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1 **TEMPORAL VARIABILITY OF A SINGLE POPULATION**
2 **CAN DETERMINE THE VULNERABILITY OF**
3 **COMMUNITIES TO PERTURBATIONS**

4
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17 **Summary**

18

- 19 1. Many aspects of global change affect the variability of species population densities, in
20 terms of both the magnitude and pattern of density fluctuations. However, we have limited
21 empirical understanding of the consequences of altered temporal variability of
22 populations, independent of changes in their mean densities, for the structure and stability
23 of natural communities and the responses of ecosystems to additional stressors.
- 24 2. We used a field experiment to test the effects of altered temporal variability of a single
25 consumer species on community structure and stability. Specifically, we manipulated the
26 temporal variability of populations of a key grazer species on temperate rocky shores
27 (*Littorina littorea*), independent of their mean densities, over 12 months and measured the
28 responses of algal communities in terms of multiple measures of structure and stability.
29 Further, we tested whether consumer variability determined the effects of an additional
30 perturbation, elevated sedimentation, on algal communities.
- 31 3. The effects of sedimentation on the structure and stability of algal communities were
32 regulated by the temporal variability of consumer populations. In particular, elevated
33 sedimentation led to a decrease in algal evenness, but only when consumer densities were
34 held constant, and resulted in a decrease in the rate of local algal extinctions, but only
35 when consumer temporal variability was increased.
- 36 4. Independent of sedimentation, increased temporal variability of consumer populations led
37 to a shift in algal assemblage structure and affected the stability of algal communities in
38 terms of both compositional turnover and resistance to environmental perturbations.
39 **Further**, these effects varied according to the temporal pattern of consumer density
40 fluctuations.

41 5. *Synthesis*. Our results demonstrate that changes in the temporal variability of a single
42 species can modify multiple aspects of both the structure and stability of natural
43 communities and alter their responses to perturbations. **However**, the effects of consumer
44 variability cannot be predicted without knowledge of the temporal pattern of density
45 fluctuations. These findings have profound implications for our understanding of the
46 effects of multiple disturbances on ecosystems.

47

48 **Key-words:** algae, diversity, ecosystem functioning, field experiment, *Littorina littorea*,
49 multiple stressors, plant–herbivore interactions, rocky intertidal, sedimentation, stability

50 **Introduction**

51

52 Human-induced global environmental change is threatening the functioning and stability of
53 Earth's ecosystems and the valuable services **that** they provide (Vitousek *et al.* 1997;
54 Millennium Ecosystem Assessment 2005; Cardinale *et al.* 2012; Hooper *et al.* 2012). **In**
55 **addition to the intensification of multiple environmental stressors (IPCC 2014)**, many aspects
56 of global change are expected to alter the frequency, variance and timing of disturbances
57 (Easterling *et al.* 2000; Rhein *et al.* 2013), the **complex ecological** consequences of which
58 may be difficult to predict (Benedetti-Cecchi *et al.* 2006; García Molinos & Donohue 2010,
59 2011; Pincebourde *et al.* 2012). **In light of these concerns, there has been increasing emphasis**
60 **on the importance of spatial and temporal variability, versus the mean intensity, of ecological**
61 **processes and their environmental drivers (Benedetti-Cecchi 2003; Bertocci *et al.* 2005;**
62 **Atalah, Anderson & Costello 2007; Stier *et al.* 2013).**

63

64 **Densities of consumers and the strengths of their interactions with prey are naturally**
65 **heterogeneous in both space and time, as a result of intrinsic community dynamics and**
66 **exogenous environmental forcing (Butler 1989; Navarrete 1996; Berlow 1999; Lauzon-Guay**
67 **& Scheibling 2009). The variability of specific consumer populations may also be modified**
68 **by human activities (Adler, Raff & Lauenroth 2001; Castilla & Defeo 2001). Several common**
69 ecosystem management practices, such as those in agricultural systems, in fisheries and in
70 many forms of conservation, are based on the direct manipulation of the biomass of one, or
71 perhaps a few, focal species, altering the temporal variability of their population densities in
72 different ways. For example, the harvesting of commercial wild species in marine systems
73 often follows 'boom and bust' trends, increasing the variability in biomass of key consumers
74 (Castilla & Defeo 2001; Worm *et al.* 2006), while management of livestock tends to promote

75 the reduction of grazing variability in terrestrial systems (Adler, Raff & Lauenroth 2001).
76 Within communities that are regulated largely by interactions between herbivores and primary
77 producers, such as in marine benthic habitats and various kinds of agricultural systems
78 (Hawkins & Hartnoll 1983; Shurin *et al.* 2002), changes in grazing variability may have
79 profound consequences for ecosystem structure, functioning and stability (Benedetti-Cecchi *et*
80 *al.* 2005; Atalah, Anderson & Costello 2007).

81

82 The importance of structural properties of communities in regulating their stability has
83 comprised a key focus of both theoretical and empirical research in ecology for decades (e.g.
84 MacArthur 1955; May 1972; Montoya, Pimm & Solé 2006; Allesina & Tang 2012).

85 However, our understanding of the reciprocal relationship between community structure and
86 stability remains limited (Rooney & McCann 2012). This is, in part, because ecological
87 stability is a multidimensional concept, incorporating components such as spatial and
88 temporal variability, resistance, resilience, robustness and persistence (Table 1; Pimm 1984;
89 Ives & Carpenter 2007), but the vast majority of research has focussed on single components
90 in isolation. Recent experimental research (Donohue *et al.* 2013) has demonstrated that
91 different components of stability can be strongly related to each other, but also that the
92 strength and nature of relationships among them may be disrupted when communities are
93 exposed to strong perturbations. Therefore, simultaneous quantification of multiple
94 components of stability is needed to provide comprehensive understanding of how
95 communities may be destabilised by structural change and perturbations (Donohue *et al.*
96 2013). Theory suggests that changes in the population dynamics of key components of food
97 webs could have considerable knock-on consequences for the stability of whole ecosystems
98 (Pimm 1982; Rooney & McCann 2012). Further, empirical research has demonstrated how
99 variability in consumer–resource interactions can promote spatial variability in marine

