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Individual species provide multifaceted contributions to the stability of ecosystems

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1 **Individual species provide multifaceted contributions to the stability of**
2 **ecosystems**

3

4 LYDIA WHITE^{1,2}, NESSA E. O'CONNOR^{1,3}, QIANG YANG⁴, MARK C. EMMERSON¹ & IAN DONOHUE^{3*}

5 *¹School of Biological Sciences, Institute of Global Food Security, Queen's University*
6 *Belfast, Belfast, BT9 5DL, UK*

7 *²CNRS, UMR 7144, Station Biologique, 29680 Roscoff, France*

8 *³Department of Zoology, School of Natural Sciences, Trinity College Dublin, Ireland*

9 *⁴Department of Biology, University of Konstanz, Konstanz, Germany*

10 **Corresponding author*

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14 **Email addresses:** lwhite18@qub.ac.uk; qiang.yang@uni-konstanz.de;
15 n.oconnor@tcd.ie; m.emmerson@qub.ac.uk; ian.donohue@tcd.ie

16 **Exploration of the relationship between species diversity and ecological stability**
17 **has occupied a prominent place in ecological research for decades. Yet, a key**
18 **component of this puzzle—the contributions of individual species to the overall**
19 **stability of ecosystems—remains largely unknown. Here, we show that individual**
20 **species simultaneously stabilize and destabilize ecosystems along different**
21 **dimensions of stability, and also that their contributions to functional (biomass)**
22 **and compositional stability are largely independent. By simulating experimentally**
23 **the extinction of three consumer species from a coastal rocky shore (the limpet**
24 ***Patella*, the periwinkle *Littorina* and the topshell *Gibbula*), we found that the**
25 **capacity to predict the combined contribution of species to stability from the sum**
26 **of their individual contributions varied among stability dimensions. This implies**
27 **that the nature of the diversity-stability relationship depends upon the dimension**
28 **of stability under consideration, and may be additive, synergistic or antagonistic.**
29 **We conclude that, though the profoundly multifaceted and context-dependent**
30 **consequences of species loss pose a significant challenge, the predictability of**
31 **cumulative species contributions to some dimensions of stability provide a way**
32 **forward for ecologists trying to conserve ecosystems and manage their stability**
33 **under global change.**

34 The erosion of biodiversity is a particularly insidious consequence of human
35 activities^{1–6}. There is now widespread evidence to show that loss of biodiversity
36 leads to declines in the functioning^{4,7,8} and stability^{9–12} of ecosystems and can trigger
37 significant extinction cascades^{13,14}. Despite this general understanding, predicting

38 the consequences of individual species loss from ecosystems remains a fundamental
39 challenge in ecology^{15,16}.

40 All species are not equal. They contribute differently to the dynamics, structure
41 and function of ecosystems^{9,13,15,17–21}. The ability to partition species contributions
42 to, for example, ecosystem productivity in different ecological contexts¹⁹ has proved
43 to be of enormous benefit to research on relationships between biodiversity and
44 ecosystem functioning. However, no such framework exists for overall ecological
45 stability. Such a framework could provide the basis for a far richer understanding of
46 the frequently disparate relationships between biodiversity and stability observed in
47 both models and experiments^{22–28}. The capacity to quantify the relative extent of
48 additivity and complementarity in species contributions to stability would, for
49 example, provide considerable insight into the predictability of stability in natural
50 communities and a more contextual understanding of its relationships with diversity.

51 While the consequences of species loss has been a key focus of ecologists for
52 decades^{13,17,29–34}, this large body of theoretical and empirical understanding provides
53 limited insight into the contributions of species to the many dimensions of ecological
54 stability^{9,35}—a multidimensional concept that tries to capture the different aspects
55 of the dynamics of the system and its response to perturbations^{35,36} (Fig. 1).

