Stories told by corals, algae and sea-urchins in a Mesoamerican coral reef: degradation trumps succession

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Understanding the mechanisms that allow the permanence of coral reefs and the constancy of their characteristics is necessary to alleviate the effects of chronic environmental changes. After a disturbance, healthy coral reefs display trajectories that allow regaining coral cover and the establishment of framework building corals. Through a comparative approach, in a patch reef partially affected by a ship grounding, we analyzed the successional trajectories in affected and unaffected sectors. Fleshy algae (which do not promote the recruitment of framework-building corals), dominated the reef surface irrespective of the impact of the ship grounding incident. *Acropora* species had near-zero contribution to community structure, whereas non-framework-building corals like *Porites* sp. Had a slightly higher recruitment. Cover of coral and calcareous crustose algae decreased over time, and neither the latter nor adult coral colonies had any effect on the occurrence probabilities of small corals. Sea urchin (*Diadema antillarum*) densities were generally low, and thus unlikely to contribute to reverting algal dominance. The successional trajectories of the community in the impacted and non-impacted sectors of the coral patch reef agree with the inhibition successional mechanism, leading to the development of a degraded state dominated by fleshy algae. Probably, stability and resilience of this degraded state are high due to the ability of fleshy algae to monopolize space, along with low coral recruitment, mainly associated with the reduction of optimal recruitment surface.

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15 **Abstract**

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17 their characteristics is necessary to alleviate the effects of chronic environmental changes. After

18 a disturbance, healthy coral reefs display trajectories that allow regaining coral cover and the

19 establishment of framework building corals. Through a comparative approach, in a patch reef

20 partially affected by a ship grounding, we analyzed the successional trajectories in affected and

21 unaffected sectors. Fleshy algae (which do not promote the recruitment of framework-building

22 corals), dominated the reef surface irrespective of the impact of the ship grounding incident.

23 *Acropora* species had near-zero contributions to community structure, whereas non-framework-

24 building corals like *Porites* sp. had a slightly higher recruitment. Cover of coral and calcareous

25 crustose algae decreased over time, and neither the latter nor adult coral colonies had any effect

26 on the occurrence probabilities of small corals. Sea urchin (*Diadema antillarum*) densities were

27 generally low, and thus unlikely to contribute to reverting algal dominance. The successional

28 trajectories of the community in the impacted and non-impacted sectors of the coral patch reef

29 agree with the inhibition successional mechanism, leading to the development of a degraded state

30 dominated by fleshy algae. Probably, stability and resilience of this degraded state are high due

31 to the ability of fleshy algae to monopolize space, along with low coral recruitment, mainly

32 associated with the reduction of optimal recruitment surface.

33 **Keywords**

36   **Introduction**

37   In healthy reefs, post-disturbance recovery is featured by a steady increase in coral cover derived

38   from lateral growth or from colonization of larvae from other sources, while fleshy algae cover is

39   kept low by herbivores (Duarte et al., 2015; Hartmann, Marhaver & Vermeij, 2018; Gouezo et

40   al., 2020). The reduction of competition for space with fleshy algae mediated by sea urchins

41   (*e.g., Diadema antillarum* in the Caribbean) and herbivorous fish (*e.g.*, parrotfish), contributes to

42   the maintenance of available recruitment surface (Aronson & Precht, 2000; Edmunds &

43   Carpenter, 2001; Do Hung Dang et al., 2020). Also, efficient fleshy algae removal and the

44   availability of recruitment surface leads to the successful settlement, establishment, and

45   survivorship of morphologically complex coral species (like *Acropora palmata*, *A. cervicornis*

46   and *Orbicella* spp. in the case of Caribbean reefs), contributing to reef accretion (Toth et al.,

47   2019). However, as all coral reefs of the world have been affected by human activities (Riegl &

48   Glynn, 2020) they face increasingly harsher environments due to the augmented frequency and

49   intensity of disturbances (Arnold & Steneck, 2011; Doropoulos et al., 2012; Webster et al.,

50   2013). These changes in disturbance attributes have resulted in a reduced capacity to recover

51   coral-dominated states (Hartmann et al., 2013; Gil et al., 2016; Bruno, Côté & Toth, 2019). In

52   the Caribbean region, increases of fleshy algae cover (though dominance by other groups is also

53   possible; Knowlton, 1992, 2004) have been a constant phenomenon, ultimately reducing the

54   chances for corals to find suitable surface for settlement, survival and growth (Pineda & Caswell,

55   1997; Ferrari, Gonzalez-Rivero & Mumby, 2012; Doropoulos et al., 2016a; Evensen et al.,

56   2019).

57   Ship groundings caused by accident or negligence are complex disturbances with profound

58   effects on coral reef structure (Precht, Aronson & Swanson, 2001). The complexity of a ship

59   grounding depends mostly on ship attributes (size, weight, speed), features of the coral reef

60   affected (depth, size, and physical structure, but also its health), and the environmental

61   conditions at the moment of impact (tides, waves or storms) (Jaap, 2000; Nguyen et al., 2011).

