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Individual species provide multifaceted contributions to the stability of ecosystems

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

The erosion of biodiversity is a particularly insidious consequence of human activities[1–6]. There is now widespread evidence to show that loss of biodiversity leads to declines in the functioning[4,7,8] and stability[9–12] of ecosystems and can trigger significant extinction cascades[13,14]. Despite this general understanding, predicting the consequences of individual species loss from ecosystems remains a fundamental challenge in ecology[15,16].

All species are not equal. They contribute differently to the dynamics, structure and function of ecosystems[9,13,15,17–21]. The ability to partition species contributions to, for example, ecosystem productivity in different ecological contexts[19] has proved to be of enormous benefit to research on relationships between biodiversity and ecosystem functioning. However, no such framework exists for overall ecological stability. Such a framework could provide the basis for a far richer understanding of the frequently disparate relationships between biodiversity and stability observed in both models and experiments[22–28]. The capacity to quantify the relative extent of additivity and complementarity in species contributions to stability would, for example, provide considerable insight into the predictability of stability in natural communities and a more contextual understanding of its relationships with diversity.

While the consequences of species loss have been a key focus of ecologists for decades[13,17,29–34], this large body of theoretical and empirical understanding provides limited insight into the contributions of species to the many dimensions of ecological stability[9,35]—a multidimensional concept that tries to capture the different aspects of the dynamics of the system and its response to perturbations[35,36] (Fig. 1). Certainly, measuring how a system has changed following the addition or local extinction of a species enables quantification of the net contribution of that species to, for example, the temporal and spatial variability of biomass production (see ref. [37] for an example of how to predict the temporal variability of community biomass from that of its constituent species). However, it provides little insight into the contribution of the species to those dimensions of stability that characterize explicitly the response of systems to perturbations[35], such as their reactivity—their propensity to amplify the effects of perturbations[38,39]—and their capacity to resist and recover from those perturbations (respectively, their resistance and resilience). Such insight can only be properly gained empirically by comparing the responses of the system to independent perturbations in both the presence and the absence of the species, after transient dynamics have attenuated and the interaction network has 'rewired' following the loss (or, indeed, the addition) of the species (Fig. 1).

Here, we quantify the simultaneous contributions of different consumer species to multiple dimensions of the stability of a coastal rocky shore ecosystem (see Fig. 1 for a description of our experimental framework and Table 1 for the stability measures used and their derivation) and test whether those contributions are additive across species. Specifically, we simulated experimentally the loss of three key grazer taxa—the limpet *Patella*, the periwinkle *Littorina* and the topshell *Gibbula*—and quantified multiple stability responses of the macroalgal communities on the shore to a subsequent pulse perturbation (that is, 50% removal of total macroalgal cover). The experiment was performed in the presence and absence of each of the grazers, both separately and together, in a factorial experimental design. To maximize the ecological realism of our results, we conducted the experiment on the shoreline using natural communities structured by a diverse range of both trophic and non-trophic interactions[31,40]. We thereby caused the local extinction of various components of a larger intertidal food web in an open experimental system, which allowed immigration and recruitment of primary producers and many epibenthic consumers, including primary consumers and small predators (for example, amphipods, polychaetes and Nemertea).

We tested (1) whether the different consumer species contribute in different ways to different dimensions of ecological stability. In addition, because cumulative loss of multiple species frequently

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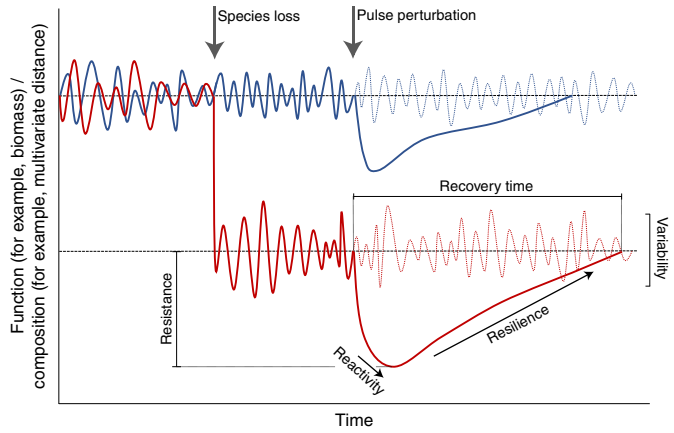

Fig. 1 | Quantification of species contributions to multiple dimensions of ecological stability. We quantified contributions of individual species to the various components of stability by comparing stability properties in plots from which species were removed (red lines) to those that experienced no 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.

alters communities in ways than cannot be predicted based on removals of single species[15,41], we explored, for multiple dimensions of stability, (2) whether the strength and/or the nature of combined contributions of taxa to stability can be predicted from the additive combination of their individual contributions.

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

Results

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

We found that *Patella* in general contributed strongly and positively to functional stability responses to our experimental pulse perturbation (Figs. 2a and 3a), but more weakly to those of compositional stability (Figs. 2b and 3b). In fact, the presence of *Patella* even strongly destabilized algal communities along some dimensions of compositional stability, for example, compositional resistance (Fig. 3b). In contrast, *Littorina* was the strongest contributor of the species we examined to compositional resistance (Fig. 3b and Extended Data Fig. 1). Even so, its presence had the most destabilizing effect on functional resilience (Fig. 3a and Extended Data Fig. 1). Finally, the contribution of *Gibbula* to the functional stability of algal communities was, in general, intermediate between those of *Patella* and *Littorina* (Figs. 2 and 3, Extended Data Fig. 1). Yet, algal community composition in plots from which *Gibbula* were removed was more reactive than in any other treatment (Extended Data Fig. 1). In other words, the presence of *Gibbula* strongly stabilized communities by reducing the reactivity of algal community composition after the pulse perturbation (Fig. 3b).