56 Certainly, measuring how a system has changed following the addition or local
57 extinction of a species enables quantification of the net contribution of that species
58 to, for example, the temporal and spatial variability of biomass production (see³⁷ for
59 an example of how to predict the temporal variability of community biomass from
60 that of its constituent species). However, it provides little insight into the

61 contribution of the species to those dimensions of stability that characterise
62 explicitly the response of systems to perturbations³⁵, such as their reactivity—their
63 propensity to amplify the effects of perturbations^{38,39}—and their capacity to resist
64 and recover from those perturbations (respectively, their resistance and resilience).
65 Such insight can only be properly gained empirically by comparing the responses of
66 the system to independent perturbations in both the presence and the absence of
67 the species, after transient dynamics have attenuated and the interaction network
68 has ‘rewired’ following the loss (or, indeed, the addition) of the species (Fig. 1).

69 Here, we quantify the simultaneous contributions of different consumer
70 species to multiple dimensions of the stability of a coastal rocky shore ecosystem
71 (see Fig. 1 for a description of our experimental framework and Table 1 for the
72 stability measures used and their derivation) and test whether those contributions
73 are additive across species. Specifically, we simulated experimentally the loss of
74 three key grazer taxa—the limpet *Patella*, the periwinkle *Littorina* and the topshell
75 *Gibbula*—and quantified multiple stability responses of the macroalgal communities
76 on the shore to a subsequent pulse perturbation (that is, 50% removal of total
77 macroalgal cover). The experiment was performed in the presence and absence of
78 each of the grazers, both separately and together, in a factorial experimental design.
79 In order to maximise the ecological realism of our results, we conducted the
80 experiment on the shoreline using natural communities structured by a diverse
81 range of both trophic and non-trophic interactions^{31,40}. We thereby caused the local
82 extinction of various components of a larger intertidal food web in an open
83 experimental system, which allowed immigration and recruitment of primary

84 producers and many epibenthic consumers, including primary consumers and small
85 predators (e.g. amphipods, polychaetes and Nemertea).

86 We tested (1) whether the different consumer species contribute in different
87 ways to different dimensions of ecological stability. In addition, because cumulative
88 loss of multiple species frequently alters communities in ways than cannot be
89 predicted based on removals of single species^{15,41}, we explored, for multiple
90 dimensions of stability, (2) whether the strength and / or the nature of combined
91 contributions of taxa to stability can be predicted from the additive combination of
92 their individual contributions.

93 Recently, it has been shown that the functional and compositional stability
94 responses of communities to perturbations —that is, the responses of, respectively,
95 biomass and species composition (Table 1)—can be largely independent^{42,43}. This is
96 likely a consequence of compensatory community dynamics occurring after
97 perturbations—fast recovery of biomass can occur in a community that has not yet
98 recovered in terms of composition and *vice versa*^{42–46}. Indeed, a recent meta-
99 analysis⁴³ found that compositional recovery from pulse perturbations tended to be
100 incomplete and far slower than functional recovery in most experiments examined.
101 Measuring multiple dimensions of both functional and compositional stability is,
102 therefore, likely to provide a far richer perspective on the overall ecological stability
103 of communities. Accordingly, we quantified the contribution of our focal grazer taxa
104 to multiple dimensions of both functional and compositional stability (Table 1),
105 examined the strength and nature of relationships between them, and tested our
106 hypotheses independently for each.

107

108 **Results**

109 Our focal consumer taxa all altered different components of the functional and
110 compositional stability responses of communities in our experimental plots in
111 different ways (Figs. 2 & 3, Extended Data Fig. 1, Supplementary Tables 1 & 2).
112 Though the presence of grazers, individually or in combination, did not modify the
113 temporal variability of macroalgal assemblages, nor the spatial variability of their
114 biomass, their presence in general reduced the spatial variability of macroalgal
115 assemblages (SNK post-hoc tests; $P < 0.001$; $n = 8$, Supplementary Table 2; Fig. 3,
116 Extended Data Fig. 1).

117 We found that *Patella* in general contributed strongly and positively to
118 functional stability responses to our experimental pulse perturbation (Figs. 2a & 3a),
119 but more weakly to those of compositional stability (Figs. 2b & 3b). In fact, the
120 presence of *Patella* even strongly destabilised algal communities along some
121 dimensions of compositional stability (*e.g.* compositional resistance, Fig. 3b). In
122 contrast, *Littorina* was the strongest contributor of the species we examined to
123 compositional resistance (Fig. 3b, Extended Data Fig. 1). Even so, its presence had
124 the most destabilising effect on functional resilience (Fig. 3a, Extended Data Fig. 1).
125 Finally, the contribution of *Gibbula* to the functional stability of algal communities
126 was, in general, intermediate between those of *Patella* and *Littorina* (Figs. 2 & 3,
127 Extended Data Fig. 1). Yet, algal community composition in plots from which *Gibbula*
128 were removed was more reactive than in any other treatment (Extended Data Fig.
129 1). In other words, the presence of *Gibbula* strongly stabilized communities by

130 reducing the reactivity of algal community composition after the pulse perturbation
131 (Fig. 3b).

