

1 **Title:** Disturbance-induced changes in size-structure promote coral biodiversity

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25 **Abstract**

26 Reef-building coral assemblages are typically species-rich, yet the processes maintaining
27 coral biodiversity remain poorly understood. Disturbance has long been believed to promote
28 coral species coexistence by reducing the strength of competition. However, such
29 disturbance-induced effects have since been shown to be insufficient on their own to prevent
30 competitive exclusion. Nevertheless, Modern Coexistence Theory has revealed other
31 mechanisms by which disturbance and, more generally, environmental variation can favour
32 coexistence. Here, we formulate, calibrate, and analyze a size-structured, stochastic coral
33 competition model using field data from two common colony morphologies. These two coral
34 morphologies, tabular and digitate, differ in their size-dependent vulnerability to
35 dislodgement caused by wave action. We confirm that fluctuations in wave action can
36 promote coral species coexistence. However, using a recently proposed partitioning
37 framework, we show that, contrast to previous expectations, temporal variability in strength
38 of competition did not promote coexistence. Instead, coexistence was enabled by differential
39 fluctuations in size-dependent mortality among competitors. Frequent and intense
40 disturbances resulted in monocultures of digitate corals, which are more robust to wave
41 action than tabular corals. In contrast, infrequent or weak disturbances resulted in
42 monocultures of tabular corals. Coexistence was only possible under intermediate levels of
43 disturbance frequency and intensity. Given the sensitivity of coexistence to disturbance
44 frequency and intensity, anthropogenic changes in disturbance regimes are likely to affect
45 biodiversity in coral assemblages in ways that are not predictable from single population
46 models.

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50 **Introduction**

51 Reef-building coral assemblages are an example of the ‘paradox of the plankton’
52 (Hutchinson 1961): they can be species-rich, even though species compete for a small
53 number of limiting resources, mainly space, light, and nutrients in the water column.
54 However, the processes maintaining such high biodiversity remain enigmatic (Tanner *et al.*
55 1994; Bellwood & Hughes 2001). A classical explanation for reef coral coexistence, the
56 intermediate disturbance hypothesis (IDH), involves the periodic reduction, by disturbances,
57 in densities of dominant competitors, which frees up space for colonisation by weaker
58 competitors (Connell 1978; Aronson & Precht 1995). However, the IDH’s theoretical validity
59 has been challenged because the weakening of competition in the presence of disturbance is
60 not sufficient to promote coexistence (Chesson & Huntly 1997; Fox 2013). Long-term
61 coexistence requires that competition operates in such a way that individuals experience
62 progressively less competition, on average, as they become rare, so that they tend to recover
63 from excursions to low density. While disturbance cannot promote coexistence solely by
64 weakening competition, it produces environmental fluctuations that under some
65 circumstances can promote coexistence (Roxburgh *et al.* 2004).

66 Environmental fluctuations can favour coexistence when population growth rate
67 responds nonlinearly or sub-additively to these environmental fluctuations or competition. A
68 sub-additive response to the environment and competition means that population growth rate
69 is reduced less by competition when a species is experiencing an unfavourable environment
70 than when it is experiencing a favourable one. The higher cost of competition during
71 favourable times acts as an upper bound to population growth, while the lower cost during
72 unfavourable times acts as a lower bound. The coexistence mechanism acting via competitive
73 and environmental sub-additivity is called the *storage effect* (Chesson & Warner 1981;
74 Chesson 2000), which is known to operate in many ecological assemblages (e.g., (Cáceres

75 1997; Adler *et al.* 2006; Angert *et al.* 2009)). However, covariation between other factors or
76 demographic rates affecting population growth can also impact coexistence (Ellner *et al.*
77 2019).

78 When population growth rate responds nonlinearly to competition, the average
79 population growth can either be boosted or depressed by fluctuations in competition relative
80 to a constant environment at the mean competition (Armstrong & McGehee 1980) (i.e.,
81 *relative nonlinearity of competition*; (Chesson 2000)). Coexistence is possible when the
82 inferior competitor under average conditions gets a larger benefit from fluctuations in
83 competition than does the superior competitor, and each population, when abundant, creates
84 the conditions that favour its competitor. Coexistence via nonlinear averaging has not
85 received as much attention as the storage effect, despite being more important than non-
86 additivity under some conditions (e.g., (Miller *et al.* 2011; Letten *et al.* 2018)). Moreover,
87 until very recently, coexistence via nonlinear averaging was thought to act exclusively via
88 nonlinearities in the population growth rate's response to competition, however nonlinear
89 responses to other factors, such as the environment, can also promote coexistence (Ellner *et*
90 *al.* 2019).