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

Across all of our experimental treatments, functional stability responses of algal communities were largely independent of those of compositional stability. Although functional resistance to the pulse perturbation correlated positively with compositional resistance across our experimental plots ($P = 0.002$, reduced major axis regression, $n = 20$), no other functional stability responses correlated with their equivalent component of compositional stability (Extended Data Fig. 2).

Discussion

Our results demonstrate that species not only contribute in different ways to different dimensions of stability, but also that they can simultaneously have a stabilizing and destabilizing influence on ecosystems. *Patella* contributed positively to functional stability by enhancing resilience to perturbations yet, in parallel, destabilized communities by reducing the resistance of community composition. *Littorina* had the most destabilizing effect of all the species we examined on functional resilience, while the presence of *Gibbula* strongly stabilized community composition by suppressing the propensity for reactivity following perturbation. These results highlight the complexities and context-dependence associated with predicting the consequences of species loss from ecosystems. They also emphasize the importance of all species, and the interaction network within which they are embedded, for maintaining the over-

Table 1 | Components of ecological stability quantified in this study, their measurement and interpretation

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[9,70].	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[9,70].	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[71,72], which enhances the spatial asynchrony of ecosystem dynamics and, thus, increases stability[73,74]. High spatial asynchrony of biomass can also stabilize communities by increasing temporal invariability[75] and providing spatial insurance effects[76,77].
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 compositional log response ratio over time[47].	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 similar dynamics; resilience and recovery time were not correlated, thus we analysed them independently.

All stability components (see also Fig. 1) were calculated at plot level, based largely upon Pimm[36], Donohue et al.[9] and Hillebrand et al.[42], except for spatial variability, which could only be calculated across plots within experimental treatments separately for each algal census. Measures of functional and compositional stability were based upon, respectively, total macroalgal biomass and assemblage structure[42].

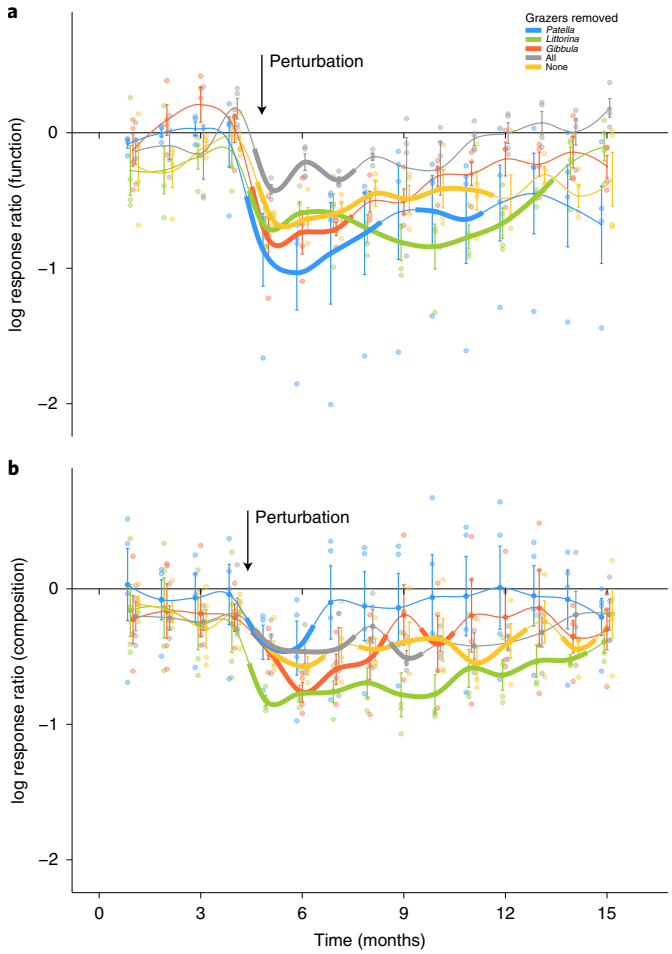

Fig. 2 | Relative responses of macroalgal communities to our experimental pulse perturbation over time. a,**b**, Mean (±s.e.m., $n=4$) log response ratios with raw data points, of the functional (total cover) (**a**) and compositional (**b**) responses of macroalgal assemblages to perturbation in plots from which different grazer taxa were removed (that is, log response ratios 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.