132 Though none of the focal grazer taxa affected functional recovery time in
133 isolation, their combined presence suppressed functional recovery (Fig. 3a; loss of all
134 three focal grazer taxa in combination led to shorter recovery times of macroalgal
135 cover [SNK post-hoc tests; $P < 0.007$, $n = 8$] relative to the treatment with no grazer
136 species losses, Extended Data Fig. 1). In fact, when present together, the three focal
137 grazer taxa had generally destabilising or neutral effects on both functional and
138 compositional stability responses to the pulse perturbation (Fig. 4). However, these
139 combined effects frequently differed—both in strength and in nature—from those
140 predicted by the additive combination of their component individual species
141 contributions to stability (Fig. 4). This result was particularly marked for functional
142 stability responses, most notably for temporal variability and resistance, where the
143 predicted cumulative contributions of the manipulated grazers was stabilizing, yet
144 their observed contributions were destabilising. This indicates clearly that, for many
145 components of stability, the combined contributions of species cannot be predicted
146 reliably from their individual contributions.

147 Across all of our experimental treatments, functional stability responses of
148 algal communities were largely independent of those of compositional stability.
149 Though functional resistance to the pulse perturbation correlated positively with
150 compositional resistance across our experimental plots ($P = 0.002$, RMA regression, n
151 = 20), no other functional stability responses correlated with their equivalent
152 component of compositional stability (Extended Data Fig. 2).

153

154 **Discussion**

155 Our results demonstrate that species not only contribute in different ways to
156 different dimensions of stability, but also that they can simultaneously have a
157 stabilizing and destabilising influence on ecosystems. *Patella* contributed positively
158 to functional stability by enhancing resilience to perturbations yet, in parallel,
159 destabilised communities by reducing the resistance of community composition.
160 *Littorina* had the most destabilising effect of all the species we examined on
161 functional resilience, while the presence of *Gibbula* strongly stabilized community
162 composition by suppressing the propensity for reactivity following perturbation.
163 These results highlight the complexities and context-dependence associated with
164 predicting the consequences of species loss from ecosystems. They also emphasise
165 the importance of all species, and the interaction network within which they are
166 embedded, for maintaining the overall multidimensional stability of ecosystems. No
167 single component of stability would have captured the complex ecological responses
168 to our experimental pulse perturbation. The fundamental insight needed for
169 effective management of ecosystem stability therefore demands consistently
170 multidimensional assessment of ecological responses to disturbance^{12,35}.

171 Metrics of functional and compositional stability varied considerably and were,
172 as expected, generally independent. Our results are broadly consistent with those of
173 Hillebrand *et al.*⁴², who found that functional resilience and temporal variability of
174 freshwater plankton communities were independent of their equivalent component
175 of compositional stability, but also that functional and compositional resistance
176 correlated positively. They are also consistent with a recently documented general

177 tendency towards independence of recovery rates of community biomass and
178 species composition following pulse perturbations⁴³, which highlights the
179 importance of considering the timescales of ecological responses to perturbations,
180 across which our predictive capacity can vary considerably^{47–49}. Managing systems
181 for functional stability may, therefore, have negative consequences for
182 compositional stability and *vice versa*, a finding that has profound implications for
183 policymakers needing to prioritise certain components of stability over others to
184 meet relevant goals³⁵. For example, managing to optimise only compositional
185 stability, such as preserving species composition or diversity within a protected area,
186 will not necessarily improve functional stability, and could have detrimental
187 consequences for the stability of biomass and productivity²⁸. Focusing on either
188 functional or compositional stability in isolation risks an incomplete understanding of
189 the effects of perturbations on ecosystems, coupled with strong likelihood of
190 underestimating their overall impacts⁴².