62   Among the impacts of ship groundings on coral reefs, physical damage and pollution by oil or

63   cargo spill are noteworthy (Precht, Aronson & Swanson, 2001; Schroeder et al., 2008; Lirman et

64   al., 2010), with contrasting effects on the system's dynamics. Consequently, recovery can occur

65   through intense coral recruitment as fast as five years (Gittings, 1990) or be completely absent in

66   the same timeframe (Lirman et al., 2010). Overall, following ship groundings two general

67   complementary patterns have been reported: (1) the longer the time after the disturbance, the

68   larger is coral cover (Riegl, 2001); and (2) opportunistic species start pre-empting the available

69   space (Smith, 1985). In a context of widespread coral reef degradation, a ship-grounding, when

70   having purely physical effects (*i.e.*, with chemical damage being absent), could open new

71   opportunities to shift the dynamics of a degraded coral reef towards one favoring a state

72   dominated by corals, especially those that increase the reef-framework accretion. For the latter to

73   occur an optimal cover of coral recruitment surface is required, provided by crustose calcareous

74   algae (CCA) (Ritson-Williams et al., 2010, 2014), recruitment of reef-building corals, and an

75   efficient control of fleshy algae.

76   Using as example a coral reef patch under a no-take scheme since it was partially affected by a

77   ship-grounding, here we ask whether in the reef's affected portion a community dominated by

78   corals is developing, especially of coral species capable of contributing to reef accretion or, on

79   the contrary, the developing community continues to be representative of degraded reefs. To

80 answer this question, we established two objectives. First, we assessed the occurrence

81 probabilities of small colonies as a proxy of coral recruitment (Edmunds, 2021), particularly of

82 framework-building (FB) corals, both in the impacted and non-impacted sectors of the patch

83 reef, relative to the cover of adult coral colonies and different algal groups (CCA, fleshy algae).

84 Second, we assessed the relationship of algae that either promote (*i.e.*, CCA) or prevent (*i.e.*,

85 fleshy, turf, branching coralline and crustose non-coralline algae, hereinafter referred to

86 collectively as non-CCA) with juvenile coral occurrence. Derived from the current degradation

87 patterns in Caribbean coral reefs (Alvarez-Filip et al., 2015), we expected to find evidence for a

88 relatively unsuccessful re-establishment of a healthy coral-dominated patch reef.

89 **Materials & Methods**

90 **Study site**

91 This study was conducted in the 'Parque Nacional Costa Occidental de Isla Mujeres, Punta

92 Cancún y Punta Nizuc' (hereinafter Cancún National Park or CNP), in northern Quintana Roo

93 state, Mexico (21° 09' 41.5" N, 86° 44' 27.6" W) (Fig. 1a). In 1997, the *Leeward* vessel (159 m

94 long, 25 600 tons, capacity for 650 passengers; Cities, 2022) impacted the Cuevones patch reef

95 (Fig. 1b), dislodging the biota of 465.5 m^2 from its substrate. The vessel's integrity was not

96 compromised (neither oil, fuel nor cargo spilled into the water), thus non-physical long-term

97 impacts were discarded. Prior to the ship grounding, the dominant species in the patch were

98 *Porites astreoides*, *Acropora palmata*, *A. cervicornis* and *Orbicella annularis* (Reefkeeper,

99 1997). Yet, just before the impact, the patch had begun to show early signs of its transit towards

100 an algae-dominated state (Victoria-Salazar et al., 2017).

101 As only one portion of the patch was affected and the impacted sector (IS) was a long but

102   relatively narrow stripe, a contiguous non-impacted sector (NS) along its longest axis was used

103   as a reference and assumed to be the closest source of larvae for IS (Fig. 1c). Every six months

104   (February and August 2013, and February and September 2014), 20 out of 40 1-m^2 permanent

105   quadrats, marked with stainless steel pins, were randomly selected within each sector and used to

106   record the cover of small corals, coral adults, and algae, as well as the abundance of the sea

107   urchin *Diadema antillarum*. The selection of the non-impacted reference sector relied on three

108   grounds. First, Victoria-Salazar et al. (2017) analyzed the historical records of the changes in the

109   Cuevones reef community prior to the ship grounding. The authors found no significant

110   differences in community structure of hard corals between the impacted and the non-impacted

111   sectors used here (NS and NI in Fig. 1), which were dominated by opportunistic corals and

112   fleshy algae with covers > 50%. Second, passive transport of coral propagules (coral larvae or

113   fragments) is strongly linked to the current; in Cuevones, the direction of the current facilitates

114   propagule transport from NS to IS (Fig. 1c). Thirdly, colonization often starts from the margins

115   between impacted and non-impacted areas (Fox & Caldwell, 2006). As only one portion of

116   Cuevones was affected, NS is the portion of the patch reef having the longest contact with the

117   impacted sector; given this long margin and the direction of the current, NS is arguably the main

118   (if not the only) local source of propagules.

119

120   **Data Collection**

121   **Adult Coral Cover and Sea Urchin Abundance**

122   Randomly selected 1-m^2 quadrats were delimited on the reef surface and information for all

123   complete or fractional adult colonies occurring in them was recorded. For each colony two

124   diameters (the longest and one perpendicular to it) were measured with a graduated tape. Colony

125 cover area calculations were based on these diameters (rounded to the nearest cm) by

126 approximation to an ellipse (eq. 1):

127 *Colony cover* = (*dmax* × *dper*)/4 (Eq. 1)

128 where *dmax* is the maximum diameter and *dper* is the diameter perpendicular to it. Next,

129 proportional coral cover was obtained by dividing coral area (cm^2) by the quadrat's area (10,000

130 cm^2). All *Diadema antillarum* individuals roaming within each quadrat were tallied.