100 intertidal communities (Berlow 1999; Benedetti-Cecchi 2000; Benedetti-Cecchi *et al.* 2005).
101 Consumer variability may also affect other components of stability, such as temporal
102 variability, indirectly via shifts in assemblage structure or diversity (Jiang & Pu 2009; Rooney
103 & McCann 2012). Currently, however, we have little empirical understanding of the
104 consequences of alterations to the variability of consumer populations, independent of
105 changes in their mean densities, for the multidimensional stability of natural communities.
106
107 Here, we examine how altering the temporal variability of populations of a key consumer
108 species, independent of changes in their mean densities, affects the structure and multiple
109 components of the stability of communities in a natural ecosystem. Specifically, we
110 manipulated the temporal variability of a key grazer, the periwinkle *Littorina littorea*,
111 experimentally in natural rocky intertidal communities and examined the responses of both
112 microalgal and macroalgal assemblages to subsequent perturbation in the form of
113 sedimentation. *Littorina littorea* plays a significant role in the dynamics of benthic
114 communities in the north Atlantic (Bertness 1984; Jenkins *et al.* 2008; O'Connor *et al.* 2015)
115 and is subjected to unregulated harvesting in many areas (McKay & Fowler 1997; Cummins
116 *et al.* 2002). This can promote high population variability over small spatial and temporal
117 scales in intertidal habitats (Johnson *et al.* 2008). In addition to anthropogenic impacts on the
118 abundance and variability of key consumer species, coastal habitats are also subjected to a
119 variety of interacting abiotic pressures at local and global scales (Thompson, Crowe &
120 Hawkins 2002; Halpern *et al.* 2008). Sedimentation, arising from both natural and
121 anthropogenic processes, is a particularly widespread and pervasive form of disturbance that
122 has profound consequences for the structure and dynamics of coastal marine ecosystems,
123 including rocky shores (Airoldi 2003). Further, as a result of human activities that enhance
124 riverine inputs and exacerbate coastal erosion, sediment loading in coastal areas is expected to

125 increase over the coming decades throughout the globe (Thompson, Crowe & Hawkins 2002).
126 Despite the potential for such abiotic stressors to interact with important consumer-driven
127 processes (Bertness 1984; Airoldi & Hawkins 2007; O'Connor & Donohue 2013; Mrowicki
128 & O'Connor 2015), it is not yet known how altered patterns of consumer variability modify
129 the responses of natural communities to perturbations.

130

131 Based on previous empirical research examining the responses of assemblages to increased
132 temporal variability of consumers in aquatic systems (e.g. Butler 1989; Navarrete 1996;
133 Atalah, Anderson & Costello 2007), we hypothesised that changing the temporal variability
134 of *L. littorea* populations, independent of their mean densities, would alter the biomass and
135 structure of natural algal assemblages. Additionally, we expected that increased consumer
136 population variability would destabilise algal assemblages in terms of multiple components of
137 their stability, either directly or indirectly via changes in community structure, as well as
138 determine their responses to perturbation in the form of elevated sedimentation. Given that the
139 dynamics of marine communities often depend strongly on the timing of consumer and
140 environmental variability (Bertocci *et al.* 2005; Stier *et al.* 2013), we also explored whether
141 the effects of changes in consumer variability were regulated by the timing of fluctuations in
142 population density.

143

144 **Materials and Methods**

145

146 *Experimental site*

147

148 The experiment was conducted on a moderately exposed rocky shore at Rush, Co. Dublin, on
149 the east coast of Ireland (53.524°N, 6.078°W). The shore comprised a mosaic of patches of

150 bare emergent substratum, barnacles (predominantly *Austrominius modestus* and *Semibalanus*
151 *balanoides*) and mussels (predominantly *Mytilus edulis*). Macroalgal assemblages consisted
152 mostly of red algal turfs (*Mastocarpus stellatus*, *Osmundea* spp. and *Gracilaria gracilis*)
153 interspersed with green filamentous species (*Cladophora rupestris*, *Ulva* spp. and
154 *Chaetomorpha linum*), overlain by sparse canopies of brown macrophytic algae (*Fucus*
155 *vesiculosus*). Encrusting macroalgae (*Lithothamnium* spp. and *Ralfsia verrucosa*) were
156 common on bare rock and barnacles. By far the most abundant gastropod grazer on the shore
157 was the common periwinkle, *Littorina littorea* (hereafter '*Littorina*'; density $300.8 \pm 24.5 \text{ m}^{-2}$
158 [mean \pm SE; $n = 16$]). Other grazers were present at much lower densities, including the
159 topshell *Gibbula umbilicalis* ($36.8 \pm 7.3 \text{ m}^{-2}$), the limpet *Patella vulgata* ($16.0 \pm 3.7 \text{ m}^{-2}$) and
160 other littorinids, such as *L. saxatilis* and *L. obtusata*.

161

162 *Experimental design*

163

164 We established 40 experimental plots ($35 \times 35 \text{ cm}$) within mussel beds around mid-tidal level
165 (ca. 2.0 m above Chart Datum). To enable the manipulation of consumer densities, plots were
166 enclosed by 12 cm-high cages, consisting of square fences with attached lids, constructed
167 from stainless steel mesh (0.9 mm wire diameter, 4.17 mm aperture, 67% open area) fixed to
168 the substratum with screws and washers. The cages were used to restrict the movement of
169 adult *Littorina* while allowing exposure to natural environmental dynamics and access to
170 smaller mobile consumers, including annelid and nemertean worms, amphipods and juvenile
171 gastropod grazers, in addition to propagules of sessile benthic fauna and algae. One month
172 prior to the commencement of the experiment, mussels and associated sediment, fauna and
173 algae were transplanted into cages from an adjacent area on the shore to ensure that the initial

174 cover of mussels within cages ($61.4 \pm 1.0\%$ [mean \pm SE]) was similar in all treatments and
175 representative of background abundances on the shore (O'Connor *et al.* 2013).

176

177 To increase the applicability of our findings to real-world ecosystems, we established an
178 additional eight uncaged manipulated plots, which enabled the comparison of consumer
179 variability and algal assemblage dynamics in our caged plots with natural patterns on the
180 shore. The uncaged plots were interspersed haphazardly among the caged plots and contained
181 similar cover of mussels (range 53–78%). The uncaged plots were, however, not used as true
182 procedural controls for detecting cage artefacts because it was not possible to manipulate, *a*
183 *priori*, consumer variability within caged plots independent of the mean density to reflect
184 robustly the natural spatiotemporal dynamics at similar spatial scales on open areas of the
185 shore. Nonetheless, we opted to conduct our experiment on open natural communities in the
186 field because field experiments have a distinct advantage over laboratory- or mesocosm-based
187 studies with regards to the incorporation of natural environmental heterogeneity and enhanced
188 realism (Naeem 2008). Further, numerous studies conducted on this shore and elsewhere
189 using an identical cage design have demonstrated an absence of cage effects on the structure
190 and stability of algal assemblages over similar or longer timescales (e.g. O'Connor & Crowe
191 2005; O'Connor *et al.* 2011, 2013; Donohue *et al.* 2013).

