressors, or whether they behave in a less predictable manner is
53 also unclear. Another open question is whether trophic position—a key determinant of the
54 structural robustness of ecological networks (Borrvall et al., 2000; Borrvall & Ebenman,
55 2006, 2017; Sanders et al., 2013; Donohue et al., 2017)—might be a useful general predictor
56 of species contributions to ecosystem stability. Through the removal of top-down control,
57 loss of predator species can, for example, affect ecosystems very differently than loss of
58 other consumers (Chen et al., 2020), increasing the vulnerability of key ecosystem processes
59 (Estes et al. 2011; Ross et al., 2022) and destabilising the overall system (Donohue et al.
60 2013; 2017) in distinct ways. Thus, understanding the extent to which the contributions of
61 individual species to stability may be determined by their trophic position would comprise a

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

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

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

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

99 The functional and compositional stability responses of communities to disturbance
100 —that is, the responses of, respectively, total biomass and species composition (Table 1)—
101 can be largely independent (Hillebrand et al., 2018; Hillebrand & Kunze, 2020; White et al.,
102 2020). This is because environmental change often affects the density or biomass of
103 populations before triggering compositional change (Gaston & Fuller, 2008; Hillebrand et al.,
104 2008; Hull et al., 2015). Total biomass and productivity can also remain relatively constant
105 despite considerable turnover in species composition, while fast recovery of biomass can
106 occur in a community that has not yet recovered in terms of composition (Hillebrand &
107 Kunze, 2020). We therefore quantified the contribution of whelks and gastropod grazers to
108 multiple dimensions of both functional and compositional stability (Table 1), examined the

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

111

112 **Methods**

113 *Experimental design*

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

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

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

136 Press perturbations of nutrient enrichment and elevated sedimentation were
137 applied six months after the commencement of the experiment to allow sufficient time for
138 our consumer manipulations to take effect and avoid transient dynamics (Donohue et al.,
139 2013). The perturbations were maintained for six months (Fig. 1). Plots were then
140 monitored for a further three-month 'recovery' phase after perturbations had ceased,
141 resulting in a total experiment duration of 15 months. Our experimental design established
142 two levels of both nutrient enrichment (ambient and enriched) and sedimentation (ambient
143 and elevated). Nutrient enrichment was achieved by the addition of slow release fertiliser
144 pellets (11N:11P:18K, Osmocote®) in plastic mesh cases (10 cm X 10 cm) to enriched
145 treatments (following Worm et al., 2000; Atalah & Crowe, 2010; Vye et al., 2017). Empty
146 mesh cases were added to non-enriched experimental plots to control for any experimental
147 artefacts caused by the presence of the bag rather than the nutrients. One hundred and
148 sixty grams of fertiliser was added to enriched plots and replaced every 8–12 weeks to
149 sustain elevated concentrations of nutrients in appropriate treatments for the duration of
150 the experiment (O'Connor & Donohue, 2013; O'Connor et al., 2015; Vye et al., 2017). After
151 four weeks, samples were taken from the water column directly above each plot on an
152 ebbing tide to test the effectiveness of this method. Water samples from plots with added
153 fertiliser had significantly (Kruskal-Wallis test, $P < 0.001$) greater concentrations of dissolved
154 inorganic nitrogen (mean \pm SE = $4.60 \pm 0.07 \mu\text{m L}^{-1}$) than ambient treatments (2.53 ± 0.28
155 $\mu\text{m L}^{-1}$). This increase of approximately 70% is consistent with those in previous enrichment
156 studies (Worm et al., 2000b; Sugden et al., 2008; White et al., 2018).

157 Elevated sedimentation was achieved by adding 800 g sediment, collected from an
158 adjacent sandy shore, to plots weekly for six months. This sedimentation rate, equivalent to
159 $\sim 800 \text{ g m}^{-2} \text{ d}^{-1}$, is almost twice the level considered the upper limit experienced by coastal
160 habitats close to populated areas (Airoldi & Virgilio, 1998; Connell, 2005), though it is well
161 below the levels recorded around harbours ($\sim 2000 \text{ g m}^{-2} \text{ day}^{-1}$; Irving & Connell, 2002).
162 Weekly additions of sediment, therefore, mimicked the effects of storms with intermittent
163 pulses in areas with considerable coastal infrastructure. Consumer loss, nutrient enrichment
164 and sedimentation were all crossed fully in our experimental design, yielding a total of 12
165 caged treatment combinations, each replicated five times (Table S1).