131

132 **Small Corals**

133 To search for small corals, a 50 × 50 cm PVC frame was attached to the southern pin of the 20 1-

134 m^2 quadrats placed in each sector (Fig. 1d). The PVC frame was divided into twenty-five 10 × 10

135 cm units. In each quadrat we carefully searched for all hard-coral small colonies with a diameter

136 ≤ 4 cm (Acosta, Dueñas & Pizarro, 2011; Edmunds, 2021). While we recognize that colony

137 fragmentation, mortality or contraction may obscure small coral counts, we also based our

138 decision to consider a colony depending on its context, *i.e.*, we examined whether each small

139 coral was associated with a colony fragment, or with colonies with signs of mortality or

140 contraction. Once a small coral was sighted it was identified to genus level. Colony cover was

141 approximated to a circle and a small coral proportional cover (*scp*) was calculated for each

142 genus, as follows:

143 $scp = \Sigma_i csc_i/sampling\ area$ (Eq. 2)

144 where csc_i is the cover (cm^2) of the *i*-th small coral and sampling area is 2500 cm^2.

145

146   **Algal Cover**

147   We assessed algal cover in five randomly selected 10 × 10 cm sampling units, in which we

148   recorded the cover of the benthic groups underneath an acrylic plate (to the nearest cm^2) with a

149   1-cm resolution grid. Algal cover was classified into two categories according to their functional

150   group: (1) algae promoting coral recruitment, which only included CCA; and (2) non-CCA

151   algae, which included the aforementioned fleshy macroalgae (FA), turf algae (TA), branched

152   coralline algae (BCA), and crustose non-coralline algae (CnCA). We used these data to

153   independently calculate the proportional contribution of each algal category (*pac*) to reef surface

154   by quadrat in the space not occupied by adults or recruit coral colonies:

155    $pac_{CCA} = (1 - crp)\ \Sigma_i\ pac_i^{CCA}/500$, and

156    $pac_{non\text{-}CCA} = (1 - crp)\ \Sigma_i(pac_i^{FA} + pac_i^{TA} + pac_i^{BCA} + pac_i^{CnCA})/500$, (Eqs. 3)

157   where pac_{CCA} is the proportional cover of CCA, $pac_{non\text{-}CCA}$ is the proportional cover of non-

158   recruitment-promoting algae, ac_i^j is the cover of algal functional group j (*i.e.*, CCA, FA, TA,

159   BCA or CnCA) in the i-th sampling unit, crp is the proportion occupied by corals, and $1 - crp$ is

160   the proportion of space not occupied by corals.

161

162   **Data Analysis**

163   **Benthic Community Structure**

164   Through a multivariate approach, we assessed the current differences and similarities in the

165   cover of the benthic community (which includes hard corals and algal groups) developing in the

166   non-impacted sector and the impacted sector 16 years after the ship grounding. Using a

167   dissimilarity matrix based on the Bray-Curtis index, a two-way PERMANOVA test was

168   computed (9999 permutations), with date and condition as fixed factors. When significant

169   differences were detected, pairwise comparisons were performed. All tests were computed with

170   PRIMER V6 and the PERMANOVA+ add-on (Clarke & Gorley, 2006). We used a principal

171   coordinate analysis (PCoA) for sampling date and condition (impacted vs. non-impacted) to

172   achieve a clear visualization of between-sector differences; we also plotted benthic groups

173   strongly correlated with the ordination axes (Spearman $r_s > 0.5$).

174

175   **Small Corals**

176   To assess occurrence probabilities of small corals for FB and NFB corals and their relationship

177   with sector condition, CCA and adult coral covers, we tested 12 models (S1) using binomial

178   (logit-link) regressions with the 'stats' package in R (Core Team, 2017). The selection of the best

179   model was based on the Bayesian Information Criterion (BIC); if more than one model were

180   similarly supported, a full averaging approach was used based on BIC weights (Symonds &

181   Moussalli, 2011).

182

183   **Short-Term Changes**

184   The cover proportions of the surveyed benthic groups were classified into four categories nested

185   in pairs: (1) proportion of coral cover, irrespective of its role in reef development; (2) proportion

186   of framework-building coral cover (nested to category 1); (3) proportion of algae, irrespective of

187   their role in promoting coral recruitment; and (4) proportion of algae promoting coral

188   recruitment (nested to category 3). All proportional data were transformed to fit the standard

189   interval unit (using Eq. 4) (Cribari-Neto & Zeileis, 2010), except for algae cover proportion,

190   which fitted the interval in their original form:

191        $p' = (p(n-1) + 0.5) / n$ (Eq. 4)

192   where p is the observed proportion, and n is sample size.

193   The proportion of each category was modelled using a mixed beta (logit-link) regression, with

194   date, sector condition, and sea urchin abundance as fixed factors, and quadrat as random

195   intercept (Cribari-Neto & Zeileis, 2010). To fit the model to the data, a Markov Chain Monte

196   Carlo (MCMC) method was performed using JAGS (Plummer, 2003) via the 'R2jags' package

197   (Su & Yajima) in R. For each posterior distribution 60 chains were computed, each with 50 000

198   iterations (with a burn-in of 10 000 iterations and a thinning of 10). Diffuse normal priors were

199   used for the fixed and random parameters. In turn, for the standard deviation a half-Cauchy

200   distribution was used. In total, eight models were fitted for each response variable (S2); in this

201   case, the null model considered time and condition.

