

1 Running Head: Matias et al.: Rare species made common

2 Increasing density of rare species of intertidal  
3 gastropods: tests of competitive ability compared  
4 with common species

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10 ABSTRACT:

11 Many assemblages contain numerous rare species, which can show large increases in  
12 abundances. Common species can become rare. Recent calls for experimental tests of  
13 the causes and consequences of rarity prompted us to investigate competition between  
14 co-existing rare and common species of intertidal gastropods. In various  
15 combinations, we increased densities of rare gastropod species to match those of  
16 common species to evaluate effects of intra- and interspecific competition on growth  
17 and survival of naturally rare or naturally common species at small and large  
18 densities. Rarity *per se* did not cause responses of rare species to differ from those of  
19 common species. Rare species did not respond to the abundances of other rare  
20 species, nor show consistently different responses from those of common species.  
21 Instead, individual species responded differently to different densities, regardless of  
22 whether they are naturally rare or abundant. This type of experimental evidence is  
23 important to be able to predict the effects of increased environmental variability on  
24 rare as opposed to abundant species and therefore, ultimately, on the structure of  
25 diverse assemblages.

26 KEY WORDS: Additive-design • Competition • Gastropods • Species-abundance •  
27 Rarity

28 INTRODUCTION

29 The distributions and abundances of species are core topics of study in  
30 ecology (Andrewartha & Birch 1954). Generally, assemblages have relatively few  
31 common species and many relatively rare species (e.g. Rabinowitz et al. 1986, Gaston  
32 1994). Common species often occupy many sites, whereas rare species can occur in  
33 only a few sites over a limited geographical range (Gaston 1994), or be widespread,  
34 but in small abundance everywhere (e.g. MacArthur & Wilson 1967).

35 Rare species, however defined, have been suggested to be more vulnerable to  
36 extinction, but many persist for long periods in small numbers and/or few places.  
37 Mechanisms for long-term maintenance of rarity are not, however, well understood.  
38 Also, relatively few studies have attempted to understand the effects of increased  
39 abundance of naturally rare species on other species in an assemblage, especially in  
40 marine assemblages.

41 The competitive ability of rare species has been suggested as a mechanism to  
42 compensate for their small densities, by reducing the probability of extinction at local

43 scales (Rabinowitz et al. 1986). Myers & Harms (2009), in contrast, suggested that  
44 individuals in small populations may not encounter other individuals frequently  
45 enough for intra-specific competition among different rare species to be important. No  
46 general relationship between abundance and competition exists, because many studies  
47 have contradictory conclusions (see review by Gaston & Kunin 1997). There are clear  
48 patterns in competition between larger versus smaller organisms and for invertebrates  
49 versus vertebrates (reviews by Connell 1983, Schoener 1983), but there has been no  
50 comparable analysis of competitive ability of rare versus abundant species.

51 Rare species are often difficult to study and most studies have been  
52 mensurative, involving biotic characteristics (e.g. Rabinowitz 1978), abiotic variables  
53 (e.g. Virtanen & Oksanen 2007) or disturbance regimes (e.g. Clarke & Patterson  
54 2007). Not all studies tested clear hypotheses (but see Gotelli & Simberloff 1987);  
55 many simply documented correlations. Exceptions are Fischer & Matthies (1998),  
56 who suggested a genetic basis for rarity of *Gentianella germanica*, Bruno (2002), who  
57 demonstrated that requirements for habitat limited the distributions of rare beach  
58 plants, and Boeken & Orenstein (2001) and Myers & Harms (2009), who each tested  
59 experimentally the role of rare species in recovery of plant communities. There have,  
60 however, been fewer manipulative studies of the role of rare species in assemblages of  
61 animals, although Angel et al. (2006) showed the effect of biotic disturbance in  
62 maintaining the rare limpet *Siphonaria compressa* in a suboptimal habitat.

63 It is often simply accepted that abundant species are competitively dominant  
64 over rare species (e.g. Lin & Liu 2006), but it is always necessary to test such  
65 hypotheses. Competition can only occur when abundances of potential competitors  
66 are large relative to availability of necessary resources. Species that have small  
67 populations are less likely to have encounters with conspecifics than are species with  
68 large local abundances. Thus, competition within and among rare species may be  
69 unlikely to be important (Myers & Harms 2009).

70 Many intertidal assemblages have numerous species which: (1) are  
71 taxonomically related, (2) have similar requirements for habitat or food and (3)  
72 interact strongly through competition, predation and other biological interactions. Yet,  
73 these assemblages typically contain many species with very small abundances.  
74 Nevertheless, these species persist temporally and spatially, even when documented to  
75 be competitively inferior (Espinosa et al. 2006), or when they have very stringent  
76 requirements for habitat (e.g. Angel et al. 2006).

77 Rare gastropods can show greater small-scale variability and less large-scale  
78 variability than do common species (Chapman & Underwood 2008), although this is  
79 not consistent among assemblages (e.g. Chapman et al. 2005). Some rare species are  
80 competitively dominant (Olabarria & Chapman 2001), although this may be modified  
81 by preferences for different microhabitats (Olabarria et al. 2002).