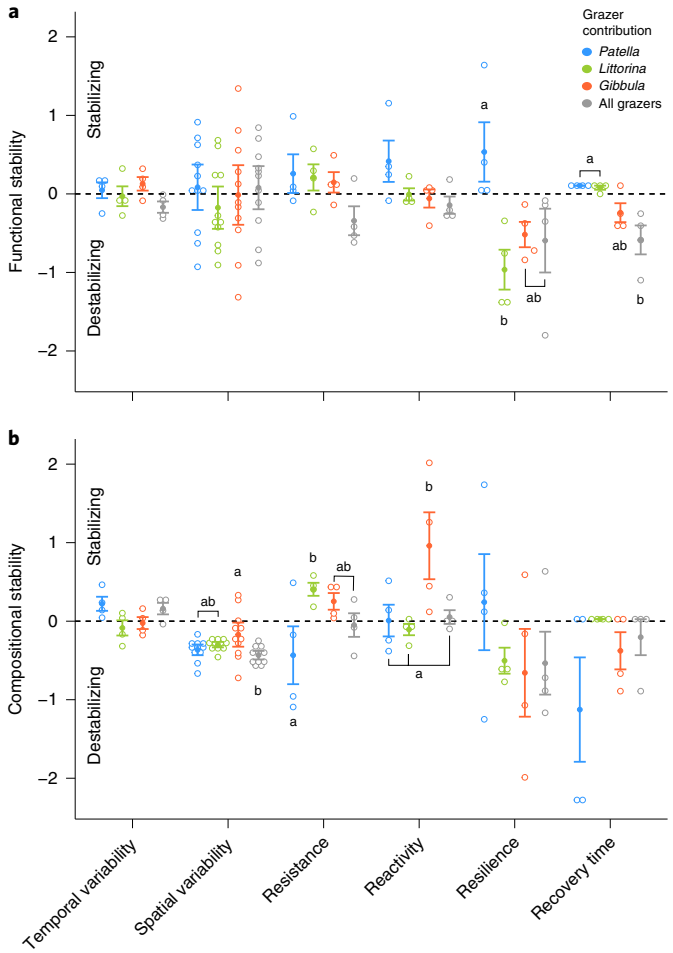

Fig. 3 | Species contributions to multiple components of ecological stability. a,**b**, Mean (±s.e.m., $n=4$ for all measures except spatial variability, for which $n=11$) log response ratios, with raw data points, indicating contributions of grazer species, both individual and combined, to multiple components of functional (**a**) and compositional (**b**) stability. Data points above the dashed horizontal line indicate a stabilizing 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 destabilizing 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).

all multidimensional stability of ecosystems. No single component of stability would have captured the complex ecological responses to our experimental pulse perturbation. The fundamental insight needed for effective management of ecosystem stability therefore demands consistently multidimensional assessment of ecological responses to disturbance[12,35].

Metrics of functional and compositional stability varied considerably and were, as expected, generally independent. Our results are broadly consistent with those of Hillebrand et al.[42], who found that functional resilience and temporal variability of freshwater plankton communities were independent of their equivalent component of compositional stability, but also that functional and compositional resistance correlated positively. They are also consistent with a recently documented general tendency towards independence of recovery rates of community biomass and species composition following pulse perturbations[43], which highlights the importance of considering the timescales of ecological responses to perturbations, across which our predictive capacity can vary considerably[47–49]. Managing systems for functional stability may, therefore, have negative consequences for compositional stability and vice versa, a finding that has profound implications for policymakers needing to prioritize certain components of stability over others to meet relevant goals[35]. For example, managing to optimize only compositional stability, such as preserving species composition or diversity within a protected area, will not necessarily improve functional stability, and could have detrimental consequences for the stability of biomass and productivity[28]. Focusing on either functional or compositional stability in isolation risks an incomplete understanding of the effects of perturbations on ecosystems, coupled with a strong likelihood of underestimating their overall impacts[42].

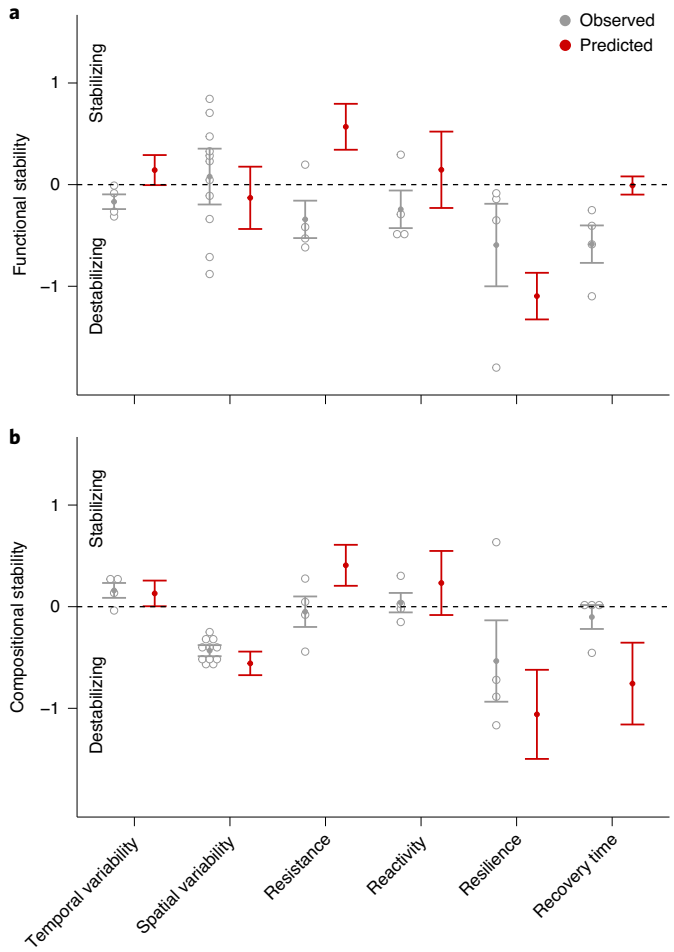

Fig. 4 | Comparison of observed combined contributions of multiple grazer species to stability to those predicted from the additive combination of individual taxa. a,**b**, Mean (±s.e.m., $n=4$, for all measures except spatial variability, for which $n=11$) log response ratios indicating observed contributions 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 functional (**a**) and compositional (**b**) stability (see Methods for details on how predicted combined species contributions were calculated).

Although combined contributions of multiple species to some dimensions of stability were additive, many combined contributions—particularly to functional stability responses—could not be predicted reliably from the additive contributions of individual species, with some predictions severely under- or overestimating stability. This is broadly consistent with the disparate relationships between diversity and stability found in both models and experiments[22–27], and also provides a mechanism for explaining how the relationship between species diversity and ecological stability can vary simultaneously among multiple stability dimensions[28]. Further, this finding also reflects our understanding of the individual and cumulative effects of species on multiple ecosystem functions[15,19], and is probably a consequence of idiosyncratic interactions between our focal consumers. In fact, single species frequently contributed more strongly to stability than the simultaneous combinations of multiple species, highlighting the significant challenges associated with predicting the impacts of cumulative species losses on ecosystems under global environmental change.