192

193 Three experimental treatments were established in August 2012 to test the effects of
194 consumer variability on algal assemblages over 12 months. Importantly, the mean density of
195 *Littorina* was identical in all of our experimental plots (both caged and uncaged) over the
196 duration of the experiment, mimicking the mean background density on the shore (Fig. 1a,b),
197 and was unconfounded from the manipulation of consumer variability (Fig. 1c). In the
198 'constant' treatment, *Littorina* density was maintained at 30 individuals per plot for the

199 duration of the experiment to mimic situations where the density of consumers is relatively
200 constant over time. We established two ‘variable’ treatments to test the importance of the
201 temporal pattern of consumer density fluctuations. *Littorina* density in both of these
202 treatments alternated between 15 and 45 individuals per plot every two months (Fig. 1a). This
203 was within the range of background densities observed in preliminary surveys at the
204 experimental site (128–464 m⁻²). The ‘variable₁’ treatment commenced with 15 *Littorina*
205 individuals per plot, while the ‘variable₂’ treatment commenced with 45 (Fig. 1a). All
206 experimental densities were based on adult individuals (> 5 mm) because it was impractical to
207 manipulate juveniles smaller than the cage mesh size. The mean density of juvenile *Littorina*
208 was quantified over the duration of the experiment and did not vary among our caged biotic
209 variability treatments (ANOVA; MS = 0.44, $F_{2,17} = 0.39$, $P = 0.681$).

210

211 To test whether variability in consumer population densities altered the responses of
212 communities to disturbances, we established two sedimentation treatments (‘ambient’ and
213 ‘elevated’) four months after the commencement of the experiment. The elevated
214 sedimentation treatment involved the monthly addition of 400 g dry mass of sandy sediment,
215 collected from an adjacent sandy shore, to each respective plot until the end of the experiment
216 (12 months). This sedimentation rate, equivalent to ca. 100 g m⁻² d⁻¹, is within the range
217 experienced by coastal habitats in the vicinity of populated areas (Airoldi & Virgilio 1998;
218 Connell 2005). **Instead of a temporally consistent increase in sedimentation above**
219 **background levels, which would have been impossible to maintain for the duration of the**
220 **experiment, this treatment was manifested as a pulse disturbance, whereby the full quantity of**
221 **sediment was applied to each respective plot at low tide and then apparently washed away by**
222 **the incoming tide.** The two sedimentation treatments were crossed fully with the three biotic
223 variability treatments, yielding a total of six treatments in a factorial design. Eight replicate

224 caged plots were assigned randomly to each of the four treatment combinations involving the
225 constant and variable₁ consumer variability treatments. However, owing to practical
226 limitations on the number of plots that could be maintained during the experiment, it was not
227 possible to allocate such a large number of replicates to all treatments. Consequently, four
228 replicate caged plots were assigned randomly to the remaining two treatment combinations
229 involving the variable₂ treatment.

230

231 The percent cover of macroalgal species was estimated monthly using a 25 × 25 cm quadrat
232 with 64 intersections, positioned centrally within cages to avoid sampling edge effects.

233 Species present within the quadrat but not occurring underneath any of the intersections were
234 assigned a value of 1% (O'Connor & Crowe 2005). Slate tiles (10 × 10 × 1 cm) were either
235 attached inside cages or fixed to the substratum adjacent to uncaged plots four months after
236 the commencement of the experiment to monitor the development of epilithic biofilms.

237 Microalgal biomass on the tiles was quantified monthly *in situ* by measuring chlorophyll *a*
238 concentrations with a benthic fluorometer (BenthoTorch, bbe Moldaenke GmbH,
239 Schwentinental, Germany). This method has been shown to provide reliable estimates of total
240 microalgal biomass in marine intertidal systems (Kahlert & McKie 2014), and enables the
241 differentiation of component microalgal groups (diatoms, cyanobacteria and chlorophytes)
242 based on their fluorescence excitation spectra (Aberle *et al.* 2006). Mean values for each plot
243 were calculated from three haphazardly-spaced readings per tile because the distribution of
244 epilithic microalgae is highly heterogeneous at small scales (Hutchinson *et al.* 2006).

245 Quantification of all response variables commenced four months after the establishment of the
246 experiment (i.e. from December 2012 to August 2013) to avoid transient dynamics (Donohue
247 *et al.* 2013).

248

249 *Data analyses*

250

251 Given the dynamic nature of algal communities on rocky shores and their rapid responses to
252 fluctuations in physical and biological conditions at scales relevant to this study (e.g. Hawkins
253 & Hartnoll 1983), focussing on primary producer assemblages allowed us to maximise the
254 probability of detecting shifts in ecosystem functioning and stability (Borrvall & Ebenman
255 2006; Donohue *et al.* 2013). Therefore, we used the total biomass of microalgae and the total
256 cover, taxonomic richness, Simpson's evenness ($1-\lambda$) and assemblage structure of macroalgae
257 at the end of the experiment as proxies for shifts in ecosystem functioning. There were no
258 significant differences in any of these variables among treatment combinations (including
259 between caged and uncaged plots) at the start of the experiment (Table S1 in Supporting
260 Information).

261

262 We quantified up to six components of ecological stability for algal assemblages (Table 1):
263 spatial and temporal variability of total biomass were calculated for both micro- and
264 macroalgal assemblages, while the number of local species extinctions and invasions,
265 compositional turnover and resistance to environmental fluctuations were determined for
266 macroalgal assemblages only, owing to low taxonomic resolution of the microalgal data. Both
267 spatial and temporal variability were detrended to avoid the potentially confounding effects of
268 transient or seasonal shifts in algal abundance over the duration of the experiment. This was
269 achieved by using the residuals from linear regressions of total algal abundance (microalgal
270 biomass or macroalgal cover) against time, rather than algal abundance *per se* (Tilman, Reich
271 & Knops 2006; Donohue *et al.* 2013).

272

273 We tested for effects of the nature and timing of variability in consumer densities and for
274 interactions between these and sedimentation on measures of each of the structure,
275 functioning and stability of algal communities. Our statistical models incorporated two fully-
276 crossed factors, consumer variability (fixed, three levels: constant, variable₁ and variable₂)
277 and sedimentation (fixed, two levels: ambient and elevated). In the case of spatial variability,
278 for which data were not associated with individual plots, month was included as a random
279 factor in all analyses to account for variation among survey dates.