82 To investigate effects of changing densities on survival of naturally rare or  
83 naturally common gastropods, we manipulated the relative abundances of some  
84 common and rare species in pair-wise combinations to measure relative survival  
85 under conditions when abundances of rare species are increased to match the densities  
86 of common species. It has already been established that these species may exhibit  
87 interspecific competition (Olabarria & Chapman 2001). The models proposed to  
88 explain natural abundances of these common and rare species (and the tested  
89 hypotheses derived from them) were:

- 90 (1) Common and rare species have different natural abundances because rare species  
91 have more specific requirements for resources or individually need more resources  
92 than do common species. Therefore, rare species are more affected by  
93 intraspecific competition. Survival of rare species should be less than that of  
94 common species when densities of each type are at the natural densities of  
95 common species (Hypothesis 1). If densities of either type are increased to be  
96 greater than natural densities of common species, common species should have  
97 greater survival (Hypothesis 2);
- 98 (2) Rare species have smaller abundances because they are negatively influenced by  
99 competition from common species, but common species are less affected by other  
100 common, or by rare species. Rare species are therefore predicted to have  
101 decreased survival when kept with increased densities of common species  
102 (Hypothesis 3). In contrast, common species should not be as much affected when  
103 with enhanced densities of common or of rare species (Hypothesis 4);
- 104 (3) Alternatively, there is no general consequence of being rare that causes rare  
105 species to differ from common species when kept at similar enhanced densities or  
106 in the presence of other common or rare species. In this case, there will be no  
107 effects of being rare versus being common, or effects should be idiosyncratic  
108 (species respond differently, regardless of whether they are naturally rare or  
109 abundant; Hypothesis 5).

110 These predictions were tested by manipulating densities of combinations of  
111 common and rare intertidal gastropods in experimental assemblages. This design  
112 distinguished between asymmetrical intra- and interspecific effects of competition for  
113 common and rare species (e.g. Underwood 1986).

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## MATERIALS AND METHODS

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### Frequency and relative abundance of rare species

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We used microgastropods, with an adult shell size of 0.7 to 3.0 mm. There are many species of microgastropods in coralline turfs on rocky shores all over the world, including southeast Australia (e.g. Kelaher et al. 2001). Data collected previously from assemblages colonizing coralline turfs (Matias et al. 2007) were used to determine the frequency of occurrence of different species of gastropods, so that they could be reliably defined as rare or common. A species was defined to be rare when its abundance was <1% of all individuals of all species of microgastropods over all samples. Densities of the rare species were consistently <4 per 225 cm<sup>2</sup> of turf. Common species were found in relatively large abundances (>15 per 225 cm<sup>2</sup> of turf); these also occurred in >90% of these samples (with numbers of samples >20 in all cases). Using these definitions, 4 species of gastropods were chosen and their densities per 225 cm<sup>2</sup> (mean  $\pm$  SD) estimated (Fig. 1):

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(1) Common species 1, C1: *Eatoniella atropurpurea* (Frauenfeld, 1867);  $21.2 \pm 17.6$ ;

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(2) Common species 2, C2: *Amphithalamus incidatus* (Frauenfeld, 1867);  $15.7 \pm 10.3$ ;

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(3) Rare species 1, R1: *Alaba opiniosa* (Iredale, 1936);  $1.2 \pm 2.6$ ;

133 (4) Rare species 2, R2: *Eatonina rubrilabiata* (Ponder & Yoo, 1980;  $3.7 \pm 5.5$ .  
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135 To collect snails for experiments, patches of coralline turfs were sampled from  
136 intertidal platforms at the Cape Banks Scientific Marine Research Area, Botany Bay,  
137 New South Wales, Australia. Artificial surrogates of coralline turfs (synthetic grass)  
138 were also deployed to collect extra specimens, minimizing the need to remove  
139 excessive amounts of natural turfs from the shore. Artificial turfs, deployed 6 wk prior  
140 to the experiment, were rapidly colonized by gastropods in similar densities to those  
141 in natural turfs (Kelaher et al. 2001). All samples were washed under running water  
142 through a 500  $\mu\text{m}$  sieve. Strained gastropods were carefully sorted to species.

143 In total, ~10 000 gastropods were sorted to get the required numbers of each  
144 species. Twenty random sub-samples of ~100 individuals were identified and counted  
145 to provide estimates of relative abundances for each species. Abundant species were  
146 *Eatoniella atropurpurea* (55% of individuals) and *Amphithalamus incidatus* (42%).  
147 *Alaba opiniosa* (<1%) and *Eatonina rubrilabiata* (<1%) were amongst the least  
148 abundant species. These counts demonstrate that the species defined to be common or  
149 rare were consistently and correctly categorized in natural and in artificial habitats.  
150 Examination of data from extensive sampling and experiments over several years in  
151 other studies on similar assemblages including these species (Chapman & Underwood  
152 2008 and their unpubl. data) showed that the rare species were always rare and  
153 common species always common.

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### 156 **Experimental set-up**

157 In addition to turfs, the experimental species readily colonize bare rocky  
158 surfaces, where these are protected from desiccation. They also grow well on cores of  
159 rock in the laboratory (Olabarria & Chapman 2001). Therefore, cores (~1 to 2 cm  
160 deep, 3 cm diameter) were drilled out of 3 cm thick sandstone slabs previously  
161 attached to an intertidal platform at Cape Banks. These slabs had been in the field  
162 since November 2006 and were covered with algal biofilm. To check that similar  
163 amounts of biofilm were on the cores at the start of the experiment, algal biomass was  
164 estimated using Digital CIR quantitative imaging (see details in Murphy &  
165 Underwood 2006), which enabled rapid *in situ* measurements of chlorophyll *a* (as an  
166 index of biomass of micro-algae). This was repeated at the end of the experiment.