202

203   **Results**

204

205   **Benthic Community Structure**

206   The community structure differed significantly between the impacted and non-impacted sectors

207   of the patch reef (pseudo-F = 6.59, d.f. = 1, p < 0.001), and changed over time (pseudo-F = 3.60,

208   d.f. = 3, p < 0.001). These differences were clearly reflected by the separation between sectors

209   and sampling dates in the PCoA (Fig. 2). Over the entire duration of the study, fleshy algae

210   dominated in both sectors, followed by turf algae (S6 and S7). Regarding corals, *Porites*

211   *astreoides* was the most important contributor to the benthic cover of all recorded species. The

212   contribution of FB corals to benthic cover was negligible in both sectors.

213

Small Corals

215 Over the two-year period, only 79 small corals were recorded. *Acropora* (mean diameter ± SD =

216 2.48 ± 0.715 cm, $n = 6$) was the only FB genus occurring in both sectors and its contribution to

217 recruitment was minimal (S8). Conversely, *Porites* (mean diameter ± SD = 2.35 ± 0.978 cm, $n =$

218 61) was the dominant genus in the small coral community in both sectors at all sampling dates.

219 Other genera recorded were *Agaricia* (mean diameter ± SD = 2.60 ± 0.710 cm, $n = 9$) and

220 *Millepora* (mean diameter ± SD = 2.05 ± 0.764 cm, $n = 4$). Models showed that FB corals had

221 the lowest occurrence probabilities on the reef and a lack of relationships with sector condition,

222 adult colony cover, or the cover proportion of the recruitment promoting algae (Fig. 3a, S3). Our

223 models also showed higher occurrence probabilities for NFB than for FB corals; however, no

224 single explanatory variable had an effect on this probability (Fig. 3b, S3).

225

Short-Term Changes of Functional Groups

227

228 Algae were the main contributors to cover (ca. 70%) in the four sampling dates (Fig. 4e-h). non-

229 CCA algae were the main contributors to algal cover with > 50% of the area in both sectors at all

230 sampling dates. By contrast, CCA algae did not exceed 15% of proportional cover in both sectors

231 at the four sampling dates (Fig. 4e, f). Mean coral cover ranged between 10 and 16% in the

232 impacted sector, and between 20 and 26% in the non-impacted one. FB corals had the lowest

233 proportional cover during the entire study period (IS, 1.3–3.4%; NIS, 5–10%; Fig. 4a, b), whilst

234 NFB corals had higher covers (IS, 10–14%; NIS, 14–21%; Fig. 4c, d). Across sampling dates,

235   mean *Diadema antillarum* density ranged between 0.04 and 0.81 ind. m^{-2}, with virtually no

236   difference between sectors.

237   Models for all benthic groups achieved a good mixing of the 60 MCMC chains, and model

238   validation did not reveal any problem with dispersion of residuals. BIC weights showed that M1

239   (*i.e.*, sector condition and date) had the highest value for three of the four variables (S4), and it

240   represented the only candidate model for coral proportional cover ($w = 0.891$, S4). For FB corals,

241   algae as a whole and CCA alone, the full average model showed that condition and date were the

242   strongest covariates explaining changes in all benthic categories examined (S5). Models showed

243   that FB corals and non-recruitment algae had the lowest and the highest cover proportions,

244   respectively, among all response variables and throughout the study period (Fig. 4a, b, g, h). The

245   model for FB corals showed that their cover proportion decreased in both sectors; in the

246   impacted sector there was a 0.2% reduction, whilst in the non-impacted sector cover reduction

247   was considerably higher (1.2%) (Fig. 4a, b); in the case of NFB corals, cover reduction was

248   similar for both the impacted and non-impacted sector (2 and 3%, respectively) (Fig. 4c, d).

249   Regarding algal categories, non-CCA increased their cover proportion over time and were larger

250   in the impacted sector (Fig. 4g, h). By contrast, the cover proportion of CCA decreased over time

251   (Fig. 4e, f). The effects of *D. antillarum* on all four response variables assessed were modest,

252   probably due to the overall low abundances within quadrats, reflected in a high frequency of

253   quadrats devoid of sea urchins compared with a few quadrats with sea urchin densities as high as

254   5 ind. m^{-2} (Fig. 4, S5). Interactions between time and sea urchin densities were variable but

255   overall weak for all response variables, except in the case of cover proportion of FB corals, as

256   shown by the inclined isolines in Figure 4a, b; positive slopes in these isolines imply that higher

257   sea urchin densities delayed the decrease of coral cover over time by about two months. For

258   example, the mean cover proportion recorded in February 2013 (1.1%) was reached between

259   April and May in quadrats with a sea urchin density of 5 ind. m^{-2} (Fig. 4a).

260

261   **Discussion**

262

263   Based on the information gathered in a patch reef 16 years after it was affected by a ship

264   grounding, our results confirmed that this community is still dominated by fleshy algae and non-

265   reef building corals, as anticipated. This implies that the sector affected by the incident, despite

266   the no-take protection status it enjoys since, is dominated by species that do not contribute to the

267   recovery of a physically complex state dominated by reef-building corals. Instead, coral species

268   with low contribution to reef accretion, like *Porites astreoides* and fleshy algae, are the main

269   contributors to live cover in this sector. The present condition seems to be caused by the low

270   recruitment probability (as inferred from the low occurrence probabilities of small corals), low

271   cover, and the continued loss of FB corals, all of which is reflected in the increasing cover of

272   NFB corals, but more importantly, in the dominance of non-CCA. Moreover, our results showed

273   that cover of non-CCA is increasing and gradually replacing the non-framework building corals.

274   Notably, this pattern was evident in both sectors regardless of disturbance history, the protection

275   status of this marine area, or the presence of NFB coral species, such as *Porites astreoides*.

