

1 Impacts of a prolonged marine heatwave and chronic local human
2 disturbance on juvenile coral assemblages

3 Short title: Multiple stressor impacts on juvenile corals

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21 **Abstract**

22 Coral reefs are threatened by climate change and chronic local human disturbances. Although
23 some laboratory studies have investigated the effects of combined stressors, such as nutrient
24 enrichment and heat stress, on growth and survival of early life stage corals, *in situ* studies
25 remain limited. To assess the influence of multiple stressors on juvenile corals, we quantified
26 densities of corals ≤ 5 cm at 18 forereef sites with different exposure levels to underlying chronic
27 local human disturbance before, during, and after the 2015-2016 El Niño. This marine heatwave
28 caused prolonged heat stress and devastating losses of coral cover at our study site, Kiritimati, in
29 the central equatorial Pacific Ocean. In total, we enumerated 7732 juvenile corals from 13
30 different families. Over 80% of corals were from four families: 70% from Agariciidae,
31 Merulinidae, or Poritidae, which all have stress-tolerant life history strategies, and 11% from
32 Acroporidae which has a competitive life-history strategy. Both local disturbance and heat stress
33 were significantly negatively related to juvenile coral densities. Prior to the heatwave, juvenile
34 densities were on average 72% lower at the most disturbed sites (7.2 ± 1.9 m²) compared to the
35 least disturbed ones (15.3 ± 3.8 m²). Overall, juvenile corals had a lower bleaching prevalence
36 and lower mortality during the heatwave when compared to their adult counterparts. Still, the
37 heatwave resulted in the loss of half (50%) of all juvenile corals, with competitive and weedy life
38 history strategy corals undergoing greater declines than stress-tolerant ones. Although juvenile
39 coral densities increased slightly in the year following the heatwave, the effect was statistically
40 non-significant. Our results highlight the influence of local chronic anthropogenic and climate
41 change-driven marine heatwaves on juvenile coral densities.

42 **Introduction**

43 Coral reefs are increasingly impacted by the effects of climate change, which are overlaid
44 on chronic regional and local scale anthropogenic pressures [1,2]. Recent marine heatwaves,
45 notably the 2015-2016 El Niño, have caused mass coral bleaching and extensive mortality [3–5].
46 The persistence of coral reefs is dependent on the recovery of corals, which can be driven by
47 coral recruitment and the population dynamics of juvenile corals [6–8]. But while heatwave
48 impacts have been documented extensively for adult corals, there has been comparatively less
49 research on the effects of heat stress on juvenile corals. Previous studies have demonstrated that
50 the demographics of juvenile corals can strongly influence recovery trajectories [6,7,9], with
51 surviving juvenile corals rising through size classes, with corresponding increases in brood stock
52 and reproductive output [10], to repair stock-recruitment relationships disrupted by the loss of
53 adult colonies [10,11]. Studies of long-term reef recovery following the 1998 El Niño in the
54 Indian Ocean (Scott Reef, Western Australia and the Maldives) found that juvenile corals
55 stimulated reef recovery within 10-12 years of the event [10,12,13], and were likely especially
56 critical on these isolated reefs that are reliant on self-seeding [10,14]. Overall, however, given
57 their importance for recovery dynamics, and the lack of studies, there is a need to better
58 understand the effects of climate change-amplified heat stress, and its interplay with local
59 anthropogenic disturbance, on juvenile corals.

60

61 Although studies from several regions, including the Caribbean, Mediterranean, Japan,
62 Thailand, and Australia [15–18], have shown that juvenile corals can have greater heat stress
63 tolerance than their conspecific adults, the reasons underlying this difference remain unclear
64 [15–17]. Mumby [15] hypothesized that this enhanced survival could be due to reduced

65 irradiance levels due to their cryptic microhabitats or capacity for heterotrophic feeding to
66 replace lost autotrophic nutrition during bleaching. Further research has suggested additional
67 mechanisms based on properties such as being non-reproductive, which may allow for more
68 energy invested into maintenance [18], and the relatively flat [19] and small colonies of juveniles
69 which allow for faster elimination of toxic by-products by mass transfer [20]. In addition to
70 exploring mechanisms for survival, a few studies have investigated the effects of heat stress on
71 juvenile corals. Two experimental laboratory studies investigated the effects of short term heat
72 stress and found that it resulted in sub-lethal stress and negative allometric growth scaling in
73 *Porites* [21,22], whereas another study found increases in both growth and mortality in *Acropora*
74 after over a month of elevated temperatures [23]. A comprehensive understanding of bleaching
75 resilience mechanisms and heat stress effects in juvenile corals remains unresolved.