167 Five replicate cores were randomly assigned to each treatment (Table 1) and  
168 each core was enclosed in a mesh of 500  $\mu\text{m}$  to prevent snails from escaping. As a  
169 control test, 5 cores without snails were similarly enclosed with mesh. The experiment  
170 was left in running water in large aquaria, with plenty of space between cores, for 40  
171 d (April to July 2008) under a 10 h light: 14 h dark cycle to mimic natural daylight

172 and ambient water temperature (mean  $\pm$  SD = 18.8  $\pm$  1.3°C). This experimental set-up  
173 was previously used successfully to investigate survival of microgastropods at  
174 different densities (Olabarria & Chapman 2001). Previous studies have demonstrated  
175 that abundances of these small gastropods are dominated by small-scale (10s of cm)  
176 variation (Chapman & Underwood 2008), which also suggests that the size of these  
177 experimental units is entirely appropriate for examining competition among these  
178 species (see also Olabarria & Chapman 2001). Although there may be potential  
179 effects on the behaviour of gastropods due to handling and marking (see Chapman &  
180 Underwood 1992), the techniques used here have been used successfully in previous  
181 experiments (e.g. Olabarria & Chapman 2001).

182 Survival was defined by examining each individual gastropod under the  
183 microscope for signs of life, i.e. emergence or coherent movement of the foot. Four  
184 individuals of each species in each treatment were marked at the start of the  
185 experiment using enamel paint. Snails were submersed in seawater as soon as the  
186 paint was dry and any that did not emerge within 2 min were discarded and replaced  
187 by another marked individual (Olabarria & Chapman 2001). Each shell was measured  
188 from its apex to the lower lip of the opercular aperture, using an eyepiece micrometer  
189 (measurement error 0.001 mm). Growth was calculated as the size-specific rate of  
190 growth of each individual (final size/initial size) and transformed to natural  
191 logarithms.

## 192 **Design of the experiment**

193 Experimental treatments were sets of 1 or 2 species at different densities  
194 (Table 1). Based on previous experimens, standard density (4 individuals) was  
195 increased by adding 12 individuals, which was expected to be large enough to affect  
196 survival or growth (Olabarria & Chapman 2001). Treatments allowed comparisons of  
197 inter- and intraspecific competitive interactions, but it was not possible to set up all  
198 possible combinations between rare species (Table 1) because not sufficient  
199 individuals of each rare species could be collected. All comparisons necessary to test  
200 the hypotheses described above were made using analyses of variance, which differed  
201 among the different tests; the details of the analyses are given in the Results.

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## **RESULTS**

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### **Effects of density of conspecifics**

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Hypothesis 1 predicted that, at natural densities of common species, rarer species would survive less. There was, in fact, no difference among species at a density of 4 individuals per core (Fig. 2, Table 2). At increased densities, common

208 species were predicted to survive better than rare species (Hypothesis 2), but survival  
209 of all species was similarly lower in treatments with increased densities,  
210 independently of whether species were common or rare (Fig. 2, Table 2; note that  
211 there was no interaction between Type of species and Density). These results do not  
212 support Hypotheses 1 or 2, that rare species would be more affected by intraspecific  
213 competition. Instead, the results support Hypothesis 5, that being rare or common  
214 makes no difference to intraspecific competition.

215 Mean growth differed between species. Density had no effect on growth of C1  
216 (*Eatoniella atropurpurea*), C2 (*Amphithalamus incidatus*) or R1 (*Alaba opiniosa*),  
217 but, unusually, when averaged over all treatments, mean growth of the rare species,  
218 R2 (*Eatonina rubrilabiata*) was significantly greater at the larger density (Student-  
219 Newman-Keuls [SNK] test in Table 3; note the significant Density  $\times$  Species (Type)  
220 interaction).

### 221 **Competition from common species**

222 We hypothesized that rare species should have decreased survival when kept  
223 with large densities of common species (Hypothesis 3), but that common species  
224 should be less affected when kept with other common species or with large densities  
225 of rare species (Hypothesis 4).

226 There were, in fact, no general differences between survival of common and  
227 rare species when kept with larger densities of either of the 2 common species (Fig.  
228 3). There were, however, significantly different patterns of survival for the individual  
229 species in each category [note the Treatment  $\times$  Species (Type) interaction; Table 4].  
230 There was significantly less survival of common species C1, *Eatoniella atropurpurea*,  
231 when with increased densities of either common species. Survival of the second  
232 common species, *Amphithalamus incidatus*, was, however, only significantly reduced  
233 by increased density of conspecifics. Both rare species (R1, *Alaba opiniosa* and R2,  
234 *Eatonina rubrilabiata*) survived significantly less when with increased densities of  
235 either of the common species, which did not differ in their effects (Table 4, Fig. 3).

236 *Eatoniella atropurpurea* (C1) had a larger effect on itself and on the 2 rare  
237 species than on the other common species (Table 4). The increased density of the  
238 second common species C2 (*Amphithalamus incidatus*) caused greater interspecific  
239 and intraspecific reductions in density than was caused by C1.