276   Importantly, this process seems to be occurring also on a fraction of Cuevones currently under a

277   coral restoration program (Padilla-Sousa et al., 2018), where coral cover has increased because

278   of the introduction of coral fragments, but with a low contribution of FB species to the small

279   coral community (Perera-Valderrama et al., 2016). Under these circumstances, Cuevones may

280   not be able to recover a coral-dominated state without intervention. If regional factors causing

281   detrimental changes (*e.g.*, coastal development or highly intense tourism) in coral reefs persist

282   for a long time or become permanent, this and other Caribbean reefs will very likely continue to

283   display algae-dominated community states, thus jeopardizing the success of coral restoration

284   programs (Ware et al., 2020).

285   In Caribbean reefs, the loss of resilience and the consequent development of degraded states

286   have been driven by a combination of anthropogenic stresses, ranging from eutrophication to

287   decimation of herbivores, all of which has resulted in significant declines in FB coral species

288   populations (Jackson et al., 2014). This loss of coral cover releases space that becomes available

289   to algal colonization, while negative feedback from herbivores remains low. In turn, the presence

290   of fleshy and turf (non-CCA) algae deters coral recruitment and reduces coral recruit survival

291   (Steneck, Arnold & Mumby, 2014; Olsen, Sneed & Paul, 2016). These algal groups favor the

292   dominance of disturbance-tolerant coral species with broad ecological plasticity (Alvarez-Filip et

293   al., 2013). Such a role has serious ecological implications for reef accretion and the ecosystem

294   services they provide (Kennedy et al., 2013; Perry et al., 2013, 2015). A further consequence of

295   this replacement is the local extinction of corals, ultimately resulting in the absence of refuges

296   necessary to sustain other reef inhabitants (Vermeij, 2006; Green, Edmunds & Carpenter, 2008;

297   Alvarez-Filip et al., 2013; Perry et al., 2015).

298   The ultimate effect of the ship grounding on the Cuevones patch reef was to catalyze the shift in

299   dominance in the impacted sector from a FB coral-dominated state towards a degraded state

300   dominated by non-CCA and NFB coral species (Victoria-Salazar et al., 2017). In this state, NFB

301   species such as *Porites astreoides* would be able to colonize the reef surface due to its ability to

302   develop healthy populations in harsh environments (Green, Edmunds & Carpenter, 2008; Olsen,

303   Sneed & Paul, 2016). In this study, the analysis of occurrence probabilities of small corals

304   suggests that recruitment of FB species (i.e., *Acropora* and *Orbicella* species) is so low that they

305   make a near-zero contribution to coral community structure, and that those few corals that reach

306   an adequate substrate did not thrive even under the infrequent circumstances where CCA cover

307   was as high as 40% (Fig. 3a). Instead, NFB species had higher chances to contribute to the

308   recruit community.

309   Several factors have been recognized to drive coral larval settlement, among which

310   sedimentation, interspecific competition with fleshy algae and other groups, available space for

311   settlement, chemical cues, and connectivity with other reef communities that supply coral

312   propagules are noteworthy (Ferrari, Gonzalez-Rivero & Mumby, 2012; Tebben et al., 2015

313   Suchley & Alvarez-Filip, 2017). At Cuevones, low recruitment apparently results from a

314   combination of several factors. First, autogenic recruitment could be limited due to the low

315   proportional cover of adult colonies in both sectors (S6), which is reflected by the null

316   contribution of adult coral cover as an explanatory variable for settlement success. Second,

317   connectivity (as measured through genetic diversity among FB coral populations), an important

318   factor promoting coral reef resilience (Elmhirst, Connolly & Hughes, 2009; Manikandan et al.,

319   2017), appears to be low (Domínguez-Maldonado et al., 2022), although the genetic evidence for

320   such lack of connectivity is scarce. Causes of connectivity failure may be related to the reduction

321   of larval sources in the Mesoamerican Reef System, where only one site (Limones reef, also in

322   northern Quintana Roo) has been reported to sustain a healthy population of *Acropora palmata*

323   (Rodríguez-Martínez et al., 2014), with a high potential fecundity but low recruitment (Acevedo-

324   Rosas, 2017). A third factor apparently involved is related to the low amount of recruitment

325   substrate available for FB species, which also decreased over time (Fig. 4e, f). This latter factor

326   could have an enhanced effect in Cuevones; despite the abundance of NFB species and their high

327 reproductive rate, the available space for coral larval settlement is dwindling and turning into

328 non-recruitment substrate (Fig. 4e-h).

329 Settlement, survivorship and growth opportunities for FB coral recruits (e.g., *Acropora palmata*

330 and *Orbicella annularis*), which are more selective in choosing a settlement substrate than NFB

331 species (Olsen, Sneed & Paul, 2016), depend strongly on the grazer-mediated reduction of algal

332 cover (Doropoulos et al., 2016b; Suchley & Alvarez-Filip, 2017). In this study, only a few

333 quadrats had urchin densities as high as 5 ind. m^{-2}, whereas quadrats with low abundances of this

334 sea urchin were frequent, with densities ranging from 0 to 3 ind. m^{-2} (see Fig. 4). Sea urchin

335 distribution depends on the complexity of the coral colony, with physically more complex coral

336 colonies offering more refuge space (Dunn et al., 2017). Thus, given the dominance of sub-

337 massive coral species observed at Cuevones, the only available space usable by sea urchins are

338 the crevices and the few remaining standing *Acropora palmata* skeletons. The low refuge

339 availability leads to the exclusion of these herbivores, with negative impacts on coral recruitment

340 (Doropoulos et al., 2016b).