191 Though combined contributions of multiple species to some dimensions of
192 stability were additive, many combined contributions—particularly to functional
193 stability responses—could not be predicted reliably from the additive contributions
194 of individual species, with some predictions severely under- or over-estimating
195 stability. This is broadly consistent with the disparate relationships between diversity
196 and stability found in both models and experiments^{22–27}, and also provides a
197 mechanism for explaining how the relationship between species diversity and
198 ecological stability can vary simultaneously among multiple stability dimensions²⁸.
199 Further, this finding also reflects our understanding of the individual and cumulative
200 effects of species on multiple ecosystem functions^{15,19}, and is likely a consequence of

201 idiosyncratic interactions between our focal consumers. In fact, single species
202 frequently contributed more strongly to stability than the simultaneous
203 combinations of multiple species, highlighting the significant challenges associated
204 with predicting the impacts of cumulative species losses on ecosystems under global
205 environmental change.

206 Our experiment was done using natural communities in the field and, as such,
207 maximised ecological realism in so far as possible⁴⁰. Our findings are, nonetheless,
208 from a single system over a 15-month duration, and both biological and
209 environmental context can strongly influence the conclusions of field
210 experiments^{16,48,50–54}. The generality of our findings therefore needs to be explored
211 in other systems. The experimental framework presented here could also be
212 extended to observational studies of, for example, invasion or species loss.
213 Comparing the response of rock pool communities that have been invaded by an
214 invasive alga to various anthropogenic stressors with those that have yet to be
215 invaded could provide insight on the invasive's capacity to destabilise surrounding
216 communities⁵⁵. Similarly, exploring invaded and uninvaded grassland communities
217 and their responses to perturbations will allow identification of stabilising and
218 destabilising invaders and a potential way to prioritise their management. The
219 framework may also be applicable to exploration of time series, in particular if
220 information on local pressures or perturbation events is known. For example, effects
221 of an oil spill on macrobenthic communities could be explored where the presence
222 of species of interest vary among sampling sites, thus enabling quantification of the
223 contribution of those species to resistance and recovery from such events^{56,57}.

224 Our results demonstrate that individual species moderate the stability of
225 ecosystems in a variety of ways, and can simultaneously contribute both positively
226 and negatively to stability. This makes predicting and managing the consequences of
227 their loss an especially challenging task. The frequently non-additive and context-
228 dependent nature of cumulative species contributions to ecological stability
229 exacerbates this problem even further. Even though combined species contributions
230 to some dimensions of stability may be predictable, the multifaceted consequences
231 of species loss present a significant challenge to ecologists trying to conserve
232 ecosystems and maintain or enhance their stability under global change.

233

234 **Methods**

235 *Study site*

236 Our experiment took place on an exposed Atlantic rocky shore at Glashagh
237 bay, Fanad, Co. Donegal, Ireland (55°26'5''N, 7°67'5''W) over 15 months from May
238 2016. The shore comprised a large gently sloping granitic platform covered by a
239 network of barnacles, macroalgae and bare rock⁴¹, typical of exposed shores in the
240 region⁵⁸, with small patches of juvenile mussel beds present around the mid-shore
241 region (2.0 – 2.5 m above Chart Datum). Discrete shallow rock pools were
242 widespread throughout the intertidal zone, dominated by turfs of upright calcareous
243 algae (*Corallina officinalis*). These supported a diverse macroalgal assemblage,
244 including fine (*e.g. Ceramium nodulosum*), coarse (*e.g. Osmundea hybrida*) and
245 ephemeral (*e.g. Porphyra umbilicalis*) red algae, perennial (*e.g. Codium fragilis*) and
246 ephemeral (*e.g. Ulva compressa, Bryopsis spp.*) green algae and brown canopy algae

247 (e.g. *Fucus serratus*, *Cystoseira tamariscifolia*). Encrusting macroalgae (*Lithothamnium*
248 spp.) covered most remaining bare rock.

249 Grazing gastropods were common and widespread across the shore. The most
250 abundant species in rock pools were the China limpet *Patella ulyssiponensis*,
251 common periwinkle *Littorina littorea* and topshell *Gibbula umbilicalis*. Other
252 gastropod species, including *P. vulgata*, *L. saxatilis*, *L. obtusata* and *G. cineraria*,
253 were also present as well as non-gastropod grazers such as chitons, amphipods,
254 harpacticoids and isopods.