91 In coral assemblages, hydrodynamic disturbances strongly affect assemblage structure
92 (Connell *et al.* 2004), mainly by imposing mortality pulses that affect top-heavy colonies
93 more than bottom-heavy ones (Madin & Connolly 2006a). Consequently, susceptibility to
94 wave action is morphology- and size-dependent (Massel & Done 1993; Madin & Connolly
95 2006a; Madin *et al.* 2014). Since top-heavy colonies, such as those of species with a tabular
96 morphology, tend to grow faster than bottom heavy colonies (Dornelas *et al.* 2017) and can
97 monopolize space on the reef crest in the absence of hydrodynamic disturbances (Baird &
98 Hughes 2000), periodic hydrodynamic disturbances have long been thought to prevent the
99 exclusion of bottom-heavy competitors (Connell 1978). Moreover, because top-heavy

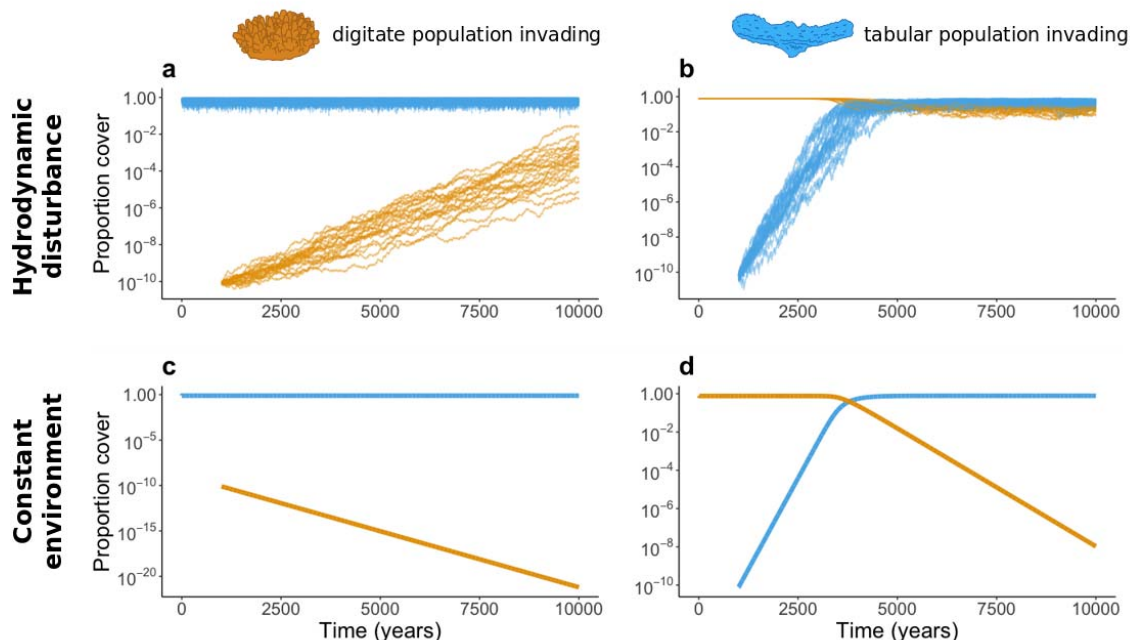
100 colonies increase in susceptibility to mechanical dislodgement with increasing colony size,
101 storms affect the largest, most fecund sizes disproportionately, further affecting superior
102 competitors. Therefore, the effect of hydrodynamic disturbances on coexistence acts in two
103 ways: clearing space for larvae to settle and altering, not just the relative number of colonies
104 of each competitor, but also the populations' size structures. While the presence of periodic
105 disturbance is not sufficient to promote coexistence (Chesson & Huntly 1997; Fox 2013), if a
106 competitors' population growth rates respond nonlinearly or non-additively to factors (e.g.,
107 competition) or demographic rates (e.g., survival) that fluctuate with disturbance, disturbance
108 could promote coexistence between coral morphologies.

109 Here, we calibrated a competition model using field demographic data for two
110 common coral morphologies (Madin *et al.* 2014; Álvarez-Noriega *et al.* 2016; Dornelas *et al.*
111 2017) and simulated hydrodynamic disturbances using a local 37-year wind record. Using
112 model simulations, we first investigated whether or not coexistence was possible in the
113 presence of hydrodynamic disturbance. Then, having found that it was, we identified the
114 fluctuation-dependent mechanisms responsible for coexistence by decomposing competitors'
115 population growth rates into contribution from each of the different fluctuating components:
116 competition, size structure, and the interaction between the two. We chose tabular *Acropora*
117 as the model morphology for corals that are fast growing, good competitors that are highly
118 susceptible to disturbance, and digitate *Acropora* as the model morphology for slower
119 growing, more mechanically robust corals. These two morphologies are very common in the
120 wave-exposed habitats of highly diverse Indo-Pacific reefs (Done 1982; Dornelas &
121 Connolly 2008).