341 From a mechanistic perspective, community recovery depends on ecological succession and in

342 coral reefs this process may take place in one of two ways. On the one hand, facilitation (*sensu*

343 Connell & Slatyer, 1977) occurs when CCA algae dominate the reef surface. Alternatively,

344 inhibition mechanisms come into play when earlier colonizers prevent the settlement of coral

345 larvae, which represent the late successional dominant species. The answer to the question of

346 which mechanism of ecological succession operates in each coral reef largely depends on the

347 identity of earlier algal colonizers (Mumby et al., 2007; Doropoulos et al., 2016b). In our study,

348 proportional cover of non-CCA was up to eight-fold that of CCA in both sectors, and the models

349 showed that CCA decreased over time. Hence, the Cuevones seascape seems unsuitable for

350   corals to successfully settle on to. The type of benthic early successional groups is strongly

351   coupled with herbivore densities (Steneck, Arnold & Mumby, 2014; Doropoulos et al., 2016a;

352   Mumby et al., 2016). Our models also showed that, for the Cuevones patch reef, ecological

353   succession in both sectors is driven by a stabilizing mechanism that promotes fleshy-algae

354   dominance. Despite the no-take protection scheme offered by the MPA and the restoration

355   efforts, modifying this situation in the current ecological context seems unlikely. Densities of the

356   herbivore *D. antillarum* in both sectors over the entire study period were so low that its effect is

357   very likely negligible, which explains the continuous increase in the proportion cover of non-

358   CCA. In the Caribbean Sea, such low densities, even under the protected condition of an MPA,

359   have been linked to predation upon the sea urchin by fishes (Harborne et al., 2009) and a low

360   inter-population connectivity, which together translate into low local larvae availability

361   (Carpenter & Edmunds, 2006).

362   In summary, this study shows that the community that is developing in the damaged sector of the

363   Cuevones patch reef has been following a successional trajectory that seems to be in accordance

364   with a stabilizing mechanism (Pulsford, Lindenmayer & Driscoll, 2016), characterized by the

365   dominance of coral recruitment inhibition processes. Cover of non-recruitment promoting algae

366   (non-CCA), the group that encompasses fleshy and turf species, has increased over time,

367   occupying most of the substrate and reducing the availability of suitable space for coral

368   establishment. By contrast, CCA cover, which is necessary for the successful establishment of

369   FB coral larvae, decreased over time. It is important to note that these algal patterns are

370   consistent across the different sector in Cuevones, regardless of their disturbance history.

371   Previous studies have shown the existence of herbivore-mediated shifts between inhibition and

372   facilitation mechanisms (Doropoulos et al., 2016b). At Cuevones, although higher *D. antillarum*

373 densities were associated with reductions in non-CCA, the overall abundance of this herbivore

374 was very low. Interestingly, however, quadrats having between one and three sea urchins showed

375 a high variation in algal cover, suggesting that the abundance of this herbivore is currently below

376 the minimum threshold needed for this species to have a regulatory effect on such cover

377 (Edmunds & Carpenter, 2001; Mercado-Molina et al., 2015). The permanent analysis of

378 ecological succession in this and other coral reefs affected by a variety of disturbance agents will

379 provide insights into the processes leading to the loss of resilience in these complex and highly

380 diverse ecological systems. More importantly, it will help us understand why the dynamics of

381 new degraded states, mainly characterized by the absence of the original species, hampers the

382 return to the original state.

383

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Figure 1

Study area and sampling details.