280

281 Permutational analysis of variance (perANOVA; Anderson 2001a), based on Euclidean
282 distance matrices, was used to test hypotheses involving univariate metrics of ecosystem
283 functioning and stability. Homogeneity of data was assessed prior to analysis using Levene's
284 test and data were transformed as necessary to stabilise heterogeneous variances. We used
285 permutational procedures rather than conventional ANOVA in our analyses because they do
286 not rely on the normality of error distributions, an assumption to which univariate ecological
287 data often do not conform (Anderson 2001a), and because these methods have been shown to
288 be significantly more robust for the analysis of unbalanced datasets than other resemblance-
289 based permutation methods (Anderson & Walsh 2013). We tested the consistency of the
290 perANOVA results by comparing pseudo-*F* values obtained for all terms against distributions
291 of *F*-values obtained from conventional ANOVAs performed on 10⁴ balanced datasets (*n* = 4)
292 sampled randomly from the full dataset. All relevant test statistics were within the 95%
293 confidence intervals derived from this procedure (Table 2).

294

295 We tested for differences in the structure of macroalgal assemblages using permutational
296 multivariate analysis of variance (PERMANOVA; McArdle & Anderson 2001; Anderson
297 2001b) based on Bray-Curtis dissimilarities and calculated from log₁₀(*x*+1)-transformed

298 abundance data to reduce the influence of dominant taxa (Clarke & Warwick 2001). The
299 analysis was performed with 9,999 permutations of residuals under a reduced model and was
300 based on Type II sums of squares, as recommended for unbalanced factorial designs
301 (Langsrud 2003). Owing to low numbers of unique permutations in some cases, statistical
302 significance was assessed using *P*-values obtained via Monte Carlo simulations rather than
303 from permutation-based empirical distributions (Anderson & Robinson 2003). Post hoc
304 permutational *t*-tests were used to resolve pairwise differences among levels of significant
305 terms and the relative contributions of algal taxa to differences between treatments were
306 determined using similarity of percentages analysis (SIMPER; Clarke 1993).

307

308 Analyses were conducted in R (version 3.0.1; R Development Core Team 2013), except for
309 distance-based perANOVAs and PERMANOVAs, which were performed using the
310 PERMANOVA+ add-on in PRIMER (version 6.1.13; PRIMER-E Ltd., Plymouth, UK).

311

312 **Results**

313

314 Temporal variability of *Littorina* populations determined the effects of sedimentation on the
315 structure and stability of algal assemblages (Table 2). Macroalgal evenness was reduced by
316 elevated sedimentation when *Littorina* density was constant, but not when *Littorina* densities
317 were variable (perANOVA; consumer variability \times sedimentation: $P = 0.035$; Table 2a; Fig.
318 2a). Elevated sedimentation also decreased the number of local extinctions of macroalgal
319 species in both of the variable treatments but not in the constant treatment (consumer
320 variability \times sedimentation: $P = 0.015$; Table 2b; Fig. 2b). Although consumer variability and
321 sedimentation interacted to affect the spatial variability of both microalgal ($P = 0.030$) and
322 macroalgal ($P = 0.012$) assemblages (Table 2b), post hoc tests were inconclusive and revealed

323 no significant ($P < 0.05$) differences between ambient and elevated sedimentation for any of
324 the three consumer variability treatments (Fig. 2c,d). A decrease in macroalgal spatial
325 variability in response to elevated sedimentation was, however, bordering on statistical
326 significance in the variable₂ treatment (perANOVA post hoc test; $t = 2.28$, $P = 0.052$).

327

328 Independently of sedimentation, increased temporal variability of *Littorina* populations
329 resulted in a shift in macroalgal assemblage structure (PERMANOVA; $P = 0.012$; Table 2a),
330 but this effect depended on the temporal pattern of consumer density fluctuations.

331 Specifically, the ‘variable₂’ treatment (i.e. commencing with low *Littorina* density), but not
332 the ‘variable₁’ treatment (i.e. commencing with high *Littorina* density), differed from the
333 ‘constant’ treatment in terms of macroalgal assemblage structure at the end of the experiment
334 (PERMANOVA post hoc test; $t = 1.66$, $P = 0.024$). This difference was driven by greater
335 cover of red (*Osmundea* spp. and *Mastocarpus stellatus*) and green (*Ulothrix* sp.) turf-
336 forming species and encrusting coralline species (‘*Lithothamnia* spp.’) in the variable₂
337 treatment compared to the other treatments (SIMPER; Table S2).

338

339 The nature and temporal pattern of *Littorina* population variability also affected, independent
340 of sedimentation, the compositional turnover of macroalgal assemblages (perANOVA; $P =$
341 0.010 ; Table 2b) and their resistance to perturbations in the form of natural environmental
342 fluctuations ($P = 0.045$; Table 2b). Although post hoc tests were unable to resolve differences
343 among groups fully, algal assemblages in the variable₂ treatment appeared to have increased
344 compositional turnover relative to those in the constant treatment (Fig. 2e) and lower
345 resistance to perturbations compared to those in the variable₁ treatment (Fig. 2f).

346

347 **Discussion**

348

349 Our results demonstrate that **altered patterns of** temporal variability in the population density
350 of even a single consumer species can, independent of its mean density, affect multiple
351 aspects of both the structure and stability of natural communities and determine their
352 responses to **other** perturbations. **Additionally**, we show that the effects of consumer
353 population variability depend on the timing of density fluctuations, **which, in general,**
354 **appeared to be more important than variability *per se*.** These findings have important
355 implications for our understanding of the factors governing ecological responses to
356 perturbations. In particular, our results indicate that predicting the effects of disturbances on
357 ecosystems requires knowledge of the patterns of variability in species populations.

358

359 We found that the effects of sedimentation on the structure and stability of algal assemblages
360 were determined by variability in the densities of *Littorina littorea* populations, independent
361 of their mean densities. Further, it appeared that the **variability *per se***, rather than temporal
362 pattern, of consumer **densities** drove this interaction. When consumer densities were held
363 constant, elevated sedimentation resulted in a decline in macroalgal evenness, which can be
364 explained by a reduction in the recruitment and/or survival of less tolerant species and a
365 subsequent shift in dominance towards more resistant species (Airoldi 2003). **Mechanisms by**
366 **which sediment can affect algal species directly include damage to or loss of individuals via**
367 **scouring and abrasion, reduced availability of stable substratum as a result of sediment build-**
368 **up, and restricted access to light, oxygen and nutrients owing to burial and smothering**
369 **(Airoldi 2003).** Although sedimentation can directly impair the feeding activity of gastropod
370 grazers such as limpets (Airoldi & Hawkins 2007), it may have weaker effects on more
371 mobile species, particularly at greater densities. In fact, *L. littorea* has been shown to
372 'bulldoze' accumulated sediment from rocky substrata, indirectly inhibiting the development