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### 241 **Effects of increasing density of common or rare species**

242 The effects on survival and growth of increased densities of common or rare  
243 species were examined in several analyses. As it was impossible to create all  
244 treatments involving increased densities of rare species (see Materials and methods),  
245 each of the rare species was examined in a separate analysis. First, the effect of  
246 enhanced density of R1 (*Alaba opiniosa*) was compared with the effects of increased  
247 density of the common species. The analysis was asymmetrical (Underwood 1992)  
248 because there were 2 species nested in the type 'Common', but only 1 rare species.  
249 There was, in fact, no systematic difference due to being common or rare (analysis not  
250 shown; Type was not significant at  $p > 0.25$ ). The interaction of Treatment (+C1,  
251 +C2, +R1) and Species (C1, C2) was significant ( $F_{3, 48} = 6.54$ ,  $p < 0.001$ ). Thus,  
252 particular species had different effects on other species,

253 When at enhanced density, the first common species (C1, *Eatoniella*  
254 *atropurpurea*) significantly reduced survival of itself (i.e. intraspecific competition)  
255 and of the second rare species (R2, *Eatonina rubrilabiata*) but had no effect on the  
256 other common species and the first rare species (R1, *Alaba opiniosa*; Table 5, Fig. 3).  
257 In contrast, the other common species (C2, *Amphithalamus incidatus*) caused  
258 significantly reduced survival of each of the common species, but had no significant  
259 influence on survival of the rare species R1 (Table 5). The first rare species (R1, *A.*  
260 *opiniosa*) showed the same pattern as C1—it reduced survival of C1 and of itself, but  
261 not of the other common species, C2 (Table 5).

262 The analysis of the second rare species (R2, *Eatonina rubrilabiata*) showed a  
263 different pattern of competition from that shown by R1. It reduced survival of itself  
264 (i.e. intraspecific competition) and of the common species C1 (*Eatoniella*  
265 *atropurpurea*), but had no influence on survival of the other common species.

266 Thus, all 4 species caused increased intraspecific reductions in survival and  
267 had various influences on other species. There was no general pattern that could be  
268 attributed to being rare or common and the same pattern was shown by 1 rare and 1  
269 common species.

270 Similar analyses of growth showed no significant effects of enhanced density  
271 of any species on any other species (analyses not shown, but all tests not significant at  
272  $p > 0.25$ ).

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### 276 Chlorophyll as an index of food

277 At the start of the experiment, biomass of chlorophyll *a* did not significantly  
278 differ among experimental treatments (smallest and largest means  $\pm$  SE of chlorophyll  
279 were  $1.05 \pm 0.14$  and  $1.69 \pm 0.04 \mu\text{g cm}^{-2}$ ; analysis of variance, not presented here,  $p$   
280  $> 0.05$ ). Similarly, at the end of the experiment, there were again no differences  
281 (analysis of variance,  $p > 0.05$ , not presented; smallest and largest means were  $0.86 \pm$   
282  $0.08$  and  $1.63 \pm 0.15 \mu\text{g cm}^{-2}$ ). Thus, amount of food at the start and throughout the  
283 experiment did not differ for different species and densities. Changes in chlorophyll  
284 on each core were therefore uninformative.

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## DISCUSSION

287 To investigate how rare and common species might differ ecologically, we  
288 examined the effects of intra- and interspecific competition at normal and enhanced  
289 densities. Competitive interactions between the species examined were not generally  
290 determined by whether species were naturally common or rare. Common and rare  
291 species responded in the same way to increased densities of conspecifics (rejecting  
292 Hypothesis 2) and to natural densities of common species (rejecting Hypothesis 3).  
293 Thus, changes in densities of either type of species were similarly influenced by  
294 intraspecific competition. Similarly, common and rare species showed similar  
295 responses to larger densities, regardless of whether the increased densities were due to  
296 common or rare species (clearly rejecting Hypothesis 4). There was no evidence that  
297 natural rarity per se caused rare species to differ from common species in their  
298 responses to changes in densities of other species. Nor did rare, as opposed to  
299 common species have different effects on other species. The results strongly support  
300 the model that individual species respond differently, regardless of whether they are  
301 naturally rare or abundant (supporting Hypothesis 5) and, thus, that species showed  
302 idiosyncratic results (Emmerson et al. 2001).

303 Competitive interactions were expected (Olabarria & Chapman 2001) and,  
304 despite there being no pattern of change in abundance of microfloral food,  
305 intraspecific competition was found for all 4 of the species tested. All 4 were also  
306 involved in at least 1 interspecific competitive interaction. Thus, the experiment was  
307 sufficient to test for differences in competition between rare and common species.

308 Growth was generally not affected by competition from any species,  
309 regardless of their natural abundance. The only exception was 1 rare species,  
310 *Eatonina rubrilabiata*, which increased growth at larger densities of conspecifics.  
311 This is anomalous and is difficult to propose ecological processes that would allow  
312 greater growth when resources are under greater pressure. Possibly, more grazing  
313 associated with greater densities can enhance supplies of food (e.g. Branch 1984;  
314 Firth & Crowe 2010), although the measures of available food in the experimental  
315 treatments did not show greater standing stock of food for *E. rubrilabiata* at the large  
316 density. Standing stock is not, however, necessarily indicative of production. Overall,  
317 however, growth over the period of the experiment did not appear to be related to  
318 whether these grazers were naturally common or rare. As we used adult individuals  
319 only, growth during the experiment was expected to be small.