Our experiment was done using natural communities in the field and, as such, maximized ecological realism as far as possible[40]. Our findings are, nonetheless, from a single system over a 15-month duration, and both biological and environmental context can strongly influence the conclusions of field experiments[16,48,50–54]. The generality of our findings therefore needs to be explored in other systems. The experimental framework presented here could also be extended to observational studies of, for example, invasion or species loss. Comparing the response of rock pool communities that have been invaded by an invasive alga to various anthropogenic stressors with those that have yet to be invaded could provide insight on the invasive's capacity to destabilize surrounding communities[55]. Similarly, exploring invaded and uninvaded grassland communities and their responses to perturbations will allow identification of stabilizing and destabilizing invaders and a potential way to prioritize their management. The framework may also be applicable to exploration of time series, in particular if information on local pressures or perturbation events is known. For example, the effects of an oil spill on macrobenthic communities could be explored where the presence of species of interest vary among sampling sites, thus enabling quantification of the contribution of those species to resistance and recovery from such events[56,57].

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

Methods

Study site. Our experiment took place on an exposed Atlantic rocky shore at Glashagh Bay, Fanad, County Donegal, Ireland (55° 26′ 5″ N, 7° 67′ 5″ W) over 15 months from May 2016. The shore comprised a large gently sloping granitic platform covered by a network of barnacles, macroalgae and bare rock[41], typical of exposed shores in the region[58], with small patches of juvenile mussel beds present around the mid-shore region (2.0–2.5 m above Chart Datum). Discrete shallow rock pools were widespread throughout the intertidal zone, dominated by turfs of upright calcareous algae (*Corallina officinalis*). These supported a diverse macroalgal assemblage, including fine (for example, *Ceramium nodulosum*), coarse (for example, *Osmundea hybrida*) and ephemeral (for example, *Porphyra umbilicalis*) red algae, perennial (for example, *Codium fragilis*) and ephemeral (for example, *Ulva compressa, Bryopsis* spp.) green algae and brown canopy algae (for example, *Fucus serratus* and *Cystoseira tamariscifolia*). Encrusting macroalgae (*Lithothamnia* spp.) covered most remaining bare rock.

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

Experimental design. Forty experimental plots were established in rock pools on the shore around mid-tidal level across approximately 100 m of shoreline, with a minimum of 2 m between plots. Plots were enclosed by cages (35 × 35 cm^2, 12 cm high) constructed from stainless steel mesh (0.9-mm-diameter wire, 4.17 mm aperture, 67% open area) fixed to the substratum with screws and washers. This enabled us to restrict the movement of our focal grazer species into and out of plots, while allowing access to smaller mobile consumers, including annelid and nemertean worms, amphipods and juvenile gastropod grazers, in addition to propagules of sessile benthic fauna and algae. This cage design has been used extensively and successfully to manipulate consumer presence on rocky shores with no consequences for algal community structure or stability[13,16,17,41,51,59]. Plots were situated in separate shallow pools of similar area (range 0.5–5.0 m^2) and depth (<12 cm) and included in excess of 60% (mean ± s.e.m., 66 ± 2.4%) coverage of coralline algae.

The experiment involved the single and combined removal of three focal gastropod grazer taxa from rock pools. There was no experimental

compensation for the loss of a particular species, or artificial increase in biomass of the remaining species, akin to additive designs. Unlike substitutive designs, additive designs avoid confounding intra- and interspecific interactions with changes in diversity[60] and our design ensured that interspecific differences in standing stock were represented[52]. Five grazer removal treatments were assigned randomly to plots: one non-removal treatment requiring no removal of species; three single species removal treatments involving removal of either *Patella* spp., *L. littorea* or *G. umbilicalis*, and one combined removal treatment in which all three focal grazer taxa were removed simultaneously. Every experimental treatment was replicated four times. Due to difficulties in differentiating *P. ulyssiponensis* and *P. vulgata*, particularly juveniles, in plots without causing considerable disturbance and probable death, we did not discriminate between the two limpet species in our experiment. *P. ulyssiponensis* dominated in rock pools, although *P. vulgata*, which tends to disperse onto emergent rock[61], were also present in pools at much lower densities (<15%). All experimental grazer densities were based on adult sizes because of difficulties associated with effectively manipulating juveniles, and were based on natural densities found in rock pools during preliminary surveys of the experimental site (that is, *Patella*, $52.1 \pm 11.7\ m^{-2}$; *Littorina*, $80.6 \pm 19.1\ m^{-2}$; *Gibbula*, $20.8 \pm 4.9\ m^{-2}$). Grazer abundances within our experimental plots were therefore as follows: seven *Patella* individuals, ten *Littorina* and three *Gibbula*. Where appropriate, grazer populations were supplemented with additional individuals to meet target densities.