122

123 **Results and Discussion**

124 In our model, coexistence of tabular and digitate corals was only possible in the
125 presence of hydrodynamic disturbance (Fig. 1). In a variable environment, both competitors
126 had a positive population growth rate when they were rare and the other competitor was a
127 resident (Fig. 1-a & b). This implies that if the population of either competitor reaches very
128 low densities, it will be able to recover and avoid extinction in the presence of the other
129 competitor, which is abundant (or at least at its long-term abundance in monoculture).
130 However, in a constant environment, one of the competitors was unable to recover from low
131 densities (Fig. 1-c & d). Indeed, with our model, we find no region of parameter space where
132 coexistence could occur in the absence of fluctuations (see Methods). To investigate the
133 mechanism by which hydrodynamic disturbance was driving coexistence, we isolate the
134 effects of the different sources of fluctuations in our model on invader growth rate. We
135 quantified the approximate contribution of the two main fluctuating factors affected by wave
136 action: competition (i.e., proportion of free space) and size-dependent mortality due to
137 disturbance, as well as the additional contribution of both factors fluctuating together (i.e.,
138 their interaction). To do this, we used a recent quantitative framework (Ellner *et al.* 2019)
139 that relies on simulations rather than mathematical approximations, thus allowing for higher
140 model complexity than previous frameworks (e.g.,(Chesson 1994)).
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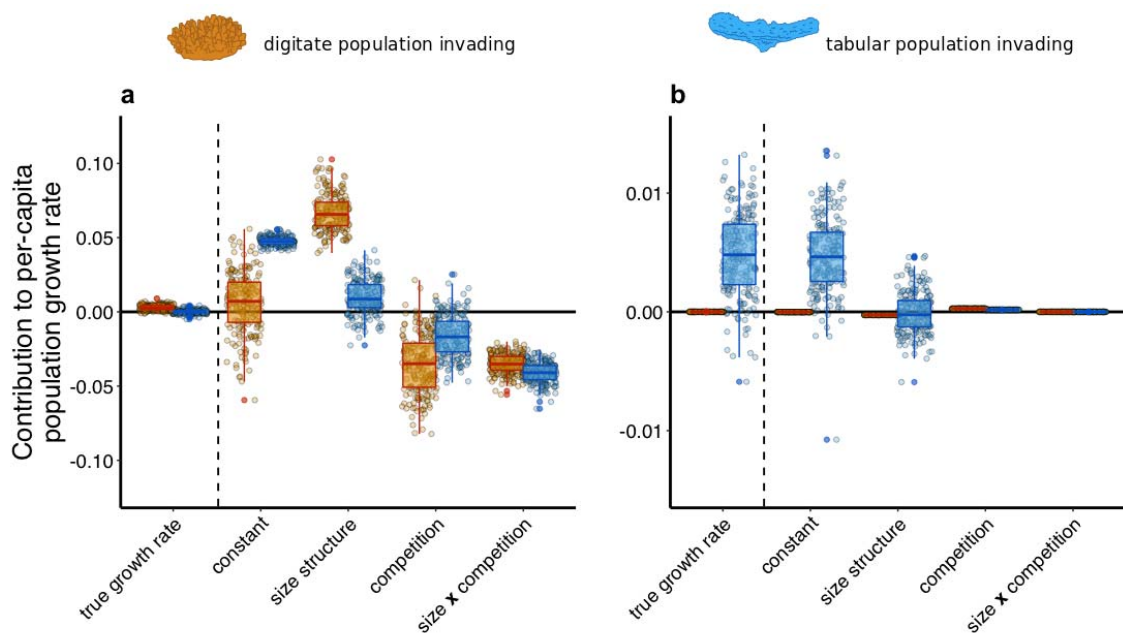


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143 **Figure 1.** Proportion of space occupied through time following an invasion. The trajectories
144 of the digitate and tabular populations are in orange and blue, respectively. Panel a- Digitate
145 population invading a tabular resident in the presence of environmental fluctuations. Panel b-
146 Tabular population invading a digitate resident in the presence of environmental fluctuations.
147 Panel c- Digitate population invading a tabular resident at the mean size-dependent survival
148 rates (constant environment). Panel d- Tabular population invading a digitate resident at the
149 mean size-dependent survival rates (constant environment). Note that the scale is different in
150 Panel c. In panels a & b, each line represents one simulation (out of 20), in panels c & d, all
151 simulations follow the same trajectory. These simulations were run for 10,000 years (with
152 invasion after 2000 years) to show the full dynamics of invasion, but were run only for 2300
153 years (300 years following invasion) for all other analyses.
154

155 Contrary to the prevailing understanding of how disturbance promotes coexistence,
156 fluctuations in free space actually had a coexistence-inhibiting effect (i.e., a negative effect
157 on the invader growth rate; Fig. 2-a, Fig. S6), relative to the constant free space model where
158 average free space from the stochastic simulation was imposed every year. Rather, invasion
159 and establishment of the digitate population depended on the beneficial effect of fluctuations
160 in size structure caused by differences in size-dependent susceptibility to disturbance (which
161 was the only term >0 for the digitate population; Fig. 2-a). The positive contribution of
162 fluctuations in size structure counteracted the negative effects of fluctuations in free space
163 and size structure varying jointly on the digitate population's invasion growth rate.

164 Conversely, the invasion growth rate of the tabular population was positive solely because it
165 had a positive per-capita growth rate under average conditions (Fig. 2-b). Since the digitate
166 population was not vulnerable to hydrodynamic dislodgment, fluctuations were negligible
167 when this population was dominant, and therefore did not affect population growth.
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170 **Figure 2.** Partitioning the contributions to per-capita population growth (r). Contribution of
171 the different sources of variation to mean population growth rate ('true population growth')
172 following Ellner et al. 2019 (Ellner *et al.* 2019) when a digitate population invades a tabular
173 resident (Panel a), and when a tabular population invades a digitate resident (Panel b).
174 *Constant* refers to the population growth rate at mean values of free space and competitors'
175 size structures. *Size structure* represents the contribution of fluctuations in size structure to
176 population growth rate when competition is constant (at its mean value). Similarly,
177 *competition* represents the contribution of fluctuations in the amount free space when size
178 structures are fixed at their mean values for each competition. *Size structure* and *competition*
179 are the main effects. *Size x competition* represents the contribution of the simultaneous
180 fluctuation of competition and size structure that is independent of their main effects. The
181 true population growth rate is the sum of *constant*, *size structure*, *competition*, and *size x*
182 *competition*, and it is equal to the mean population growth rate when size structure and
183 competition fluctuate (). See methods for more details. The digitate and tabular populations
184 are represented by orange and blue colours, respectively. Each point represents the one
185 simulation (200 simulations in total), and the box plots show their distribution.
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To understand how environmental fluctuations induced a stabilizing coexistence