(a) General and (b) detailed location of the Cancún National Park (CNP), Quintana Roo, eastern Mexico. (c) Cuevones patch within CNP and location of the impacted (IS) and the non-impacted (NS) sector, where the study was conducted; the arrows show the direction of the current. (d) Example of a sampling unit for coral and algal cover, and sea urchin density.
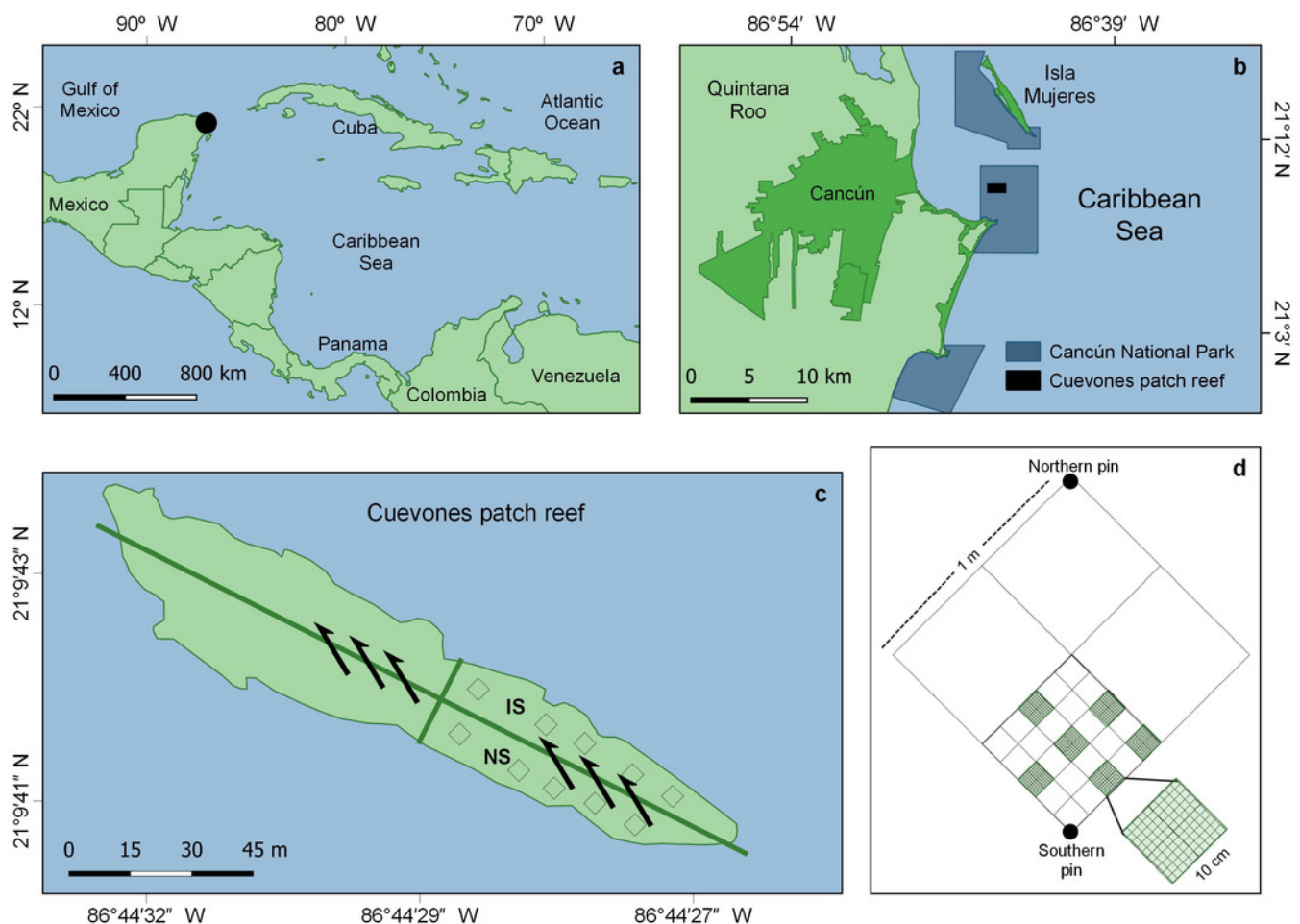
Figure 2

Results of the Principal Coordinates Analysis (PCoA).

Community cover recorded in four dates in the impacted and non-impacted sectors of the Cuevones patch reef. Lines represent Spearman correlations of those benthic groups with r_s > 0.6. BCA, branched coralline algae; FA, fleshy algae. Full species names: *Millepora complanata* and *Porites astreoides*.
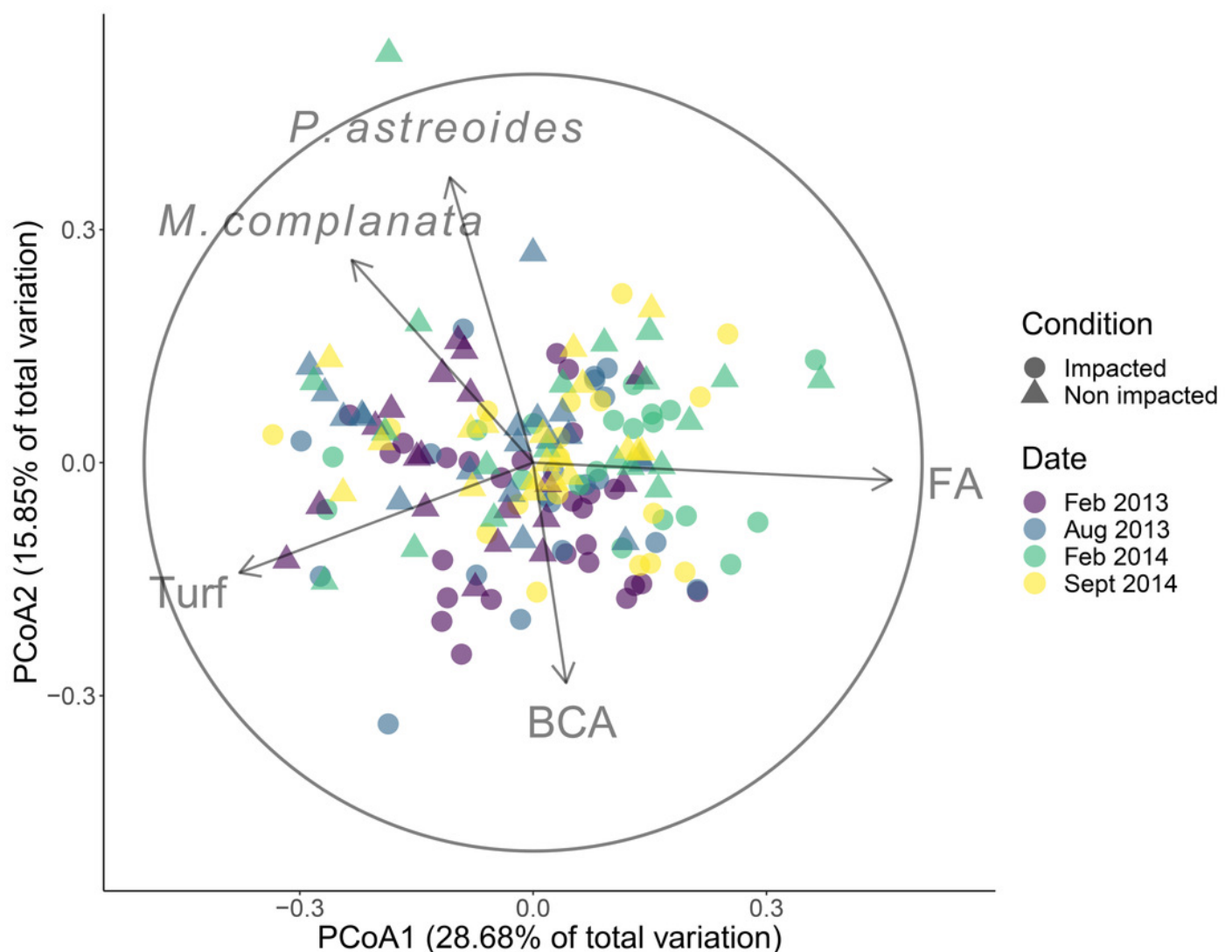
Figure 3