76

77 Juvenile survival through heat stress [7,18], and contributions to reef recovery through
78 increases in coral cover [7], vary substantially amongst coral species and life history types. For
79 example, a study by Doropoulos and colleagues [7] on the Great Barrier Reef, Australia found
80 that when reef recovery is characterized by increases in coral cover, brooders may not
81 considerably contribute to reef recovery due to their small colony sizes [7,24] despite their other
82 ‘weedy’ life history characteristics (e.g., rapid generation times, opportunistically colonizing
83 recently disturbed habitats) [24,25]. Rather, corals such as *Acropora*, that exhibit a ‘competitive’
84 life history strategy, grow large colonies, and excel at colonizing [24] can contribute
85 considerably to coral cover [7], and thus play a major role in reef recovery. In comparison,
86 massive corals that have a ‘stress-tolerant’ life history strategy often survive disturbance events
87 [24], but do not contribute appreciably to increases in coral cover because of their slow growth

88 rates [7].

89

90 Like adult corals, local factors, both natural and anthropogenic, can also affect the growth
91 and survivorship of juvenile coral. A heat stress experiment investigated the influence of a
92 simulated river plume and terrestrial runoff nutrient enrichment event on 4-month-old corals and
93 found an antagonistic effect leading to reduced mortality rates [23]. This supports one of
94 Mumby's [15] hypotheses, as nutrients can be taken up by plankton communities which in turn
95 are heterotrophically fed on by corals [reviewed in 26], potentially supplementing reduced
96 autotrophic nutrition that is lost during bleaching [15]. However, on reefs in Barbados with
97 human induced eutrophication and sedimentation, juvenile coral abundance was lower than on
98 less eutrophic/low sediment reefs [27]. The effects of macroalgae may be the most well studied
99 local factor on juvenile corals, and not unlike recruits or adult corals the effects are negative and
100 result in slowed growth and decreased survivorship [21,28,29]. In turn, decreases in macroalgae
101 levels have led to increased juvenile coral abundances [28,30]. Currently there is a lack of
102 research on the impact of local factors have on the survival of juvenile corals which have
103 important implications for reef recovery on chronically disturbed reefs.

104

105 Here, we aimed to fill a gap in the understanding of how multiple stressors affect the
106 densities of different species of juvenile corals encompassing different life history strategies. To
107 do so, we capitalized on a prolonged marine heatwave that occurred on Kiritimati (Christmas
108 Island) during the 2015-2016 El Niño, which was overlaid on the atoll's chronic disturbance
109 gradient [31,32]. Kiritimati is geographically isolated, and thus is largely reliant on self-seeding
110 for coral recruits [33,34]. We censused juvenile corals via video assays at 18 sites along the

111 disturbance gradient before, during, and one year after the El Niño. This ecosystem-scale natural
112 experiment allowed us to examine the impacts of prolonged heat stress on juvenile corals at sites
113 exposed to different intensities of local human disturbance, and its effect on an isolated island's
114 initial reef recovery. We hypothesized that due to lower overall coral cover, decreased reef
115 structural complexity and lower water quality [31] in areas with high human disturbance that,
116 prior to the heatwave, these sites would have reduced juvenile coral densities. We also
117 hypothesized that while elevated water temperatures would lead to a significant decline in
118 juvenile corals: 1) bleaching and mortality would be reduced in juvenile corals compared to their
119 adult counterparts due to their small morphology and microhabitats; and 2) mortality would vary
120 amongst coral taxa, with a higher survival of stress-tolerant juvenile corals and increases in the
121 year following the El Niño in weedy coral densities.

122

123 **Materials and Methods**

124 **Study area and design**

125 We quantified juvenile coral density by surveying their densities before, during, and after
126 the 2015-2016 El Niño-induced heatwave, at eighteen shallow forereef (10-12 m isobath) sites
127 spanning a gradient of local human disturbance on Kiritimati (Christmas Island, Republic of
128 Kiribati). Kiritimati, a remote coral atoll in the central equatorial Pacific Ocean (01°52'N,
129 157°24'W), is the world's largest atoll by land mass (388 km²; 150 km in perimeter; Fig 1). Sites
130 were surveyed at three time points prior to impacts of the El Niño (two years before (July 2013;
131 16 sites), 1 year before (August 2014; 9 sites), and at the beginning (May 2015; 8 sites)), then
132 resurveyed two months (early, July 2015; 13 sites) and 10 months (late, March 2016; 11 sites)

133 into the heatwave, and again approximately 14 months after the end of the heatwave (1 year
134 after; July 2017; 18 sites) (S1 Fig and S1 Table). Although not all sites were surveyed at each
135 time point due to inclement weather conditions that prevented safe boat and/or diving access, the
136 full set of eighteen sites were surveyed at least once before and once after the heatwave for direct
137 comparability. The field research was conducted with permission from the Government of the
138 Republic of Kiribati through permit numbers 008/13, 007/14, 001/16, 003/17.