Our experimental design comprised two levels of perturbation (that is, perturbed and unperturbed). Perturbed plots had 50% macroalgal cover removed manually with a chisel as a single pulse perturbation event four months after grazer treatment manipulation. Previous consumer species loss experiments in similar coastal systems have found that four months is generally sufficient for transient dynamics to attenuate[9,13]. Half of the substratum was cleared in a single patch in perturbed plots, and the orientation of this patch was randomized among plots. The aim of the perturbation was to simulate a single extreme storm event, similar to disturbance events employed in previous studies[62,63]. Our perturbation treatment was crossed fully with the five grazer removal treatments, giving a total of ten treatments in a full-factorial design, each replicated four times. The perturbation caused significant shifts in macroalgal cover (analysis of variance (ANOVA); $F_{1,38} = 90.69$, $P < 0.0001$) and assemblage structure (permutational multivariate analysis of variance (PERMANOVA); pseudo-$F_{1,38} = 11.06$, $P = 0.0001$). This was consistently underpinned by higher relative abundance of *C. officinalis* in perturbed plots in all treatments from which grazers were removed, although the loss of different grazer taxa also moderated how macroalgal assemblage composition responded to the perturbation (Supplementary Table 3).

To enable detection of experimental artefacts arising from the use of cages, we established an additional eight open plots (four of which were allocated to the perturbed treatment and four to the unperturbed), marked at the corners with screws, thus remaining open to natural densities of mobile organisms on the shore. These were interspersed haphazardly among the caged plots, enabling us to compare consumer and algal assemblage dynamics within caged plots with those on the natural shore over the duration of the experiment. The dynamics of both algal cover and assemblage structure was similar in both the uncaged plots and the caged plots with no grazer removals (Extended Data Fig. 3) and we found no differences in any measure of functional or compositional stability between the two treatments (Supplementary Table 4).

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

We quantified six components of ecological stability (Table 1), separately for both total algal cover (as a proxy for total algal biomass) and assemblage structure as measures of, respectively, functional and compositional stability[42]. Contributions of grazers to algal stability were then quantified as the inverse of stability responses calculated from log response ratios of function and composition in perturbed and unperturbed treatments following the experimental pulse perturbation (after month 5; Figs. 1 and 2; that is, a strong destabilizing effect of the pulse perturbation in plots from which a species was removed compared to when it was present implies that the species contributes strongly and positively to that component of ecological stability).

We predicted the combined contribution of species to the various dimensions of stability based upon the sum of their individual contributions[65], effectively testing for transgressive over- (or under-) yielding of stability by comparing observed ecosystem stability in the presence of a mixture of grazers to their expectations from monocultures[19]. As we quantified the consequences of species loss using an additive experimental design, the manipulation of grazer biomass in our combined species loss treatment was equivalent to the additive combination of that in the individual species loss treatments. First, we calculated the difference in stability values between plots from which individual grazer taxa were removed and the mean values from plots with no grazer removals. We then randomly selected combinations of these deviations from each of the three constituent single grazer loss treatments (that is, one measurement selected randomly from one of the plots belonging to each single grazer loss treatment) by bootstrapping (1,000 times) and adding to mean stability values in treatments from which no grazers were removed. Log response ratios of bootstrapped predicted values relative to plots from which no grazers were removed were compared with observed combined removal results, after correcting for original sample size ($n = 4$).

ANOVA was used to test for effects of grazer treatment on temporal variability, resistance, reactivity, resilience and recovery time, separately for functional and compositional stability components (see Table 1 for descriptions of these stability measures). Linear mixed models were used to test for effects of grazer loss on spatial variability, with month incorporated as a random factor. Before analyses, data normality and homoscedasticity were assessed using, respectively, Shapiro–Wilk and Levene's tests. Data were transformed where necessary: functional spatial variability, functional resistance and compositional recovery time were squared, functional resilience was cube-rooted and compositional resilience square-rooted to meet analytical assumptions. SNK tests were used to make post-hoc comparisons among levels of significant terms, with the exception of spatial variability, where pairwise comparisons between levels were carried out using least mean squared estimates.

PERMANOVA[66,67] was used to test for effects of grazer loss on macroalgal assemblages in unperturbed treatments and also for effects of our experimental perturbations. Post-hoc pairwise *t*-tests were used to reveal differences between levels of significant terms, and the relative contributions of individual macroalgal species to differences among treatment groups were determined using similarity of percentages analyses[68].

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data supporting the findings of this study are available in the Zonodo digital repository[69].

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Author contributions

L.W., N.E.O'C. and I.D. designed the research. L.W. performed the experiment and analysed the data. L.W. and I.D. led the writing, with contributions from N.E.O'C., Q.Y. and M.C.E.