effect, it is important to recognize that each species was favoured at different levels of

environmental variation. Hydrodynamic disturbance increased the digitate population's

growth rate, while the tabular population performed best when environmental variation was

low (i.e., under average conditions). When abundant, each population created the conditions

that favoured its competitor, allowing the latter to increase in abundance. When the digitate

population was rare, the high abundance of tabular corals induced large fluctuations in

competition – specifically, via the dislodgment of large tabular corals, and an associated

reduction in reproductive output of the tabular population – which favoured the digitate

population. Conversely, when the tabular population was rare and the mechanically-stable

digitate population was abundant, resource fluctuations were minimal. This favoured tabular

corals, whose per-capita population growth rate was higher at the mean resource level, as

well as in the absence of disturbance. These dynamics are consistent with empirical

observations. Tabular corals grow faster than digitate corals (Dornelas *et al.* 2017) and reach

larger colony sizes that are very fecund (Álvarez-Noriega *et al.* 2016). In periods of low

hydrodynamic disturbance, tabular species can dominate the reef crest (Baird & Hughes

2000). However, hydrodynamic disturbances affect the large, very fecund, tabular colonies

most strongly (Madin & Connolly 2006a) and, consequently, the relative abundances of

digitate corals tend to increase after disturbances that dislodge tabular corals (Muko *et al.*

2013). Our findings are also consistent with changes in the relative abundance between

species following disturbance in the Caribbean (Aronson & Precht 1995) and the recovery of

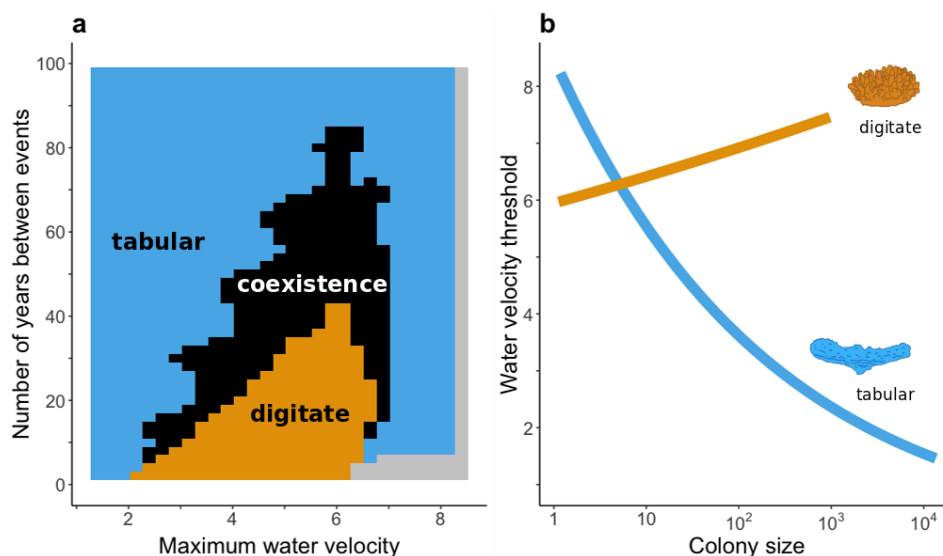
species richness following strong hydrodynamic disturbance on the GBR (Connell *et al.*

2004).

According to the IDH (Connell 1978), coexistence should be more likely at

intermediate levels of disturbance because high disturbance eliminates susceptible species,

214 while low disturbance allows dominant competitors to exclude inferior ones. Sensitivity
215 analysis indicates that fluctuation-dependent coexistence creates such a relationship in our
216 model: if disturbance is weak or very infrequent, the tabular population outcompetes the
217 digitate population; if disturbance is very frequent, the digitate population outcompetes the
218 tabular population (Fig. 3-a). Coexistence was possible for a wide range of disturbance
219 frequencies and intensities but, as expected, the more intense the disturbance, the less
220 frequent it could be and vice-versa. Once disturbance was sufficiently intense to dislodge
221 most of the digitate colonies (i.e. only the largest sizes would survive; Fig. 3-b), the digitate
222 population was again unable to invade a tabular resident, despite most tabular colonies being
223 dislodged too (Fig. 3- a & b). This occurred because the rapid growth of surviving small
224 tabular colonies favoured their population recovery over that of digitate populations, for
225 extreme disturbance regimes that dislodged even digitate colonies.