320 Our results are contrary to the expectation that small natural abundances of  
321 rare species are a direct result of competition (reviewed by Gaston & Kunin 1997),  
322 and that inferior competitive ability of rare species (e.g. rare grasses in American  
323 prairies, Rabinowitz et al. 1984) is a general explanation for rarity (see review by  
324 Lyons et al. 2005). In contrast, our results are consistent with those of Angel et al.  
325 (2006), who found no evidence that spatial distribution or abundance of the rare  
326 limpet *Siphonaria compressa* and the common gastropod *Assiminea globulus* were  
327 determined by interspecific competition. They also do not support previous  
328 suggestions that interspecific competition between individuals of the common limpet  
329 *Patella caerulea* and of the rare limpet *P. ferruginea* is the most likely explanation for  
330 the coexistence of these 2 species (Espinosa et al. 2006).

331 Most studies of competition between rare and common species have used  
332 experimental reductions of densities of the common species (e.g. Boeken & Shachak  
333 2006, Myers & Harms 2009), or manipulated densities of rare species via propagules,  
334 e.g. seeds (Bruno 2002). This is possibly because of the work necessary to increase



335 numbers of rare species, because of ethical constraints with manipulating densities of  
336 rare species, or because densities of rare species could not be maintained during  
337 experiments. This study overcame such difficulties, but, as with all laboratory  
338 experiments, any interpretation of results with respect to the real world must be made  
339 with care (e.g. Connell 1974). The limitations were reduced by minimizing  
340 disturbances and by making the size of the experimental units similar to that of many  
341 small patches of natural habitat in which these species live.

342 Although only 2 rare and 2 common species were studied here, the variation  
343 between the 2 species of each type was large. The individual rare species showed  
344 similar large amounts of difference in their competitive interactions, as did the 2  
345 common species. Therefore, it is not likely that different conclusions could have been  
346 reached, if more species had been tested.

347 To our knowledge, our study presents the first experimental test of the effects  
348 of commonness and rarity on inter- and intraspecific competition between co-  
349 occurring species randomly selected from natural assemblages.

350 Idiosyncratic differences between different species within the common or rare  
351 category should not necessarily be surprising. Chapman & Underwood (2008) showed  
352 no general patterns of colonization across multiple spatial scales for common and rare  
353 species of similar microgastropods, but considerable variation among species within  
354 each of these categories. Neither of the 2 common species studied here showed the  
355 same patterns observed by Chapman & Underwood (2008), and 1 of the rare species  
356 (*Eatonina rubrilabiata*) showed no spatial variation in abundance. Many recent  
357 studies of the diversity-identity problem (e.g. Cardinale et al. 2006) have shown that  
358 different species have different effects on ecological processes, often with 1 species  
359 being responsible for a lot of the pattern perceived as an outcome of the assemblage  
360 (e.g. Bruno et al. 2006). We may, therefore, make more progress into understanding  
361 causes of rarity if we stop attempting to force species into either of these categories  
362 (Gaston 1994) and attempt more experiments with multiple species to identify the  
363 range of individual responses.

364 These findings thus expand our understanding of the role of rare species and  
365 are relevant to several branches of current ecological research. In order to support the  
366 argument that biological diversity must be conserved to maintain ecosystem  
367 functioning, research must be able to demonstrate that rare species—the great  
368 majority of species in assemblages—also make significant contributions (Lyons et al.  
369 2005, Benedetti-Cecchi et al. 2008). These rare species have the potential to make  
370 significant contributions to ecological functions because they responded in the same  
371 way as common species. If persistence of rare species at small abundances can  
372 promote resistance or resilience to external stress or perturbations (Benedetti-Cecchi  
373 et al. 2008), their different environmental requirements and preferences could increase  
374 resilience in ecosystem functioning under perturbations that favour them over  
375 previously dominant species (Walker 1992).

376 It has also been suggested that reductions in density-dependent processes (e.g.  
377 competition) have a positive effect on rare species during adverse environmental  
378 conditions by reducing the risk of extinction and vulnerability to environmental  
379 instability (e.g. Benton et al. 2001, Benedetti-Cecchi et al. 2008). Recent studies  
380 showed that variability in assemblages depends on the relative contribution of rare  
381 and common species to spatial and temporal dynamics, suggesting that rare species  
382 may affect temporal changes in assemblages because of their susceptibility to

383 fluctuations in environmental conditions (e.g. Easterling et al. 2000, Benedetti-Cecchi  
384 et al. 2006).

385         Understanding how species with small geographic ranges, specialized habitat  
386 requirements and small local abundances have persisted through time (e.g. Harrison et  
387 al. 2008), will advance our knowledge of species' responses to adversity.