139

140 **Fig 1. Map of shallow forereef study sites on Kiritimati (Christmas Island), categorized by**
141 **level of chronic local human disturbance.** Village populations (red circles) are represented by
142 bubble size and windward sites are denoted by a thick black border around site. Inset shows
143 Kiritimati's location in the equatorial central Pacific Ocean (open triangle).

144

145 Chronic local human disturbance around the island was previously quantified [31,35]
146 using a combined quantitative metric that incorporated both the human population within 2 km
147 radius [36] of each site (as a proxy for localized impacts e.g. sewage inflow) [31,35] and fishing
148 intensity data [32]. We modelled local human disturbance using this continuous metric, and for
149 visualization used five local human disturbance categories (assigned previously from the
150 continuous metric), which should be regarded as being relative to other sites rather than absolute
151 levels of human disturbance [31]. Thermal stress, in degree heating weeks, was quantified from
152 *in-situ* temperature data, collected from temperature loggers (SBE 56, Sea-Bird Scientific \pm
153 0.001°C precision) deployed at monitored sites around the island, with at least one logger in each
154 of the disturbance levels [further details in 37]. The heat stress from the 2015-2016 El Niño
155 peaked at 27 Degree Heating Weeks (DHW) on Kiritimati, and temperatures were continuously

156 elevated between June 2015 and April 2016 [37] with minimal differences in heat stress across
157 sites (< 1.1 DHW) [31,37]. This prolonged heat stress resulted in an 89% loss of coral cover
158 across the atoll [31].

159

160 In addition to local disturbance, oceanographic factors also vary around the atoll. We
161 used site level net primary productivity (NPP; mg C m⁻² day⁻¹) data extracted from the Marine
162 Socio-Environmental Covariates (MSEC) open source data product, derived from NOAA
163 CoastWatch and calculated over a 2.5 acrmin grid (<https://shiny.sesync.org/apps/msec/>; [38]). In
164 lieu of comprehensive site-level wave exposure data, we defined site-level exposures based on
165 the dominate wind direction (southeasterly; [39]), with sheltered sites on the west side of the
166 island grouped as leeward, and exposed sites on the north and east coasts as windward, following
167 [31,35,40].

168

169 **Juvenile coral survey**

170 At each site, we surveyed juvenile corals along two 25 m transects. Up to ten 1 m²
171 gridded quadrats were set at predetermined random points along the transects and filmed
172 following the protocol in Mumby and colleagues [41], with the modification of 10 cm swaths
173 instead of 20 cm (n = 732 videos total, S1 Table and S2 Fig); more than ten quadrats were
174 surveyed at site VH1 to account for the high prevalence of sand at that site. Videos were
175 randomly analyzed by one of three trained individuals (KLT, NFP, NCOB), who identified each
176 coral to the lowest possible taxonomic unit and measured its 2D horizontal size (i.e., widest
177 width) using the software Tracker (physlets.org/tracker/; [42]; Fig 2); KLT also checked
178 identifications to ensure consistency amongst observers. A juvenile coral was distinguished as

179 being a new colony—rather than a fragment of a colony that experienced partial mortality—by
180 inconsistencies with the surrounding area (i.e., dead skeleton). We defined juvenile corals as
181 those with ≤ 5 cm maximum width. While this size classification is somewhat arbitrary in regards
182 to maturity of corals, it is a commonly used size classification in juvenile and young coral studies
183 [e.g., 7,18,45,46]. Corals that were not fully inside a quadrat were removed from the dataset.
184 When available, life history traits for identified corals were assigned as in Baum and colleagues
185 [31], based upon the Coral Trait Database (<https://coraltraits.org>; [24]) to classify species found
186 in the database, and extracted life histories for other species based on the family (S2 Table).
187 Three coral taxa (n = 42 individuals total) could not be assigned to a life history strategy and thus
188 were removed from statistical analysis. In addition, corals with unresolved identifications or life
189 history assignments (e.g., when coral could only be identified to family and a life history could
190 not be assigned to the family due to multiple strategies within the family) were removed from
191 statistical analysis (n = 317; 4.1% of the data). Generalists (n = 5) and soft coral (n = 38) were
192 excluded from our statistical analysis due to low densities.