226

227 **Figure 3.** Effect of frequency and intensity of disturbance on species coexistence. Panel a-
228 Competitive outcomes depending on the intensity (maximum water velocity; ms^{-1}) and
229 frequency (number of years between disturbance events) of disturbance. Colours indicate
230 combinations of competitive outcomes: the digitate population outcompetes the tabular
231 population in orange areas, the tabular population outcompetes the digitate population in blue
232 areas, in grey areas both competitors go extinct, and coexistence is possible in black areas.
233 Panel b- Minimum water velocity required to dislodge a colony depending on colony size
234 (cm^2) (estimates are from (Madin *et al.* 2014)). The orange line shows the relationship for the
235 digitate colonies and the blue line shows the relationship for the tabular colonies.

236 The contribution of nonlinear responses of population growth rates to coexistence has
237 received considerably less attention than the contribution of nonadditive responses (mainly
238 the storage effect). Nonlinear responses to coexistence were initially thought to be more
239 limited than for the latter (Chesson 1994), although recent studies suggest otherwise (Letten
240 *et al.* 2018; Hallett *et al.* 2019; Zepeda & Martorell 2019). Importantly, the contribution of
241 nonlinear responses to coexistence was thought to be limited to competition (e.g., (Chesson
242 1994, 2000)) until very recently (Ellner *et al.* 2019). In our model, fluctuations in competition
243 were limiting, rather than promoting, coexistence (Fig. 2-a). Since coral demographic rates
244 are tightly linked with colony morphology (Madin *et al.* 2014; Álvarez-Noriega *et al.* 2016),
245 we expect our results to hold for competition between any species of these morphologies.
246 Tabular and digitate corals of the genus *Acropora* have a widespread distribution across the
247 Indo-Pacific and are abundant in wave-exposed reef environments (Done 1982). More
248 broadly, our findings highlight the potential for nonlinear responses in population growth rate
249 to promote coexistence whenever differences in mechanical stability produce differential
250 fluctuations in size structure, as long as those fluctuations disadvantage the population with
251 the higher intrinsic growth rate under average conditions. Because overtopping growth forms
252 tend to be both fast-growing and mechanically unstable (Jackson 1979), nonlinearities are
253 likely to play a role in competition involving species with these growth forms.

254 Disturbance has long been thought to be an important contributor to coral species
255 coexistence (Connell 1978), but the lack of a mechanism has made this idea controversial in
256 recent years (Chesson & Huntly 1997; Fox 2013). We show that environmental fluctuations
257 can promote coexistence of species that differ in their size-dependent susceptibility to
258 disturbance, limiting the ability of superior competitors to form monocultures and exclude
259 inferior competitors. While other mechanisms are likely to operate to promote coexistence in
260 coral assemblages (including spatial heterogeneity (Hoogenboom *et al.* 2011) and

261 asymmetries and fluctuations in metapopulation connectivity (Salomon *et al.* 2010)), the fact
262 that hydrodynamic disturbances' transient effects on coral assemblages are large in
263 magnitude and consistent with the model analysed here suggests that the contribution made
264 by hydrodynamic disturbance to coexistence in wave-exposed habitats with fast-growing,
265 top-heavy coral species might be substantial. If so, anthropogenic changes that alter
266 hydrodynamic disturbance regimes (Knutson & Tuleya 2004) or species' skeletal densities
267 and therefore their vulnerability to mechanical disturbance (Madin *et al.* 2012) are likely to
268 affect coral assemblages in ways that will not be captured by commonly used methods of
269 projecting reef futures, which either consider coral cover to be a single population, or which
270 aggregate the projections of single-species models. Moreover, size-dependent responses to
271 the environment are common in nature (Tredennick *et al.* 2018), and are likely to vary among
272 species. For instance, trees differ in their size-dependent response to drought (Zang *et al.*
273 2012) and size-dependent fishing pressure affects fish species differently (Genner *et al.*
274 2010). Consequently, effects of episodic mortality agents on coexistence via nonlinearities in
275 population growth rates are likely to be more widespread in nature than currently recognised.

276

277 **Methods**

278

279 Analysis overview

280 First, we specified the competition model and parameterised demographic rates and the
281 disturbance regime. Then, we did an invasibility analysis in the presence of environmental
282 fluctuations to test whether coexistence was possible, and we compared it to an invasibility
283 analysis in a constant environment to investigate if coexistence was mediated by
284 environmental fluctuations. After determining that coexistence was fluctuation-dependent,
285 we decomposed population growth rate into the contribution of: 1) demographic rates at

286 constant (average) conditions, 2) fluctuating size structures, 3) fluctuating competition
287 (proportion of occupied space), and 4) joint fluctuation of competition and size structures.
288 Finally, to test whether competitive outcomes were dependent on the strength and frequency
289 of the disturbance regime, we did invasibility analyses over a range of wind intensities and
290 frequencies. See Figure S1 for a diagrammatic summary of our approach. We explain each
291 step in detail below.