255

256 *Experimental design*

257 Forty experimental plots were established in rock pools on the shore around
258 mid-tidal level across approximately 100 m of shoreline, with a minimum of two
259 metres between plots. Plots were enclosed by cages (35 x 35 cm, 12 cm high)
260 constructed from stainless steel mesh (0.9 mm wire diameter, 4.17 mm aperture,
261 67% open area) fixed to the substratum with screws and washers. This enabled us to
262 restrict the movement of our focal grazer species into and out of plots, while
263 allowing access to smaller mobile consumers, including annelid and nemertean
264 worms, amphipods and juvenile gastropod grazers, in addition to propagules of
265 sessile benthic fauna and algae. This cage design has been used extensively and
266 successfully to manipulate consumer presence on rocky shores with no
267 consequences for algal community structure or stability^{13,16,17,41,51,59}. Plots were
268 situated in separate shallow pools of similar area (range 0.5 – 5.0 m²) and depth (<
269 12 cm) and included in excess of 60% (mean ± S.E.: 66 ± 2.4%) coverage of coralline
270 algae.

271 The experiment involved the single and combined removal of three focal
272 gastropod grazer taxa from rock pools. There was no experimental compensation for
273 the loss of a particular species, or artificial increase in biomass of the remaining
274 species, akin to additive designs. Unlike substitutive designs, additive designs avoid
275 confounding intra- and inter-specific interactions with changes in diversity⁶⁰ and our
276 design ensured that interspecific differences in standing stock were represented⁵².
277 Five grazer removal treatments were assigned randomly to plots: one non-removal
278 treatment requiring no removal of species; three single species removal treatments
279 involving removal of either *Patella* spp., *Littorina littorea* or *Gibbula umbilicalis*, and
280 one combined removal treatment in which all three focal grazer taxa were removed
281 simultaneously. Every experimental treatment was replicated four times. Due to
282 difficulties in differentiating *P. ulyssiponensis* and *P. vulgata*, particularly juveniles, in
283 plots without causing considerable disturbance and likely death, we did not
284 discriminate between the two limpet species in our experiment. *P. ulyssiponensis*
285 dominated in rock pools, though *P. vulgata*, which tends to disperse onto emergent
286 rock⁶¹, were also present in pools at much lower densities (< 15%). All experimental
287 grazer densities were based on adult sizes because of difficulties associated with
288 effectively manipulating juveniles, and were based on natural densities found in rock
289 pools during preliminary surveys of the experimental site (that is, *Patella*: 52.1 ± 11.7
290 m^{-2} ; *Littorina*: $80.6 \pm 19.1 \text{ m}^{-2}$; *Gibbula*: $20.8 \pm 4.9 \text{ m}^{-2}$). Grazer abundances within
291 our experimental plots were therefore as follows: 7 *Patella* individuals, 10 *Littorina*
292 and 3 *Gibbula*. Where appropriate, grazer populations were supplemented with
293 additional individuals to meet target densities.

294 Our experimental design comprised two levels of perturbation (that is,

295 perturbed and unperturbed). Perturbed plots had 50% macroalgal cover removed
296 manually with a chisel as a single pulse perturbation event four months after grazer
297 treatment manipulation. Previous consumer species loss experiments in similar
298 coastal systems have found that four months is generally sufficient for transient
299 dynamics to attenuate^{9,13}. Half of the substratum was cleared in a single patch in
300 perturbed plots, and the orientation of this patch was randomised among plots. The
301 aim of the perturbation was to simulate a single extreme storm event, similar to
302 disturbance events employed in previous studies^{62,63}. Our perturbation treatment
303 was crossed fully with the five grazer removal treatments, giving a total of ten
304 treatments in a full-factorial design, each replicated four times. The perturbation
305 caused significant shifts in macroalgal cover [Analysis of Variance (ANOVA), $F_{1,38} =$
306 90.69 , $P < 0.0001$] and assemblage structure [Permutational Multivariate Analysis of
307 Variance (PERMANOVA); pseudo- $F_{1,38} = 11.06$, $P = 0.0001$]. This was consistently
308 underpinned by higher relative abundance of *Corallina officinalis* in perturbed plots
309 in all treatments from which grazers were removed, though the loss of different
310 grazer taxa also moderated how macroalgal assemblage composition responded to
311 the perturbation (Supplementary Table 3).