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

174 The percent cover of individual macroalgal species was measured monthly using a
175 25x25 cm quadrat with 64 intersections, positioned centrally within cages to avoid sampling
176 edge effects. Species found within the quadrat but not present underneath any of the
177 intersections were assigned a cover value of 1% (O'Connor & Crowe, 2005). There were no
178 differences in total macroalgal cover (ANOVA; $F_{15,64} = 0.51$, $P > 0.05$) or assemblage
179 structure (PERMANOVA; Pseudo- $F_{15,64} = 0.84$, $P > 0.05$) between any caged or uncaged
180 experimental treatments at the beginning of the experiment. Whelks consumed $11.5 \pm 2.1\%$

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

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

193

194 *Data analyses*

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

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

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

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

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

247

248 **Results**

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

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

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

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

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

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

298

299 **Discussion**

300 Our results show that species may contribute differently to ecological stability when
301 ecosystems are disturbed in different ways. Moreover, our focal predator and grazers both
302 stabilised and destabilised algal communities simultaneously along different dimensions of
303 stability. Whelks stabilised communities in response to sediment but destabilised them in
304 response to nutrients, via, respectively, increasing functional spatial variability and
305 decreasing compositional spatial variability. Grazers promoted resilience to nutrients but
306 destabilised communities by increasing functional temporal variability in the absence of
307 stressors. It follows that the differing nature of the disturbances—both common stressors in
308 coastal systems (Thompson et al., 2002)—can determine how they impact macroalgae and
309 consumers, the interactions between them, and, ultimately, their contributions to the
310 overall stability of the system (Polazzo & Rico, 2021; Simmons et al., 2021). Sediment
311 physically smothers algae and reduces light availability for photosynthesis (Airoldi, 2003) but
312 might physically hinder grazing activity (Airoldi & Hawkins, 2007), whereas nutrients have
313 strong bottom-up effects stimulating algal growth that may be dampened by presence of
314 grazers but accentuated via predator-induced grazer suppression (O'Connor & Donohue,
315 2013; Rober et al., 2022). Understanding whether there are generalities in how individual
316 species or functional groups contribute to overall stability under different types of
317 disturbances is essential to disentangle these complex interactions (Rezende et al., 2021).

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

324 indirect consequence of the effects of predators on their gastropod prey (Rober et al.,
325 2022). These findings provide further evidence of the direct role played by grazers in
326 increasing spatial heterogeneity of algal communities (Kordas et al., 2017), as well as the
327 important indirect role of predators as compositional homogenisers, induced via grazer
328 suppression (Ross et al., 2022). Nonetheless, the neutral contributions of consumers to
329 functional spatial variability and lack of correlation between compositional and functional
330 spatial variability suggests that the compositional homogenisation we observed had little
331 impact on variability of total biomass in space in our study. Were compositional
332 homogenisation accompanied by decreasing complementarity among functionally dissimilar
333 communities (Villéger et al., 2014), however, consumers may drive subtle changes in other
334 aspects of ecosystem functioning, such as metabolic rates and nutrient cycling, via this
335 mechanism.

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

348 al. 2013). In our experiment, nutrients and sediments were acting on multiple different
349 components of the community, and hence their trophic and non-trophic interaction
350 networks, simultaneously. Given the importance of non-trophic interactions in driving
351 community dynamics and responses to disturbances (Kéfi et al. 2012; 2015; Donohue et al.,
352 2017), coupled with their strong context-dependence (Wirsing et al., 2021), the relative
353 influence of trophic interactions as a driver of stability may have been tempered by other
354 interaction types at our experimental site. Developing theory and testing experimental
355 frameworks in different ecological contexts are, therefore, needed both to examine the
356 generality of these findings and identify other factors that might predict the contributions of
357 individual species to stability.