292

293 Competitive model specification

294 We used integral projection models (Easterling *et al.* 2000) (IPMs) to characterise
295 community dynamics. In the model, demographic processes over each year were divided into
296 two sub-intervals: from time $t-1$ to time $t-h$ (where $h \in [1 - z, 1)$ and $z \rightarrow 0$), when
297 reproduction and larval settlement occurred, and 2) from time $t-h$ to time t , when disturbance,
298 growth, and survival occurred. In other words, reproduction occurred before growth and
299 survival. We adopted this approach because settlement usually peaks shortly (1-2 weeks)
300 after spawning (Miller & Mundy 2003; Nozawa & Harrison 2008), and thus most growth and
301 mortality of established corals would occur outside this interval. Because coral recruitment is
302 proportional to unoccupied space (Connell *et al.* 1997), we modelled the proportion of larvae
303 successfully recruiting as depending linearly on free space availability $1 - \sum_{j=1}^2 N_{j,t}$, where $N_{j,t}$ is
304 the proportion of space occupied by species j at time t . $N_{j,t}$ was calculated by integrating the
305 density of colonies of size y at time t ($n_j(y, t)$) times their planar area, and then normalizing by
306 the total habitat area (A):

$$307 \quad N_{j,t} = \frac{\int y [n_j(y, t)] dy}{A}.$$

308 (Eq. 1)

309 The density of colonies of size x at time $t-h$ for species j ($n_j(x, t-h)$) was the sum of (i)
310 the density of colonies of size x just before settlement ($n_j(x, t-1)$) and (ii) the density of

311 successful settlers of size x at time $t-h$ produced through reproduction of colonies of size x at
312 time $t-1$. The number of possible settlers was given by the integral of the fecundity kernel
313 ($F_j(x, x')$) times the size distribution at time $t-1$ ($n_j(x, t-1)$). The fecundity kernel was a surface
314 containing transitions from a parent of size x at time $t-1$ to an offspring of size x' at time $t-h$,
315 and thus it implicitly included reproductive output, larval survival, and successful settlement.
316 With the above assumptions, the density of successful settlers was:

$$317 \quad R_j(x', t-h) = (1 - \sum_{i=1}^k N_{i,t-1}) \int_0^\infty F_j(x, x') n_j(x, t-1) dx.$$

318 (Eq. 2)

319 The size distribution at time $t-h$ was then:

$$320 \quad n_j(x', t-h) = n_j(x', t-1) + R_j(x', t-h).$$

321 (Eq. 3)

322 In the second sub interval ($t-h$ to time t), the model predicted growth and survival of
323 all corals (including those newly recruited) and the proportion of space occupied by each
324 species was calculated (N_j). Survival from time $t-h$ to time t ($S_{j,t-h}(x')$) had two components: a
325 stochastic component that depends on susceptibility to the strongest yearly mechanical
326 disturbance ($D_{j,t-h}(x')$), and a deterministic component that represents ‘background’ mortality
327 ($M_j(x')$; i.e. mortality independent of mechanical disturbance):

$$328 \quad S_{j,t-h}(x') = (1 - D_{j,t-h}(x')) (1 - M_j(x')).$$

329 (Eq. 4)

329 The distribution of colonies of size y at time $t+1$ depended on the survival of colonies
330 of size x ($S_{j,t-h}(x)$) and their size-dependent growth to colony size y ($G_j(x, y)$) from time $t-h$ to
331 time t :

$$332 \quad n_j(y, t) = \int_0^\infty [S_{j,t-h}(x') G_j(x', y)] n_j(x', t-h) dx'.$$

333 (Eq. 5)

334 We modelled growth as density-independent, because no effect of competition on colony
335 growth could be detected for the modelled species at the site (Álvarez-Noriega *et al.* 2018).
336 Specifically, growth was modelled as a linear function of size on a logarithmic scale
337 ($y_i \sim \beta_0 + \beta_1 x'_i + \varepsilon_i$) using published data from the study site (Dornelas *et al.* 2017).

338

339 Parameter estimation

340 Model parameters are defined in the extended data (Table S1).

341 Growth, fecundity, and background mortality were obtained from a 5-yr data set of 30
342 colonies per species on the reef crest of Lizard Island, northern Great Barrier Reef
343 (14.699839°S, 145.448674°E). Parameter estimates were obtained from previously-published
344 analyses of these data (Madin *et al.* 2014; Álvarez-Noriega *et al.* 2016; Dornelas *et al.* 2017),
345 and are reported in the **R** scripts for this paper, which will be publicly available in Github
346 upon publication. For each growth form, demographic data of two species -*Acropora*
347 *hyacinthus* and *Acropora cytherea* for tabular corals and *Acropora cf. digitifera* and
348 *Acropora humilis* for digitate corals- were pooled for analysis (Fig. S2). *Acropora hyacinthus*
349 and *A. cf. digitifera* were among the most abundant coral species at the site (Dornelas &
350 Connolly 2008). Previous analyses indicate that growth, mortality, and fecundity all vary
351 substantially more between growth forms than between species of the same growth form
352 (Madin *et al.* 2014; Álvarez-Noriega *et al.* 2016; Dornelas *et al.* 2017).