Competing interests

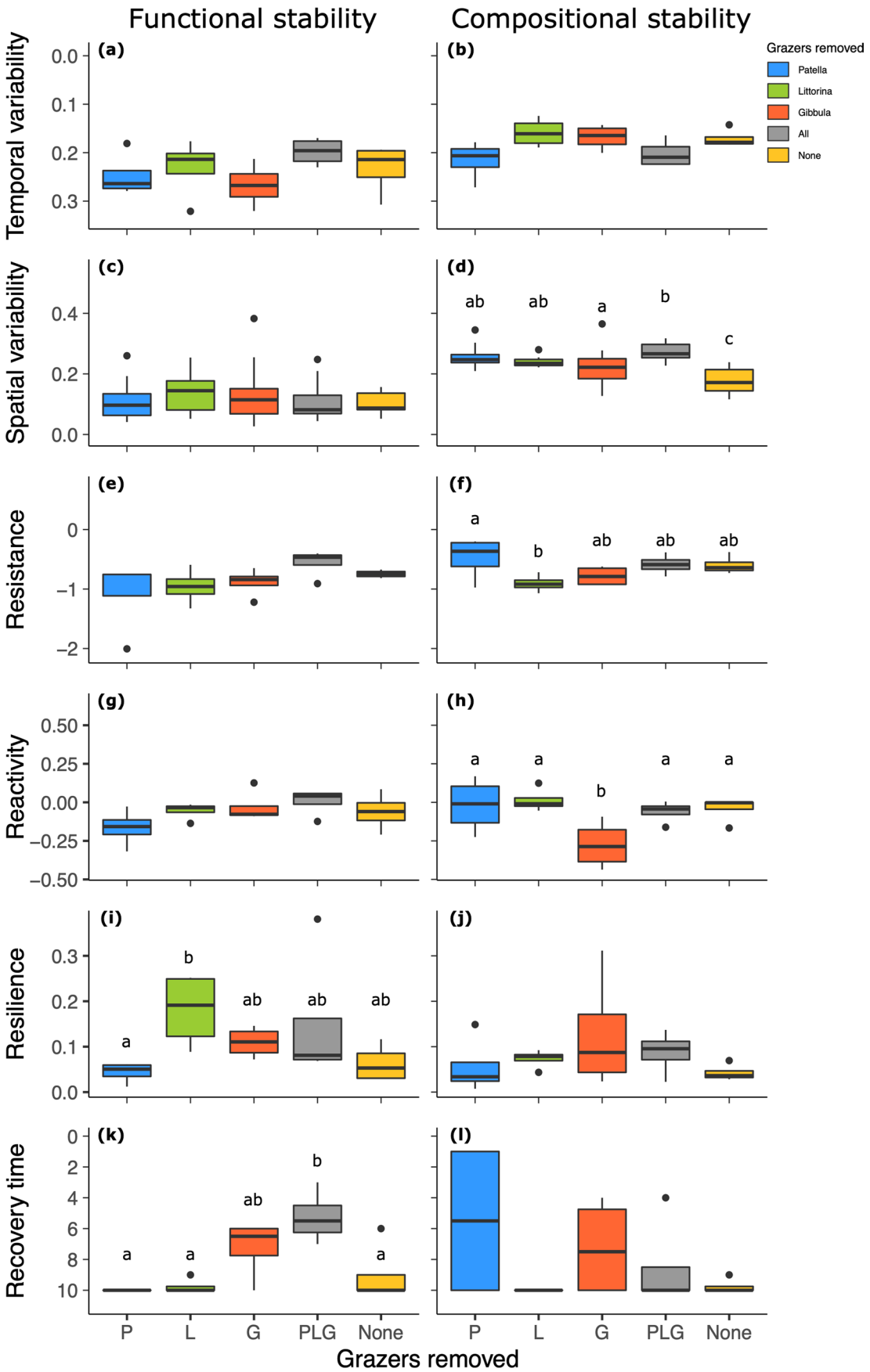
The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41559-020-01315-w.

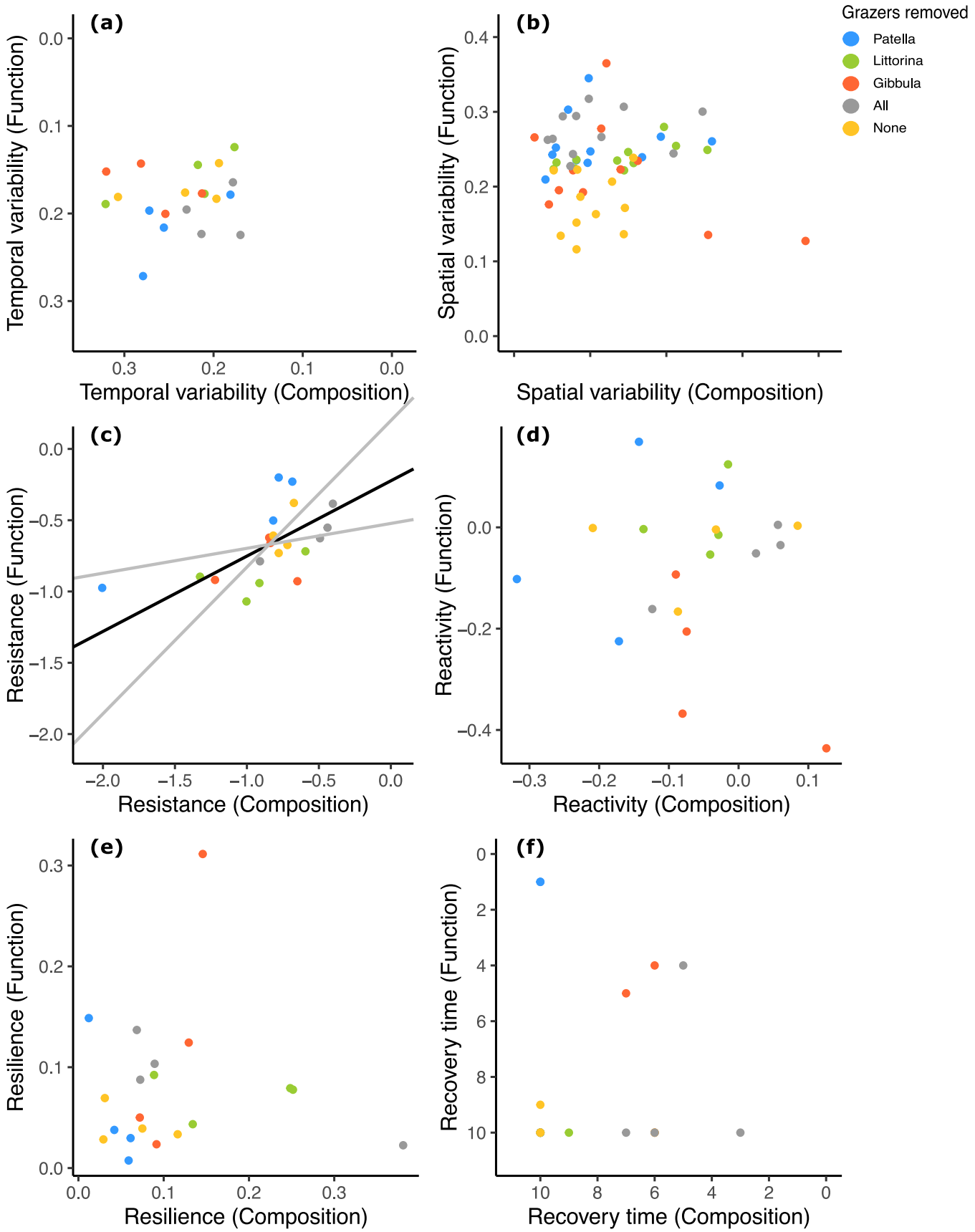
Supplementary information is available for this paper at https://doi.org/10.1038/s41559-020-01315-w.