358 Even though interactions between stressors can modify several stability dimensions
359 (Polazzo & Rico, 2021), we found that species contributions to stability under combined
360 stressors could frequently be predicted from their contributions under the individual
361 disturbances acting in isolation (that is, the observed responses to nutrients and sediments
362 in combination were statistically similar to those predicted by the sum of the responses to
363 nutrients and sediments in isolation). This suggests that predicting species contributions to
364 stability under multiple stressors may be a somewhat less complex problem than predicting
365 stability responses of entire communities. For spatial variability and compositional
366 resilience, however, stressors tended to behave antagonistically to reduce their cumulative
367 effect on stability. That is to say that the relative role of consumers in stabilising the
368 community was diminished when exposed to both stressors combined, although this varied
369 among consumers. In contrast, species contributions to all other stability dimensions under
370 multiple stressors could be predicted from the effects of individual stressors acting in
371 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

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

401 As with almost all field-based ecological experiments, our study is limited in scope by
402 its spatial scale. Recently derived general statistical scaling rules of stability (Clark et al.,
403 2021) may, however, be useful in exploring the generality and implications of our findings at
404 larger scales in space and time. Even so, our results imply that, in biologically diverse
405 systems such as rocky shores, stability varies with community structure, such that removing
406 species or altering how species interact with one another has the potential to alter these
407 scaling relationships (Jacquet et al., 2016; Arnoldi et al., 2018; Hillebrand et al., 2018; White
408 et al., 2020). Further, due to logistical constraints, our experiment considered just two levels
409 of each stressor treatment, which limited the kinds of interactions that could be identified.
410 It is evident that the intensity (Vye et al., 2015), temporal pattern (García Molinos &
411 Donohue, 2010, 2011; Mrowicki et al., 2016), and legacy effects (Jackson et al., 2021; Miller
412 et al., 2021; Ross et al., 2022) of disturbances all regulate their impacts on communities.
413 Considering multiple dimensions of disturbances within the context of ecological stability
414 must, therefore, be a priority for future research (Donohue et al., 2016; Kéfi et al., 2019, Orr
415 et al., 2022).

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

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

427

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430

431 **Conflict of interests**

432 The authors declare no competing interests.

433

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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)	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). $\frac{\mu_{t6-t12}}{\sigma_{resid\ t6-t12}}$ where $\sigma_{resid\ t6-t12}$ = The standard deviation of residuals from regression	Mean Euclidean distance from each plot on every census, to their treatment centroid. \overline{ED}_{t6-t12} where ED_{t6-t12} = Euclidian distance between a single plot in a given perturbed treatment and their own centroid on each census.	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).

666 **Figure legends**

667

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

669 **stability.** We quantified contributions of species to the various components of stability (see

670 Table 1 for detailed description of stability measures and their quantification) by comparing

671 stability properties in plots from which consumers were removed (lower red lines:

672 predatory whelk removed; upper green lines: whelk and gastropod grazers removed) to

673 those that experienced no species losses (middle blue lines). We measured stability

674 responses to our experimentally-imposed press perturbations (that is, nutrient enrichment

675 and sedimentation, both separately and together) by comparing perturbed (solid lines) to

676 equivalent unperturbed (dotted lines) plots within species removal treatments. Where a

677 dimension of stability was reduced (that is, the system was destabilised) in the absence of a

678 species compared to when it was present, this implies that the species contributes positively

679 to that dimension of stability, and *vice versa*. All stability measures were quantified

680 separately from both total macroalgal biomass and assemblage structure as dimensions of,

681 respectively, functional and compositional stability (Table 1).

682

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

684 **under different disturbance types.** Mean (\pm 95% CI, $n = 5$ for all measures except spatial

685 variability, for which $n = 7$) log response ratio, indicating contributions of predatory whelks

686 (triangles) and gastropod grazers (squares) to multiple components of (a) functional and (b)

687 compositional stability (see Fig. 1 and Table 1 for description of stability measures and their

688 quantification). Data points above the dashed horizontal line indicate a stabilising

689 contribution (that is, the presence of a consumer promoted resistance, resilience, or spatial

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

697

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

710

711 **Fig. 4. Relationships between species contributions to functional and compositional**
712 **stability components.** Analyses were pooled across consumer treatments ($n = 40$ for
713 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.