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519

520

521 Fig. 1. Frequency of occurrence of common (*Eatoniella atropurpurea* and  
522 *Amphithalamus incidatus*) and rare species (*Alaba opiniosa* and *Eatonina*  
523 *rubrilabiata*)

524

525 Fig. 2. Survival (mean + SE, n = 5) of common, *Eatoniella atropurpurea* (C1),  
526 *Amphithalamus incidatus* (C2), and rare, *Alaba opiniosa* (R1) and *Eatonina*  
527 *rubrilabiata* (R2), species of gastropods at ambient and enhanced densities. Bars with  
528 different grey shades indicate different species. \* :means differed significantly in  
529 Student-Newman-Keuls (SNK) tests at  $p < 0.05$  (see Table 2)

530

531 Fig. 3. Survival (mean  $\pm$  SE, n = 5) and growth (mean  $\pm$  SE, n = 3) of common,  
532 *Eatoniella atropurpurea* (C1), *Amphithalamus incidatus* (C2), and rare, *Alaba*  
533 *opiniosa* (R1) and *Eatonina rubrilabiata* (R2), species of gastropods in different  
534 experimental treatments. Black bars = intraspecific treatments. Different numbers on  
535 top of the bars indicate groups which differed significantly in Student-Newman-Keuls  
536 (SNK) tests at  $p < 0.05$