353 The fecundity function ($F_j(x, x')$) for species j depended on: the size-dependent
354 probability of a polyp being mature ($p_{j,x}$), the size-dependent number of oocytes per mature
355 polyp ($m_{j,x}$), the number of polyps per projected unit area (ρ_j), the projected area of the
356 colony (a_j) and the settlement probability (q_j):

$$357 F_j(x, x') = p_{j,x} m_{j,x} \rho_j a_j q_j.$$

358

(Eq. 6)

359 The settlement probability included the probability of an egg being fertilised and
360 becoming a larva, and the probability of that larva successfully settling. Since larval mortality
361 is density-independent and per-capita settlement, if affected at all, is positively affected by
362 higher larval densities(Heyward *et al.* 2002; Edwards *et al.* 2015; Doropoulos *et al.* 2017,
363 2018), we assumed no competition among larvae (i.e., successful recruitment depended on
364 unoccupied space, but not on the density of offspring seeking to settle).

365 All terms in eq. (6) except for settlement probability were obtained from Álvarez-
366 Noriega *et al.* (2016)(Álvarez-Noriega *et al.* 2016). Since there is no information available on
367 settlement probability, we fixed a value resulting in average coral cover of about 75% of each
368 morphology in the absence of competitors and in the presence of disturbance. However, we
369 considered a range of values of this parameter to ensure that settlement probabilities resulting
370 in lower average coral cover yielded consistent results (i.e., coexistence by RNC in the
371 presence of environmental fluctuations; no coexistence possible without fluctuations).

372 Mortality due to mechanical disturbance was determined by comparing each colony's
373 'Colony Shape Factor' (CSF) to the 'Dislodgment Mechanical Threshold' (DMT) imposed
374 by the yearly maximum hydrodynamic disturbance. Both quantities were derived by Madin
375 and Connolly (Madin & Connolly 2006b), and field-tested on Lizard Island, at a reef adjacent
376 to our study site. When the DMT of an event exceeds the CSF of a colony, the colony is
377 predicted to be dislodged.

378 In each year of the simulation, a random wind velocity was drawn from a gamma
379 distribution ($\alpha=2.18$, $\beta=0.35$), with parameters estimated from the distribution of a 37-year
380 wind velocity data for the Low Isles (16.383°S, 145.567°E) (from the Australian Bureau of
381 Meteorology), approximately 180 km south of Lizard Island (Madin *et al.* 2006). Water
382 velocity at the reef crest as a function of wind velocity was estimated using wind and water
383 velocity at the reef crest collected at the site(Madin *et al.* 2006). We predicted water velocity,

384 u , as a saturating function of wind velocity, v , because wave energy is limited by fetch and
385 depth:

$$u = a(1 - e^{-bv}),$$

386 (Eq. 7)

387 where a and b are fitted parameters, estimated by least-squares estimation ($a= 5.10$, $b= 0.04$;
388 Fig. S3). Using previously calibrated relationships between colony size and CSF for our
389 study species at Lizard Island (Madin *et al.* 2014), colonies were predicted to dislodge if the
390 DMT imposed by the yearly maximum wind velocity was smaller than the colony's estimated
391 CSF (Madin & Connolly 2006b). Since dislodged colonies have very low survival rates
392 (Smith & Hughes 1999), colony dislodgement was assumed to cause colony mortality.

393 Background mortality (mortality independent of mechanical disturbance) was
394 estimated from mortality data from 2009-2012 (Madin *et al.* 2014). CSF for each individual
395 colony was estimated and compared to the maximum dislodgement mechanical threshold
396 imposed by the environment that year (estimated from wind data at the site(Australian
397 Institute of Marine Science 2017)). As predicted by theory (Madin & Connolly 2006b) and
398 validated with mortality data on the reef (Madin *et al.* 2014), colonies that had CSF larger
399 than the DMT estimated for that year were assumed to have been dislodged. Colonies
400 predicted to dislodge were assumed dead and were removed from the data set from which
401 background mortality was estimated. With the remaining data, two linear models with a
402 binomial error structure were fitted for each growth form: one with colony area as an
403 explanatory variable (log-scale) and one independent of colony area. Models were compared
404 using AIC, and the best-fit model for each growth form was used in the simulations (Tables
405 S2-S3; Figs. S4-S5).

406
407 Analysis of coexistence
408

409 Partitioning the contribution of the fluctuation-dependent mechanisms using
410 analytical solutions for quadratic approximations (Chesson 1994) is unfeasible in complex
411 models (e.g. multiple-step, stage/size-dependent models); therefore, we estimated terms
412 needed for the analytical solution via simulations.

413 Overall, the finite rate of increase in cover of species j between time $t-1$ and time t
414 ($\lambda_j(t)$) in terms of proportion of occupied space (i.e. the factor by which the proportion of
415 space occupied by species j changes) is:

$$\lambda_j(t) = \frac{N_{j,t}}{N_{j,t-1}} \quad (\text{Eq. 8})$$

416 and the overall specific population growth rate ($r_j(t)$) is:

$$r_j(t) = \ln [\lambda_j(t)]. \quad (\text{Eq. 9})$$

420

421

422 Decomposing growth rate into contributions from different sources of variation

423 We follow Ellner et al. (Ellner *et al.* 2019) to decompose mean population growth rate of
424 each species (\bar{r}_j) into population growth rate at mean conditions (ε_j^0), the contribution of
425 fluctuations in competition ($\bar{\varepsilon}_j^c$), fluctuations in size-structure ($\bar{\varepsilon}_j^s$), and the interaction
426 between fluctuating competition and size-structure ($\bar{\varepsilon}_j^{wc}$):

$$\bar{r}_j = \varepsilon_j^0 + \bar{\varepsilon}_j^w + \bar{\varepsilon}_j^c + \bar{\varepsilon}_j^{wc}. \quad (\text{Eq. 18})$$

428 The approach involves computing population growth under different scenarios: one where all
429 varying factors are allowed to fluctuate, and one for each possible combination of one of
430 more of the varying factors fixed at its mean value from the stochastic simulations. The

431 population growth rates from the different scenarios are compared to quantify the
432 contribution of each factor varying on its own and in combination with other factors.