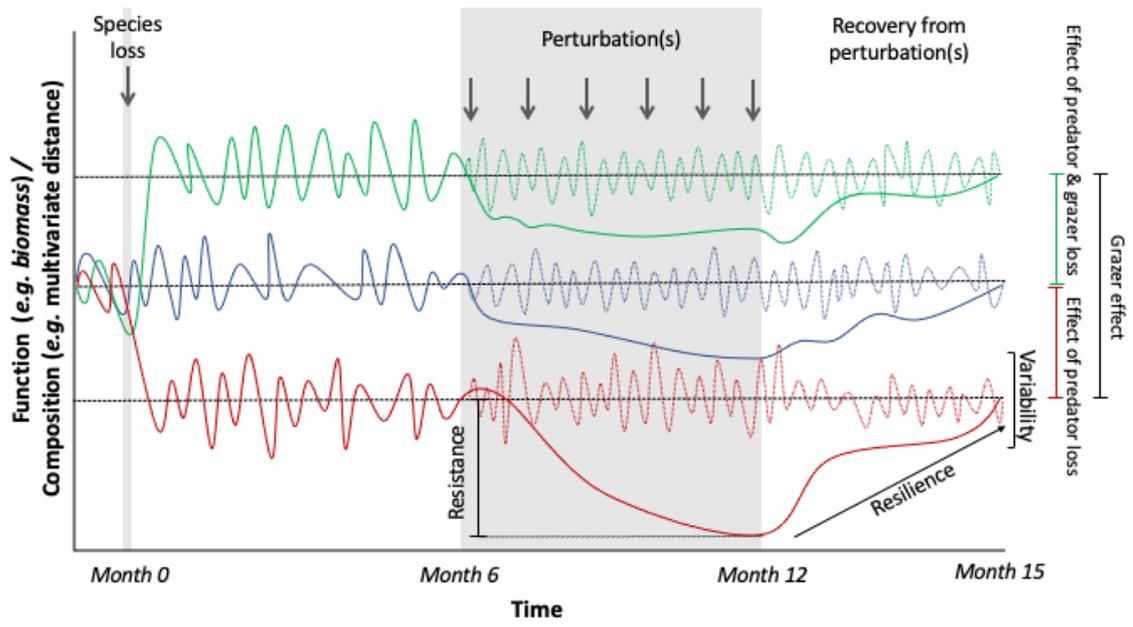


Fig. 1. White *et al.*

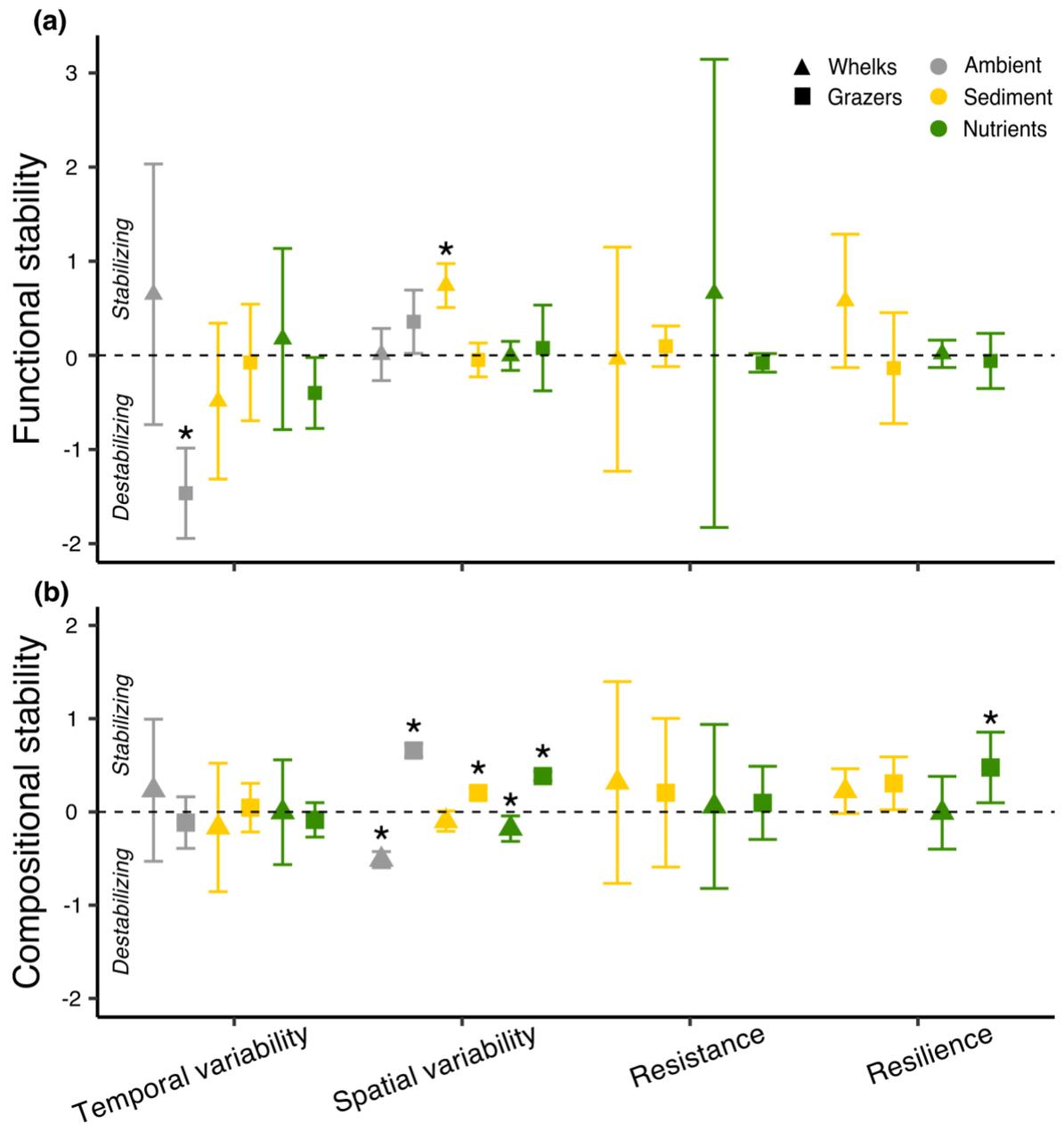


Fig. 2. White *et al.*

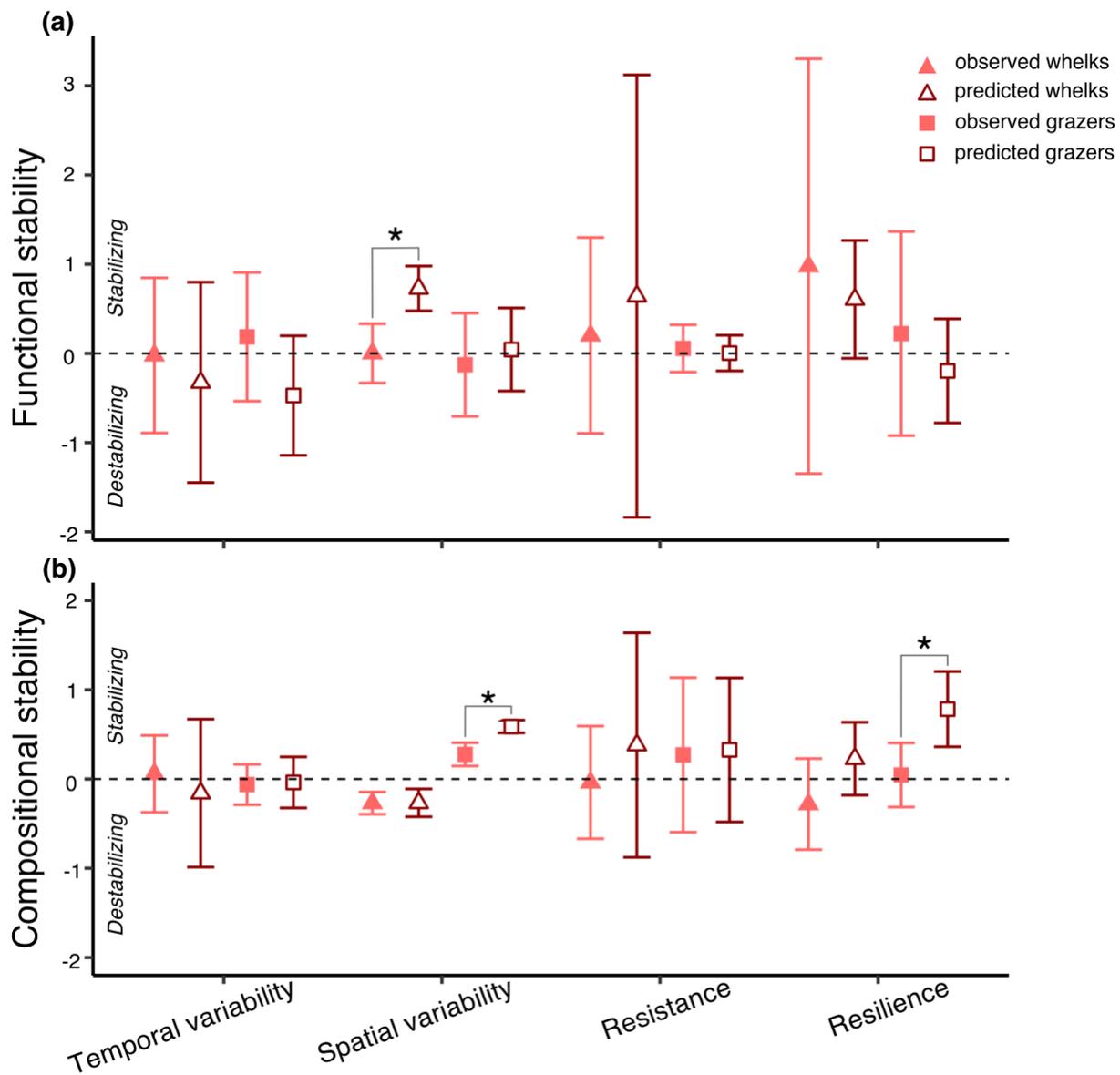


Fig. 3. White *et al.*

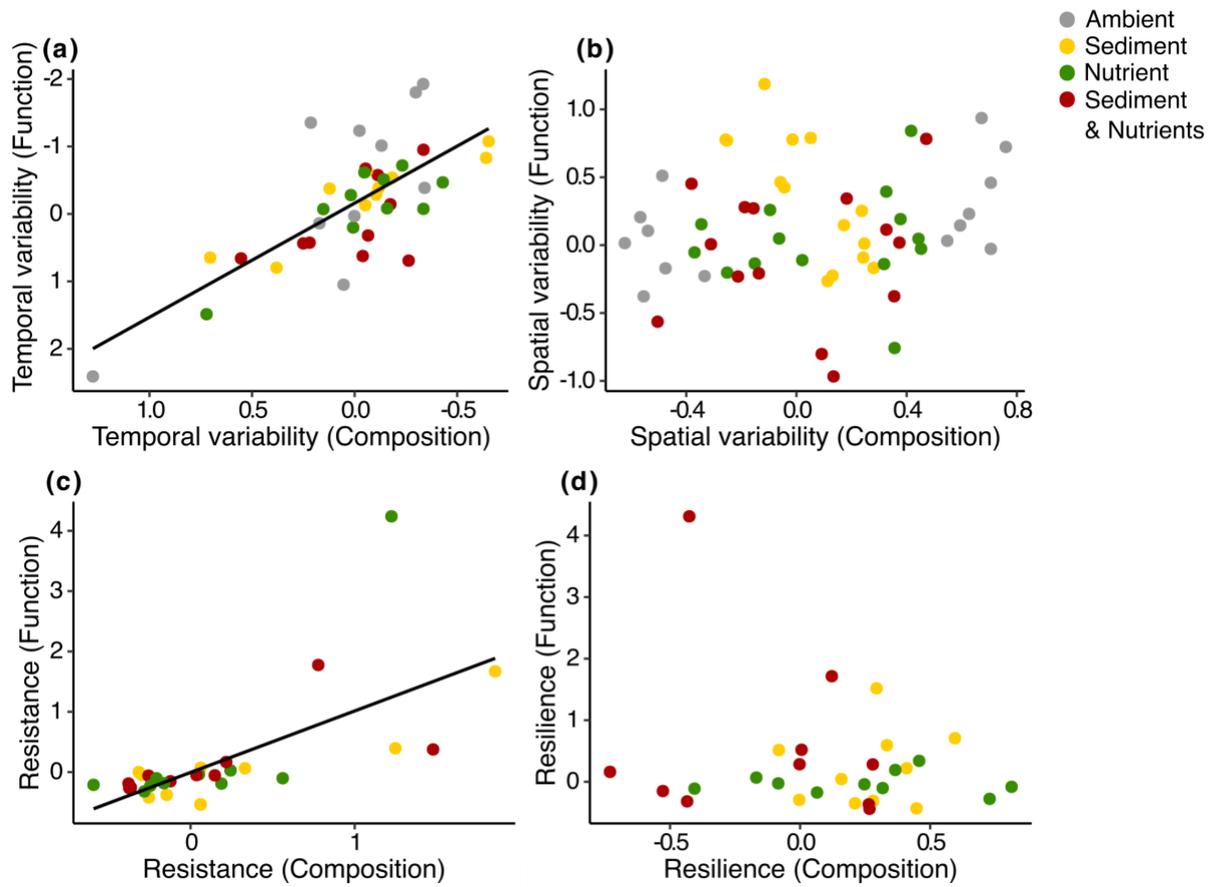


Fig. 4. White *et al.*

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 ± 14.6 m⁻² [mean \pm SE]; $n = 30$), the topshell *Steromphala umbilicalis* (13.6 ± 2.0 m⁻²), and the common