Figure 1

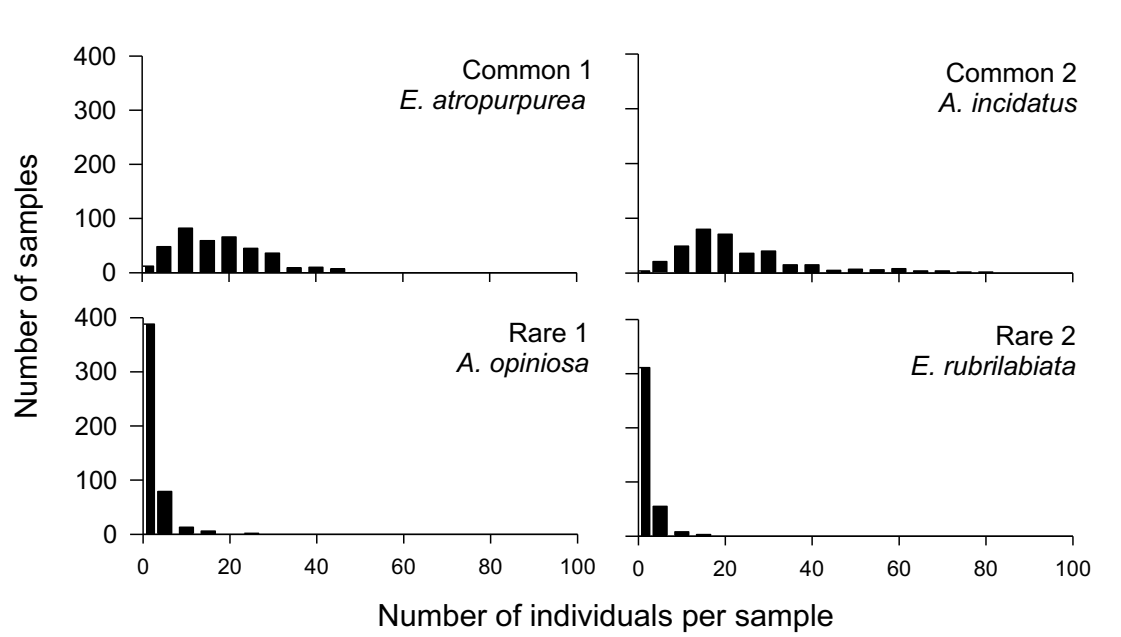


Figure 2

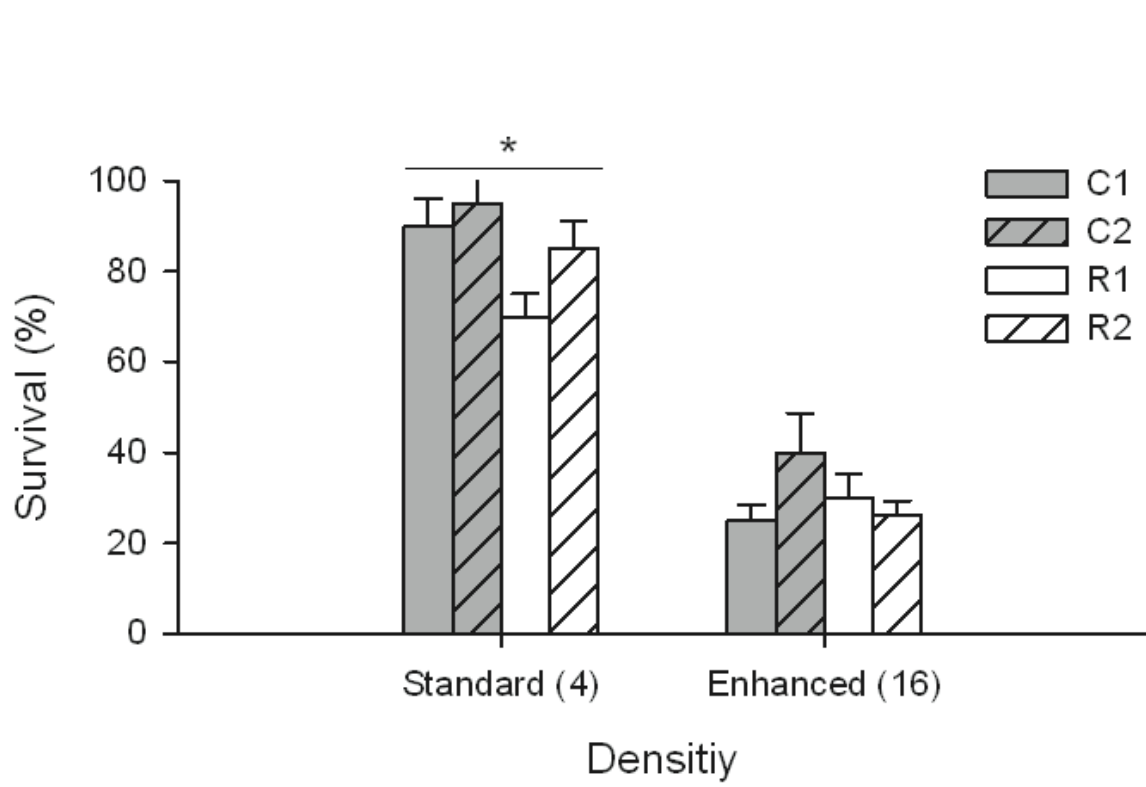
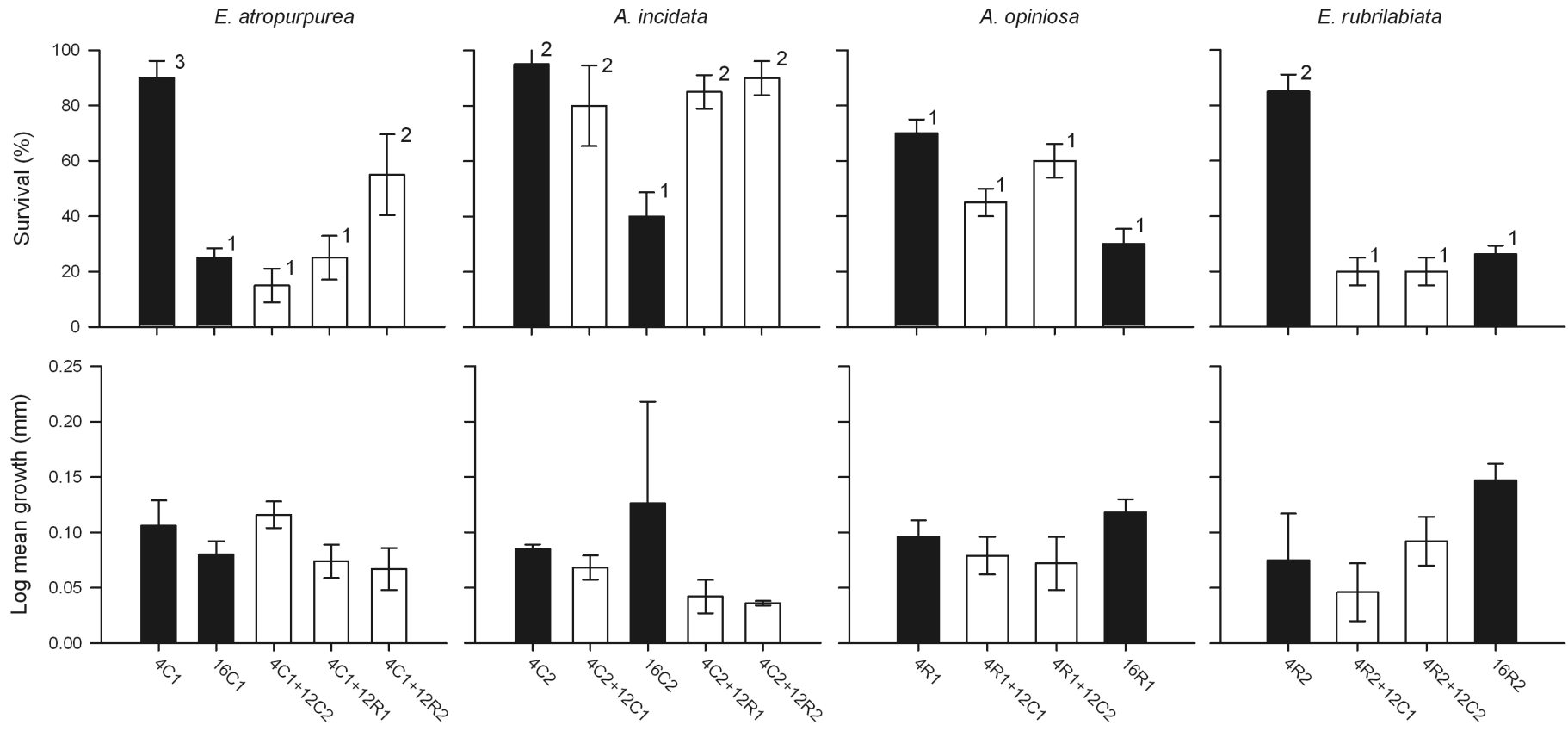




Figure 3



ble 1. Experimental treatments. To 4 individuals (standard density) each of common, *Eatoniella atropurpurea* (C1), *Amphithalamus incidatus* (C2), or rare, *Alaba opiniosa* (R1) and *Eatonina rubrilabiata* (R2), species 12 individuals each of C1, C2, R1 or R2 were added, except for the control. nd: not determined

-----Treatments -----				
Control + 0	+ 12 C1	+ 12 C2	+ 12 R1	+ 12 R2
4 C1	4 C1	4 C1	4 C1	4 C1
4 C2	4 C2	4 C2	4 C2	4 C2
4 R1	4 R1	4 R1	4 R1	nd
4 R2	4 R2	4 R2	nd	4 R2