373 of algal canopies (Bertness 1984) and mitigating the negative effects of sedimentation on
374 more susceptible ephemeral algal species (Airoldi 2003). It is therefore possible that the
375 effects of elevated sedimentation on the growth of certain algal species were negated by
376 periods of higher grazing pressure within the variable treatments, with consequences for algal
377 evenness. Consistent with this, elevated sedimentation reduced the number of local
378 extinctions of macroalgal species when *L. littorea* densities were variable, with a tendency
379 towards homogenising algal cover in space. In our study, which was conducted on open
380 emergent substrata on a moderately exposed rocky shore, there appeared to be little
381 opportunity for the extensive accumulation of sediment within experimental plots (pers. obs.).
382 Further, although we did not characterise background sedimentation rates, our elevated
383 sedimentation treatment involved the addition of quantities of sediment that were relatively
384 small in the context of natural sedimentation regimes on other temperate rocky shores
385 (Airoldi & Virgilio 1998; Connell 2005). Despite the observed responses of algal assemblages
386 to this treatment, these factors may have limited the effect of sedimentation on our other
387 measures of structure and stability. Overall, however, our results demonstrate that the
388 ecological effects of such perturbations can depend strongly on the nature of temporal
389 variability in biotic communities.

390

391 Independent of sedimentation, increased consumer variability resulted in a shift in macroalgal
392 assemblage structure relative to when consumer density was held constant. Similar results
393 have been found previously in aquatic systems where resource species differed in their growth
394 rates and susceptibility to predation and consumers exhibited prey selectivity (Butler 1989;
395 Navarrete 1996). However, this shift observed in our experiment occurred only in the
396 'variable' treatment commencing with a high consumer density (variable₂), and not in the
397 treatment commencing with a low density (variable₁). The timing of disturbance events has

398 been shown to have important consequences for the emergent structure of recovering
399 communities when species differ in terms of reproductive and phenological traits, in addition
400 to their relative susceptibilities at different life history stages (Hawkins 1981; Airoldi 2000).
401 **It is possible that differences in consumer densities between variability treatments at the start**
402 **of the experiment influenced the relative rates of establishment among algal species, resulting**
403 **in divergent successional trajectories that contributed to the observed differences in final**
404 **assemblage structure.** Additionally, the temporal coincidence between maximum grazer
405 densities and periods of peak recruitment of algal species **throughout the duration of the**
406 **experiment may have contributed to the observed** shifts in algal assemblage structure
407 (Bertocci *et al.* 2005). For example, in the variable₂ treatment, peaks in grazing corresponded
408 with the main reproductive periods of *Fucus vesiculosus*, i.e. September–October and May–
409 June (Berger *et al.* 2003). The final macroalgal assemblage structure in this treatment was
410 characterised by a relatively low abundance of this species. Similarly, differences in the
411 abundances of some algal species, particularly fast-growing ephemeral species, may be a
412 function of grazer density immediately prior to the final census date. For example, the
413 abundances of *Porphyra umbilicalis* and *Ulva lactuca*, which are preferred food items for *L.*
414 *littorea* (Lubchenco 1978), were greater in the variable₂ treatment compared to the constant
415 and variable₁ treatments. However, if patterns in final assemblage structure were based
416 predominantly on direct consumptive effects of grazing, we would expect differences to be
417 driven by such palatable ephemeral species. In contrast to this expectation, unpalatable
418 perennial species, such as *Osmundea* spp. and *Mastocarpus stellatus*, made a far greater
419 contribution to differences in assemblage structure between these treatments. This suggests
420 strongly that other indirect processes, such as competitive interactions among species, were
421 important in mediating the responses of algal communities to temporal patterns of grazing
422 (Airoldi & Cinelli 1997).

423

424 Both the compositional turnover and the extent of structural change (resistance) of algal
425 assemblages in response to environmental fluctuations depended on the temporal pattern of
426 consumer density fluctuations. There was, however, no consistent effect on overall
427 community stability of any particular treatment. Specifically, resistance to environmental
428 fluctuations appeared to be greatest in the variable₁ treatment and lowest in the variable₂
429 treatment, whereas compositional turnover was greatest in the variable₂ treatment and lowest
430 in the constant treatment. Although the underlying mechanisms are unclear, such effects may
431 occur indirectly via changes in the relative abundances of key species that modify competitive
432 interactions within the community and, therefore, contribute to multiple components of
433 stability. For example, in temperate grassland ecosystems, the existence of competitive
434 hierarchies involving dominant ‘core’ species that interact with less abundant ‘satellite’
435 species may promote biotic feedback instabilities, leading to the destabilisation (i.e. increase
436 in variability) of communities (Collins 2000). Similar processes may operate within intertidal
437 macroalgal assemblages, which are also characterised by competitive asymmetries at multiple
438 life stages (Berger *et al.* 2003; Maggi *et al.* 2012). Additionally, certain species may modify
439 the influence of exogenous environmental variability on communities in different ways, with
440 contrasting consequences for stability. In marine intertidal systems, for example, habitat
441 engineers such as mussels may enhance the transmission of environmental stochasticity
442 through communities, increasing the temporal variability of other species (Wootton 2010).
443 Conversely, on some rocky shores, canopy-forming algae may dampen oscillations in
444 physical conditions and promote asynchronous species fluctuations, resulting in decreased
445 overall community variability (Bulleri *et al.* 2012). Thus, changes in both biotic and
446 environmental feedback pathways resulting from the shift in balance away from structurally
447 important forms of perennial algae (*Mastocarpus stellatus* and *Fucus vesiculosus*), as

448 observed in the variable₂ treatment, may have contributed to the destabilisation of
449 assemblages in this treatment. In general, the mechanisms by which population variability
450 affects the stability of complex communities require further investigation, paying particular
451 attention to the relative contribution of particular species to different components of stability
452 (Ives & Carpenter 2007). Importantly, while previous studies have shown that species loss
453 can have dramatic effects on assemblage structure and stability (O’Gorman & Emmerson
454 2009; Donohue *et al.* 2013), we have shown that more subtle biotic perturbations, such as
455 changes in the temporal variability of a single key species, may also affect multiple aspects of
456 ecosystem functioning and stability.