limpet *Patella vulgata* (12.0 ± 2.1 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 ± 2.9 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		Ambient
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	Elevated
	Enriched	Ambient
		Elevated
Whelk removals		Ambient
Contained grazers (25 <i>L. littorea</i> , two <i>G. umbilicalis</i> , one <i>P. vulgata</i>) and a naturally occurring macroalgal community	Ambient	Elevated
	Enriched	Ambient
		Elevated
Whelk and grazer removal		Ambient
Excluded all focal consumers from accessing a naturally occurring algal community	Ambient	Elevated
	Enriched	Ambient
		Elevated
Open uncaged plots		Ambient
Naturally occurring algal community open to ambient densities of all focal consumers and other mobile organisms.	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	F	P	MS	Pseudo-F	P
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

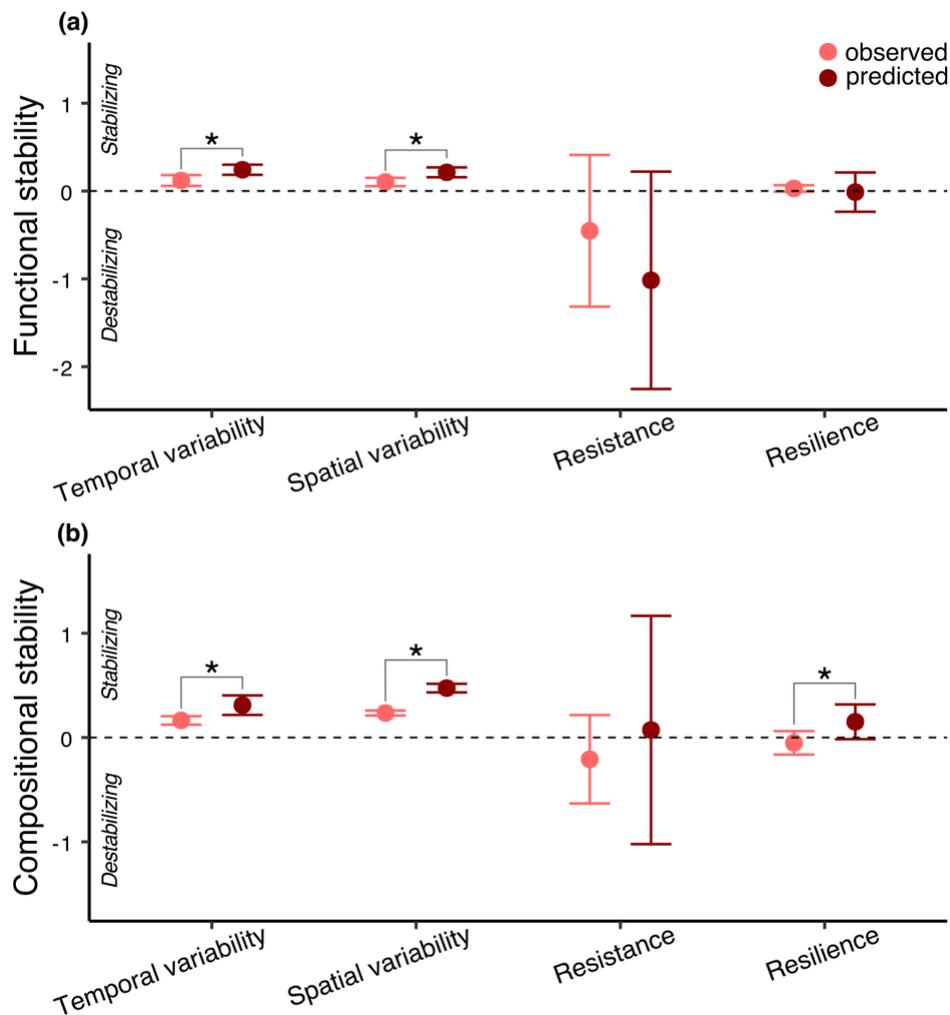


Fig. S1. Observed stability of the entire community in intact plots with no consumer removals under combined disturbances and those predicted from the additive combination of the individual disturbances acting in isolation. Mean (\pm 95% CI, $n = 5$, for all measures except spatial variability, for which, $n = 7$) 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.