312 To enable detection of experimental artefacts arising from the use of cages, we
313 established an additional eight open plots (four of which were allocated to the
314 perturbed treatment and four to the unperturbed), marked at the corners with
315 screws, thus remaining open to natural densities of mobile organisms on the shore.
316 These were interspersed haphazardly among the caged plots, enabling us to
317 compare consumer and algal assemblage dynamics within caged plots to those on
318 the natural shore over the duration of the experiment. The dynamics of both algal

319 cover and assemblage structure was similar in both the uncaged plots and the caged
320 plots with no grazer removals (Extended Data Fig. 3) and we found no differences in
321 any measure of functional or compositional stability between the two treatments
322 (Supplementary Table 4).

323

324 *Data collection and analyses*

325 We measured the percent cover of macroalgae monthly using a 25 x 25 cm
326 quadrat with 64 intersections, positioned centrally within cages to avoid sampling
327 edge effects. Species present within the quadrat but not occurring underneath any
328 of the intersections were assigned a cover value of 1%¹⁷. Total percent cover values
329 often exceeded 100% due to the multi-layered nature of macroalgal communities.
330 There were no differences in total cover (ANOVA; $F_{11,36} = 1.24$, $P > 0.05$) or macroalgal
331 assemblage structure (PERMANOVA; $Pseudo-F_{11,36} = 1.09$, $P > 0.05$) between any of
332 our experimental treatments at the beginning of the experiment. To determine
333 whether percent cover served as a reliable proxy for macroalgal biomass, we took
334 destructive samples from the central 25 x 25 cm area in each experimental plot on
335 the final sampling date to estimate biomass of each macroalgal species (excluding
336 *Lithothamnium* spp.), following drying to constant mass at 60°C. Dry biomass
337 values for *Corallina officinalis* were multiplied by 0.2 to convert them to calcium
338 carbonate-free estimates⁶⁴. There was a significant and strong linear relationship
339 between total dry biomass and total cover of macroalgae [excluding crustose
340 corallines; biomass (g m^{-2}) = $-17.89 + 0.89 \cdot \text{cover} (\%)$, $R^2 = 0.85$, $P < 0.001$, OLS
341 regression, $n = 48$].

342 We quantified six components of ecological stability (Table 1), separately for

343 both total algal cover (as a proxy for total algal biomass) and assemblage structure as
344 measures of, respectively, functional and compositional stability⁴². Contributions of
345 grazers to algal stability were then quantified as the inverse of stability responses
346 calculated from log response ratios of function and composition in perturbed and
347 unperturbed treatments following the experimental pulse perturbation (after Month
348 5; Figs. 1 & 2; that is, a strong destabilising effect of the pulse perturbation in plots
349 from which a species was removed compared to when it was present implies that
350 the species contributes strongly and positively to that component of ecological
351 stability).

352 We predicted the combined contribution of species to the various dimensions
353 of stability based upon the sum of their individual contributions⁶⁵, effectively testing
354 for transgressive over- (or under-) yielding of stability by comparing observed
355 ecosystem stability in the presence of a mixture of grazers to their expectations from
356 monocultures¹⁹. As we quantified the consequences of species loss using an additive
357 experimental design, the manipulation of grazer biomass in our combined species
358 loss treatment was equivalent to the additive combination of that in the individual
359 species loss treatments. First, we calculated the difference in stability values
360 between plots from which individual grazer taxa were removed and the mean values
361 from plots with no grazer removals. We then randomly selected combinations of
362 these deviations from each of the three constituent single grazer loss treatments
363 (that is, one measurement selected randomly from one of the plots belonging to
364 each single grazer loss treatment) by bootstrapping (1000 times) and adding to mean
365 stability values in treatments from which no grazers were removed. Log response
366 ratios of bootstrapped predicted values relative to plots from which no grazers were

367 removed were compared with observed combined removal results, after correcting
368 for original sample size ($n = 4$).