457

458 In a mesocosm experiment, Atalah *et al.* (2007) found that increased temporal variability of
459 grazing resulted in reduced total algal cover. In contrast to this, however, we found no effect
460 of consumer variability on either microalgal biomass or macroalgal cover in our field
461 experiment. Further, the temporal variability of both microalgal and macroalgal cover was
462 also unaffected by alterations to grazing variability. These results suggest that the biomass
463 and temporal variability of communities in our study were regulated more strongly by
464 processes other than variability in grazing intensity. This may be because environmental
465 heterogeneity in the field masked the effects of consumer population fluctuations on total
466 algal abundance and variability. Additionally, within diverse algal assemblages, strong
467 competitive interactions among species can result in compensatory responses (Maggi *et al.*
468 2012) whereby opposing changes in individual species abundances may underlie constant
469 total algal abundance. Indeed, we observed a shift in macroalgal assemblage structure
470 resulting from changes in the abundances of individual algal taxa, which were perhaps
471 mediated by interactions between species.

472

473 We designed our consumer variability treatments in the absence of detailed information about
474 natural fluctuations of *Littorina littorea* populations at the study site. During the course of our
475 experiment, however, our uncaged unmanipulated plots revealed background patterns of
476 population variability (Fig. 1a). While the mean density and magnitude of fluctuations of *L.*
477 *littorea* populations were both similar between uncaged and caged plots, the frequency of
478 fluctuations in our experimental manipulations was slightly greater than that observed on the
479 shore. However, differences in the responses of algal assemblages between uncaged and
480 caged plots may have been a result of artefacts from the use of cages, in concert with
481 differences between natural and manipulated patterns of consumer variability. The lack of
482 true procedural controls in our experiment, necessitated by difficulties in manipulating
483 consumer densities without the use of cages, limits how far we can extend our inferences to
484 natural communities. Despite this, examining differences among our caged treatments enabled
485 us to test the effects of consumer variability and sedimentation on natural multitrophic
486 assemblages exposed to realistic levels of natural environmental heterogeneity and open to
487 propagule supply. Within a given area, temporal variability in natural populations may occur
488 both as a result of community processes, including consumer–resource dynamics, and in
489 response to environmental heterogeneity, such as seasonal changes in conditions (Butler
490 1989; Navarrete 1996; Lauzon-Guay & Scheibling 2009). Owing to the potential for complex
491 interactions between intrinsic and extrinsic drivers of population variability, and their
492 additional effects on ecosystem functioning and stability, it is difficult to disentangle the
493 ecological role of population variability itself from other such influences in natural systems.
494 Consequently, community responses to changes in natural versus manipulated patterns of
495 consumer variability may differ. Thus, while our results demonstrate the importance of
496 consumer variability when manipulated in isolation, enhancing the applicability of these
497 findings to natural stochastic systems requires greater understanding of the modifying roles of

498 community dynamics and environmental variability. Another caveat of our study is that it
499 does not account for the potential role that population density plays in mediating the effects of
500 temporal variability. Although we separated the effects of variability and temporal pattern
501 from that of mean density, logistical constraints prevented us from testing for an interaction
502 between these variables (Benedetti-Cecchi *et al.* 2005). Further experimentation, involving a
503 range of grazer density treatments, would help to clarify the relative contribution of density to
504 the observed effects of consumer variability on community stability.

505

506 In conclusion, our study demonstrates that altered patterns of temporal variability within the
507 population of a single species may propagate through food webs to influence multiple aspects
508 of the structure, functioning and stability of communities. Importantly, we found that the
509 effects of such disturbances cannot be predicted without knowledge of the temporal pattern of
510 density fluctuations. Moreover, to our knowledge, this study is the first to show that
511 alterations to the temporal variability of single populations can determine how communities
512 respond to other perturbations. Overall, our findings indicate that the ecological impacts of
513 disturbances, which may be unpredictable because of interactions among different temporal
514 patterns of perturbations (García Molinos & Donohue 2010) as well as different types of
515 stressors (Crain, Kroeker & Halpern 2008), are mediated by patterns of temporal variability
516 within communities. Therefore, the consequences of disturbances are likely to be highly
517 context-dependent with respect to the timing of environmental fluctuations and temporal
518 coincidence of disturbance events (see also Pincebourde *et al.* 2012). Our work also
519 emphasises the value of a multidimensional view of ecological stability in facilitating a more
520 complete understanding of community responses to perturbations (Donohue *et al.* 2013). To
521 improve our predictions of the ecological impacts of perturbations in a changing world, we

522 require greater appreciation of the importance of temporal patterns of variability and, in
523 particular, the reciprocal relationship between community structure and stability.

524

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526

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531

532 **Data accessibility**

533

534 Species abundance data are available via the Dryad Digital Repository (doi:
535 xx.xxxx/dryad.xxxx).

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537

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742

743 **Supporting Information**

744

745 Additional supporting information may be found in the online version of this article:

746

747 **Table S1.** Results of tests for differences in macroalgal assemblages among treatment
748 combinations at the start of the experiment.

749 **Table S2.** Relative contributions of macroalgal taxa to differences in assemblage structure
750 between consumer variability treatments.

751

752 As a service to our authors and readers, this journal provides supporting information supplied
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Stability component	Description and quantification
Spatial variability	The coefficient of variance (CV) of total algal abundance (microalgal biomass or macroalgal cover) among experimental plots within each treatment combination on each census.
Temporal variability	The CV of total algal abundance (microalgal biomass or macroalgal cover) in each experimental plot over time.
Number of extinctions [†]	Also known as <i>structural robustness</i> . Calculated as the number of macroalgal taxa that were recorded on the first census date in each plot, but which were absent at the end of the experiment.
Number of invasions [†]	A measure of community <i>persistence</i> . The number of macroalgal taxa that were recorded at the end of the experiment in each plot, but which were absent on the first census date.
Compositional turnover [†]	The extent of change in community composition over time, integrating aspects of temporal variability, resistance, extinctions and invasions. Calculated as the mean Jaccard similarity in macroalgal community composition (based on taxonomic presence/absence data) between consecutive sampling dates for each plot.
Resistance [†]	Calculated as the reciprocal of the Euclidean distance from each experimental plot to the centroid of the uncaged unmanipulated plots at the end of the experiment, based on Bray-Curtis dissimilarity matrices calculated from $\log_{10}(x+1)$ -transformed algal abundance data. Thus, this measure represents the extent of structural change in communities in different experimental treatments in response to natural environmental fluctuations.

[†]Quantified for macroalgal assemblages only.

761 **Table 2.** Results of PerANOVAs and PERMANOVA testing the effects of consumer
762 variability (constant, variable₁ and variable₂) and sedimentation on (a) measures of
763 abundance, diversity and structure and (b) components of ecological stability of microalgal
764 and macroalgal assemblages. For univariate analyses involving unbalanced datasets, 95% CIs
765 are based on *F*-values from conventional ANOVAs performed on 10⁴ balanced datasets (*n* =
766 4) sampled randomly from the full dataset. Significant *P*-values are highlighted in bold.