Correspondence and requests for materials should be addressed to I.D.

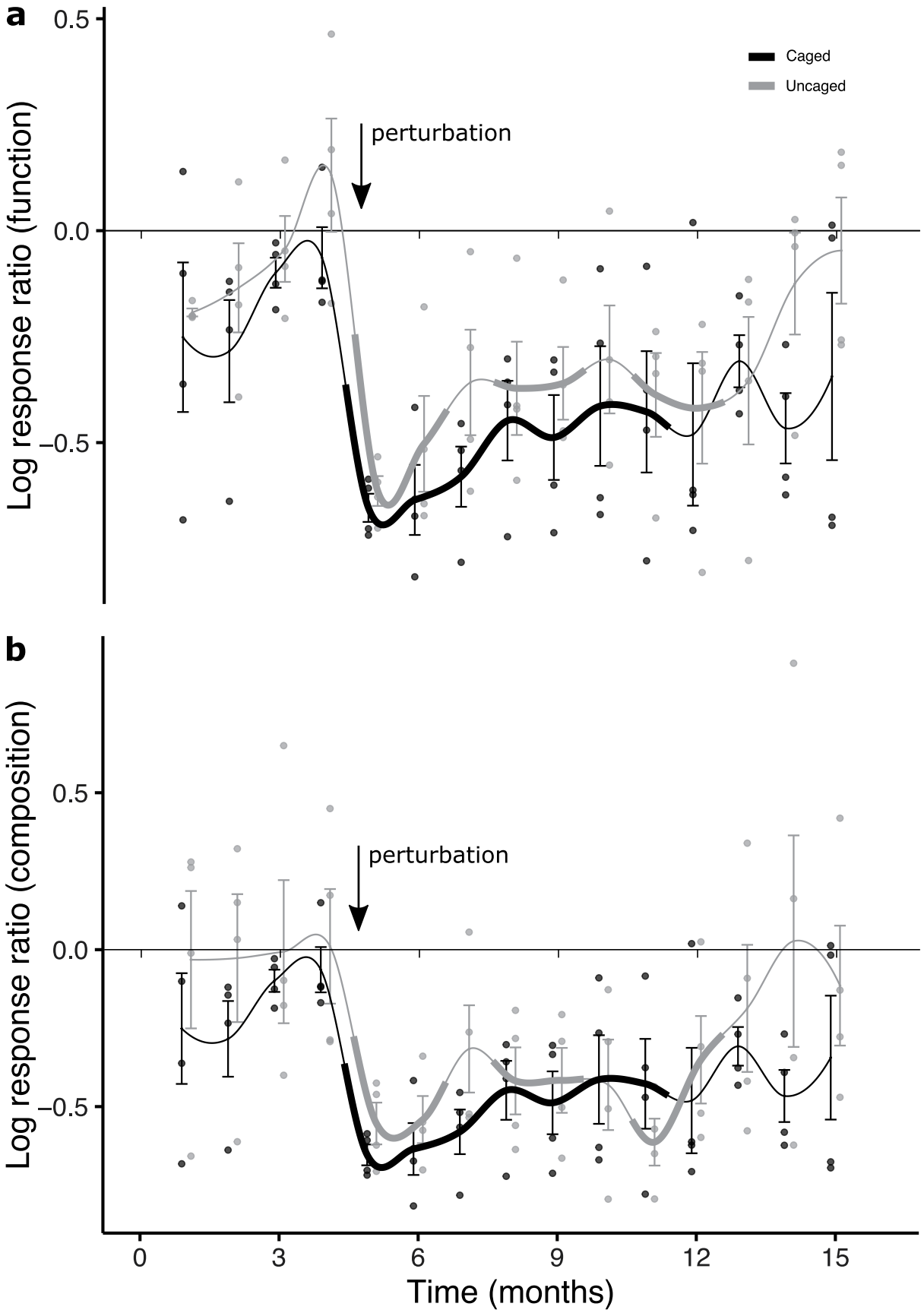


Extended Data Fig. 1 | See next page for caption.

Extended Data Fig. 1 | Functional and compositional stability responses of macroalgal assemblages in our different grazer loss treatments. Box and whisker plots ($n = 4$, for all measures except spatial variability, for which, $n = 11$) of (**a**, **b**) spatial and (**c**, **d**) temporal variability of macroalgal communities in unperturbed plots and (**e**, **f**) resistance, (**g**, **h**) reactivity, (**i**, **j**) resilience and (**k**, **l**) recovery time of macroalgal communities in response to our experimentally-imposed pulse perturbation. The centre line indicates the median, the bottom and top hinges of the box and whiskers plot correspond to the 25th and 75th percentiles, and the bottom and top whiskers extend from the hinge to the lowest and highest value, respectively (maximum 1.5× interquartile range from the hinge). Outlying points are plotted individually. Functional stability responses (**a**, **c**, **e**, **g**, **i**, **k**) were based on total macroalgal cover, whereas compositional stability responses (**b**, **d**, **f**, **h**, **j**, **l**) were based on macroalgal community composition. Stability increases from the bottom to the top of the y-axis in every case. A strong destabilising effect of the pulse perturbation in plots from which a species was removed compared to those in which it was present implies that the species contributes strongly to that component of ecological stability. Letters indicate treatments that are statistically indistinguishable from each other based on SNK tests ($P > 0.05$).