193

194 **Statistical analyses**

195 We first examined how juvenile coral densities varied around the atoll prior to the
196 heatwave, by fitting generalized linear mixed-effects models (GLMMs) to the data for the three
197 pre-heatwave timepoints, using a negative binomial error structure to accommodate
198 overdispersion in the data. We included an interaction between local human disturbance
199 (continuous) and life history strategy, along with reef exposure (leeward, windward) and NPP, as
200 fixed effects, while site was modelled as a random effect. Local human disturbance was
201 modelled as a polynomial (quadratic) relationship to allow for the possibility of a non-linear

202 relationship, although the quadratic was ultimately reduced to a linear due to AIC model
203 selection (detailed below). We also included an offset to account for differences in the total
204 number of quadrats sampled at each site.

205
206 We then tested for the influence of the heatwave on juvenile coral density by adding to
207 the above models ‘heat stress’ as an additional fixed effect (four levels: ‘before’ heatwave =
208 2013, 2014, and May 2015; ‘early’ = July 2015, ‘late’ = March 2016; and ‘after’ = July 2017),
209 and a two-way interaction between local disturbance (modelled as a quadratic) and heatwave
210 period to examine if the heatwave impact was modulated by local disturbance. We conducted
211 two sensitivity analyses to test if the heatwave effect was dependent on the exact sites sampled in
212 the various expeditions. The first sensitivity analysis included only the 9 sites that were sampled
213 in all four periods and the second included the 10 sites sampled in both the before and in the late
214 heat stress periods (S4 Table and S1 Fig). Finally, we investigated if the impacts of the heatwave
215 varied with coral life history strategy, by fitting separate ‘heat stress’ models for each life history
216 type.

217
218 All statistical analyses were conducted in R v.4.0.3 [45]. GLMMs were tested using the
219 package *glmmADMB* [46,47]. Prior to analysis, all continuous input variables were standardized
220 to a mean of zero and a standard deviation of 0.5 using the ‘rescale’ function in the *arm* package
221 [48]. AIC was used in model selection and diagnostic graphs plotting residuals using the
222 *DHARMA* package [49] were analyzed for each model presented. For each model type, we
223 present the top model according to AIC, accounting for model parsimony by selecting the model
224 with fewer fixed effects when there were two top models within 2 AIC of one another.

225

226 **Results**

227 In total, we enumerated 7732 juvenile corals (n = 7320 hard; n = 38 soft; n = 374
228 unidentifiable) from 732 census quadrat videos. Juvenile corals had an overall mean density of
229 10.7 m⁻² (± 0.74 SE) and a mean width of 2.28 cm (± 0.01 SE; S3 Fig). We identified 45 juvenile
230 coral species (or genera when species was not possible) from 13 different families (S5 Table),
231 the most common of which were *Leptoseris mycetoseroides* (2.1 ± 0.08 m⁻²), *Pavona varians*
232 (1.3 ± 0.16 m⁻²), and *Porites lobata* (1.0 ± 0.10 m⁻²) (Figs 2 and 3). Over 80% of enumerated
233 corals belonged to four families: Agariciidae (n = 2732), Merulinidae (n = 1874), Acroporidae (n
234 = 873), and Poritidae (n = 774) (S5 Table). Stress-tolerant corals were the most common at every
235 time point and accounted for almost three-quarters (73%) of the corals overall (n = 5661) (Figs 3
236 and 4). Competitive corals were the next most common (n = 1065 corals; 13.8%), followed by
237 weedy (n = 550, 7.1%), and generalists (n=5) (Fig 3).

238

239 **Fig 2. Representative photos of surveyed juvenile corals on Kiritimati throughout the**
240 **study.** The top three most common corals were **(a)** *Leptoseris mycetoseroides*, **(b)** *Pavona*
241 *variens*, and **(c)** *Porites lobata*. Panels d-f (d = *Platygyra* spp., e = *Hydnophora microconos*, f =
242 *Goniastrea stelligera*) are examples of other stress-tolerant corals. Panels g (*Acropora* spp.) and
243 h (*Pocillopora* spp.) are examples of corals with competitive life histories, and panel i
244 (*Leptastrea purpurea*) has a weedy life history strategy.

245

246 **Fig 3. Density (± SE) of 45 juvenile (≤5 cm) coral species (or genus) before (2013, 2014, and**
247 **2015b) and after (2017) the marine heatwave.** Plots **(a)** 20 most common and **(b)** rarer corals

248 are colored by life history and heatwave period. Error bar for *P. profundacella* (in panel b) after
249 the marine heatwave extends to 0.8042 m⁻². Y-axis scales vary between plots.

250

251 **Pre-heatwave juvenile corals**

252 Prior to the heatwave, overall mean juvenile coral density on the atoll ranged from 7.2 m²
253 (± 1.9 SE) at the most disturbed sites up to 15.3 m² (± 3.8 SE) at the least disturbed ones (Fig 4).