Table 2. Mean percentage survival of common and rare species at different densities of conspecifics ( $n = 5$ ); Type is a fixed factor with 2 levels (common vs. rare), Species is nested in Type (C1, *Eatoniella atropurpurea*, C2, *Amphithalamus incidatus* are common; R1, *Alaba opiniosa*, R2, *Eatonina rubrilabiata* are rare), Density is a fixed factor with 2 levels (4 vs. 16 snails per core). Main factors involved in significant interactions were not tested. Levels of significance: \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$

Source	df	MS	F
Type = Ty	1	939	2.9
Species (Ty) = Sp(Ty)	2	330	2.1
Density = De	1	29908	105.1***
Ty $\times$ De	1	282	1.0
De $\times$ Sp(Ty)	2	282	1.8
Residual	32	158	
Pooled Residual, Sp(Ty) and De $\times$ Sp(Ty)			
Density (snails per core):	4		16
Survival (mean $\pm$ SE; n = 20):		85.0 $\pm$ 3.3	30.3 $\pm$ 2.9

Table 3. Mean growth [ $\ln(\text{final size}/\text{initial size})$ ] of common and rare species at different densities of conspecifics. Type is a fixed factor with 2 levels (common vs. rare). Species is nested in Type (*Eatoniella atropurpurea*, *Amphithalamus incidatus* are common. *Alaba opiniosa*, *Eatonina rubrilabiata* are rare), Density is a fixed factor with 2 levels (4 vs. 16 snails per core). Core is a random factor nested in the combinations of Species and Density. There were 2 replicate snails in each core. Data were transformed to  $\ln(X)$  (Cochran's test:  $C = 0.6$ ,  $p < 0.01$ ). Levels of significance as in Table 2, SNK = Student-Newman-Keuls

Source	df	MS	F
Type = Ty	1	0.003	0.1
Species (Ty) = Sp(Ty)	2	0.027	10.1***
Density = De	1	0.001	0.1
Ty $\times$ De	1	0.012	1.1
De $\times$ Sp(Ty)	2	0.011	4.1*
Core [De $\times$ Sp(Ty)]	32	0.003	1.0
Residual	40	0.003	
SNK test for Density $\times$ Species(Ty); '<' indicates $p < 0.05$			
Density (snails per core):	4		16
<i>E. atropurpurea</i>	0.09 $\pm$ 0.02	=	0.07 $\pm$ 0.02
	□	□	
<i>A. incidatus</i>	0.08 $\pm$ 0.01	=	0.05 $\pm$ 0.01
<i>A. opiniosa</i>	0.09 $\pm$ 0.02	=	0.12 $\pm$ 0.01
	□	□	
<i>E. rubrilabiata</i>	0.08 $\pm$ 0.02	<	0.14 $\pm$ 0.02

Table 4. variance of survival and growth of common and rare species in treatments with different densities of common species. Type is a fixed factor with 2 levels (common vs. rare). Species is 2 species of each type nested in Type. Treatment is a fixed comparison between treatments in which zero, 12 *Eatoniella atropurpurea* (C1) or 12 *Amphithalamus incidatus* (C2) were added. Analysis of survival uses data from 5 replicate cores ( $n = 5$ ); growth data are means of 2 to 4 snails from each of 3 replicate cores ( $n = 3$ ), transformed to  $\ln(X)$ . Main factors involved in significant interactions were not tested. Sources of variation were pooled if not significant at  $p = 0.25$ . Levels of significance as in Table 2, SNK = Student-Newman-Keuls

Source	df	MS	F	df	MS	F
Type = Ty	1	844	2.2	1	0.004	1.2 <sup>a</sup>
Sp (Ty) = Sp	2	4052		2	0.000	0.1
Treatment = Tr	2	15031		2	0.003	1.2 <sup>a</sup>
Ty × Tm	2	1531	0.9	2	0.001	1.1
Tr × Sp (Ty)	4	1802	7.5***	4	0.001	0.2
Residual	48	240		24	0.003	

<sup>a</sup>Tested against pooled residual + Sp(Ty) + Tr × Sp(Ty)

SNK tests of Tr × Ty for mean survival:

Treatment	+ 0	+ 12 C1		+ 12 C2	
4 C1	90	>	25	>	15
	□		□		□
4 C2	95	=	80	>	40
	□		□		□
4 R1	70	>	45	=	60
	□		□		□
4 R2	85	>	20	=	20

Table 5. Inter- and intraspecific effects of common, *Eatoniella atropurpurea* (C1), *Amphithalamus incidatus* (C2), and rare, *Alaba opiniosa* (R1) and *Eatonina rubrilabiata* (R2), species. Data are mean survival when at a density of 4 snails per core ('4 alone') or at enhanced density (+12 snails) of each of the other species. \*: significantly different from '4 alone' (Student-Newman-Keuls, [SNK] tests,  $p < 0.05$ ) na = not available

Mean survival in treatment	4 alone	+ 12			
		C1	C2	R1	R2
Effect on:					
C1 <i>E. atropurpurea</i>	90	25*(73%)	15*(84%)	25*(73%)	55*(39%)
C2 <i>A. incidatus</i>	95	80 (16%)	40*(58%)	85 (11%)	90 (5%)
R1 <i>A. opiniosa</i>	70	45 (36%)	60 (14%)	30 (57%)	na
R2 <i>E. rubrilabiata</i>	85	20*(76%)	20*(76%)	na	26*(70%)