369 Analysis of variance (ANOVA) was used to test for effects of grazer treatment
370 on temporal variability, resistance, reactivity, resilience and recovery time,
371 separately for functional and compositional stability components (see Table 1 for
372 descriptions of these stability measures). Linear mixed models were used to test for
373 effects of grazer loss on spatial variability, with month incorporated as a random
374 factor. Prior to analyses, data normality and homoscedasticity were assessed using,
375 respectively, Shapiro-Wilk and Levene's tests. Data were transformed where
376 necessary: functional spatial variability, functional resistance and compositional
377 recovery time were squared, functional resilience was cube-rooted and
378 compositional resilience square-rooted to meet analytical assumptions. Student-
379 Newman-Keuls (SNK) tests were used to make *post-hoc* comparisons among levels of
380 significant terms, with the exception of spatial variability, where pairwise
381 comparisons between levels were carried out using least mean-squares estimates.

382 Permutational multivariate analysis of variance (PERMANOVA^{66,67}) was used to
383 test for effects of grazer loss on macroalgal assemblages in unperturbed treatments
384 and also for effects of our experimental perturbations. *Post-hoc* pairwise *t*-tests
385 were used to reveal differences between levels of significant terms, and the relative
386 contributions of individual macroalgal species to differences among treatment
387 groups were determined using similarity of percentages analyses (SIMPER⁶⁸).

388

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- 576

577 **Author contributions:** LW, NEOC and ID designed the research. LW performed the
578 experiment and analysed the data. LW and ID led the writing, with contributions
579 from all NEOC, QY and MCE.

580 **Data availability** The data supporting the findings of this study are available in the
581 Zonodo digital repository⁷⁷.

582 The authors declare no competing interests.

583

584 **Table 1. Components of ecological stability quantified in this study, their measurement and interpretation.** All stability components (see also
 585 Fig. 1) were calculated at plot level, based largely upon Pimm³⁶, Donohue et al.⁹ and Hillebrand et al.⁴², except for spatial variability, which
 586 could only be calculated across plots within experimental treatments separately for each algal census. Measures of functional and
 587 compositional stability were based upon, respectively, total macroalgal biomass and assemblage structure⁴².

Stability component	Time window of quantification	Method of quantification: Functional stability	Method of quantification: Compositional stability	Interpretation
Temporal variability	From Month 5 until end of experiment	The coefficient of variance (CV; that is, standard deviation divided by the mean) of total algal cover in each unperturbed experimental plot over time. Detrended to remove potentially confounding effects of biomass change over the duration of the experiment ^{9,69} .	Mean Euclidean distance from each experimental plot on every census, to their plot centroid, based on Bray-Curtis dissimilarity matrices calculated from algal cover data.	High values correspond to greater variability and, thus, lower stability.

Spatial variability	From Month 5 until end of experiment	The CV of total algal cover among unperturbed experimental plots within each grazer treatment combination on each census. Detrended to remove potentially confounding effects of biomass change over the duration of the experiment ^{9,69} .	Mean Euclidean distance from each experimental plot to their grazer treatment centroid, calculated separately for each census, based on Bray-Curtis dissimilarity matrices calculated from algal cover data.	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 ^{70,71} , which enhances the spatial asynchrony of ecosystem dynamics, and thus increases stability ^{72,73} . High spatial asynchrony of biomass can also stabilize communities by increasing temporal invariability ⁷⁴ and providing spatial insurance effects ^{75,76} .
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Resistance	Point of maximum deviation between perturbed and unperturbed plots	The maximum log response ratio of total algal cover in perturbed relative to unperturbed plots ^{42,47} .	The maximum 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 grazer loss treatment. Distances were calculated based on Bray-Curtis dissimilarity matrices calculated from algal cover data.	The extent of biomass (functional) or compositional change in response to perturbation. Large negative values indicate large reductions in biomass or shifts in assemblage structure following perturbation and, therefore, respectively, low functional and compositional resistance.
Reactivity	From perturbation until point of maximum deviation	Slope of linear regression of functional log response ratio over time immediately following perturbation until point of maximum deviation of perturbed from unperturbed treatment.	Slope of linear regression of compositional log response ratio over time immediately following perturbation until point of maximum deviation of perturbed from unperturbed treatment.	Increasing positive values correspond to lack of reactivity, and increased stability, whereas increasingly negative values indicate increasingly reactive systems and, thus, lower stability ³⁹ .