254 Accordingly, pre-heatwave juvenile coral density was significantly negatively influenced by
255 local human disturbance (parameter estimate = -0.520, $z = -2.432$, $P = 0.015$; S3 Table). Juvenile
256 coral densities also varied significantly with life history strategy: stress-tolerant corals were the
257 most common before the heatwave and declined as local human disturbance increased (S4 Fig),
258 competitive corals also declined along the disturbance gradient (parameter estimate: -0.643, $z = -$
259 1.972, $P = 0.049$; S3 Table) but had significantly lower densities compared to stress-tolerant
260 (parameter estimate = -1.424, $z = -11.074$, $P < 0.001$; S3 Table). While there were also
261 significantly fewer weedy juvenile corals compared to stress-tolerant ones (parameter estimate =
262 -2.499, $z = -12.608$, $P < 0.001$; S3 Table), they differed in that they significantly increased with
263 increasing local human disturbance (parameter estimate = 0.642, $z = 2.315$, $P = 0.021$; S3 Table).
264 Although there was a tendency for juvenile coral densities to increase with exposure (parameter
265 estimate = 0.104, $z = 0.462$, $P = 0.644$; S3 Table) and NPP (parameter estimate = 0.155, $z =$
266 0.599, $P = 0.559$; S3 Table) these effects were not statistically significant.

267

268 **Fig 4. Density (\pm SE) of juvenile (≤ 5 cm) corals at forereef sites on Kiritimati (Christmas**
269 **Island) across the heatwave** (Early = 2 months (July 2015), Late = 10 months (March 2016),
270 and After = ~ 1 year after (summer 2017)) for **(a, b)** all corals, **(c, d)** stress-tolerant corals, and **(e,**

271 **f**) competitive corals across the (**a, c, e**) entire island (18 sites; n = the number of quadrats
272 sampled per time point), and the (**b, d, f**) local human disturbance gradient (VL = very low, L =
273 low, M = medium, H = high, and VH = very high). Note: Not all sites could be sampled in each
274 time point. Y-axis scale varies among panels.

275

276 **Heatwave effects**

277 The 2015-2016 El Niño significantly reduced juvenile coral densities (parameter estimate
278 = -0.774, $z = -5.042$, $P < 0.0001$; Figs 4a and 6, S3 Table), resulting in the loss of half of all
279 juvenile corals by late in the event ($11.6 \text{ m}^2 \pm 1.1 \text{ SE}$ before to $5.9 \text{ m}^2 \pm 1.2 \text{ SE}$ after; 50%
280 decrease). Of the 15 coral taxa with the highest densities before the heatwave, all six with
281 competitive life histories declined by more than 80% (three by 100%; Fig 5). There was a greater
282 range of declines among the stress-tolerant taxa: only two, *Montipora* encrusting species and
283 species from the Fungiidae family had losses greater than 80% and four taxa declined by less
284 than 50%. *Dipsastraea speciosa* had the smallest loss at just over 5% (Fig 5).

285

286 **Fig 5. Overall change in density by the late heat stress time period of individual juvenile**
287 **(≤ 5 cm) coral taxa at forereef sites on Kiritimati (Christmas Island)** for the 15 most common
288 taxa before the heatwave, ordered from least to greatest change in density. Where applicable,
289 taxa colors are the same as in Baum and colleagues [31].

290

291 Declines in juvenile coral densities (from before to late in the El Niño) were lowest at
292 sites in the mid-range (20.6% at medium sites, 58.5% at low sites) of the local disturbance (Fig
293 4). The sites at the very high and very low ends of the range experienced 66.5 per cent and 68.9

294 per cent respectively (high sites not sampled in late time period; Fig 4). This resulted in a
295 significant quadratic interaction between local disturbance and heatwave for late in the heatwave
296 (parameter estimate = -6.314, $z = -2.121$, $P = 0.034$; S3 Table). This quadratic interaction was
297 also present in the juvenile coral density early in the heatwave (parameter estimate = -3.804, $z = -$
298 2.353, $P = 0.019$; S3 Table) although there were not yet decreases overall. Significant reductions
299 in juvenile coral density were only detected late in the heatwave (March 2016; parameter
300 estimate = -0.774, $z = -5.042$, $P < 0.001$; S3 Table), with none detected two months into the
301 heatwave (parameter estimate = -0.152, $z = 1.555$, $P = 0.120$; S3 Table). Approximately one year
302 after the El Niño, juvenile corals remained at significantly lower densities than prior to the event,
303 but the effect was lessened (parameter estimate = -0.298, $z = -2.892$, $P = 0.004$; Figs 4a and 6, S3
304 Table) and densities had increased relative to those late in the heatwave (Fig 4a). The significant
305 quadratic interaction between disturbance and heat stress dissolved by this time point (parameter
306 estimate = -2.310, $z = -1.409$, $P = 0.159$; S3 Table) but there was also not a linear interaction
307 (parameter estimate = -2.776, $z = -1.422$, $P = 0.155$; S3 Table). There were significantly fewer
308 competitive and weedy juvenile corals compared to stress-tolerant corals (competitive: parameter
309 estimate = -1.794, $z = -16.811$, $P < 0.001$; weedy: parameter estimate = -2.216, $z = -18.076$, $P <$
310 0.001; Fig 6, S3 Table). Neither island exposure nor NPP had significant effects on juvenile coral
311 density (Fig 6, S3 Table). In our sensitivity analyses that controlled for site, the patterns largely
312 remained the same with some differences in significance, notable differences include: the
313 interaction (both linear and quadratic) between human disturbance and the late heat stress time
314 point is significant in both site controlled models, the linear effect of human disturbance was not
315 significant when the model was controlled for sites sampled in both before and after heat stress
316 periods (S4 Table).