433 First, a simulation was run in which one population was introduced at a coral cover
434 $<10^{-9}$ in a system where the competitor had been resident for 2000 years; the simulation ran
435 for 300 years after the invasion. In this first simulation (the baseline simulation), wind
436 velocities were randomly drawn from the gamma distribution fitted to the wind velocity data
437 at Low Isles; from this simulation we estimated \bar{r}_j as the mean population growth of species j
438 from 50 years after the invasion to the end of the simulations. Competition (c), and size-
439 structure (w) (both $n(x', t - h)$ and $n(y, t + 1)$) were recorded for each year of the
440 simulation (c_t^* and $w_{j,t}^*(x)$), where $w_{j,t}(x)$ is the size distribution of colony sizes of species j
441 at time t (normalized to integrate to unity) and c_t is the proportion of free space at time t ; the
442 asterisks indicates values for the baseline simulation. Using these values, we then calculated
443 their temporal averages $\bar{w}_j(x)$ and \bar{c} and ran a simulation in which $w_{j,t}(x)$ and c_t were fixed
444 at those mean values to estimate ε_j^0 ($\varepsilon_j^0 = \frac{1}{T-I} \sum_{t=I}^T r_j(\bar{w}(x), \bar{c})$, where I is time after 50 years
445 after the invader was introduced ($I=2050$; to be consistent with the previous growth rate
446 decomposition) and T is time at the end of the simulations ($T=2300$); i.e. the mean population
447 growth calculated for this set of simulations). To maintain a constant size structure, the total
448 number of colonies of species j at time t were summed and the corresponding proportion was
449 allocated to each size to match the temporal average size structure from the stochastic
450 simulations ($\bar{w}(x)$). Here, the proportion of free space was fixed at \bar{c} during all years of the
451 simulation. To calculate $\bar{\varepsilon}_j^w$, another simulation was run where $c_t = \bar{c}$, but the size-structures
452 were set at the value recorded for the baseline simulation ($w_{j,t}(x) = w_{j,t}^*(x)$). $\bar{\varepsilon}_j^w$ was the
453 effect of fluctuations in size-structure on population growth, independent of the effect of
454 mean size-structure ($\bar{\varepsilon}_j^w = \frac{1}{T-I} \sum_{t=I}^T r_j(w_{j,t}(x), \bar{c}) - \varepsilon_j^0$). Similarly, $\bar{\varepsilon}_j^c$ (where $w_{j,t}(x) = \bar{w}_j(x)$)

455 and $c_t = c_t^*$) was estimated as the effect of competition independent of the effect of its mean
456 (Table S4 for all the relevant formulas). The interaction between w and c ($\bar{\epsilon}_j^{wc}$), was the
457 effect of both $w_{j,t}(x)$ and c_t varying together ($w_{j,t}(x) = w_{j,t}^*(x)$ and $c_t = c_t^*$), independent of
458 the effects of mean size-structure and mean competition, and of size-structure and
459 competition fluctuating on their own: $\bar{\epsilon}_j^{wc} = \frac{1}{T-I} \sum_{t=I}^T r_j(w_t(x), c_t) - \bar{\epsilon}_j^w - \bar{\epsilon}_j^c - \epsilon_j^0 \cdot \bar{r}_j$ was then
460 defined according to Eq. (18).

461

462 Sensitivity analysis: Coexistence under different disturbance frequency-intensity regimes

463 To investigate the combinations of wave disturbance frequency and intensity that allowed
464 tabular and digitate populations to coexist, we simulated invasions of both competitors under
465 a range of water velocities (i.e. disturbance intensity) with a range of years between
466 disturbances (frequencies). Water velocity ranged from 1.4 (no colonies are dislodged) to 8.5
467 ms^{-1} (all colonies are dislodged), in 0.25ms^{-1} increments; the number of years between
468 disturbances ranged from zero to 100 years in increments of 2 years. Before each invasion,
469 2000 years of simulations were run to allow the resident to reach a stable range of coral
470 cover; after each invasion, 300 years more of community dynamics were simulated.
471 Coexistence was possible if both competitors -as invaders- had a higher mean proportion of
472 space cover in the last 100 years of the simulation than in the 100 years following the
473 invasion ($\frac{1}{100} \sum_{t=2201}^{2300} N_{i,t} > \frac{1}{100} \sum_{t=2002}^{2101} N_{i,t}$). If this was true for the tabular population, but
474 not for the digitate, the tabular population was assumed to dominate; conversely, the digitate
475 population was assumed to dominate when it was able to invade a tabular population, but the
476 tabular population was not able to invade a digitate resident. See supplementary material for a
477 stochastic version of this analysis.

478

479 All simulations were done in R (R Core Team 2018) (version 3.5.2).

480

481

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496

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