Resilience	From point of maximum deviation to point of recovery	Slope of regression of functional log response ratio over time from the point of maximum displacement between perturbed and unperturbed treatments until the point of recovery. 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 ^{42,47} .	Slope of regression of compositional log response ratio over time from the point of maximum displacement between perturbed and unperturbed treatments until the point of recovery. 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 ^{42,47} .	Increasingly positive values correspond to higher resilience (and stability), increasingly negative values indicate further deviation from unperturbed plots (that is, low resilience and stability).
Recovery time	From perturbation to point of recovery	Time taken (in months) for total algal cover to return to the 95% confidence interval of the unperturbed level of the corresponding grazer treatment, estimated by fitting an order three polynomial (cubic regression) to the functional log response ratio over time ⁴⁷ .	Time taken (in months) for compositional log response ratio to return to the 95% confidence interval of the unperturbed level of the corresponding grazer treatment, estimated by fitting an order three polynomial (cubic regression) to the	Greater recovery time corresponds to low stability whereas short recovery time is associated with greater stability. Within the theoretical setting of exponential return, resilience, the rate of exponential return, is the inverse of the return time ³⁶ . We did not observe

compositional log response ratio over
time⁴⁷.

similar dynamics; resilience and
recovery time were not correlated, thus
we analysed them independently.

Figure legends

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

We quantified contributions of individual species to the various components of stability by comparing stability properties in plots from which species were removed (red lines) to those that experienced no species losses (blue lines).

We measured stability responses to our experimentally-imposed pulse perturbation (that is, resistance, reactivity, recovery time and resilience; see Table 1 for detailed description of stability measures and their quantification) by comparing perturbed (solid lines) to equivalent unperturbed (dotted lines) plots within species removal treatments. Because they do not require an explicit perturbation for their quantification, spatial and temporal variability were measured from unperturbed plots only. Where a dimension of stability was reduced (that is, the system was destabilized) in the absence of a species (red lines) compared to when it was present (blue lines), 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.

Fig. 2 | Relative responses of macroalgal communities to our experimental pulse perturbation over time.

Mean (\pm SE, $n = 4$) log response ratios (LRRs), with raw data points, of the (a) functional (total cover) and (b) compositional responses of macroalgal assemblages to perturbation in plots from which different grazer taxa were removed (that is, LRRs of perturbed compared to equivalent unperturbed plots

belonging to the same grazer manipulation treatment) over the duration of the experiment. Reduction of a dimension of stability in the absence of a species (blue, green, orange and grey lines) compared to when it was present (yellow line) implies that the species contributes positively to that dimension of stability, and *vice versa*. Thick lines indicate significant ($P < 0.05$) effects of the perturbation, based on two-sample *t*-tests and PERMANOVAs for, respectively, functional and compositional responses.

Fig. 3 | Species contributions to multiple components of ecological stability. Mean (\pm SE, $n = 4$ for all measures except spatial variability, for which $n = 11$) log response ratios, with raw data points, indicating contributions of grazer species, both individual and combined, to multiple components of (a) functional and (b) compositional stability. Data points above the dashed horizontal line indicate a stabilising contribution relative to the treatment from which no species were removed (that is, the presence of a species promoted resistance, resilience, recovery or spatial variability, or decreased temporal variability or reactivity) and those below the line indicate a destabilising contribution, whereby the presence of a species reduced stability. Where significant treatment effects were found, letters indicate where species contributions are statistically indistinguishable from each other based on SNK tests ($P > 0.05$; see also Extended Data Fig. 1).

Fig. 4 | Comparison of observed combined contributions of multiple grazer species to stability to those predicted from the additive combination of individual taxa.

Mean (\pm SE, $n = 4$, for all measures except spatial variability, for which $n = 11$) log response ratios indicating observed contributions of grazer species when present together (grey circles), with raw data points, and those predicted from the additive combination of the individual constituent taxa (red circles) to multiple components of (a) functional and (b) compositional stability (see *Methods* for details on how predicted combined species contributions were calculated).