317 **Fig 6. Generalized linear mixed model predictor coefficient effect size estimates and 95%**
318 **confidence intervals** for the overall dataset. Human disturbance was modelled as a quadratic (l=
319 linear, q = quadratic). Heat stress colors correspond with figure 4 and life history with figure 3.

320

321 Losses in juvenile corals due to the 2015-2016 El Niño varied substantially between coral
322 life histories: stress-tolerant juvenile corals experienced an average loss of 69.25% (parameter
323 estimate = -0.594, $z = -3.990$, $P < 0.0001$; S3 Table) and weedy declined by 26.57% (parameter
324 estimate = -0.720, $z = -1.575$, $P = 0.115$; S3 Table), whereas competitive coral declined by
325 96.8% (parameter estimate = -2.1042, $z = -4.954$, $P < 0.0001$; Figs 4 and S5, S3 Table). All life
326 history strategies had an increase in juvenile corals one year after the El Niño (Figs 4 and S5, S3
327 Table). Across all three life history models, the results indicate that local human disturbance
328 lowers juvenile coral density, significantly for both stress-tolerant and competitive (stress-
329 tolerant (linear): parameter estimate = -2.487, $z = -2.309$, $P = 0.021$; competitive: parameter
330 estimate = -1.169, $z = -3.318$, $P = 0.001$; weedy (linear): parameter estimate = -2.615, $z = -1.874$,
331 $P = 0.061$; S5 Fig; S3 Table). The influence of human disturbance varied between life histories
332 throughout the heatwave; there was no significant interaction for competitive corals suggesting
333 that the impact of local human disturbance did not change throughout the marine heatwave.
334 Comparatively, stress-tolerant corals had a significant quadratic relationship with human
335 disturbance early in the heatwave (parameter estimate (quadratic) = -2.301, $z = -2.204$, $P =$
336 0.028; S3 Table) that shifted into a linear relationship by the late time period (parameter estimate
337 (linear) = -3.088, $z = -1.973$, $P = 0.049$; S3 Table). Weedy corals also had a significant linear
338 interaction late in the heat wave (parameter estimate (linear): -8.700, $z = -1.971$, $P = 0.0487$; S3
339 Table and S5 Fig, S3 Table).

340 Influences of island exposure varied between life history strategies. Competitive densities
341 were significantly higher on the windward side (parameter estimate = 0.7547, $z = 2.549$, $P =$
342 0.01082; S3 Table). Weedy density patterns were the opposite with significantly less on the
343 windward side (parameter estimate = -1.158, $z = -3.750$, $P = 0.0002$; S3 Table). Stress-tolerant
344 densities patterns were slightly higher on the windward side, although not significant (parameter
345 estimate = 0.021, $z = 0.097$, $P = 0.923$; S5 Fig, S3 Table).

346

347 Bleaching of juvenile corals was less than 15% at both time points measured during the
348 heatwave (early = $14.4 \pm 0.8\%$ SE; late = $13.0 \pm 3.4\%$ SE) (Fig 7a). Before the heatwave,
349 juvenile corals on the most disturbed reefs had the highest prevalence of bleaching ($10.9 \pm 1.9\%$
350 SE). This shifted to reefs with medium human disturbance a couple months into the heatwave
351 ($16.2 \pm 1.7\%$ SE) and by the end, the lowest human disturbed reefs had the highest occurrence,
352 with nearly a quarter of the juvenile corals bleached ($24.8 \pm 13.7\%$ SE) (Fig 7b). For many of the
353 most common corals surveyed, the bleaching percentage before, early, and late in the heatwave
354 did not exceed 25%. Additionally, most juvenile coral species showed an increase in bleaching
355 early into the heatwave but decreased by the late time period. For example, *L. mycetoseroides*,
356 the most common juvenile coral, had 3.4% bleaching before which increased to 25.3% early on
357 and decreased to 9.8% by the end of the heatwave (S5 Table). Seven coral species were
358 surveyed as adults in Baum and colleagues at the same sites and time points [31]. Among those
359 species, the juvenile corals of *Platygyra* spp. had the highest proportion of bleaching before
360 (18.1%) and late (27.3%) in the heatwave, and second highest early in the heatwave (20%).
361 *Dipsastraea* spp. was highest early in the heatwave (38.4%) and was second highest before
362 (10.9%) and late (17.5%) (S5 Table).