Extended Data Fig. 2 | Relationships between functional and compositional stability properties of macroalgal assemblages. Analyses were pooled across grazer loss treatments ($n = 20$), with each point representing a single replicate plot. Significant ($P < 0.05$) relationships are indicated by the presence of a reduced major axis regression line, with associated 95% confidence intervals.



Extended Data Fig. 3 | See next page for caption.

Extended Data Fig. 3 | Responses of macroalgal communities to our experimental pulse perturbation over time in uncaged plots and caged plots from which no species were removed. Mean (± s.e.m., $n = 4$) log response ratios (LRRs), overlain with raw data points, of the (**a**) functional (total cover) and (**b**) compositional responses of macroalgal assemblages to our experimental pulse perturbation (that is, LRRs of perturbed compared to equivalent unperturbed plots within caged and uncaged treatments) in plots from caged plots with no grazer removals (black line) and open uncaged control plots (grey line) over the duration of the experiment. 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.

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☐	☒ A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
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☐	☒ Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used to collect data.
Data analysis	All statistical analyses were done using the R statistical computing environment (version 3.3.3), except for PERMANOVAs, which were done using the PERMANOVA add-on in PRIMER version 6.1.13. We used the following R packages for analyses: nlme (version 3.1.137), vegan (version 2.5-2), lsmeans (version 2.27-52), lmodel2 (version 1.7-3).

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Ecological, evolutionary & environmental sciences study design

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Study description	We factorially manipulated grazer loss (one non-removal treatment; three single removal treatments involving removal of either Patella spp., Littorina littorea or Gibbula umbilicalis and one combined removal treatment in which all three grazer taxa were removed simultaneously) and two levels of physical perturbation (i.e. perturbed and unperturbed) within 48 discrete shallow rock pools on an exposed atlantic shore. The 12 treatment combinations were each replicated 4 times.
Research sample	We surveyed the relative abundance of 60 different macroalgal taxa found within each plot. Taxa were identified to species or genus level.
Sampling strategy	We measured the percent cover of macroalgae within experimental plots periodically using a quadrat.
Data collection	We measured the percent cover of macroalgae using a 25 x 25 cm quadrat with 64 intersections, positioned centrally within plots to avoid sampling edge effects. Species present within the quadrat but not occurring underneath any of the intersections were assigned a cover value of 1%. To determine whether percent cover served as a reliable proxy for macroalgal biomass, we took destructive samples from the central 25 x 25 cm area in each experimental plot on the final sampling date to estimate biomass of each macroalgal species, following drying to constant mass at 60°C. All data were collected by LW.
Timing and spatial scale	We surveyed each experimental plot every month from May 2016 until July 2017, resulting in a time series of 15 time points over a 14 month period. This sampling regime is adequate to characterize biomass dynamics over time. Perturbed plots had 50% macroalgal cover removed manually with a chisel as a single pulse perturbation event four months after grazer treatment manipulation to allow sufficient time for transient dynamics to attenuate.
Data exclusions	No data were excluded from analyses
Reproducibility	Each treatment combination was replicated 4 times, with replicates being true biological replicates indicating biological variation.
Randomization	Experimental plots were randomly assigned to treatments. Within perturbed plots the orientation of the cleared patch was randomised among plots.
Blinding	No blinding was applied during data aquisition. However, given the high number of experimental plots and treatments, the considerable variation among plots, and the randomisation of experimental treatments across plots, no systematic observer bias is expected.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Monthly in situ surveys of algal communities were done during low Spring tides from May 2017 to July 2017. Mean monthly temperatures varied between 6.5 and 17.5 degrees Celcius and mean monthly light intensity varied from 40 to 140 lumens ft-2 in the local intertidal region during the course of the experiment, weather conditions were highly variable.
Location	Our experiment was done within shallow rock pools (depth < 12 cm) in the mid-shore region (2 - 2.5 m above Chart Datum) of an exposed Atlantic rocky shore at Glansagh Bay, Fanad, Co. Donegal, Ireland (55°26'5''N, 7°67'5''W).
Access and import/export	No access or permits were required by law for the installation of stainless steel cages on the shore, translocation of gastropods or the removal of algal samples at the end of the experiment.
Disturbance	Stainless steel cages were removed promptly from the shore at the end of the experiment to minimise disturbance to the local habitat, algal and invertebrate communities quickly colonised any patches that had been cleared as a result of the cages.

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Materials & experimental systems

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☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	The study did not involve laboratory animals.
Wild animals	No wild animals were killed as part of our study. Individuals of Patella spp., Littorina littorea and Gibbula umbilicalus were removed from selected experimental plots to other areas on the shoreline.
Field-collected samples	The study did not involve animal samples collected from the field. Gastropods were weighed and measured on the shore. Measures of functional and compositional stability were based on monthly surveys but required destructive sampling of macroalgal communities at the end of the experiment to quantify relationships between percentage cover and biomass.
Ethics oversight	Given that the study was done in the field and involved removing invertebrate grazers from plots and replacing them elsewhere on the shore, the study did not require ethical approval.

Note that full information on the approval of the study protocol must also be provided in the manuscript.