Recruit occurrence probabilities.

(a) framework-building and (b) non-framework-building corals. The average did not show any relationship between recruitment surface and occurrence probability of recruits. Shaded areas represent 95 % confidence envelopes.
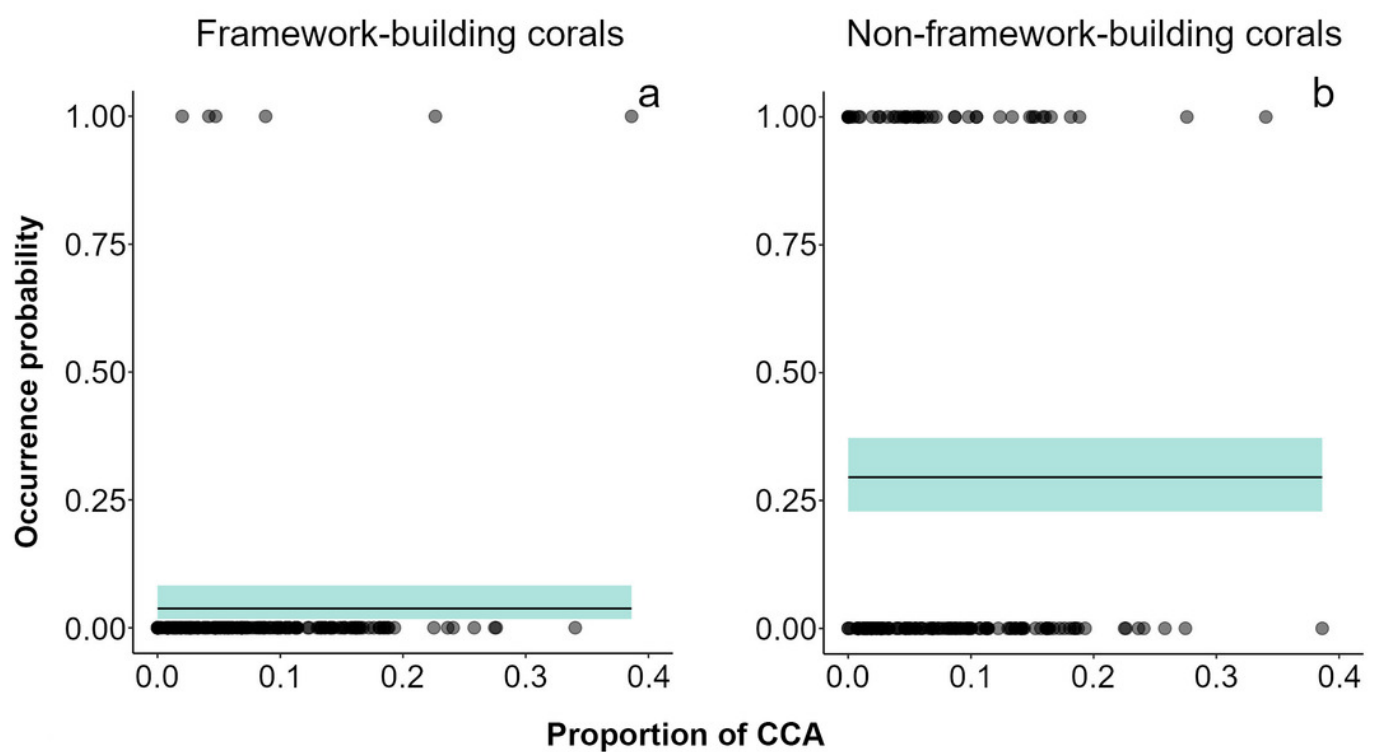
Figure 4

Heat maps of estimated successional trend of cover of four functional groups.

(a, b) framework- and (c, d) non-framework building corals, and for (e, f) CCA and (g, h) non-CCA as functions of three explanatory variables: time (the four sampling dates), sea urchin densities, and sector condition (impacted vs. non-impacted). Dots represent the original cover proportions recorded in the field. Lines in the heat maps are isolines of cover proportion (indicated by the numbers next to them) and their position denotes sea urchin density-sampling date interactions; isolines leaning to the right (i.e., positive slope) denote a positive interaction, lines leaning to the left (i.e., negative slope) denote a negative interaction, and fully vertical lines denote no interaction between these two predictor variables. Note that most samples had a sea urchin density of 0 ind. m^{-2}. Some jittering was added to recorded data points to minimize overlap.