363 **Fig 7. Density of juvenile corals visually bleaching or healthy** across the **(a)** marine heatwave
364 and **(b)** the human disturbance gradient. Heat stress colors correspond with figure 4 and human
365 disturbance colors correspond with figure 1.

366

367 **Discussion**

368 Our study provides evidence that both chronic local anthropogenic disturbance and
369 prolonged heat stress significantly reduce the density of juvenile corals on shallow forereefs.
370 Before the heatwave, there was an inverse relationship between juvenile coral densities and the
371 local disturbance gradient overall, but varying impacts of disturbance on different coral life
372 histories. The heatwave significantly reduced juvenile coral densities, and for stress-tolerant and
373 weedy corals shifted the relationship between their density and local human disturbance.
374 Juvenile coral densities appeared to be increasing (by >50%) just one year after the heatwave,
375 but the differences were not statistically significant.

376

377 The significant negative effect of local human disturbance on juvenile coral densities we
378 detected is in accordance with previous studies that have documented the negative effects single
379 [23,27,50] and multiple [30] chronic anthropogenic stressors have on juvenile corals. On
380 Kiritimati, this effect is believed to be the result of poor water quality, due to sewage and other
381 pollution outflow onto the reef [31,32,51], and direct damage from dredging at some sites [31],
382 which had substantially decreased overall coral cover and habitat complexity at the most
383 disturbed sites prior to the heatwave [31]. We note that prior to the heatwave, turf algae and
384 sediment cover were highest at the most disturbed sites, all of which can negatively impact corals
385 of all life stages [21,28,29]. Comparatively, however, examining the pre-heatwave coral

386 communities, the influence of human disturbance was greater on adults [31] than it was on
387 juveniles (this study), although the mechanism for this difference remains unclear.

388

389 The 2015-2016 El Niño caused significant mortality of juvenile corals on Kiritimati, but
390 this effect was only evident at our end of heatwave expedition (i.e. after 10 months of heat
391 stress). Juvenile corals have been known to survive a few months of heat stress [15–17,52] which
392 is hypothesized to be due to their small and flat structure increasing mass transfer off toxic by-
393 products [19,20] and being non-reproductive [18]. Despite the apparent resilience of juvenile
394 corals to short term heat stress, our study and others demonstrate juvenile coral's susceptibility to
395 long term elevated temperature conditions, similar to adult colonies [4,31,53]. Studies in the
396 Seychelles documented 48% or greater loss of juvenile corals following the 2015-2106 El Niño
397 [30,54] and a study in the Maldives recorded similarly low densities as our study (2.7 ± 4.6 to 5.8
398 ± 12.3 individuals m^{-2} ; [13]), and although they did not have pre-heatwave data, as mentioned by
399 Perry and Morgan [13], in the context of densities reported after the 1998 El Niño [55,56] these
400 are very low. On Kiritimati, recovery of juvenile corals may have occurred, as evidenced by the
401 ability of reefs on Moorea to recover despite multiple acute disturbances resulting in low juvenile
402 coral densities [57], however subsequent monitoring has been limited due to COVID-19 related
403 international travel bans from 2020 to 2023.

404

405 A comparison between the heatwave impacts we documented here to those documented
406 for adult corals by Baum et al. [31] on Kiritimati, reveals that the heatwave had a greater impact
407 on adult corals, with a higher occurrence of bleaching and 1.8 fold greater mortality in adult
408 colonies [31]. Before the 2015-2016 El Niño, overall on Kiritimati juvenile corals were more

409 frequently bleached than the adults [31], which could indicate that they were competing with
410 post-settlement stressors as the escapement size, irrespective of life-history and habitat, is 5cm
411 [7]. However, during the heatwave, the bleaching frequency in adults surpassed that of the
412 juveniles [31], possibly due to juvenile corals' hypothesized better resistance to bleaching
413 [15,17–19]. In an Australian study, Álvarez-Noriega et al. [18] also found an overall difference
414 in bleaching induced mortality between adults and juvenile corals, but that it was taxon
415 dependent. This seems to be location dependent however, as we only found *Goniastrea* spp. to
416 have the same trend on Kiritimati where the adults were more affected. The biggest difference
417 was in the Merulinidae family, where in Australia the juveniles did worse than their adult
418 counterparts, but on Kiritimati, the majority of the Merulinidae juveniles increased in density
419 while the adults declined [31]. Small colonies of *Oculina patagonica* also had higher
420 survivorship than their adult counterparts during a bleaching event in the Mediterranean [52],
421 whereas in the inner Seychelles, Dajka and colleagues [30] documented 70% mortality of
422 juveniles due to heat stress which was similar to the adult community loss on those reefs.