Variable	Source of variation	df	MS	Pseudo- <i>F</i> (95% CI)	<i>P</i>
(a) Abundance, diversity and structure					
Microalgal biomass	Consumer variability, V	2	0.37	2.81 (0.77, 6.78)	0.077
	Sedimentation, S	1	0.06	0.43 (8×10^{-4} , 2.98)	0.514
	V × S	2	0.14	1.02 (0.19, 5.00)	0.376
	Residual	34	0.13		
Macroalgae:					
Total cover	V	2	42.09	1.24 (0.12, 4.11)	0.302
	S	1	0.08	2×10^{-3} (3×10^{-4} , 2.13)	0.962
	V × S	2	4.51	0.13 (0.02, 1.96)	0.877
	Residual	34	33.99		
Species richness	V	2	0.14	0.08 (0.02, 1.49)	0.925
	S	1	0.63	0.34 (0.06, 2.36)	0.561
	V × S	2	5.72	3.16 (0.16, 5.24)	0.057
	Residual	34	1.81		
Species evenness	V	2	2×10^{-3}	0.20 (5×10^{-3} , 0.84)	0.811
	S	1	2×10^{-3}	0.26 (1×10^{-4} , 0.69)	0.613
	V × S	2	0.03	3.71 (0.68, 3.13)	0.035
	Residual	34	0.01		
Assemblage structure	V	2	2381.80	2.28 -	0.012
	S	1	791.17	0.76 -	0.608
	V × S	2	1079.10	1.03 -	0.420
	Residual	34	1044.40		
(b) Stability components					
Microalgae:					
Spatial variability	Month, M	7	40.11	17.84 -	<0.001
	V	2	6.91	3.08 -	0.060
	S	1	2.98	1.32 -	0.255
	V × S	2	8.72	3.88 -	0.029
	Residual	35	2.25		
Temporal variability	V	2	0.04	0.37 (0.01, 1.97)	0.696
	S	1	0.05	0.52 (4×10^{-4} , 1.53)	0.479
	V × S	2	0.10	0.96 (0.22, 2.34)	0.396
	Residual	34	0.10		

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(Table 2 continued)

Macroalgae:

Spatial variability	M	8	0.04	1.70 -	0.132
	V	2	0.15	7.16 -	0.002
	S	1	0.03	1.53 -	0.223
	V × S	2	0.11	4.91 -	0.014
	Residual	40	0.02		
Temporal variability	V	2	0.01	2.42 (0.69, 7.54)	0.103
	S	1	4×10^{-3}	0.66 (6×10^{-3} , 4.04)	0.415
	V × S	2	0.01	1.88 (0.33, 5.22)	0.168
	Residual	34	0.01		
No. of extinctions	V	2	3.97	7.88 (3.29, 10.32)	0.002
	S	1	3.60	7.15 (2.35, 14.49)	0.012
	V × S	2	2.42	4.80 (1.63, 5.64)	0.017
	Residual	34	0.50		
No. of invasions	V	2	4.27	2.76 (0.83, 6.27)	0.084
	S	1	4.90	3.17 (0.10, 8.35)	0.085
	V × S	2	0.77	0.50 (0.03, 2.68)	0.608
	Residual	34	1.55		
Resistance	V	2	0.32	3.39 (2.06, 5.70)	0.045
	S	1	0.01	0.12 (9×10^{-4} , 7.21)	0.746
	V × S	2	0.15	1.60 (0.46, 4.59)	0.214
	Residual	34	0.09		
Compositional turnover	V	2	0.02	5.15 (2.36, 8.59)	0.010
	S	1	0.01	1.21 (0.08, 8.99)	0.278
	V × S	2	0.01	2.38 (0.82, 6.45)	0.111
	Residual	34	4×10^{-3}		

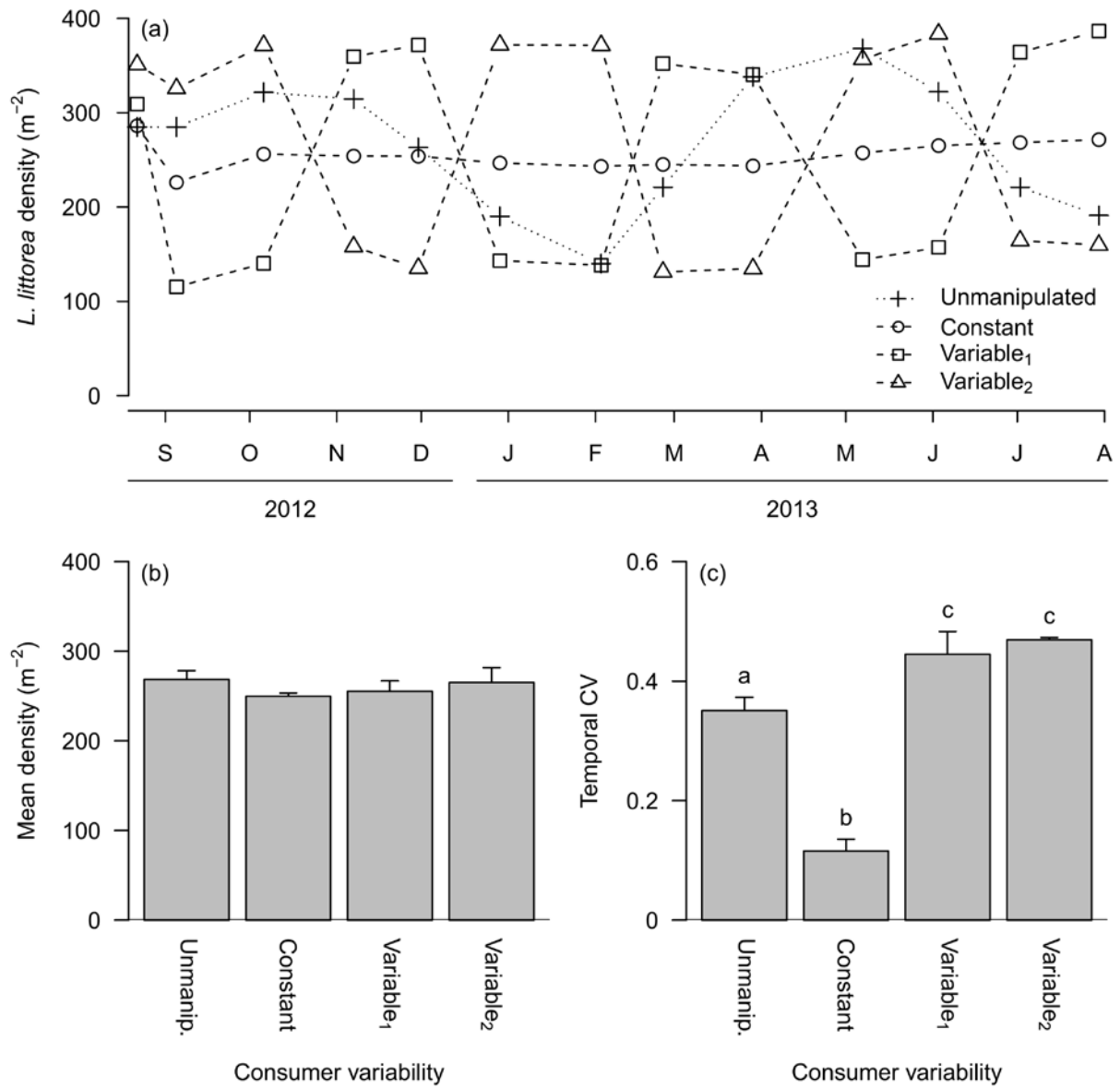
768 **Figure legends**

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770 **Fig. 1.** (a) Monthly mean densities, (b) overall mean (+ 1 SE) densities and (c) temporal
771 variability (detrended coefficient of variation; mean + 1 SE) in the density of *Littorina*
772 *littorea* over the duration of the experiment in uncaged unmanipulated plots ($n = 8$) and in
773 caged plots belonging to consumer variability treatments (constant and variable₁, $n = 8$;
774 variable₂, $n = 4$). In (c), different letters denote groups of treatments that are significantly
775 different from each other ($P < 0.05$) based on SNK tests.

776

777 **Fig. 2.** Mean (+ 1 SE) (a) Simpson's evenness ($1-\lambda$) of macroalgal assemblages, (b) number
778 of local extinctions of macroalgal species, spatial variability of (c) micro- and (d) macroalgal
779 assemblages, (e) compositional turnover of macroalgal assemblages and (f) resistance of
780 macroalgal assemblages to natural environmental fluctuations over the duration of the
781 experiment in uncaged unmanipulated plots ($n = 8$) and in caged plots belonging to consumer
782 variability treatments (constant and variable₁, $n = 8$; variable₂, $n = 4$). Results from uncaged
783 plots were not included in statistical analyses but are included here to provide additional
784 context. Asterisks indicate significant differences between groups (** $P < 0.05$) based on
785 perANOVA post hoc tests. Different letters denote groups of treatments that are significantly
786 different from each other ($P < 0.05$) based on SNK tests.



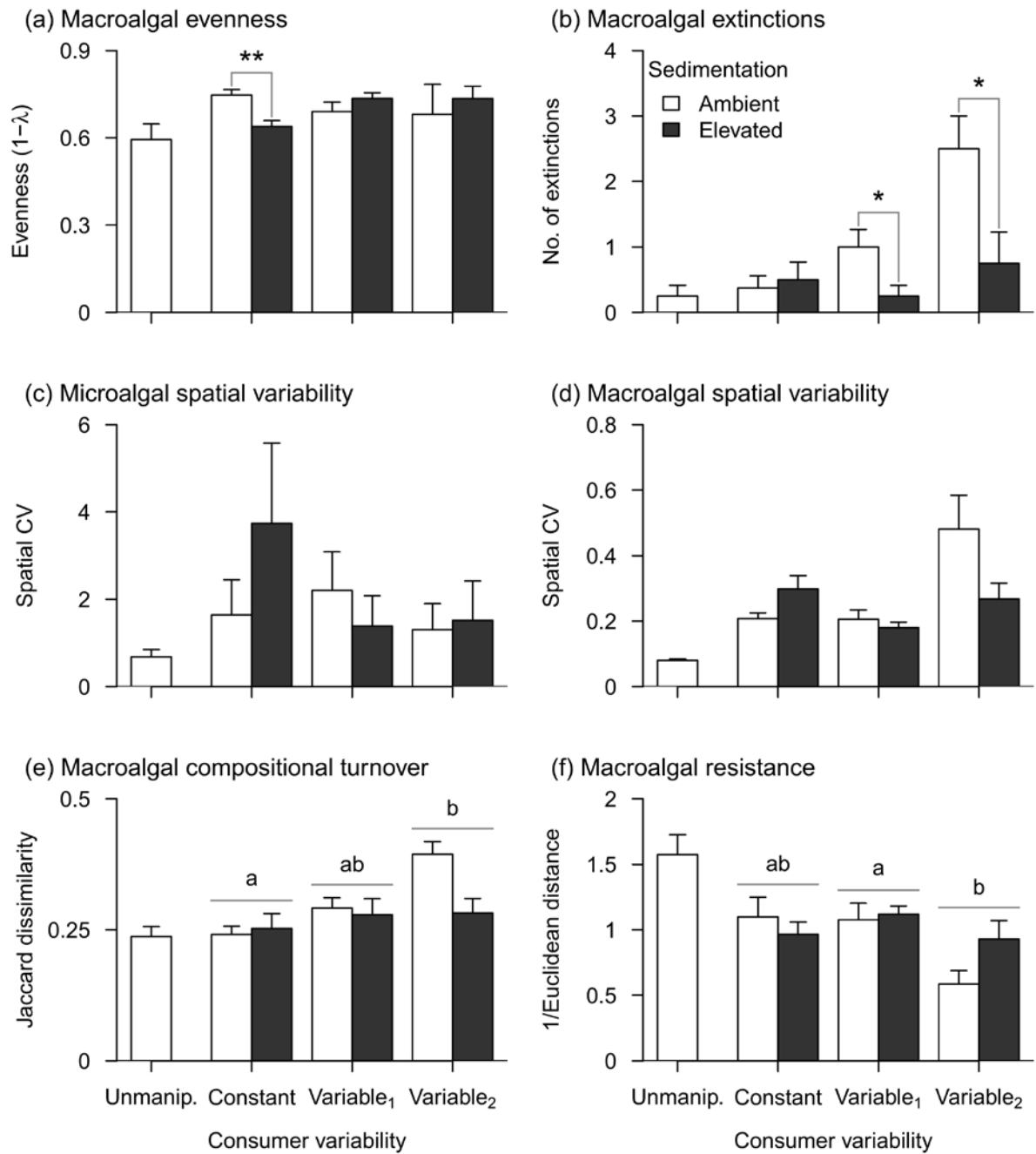
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792 **Fig. 1.** Mrowicki *et al.*



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797 **Fig. 2.** Mrowicki *et al.*