423

424 It was expected that the corals at the sites exposed to very high local disturbance before
425 the heatwave would have been the most stressed and therefore have the highest prevalence of
426 bleaching, however, the greatest prevalence of bleaching shifted along the local human
427 disturbance gradient throughout the heatwave. Interestingly, as the shift in high bleaching
428 prevalence moved to medium disturbed sites early in the event, it did not correspond with a large
429 die off of juvenile corals at the very high disturbed sites. In fact, there was an increase in juvenile
430 corals between the before and early time points. Additionally, while there was a large decline in
431 juvenile corals by the late time period across the atoll, the sites that experienced the highest

432 bleaching percentage (medium disturbed sites) at the early time point had the smallest decline
433 (~21%). This demonstrates a mismatch between bleaching prevalence and mortality levels
434 similar as to what was recorded in the adult colonies [31]. Mechanisms for this have been
435 proposed for adult colonies (e.g., resistant to bleaching but then can only survive temporarily in a
436 bleached state [58,59], symbiont switching mid heat event [35]) but to our knowledge this
437 pattern has not been documented in juvenile corals. It is possible that juveniles follow some of
438 the same mechanisms as adults but with their different physical structure [19], they may have
439 other mechanisms.

440

441 Juvenile corals with a stress-tolerant life history were dominant across the atoll at all time
442 points in this study. While for the entire coral community, Baum et al. [31] also found that stress-
443 tolerant corals dominated Kiritimati's highly disturbed reefs and all reefs after the 2015-2016 El
444 Niño, prior to the event, competitive corals dominated the lowest disturbance sites. Dominance
445 of stress-tolerant corals was also documented on reefs in the Maldives in the years immediately
446 following both the 1998 [55] and 2016 El Niños [13]. In contrast, after heatwaves other reefs
447 were dominated by competitive and weedy type corals (e.g., *Acropora* and *Pocillopora*) that
448 colonize open space on reefs and grow rapidly [10,16,57,60]; however, the timescale varies
449 globally, likely due to differences in community dynamics and severity of disturbances. Our
450 study only extended one year past the El Niño and we detected no significant increase in weedy
451 and competitive corals compared to stress-tolerant corals, similar to what was recorded on
452 nearby Jarvis Island [61]. This might indicate that recovery will be suppressed until these corals
453 can contribute significantly to recruitment, as documented on other reefs severely impacted by
454 heat stress [7,10,12,13,62] compared to reefs less impacted by extreme heatwaves [57,63]. Thus,

455 with more studies, it may be possible to roughly calculate recovery times using the severity of
456 the disturbance and composition and density of surviving juvenile corals.

457

458 Reef exposure has been shown to protect juvenile coral densities during marine
459 heatwaves as water velocity is a rate-determining step in mass transfer [20] however, high wave
460 energy can have a negative impact during recovery [64–66]. In this study, as on the Great Barrier
461 Reef [7], habitat specific stressors varyingly influenced juvenile assemblages. The sites located
462 along the windward shores had higher densities of competitive corals possibly due to these sites
463 being dominated by adult competitive corals [31] and coinciding with a lack of local human
464 disturbance resulting in low competition with macroalgae. In contrast, weedy corals had higher
465 densities on the leeward and more disturbed shores, which is a common trend around the world
466 [7,24,67–70].

467

468 Overall, our study demonstrates the negative impacts that a prolonged heatwave and
469 localized chronic anthropogenic stress had on juvenile corals. This study also highlights
470 differences in impacts amongst juvenile corals with different life history strategies. Given the
471 importance of juvenile corals for reef recovery, continued studies of the impacts of these
472 stressors, the mechanisms by which they affect juvenile corals, and ongoing monitoring of their
473 contributions to reef recovery trajectories is needed.

474

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484

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683

684 **Supporting information**

685 **S1 Fig. Map of reef study sites on Kiritimati (Christmas Island) sampled at each heat stress**
686 **time point** (Before = 2 years before – start (summer 2013, summer 2014, April/May 2015),
687 Early = 2 months (July 2015), Late = 10 months (March 2016), and After = ~1 year after
688 (summer 2017). The sites are divided into five levels of local human disturbance. Village
689 population (red circles) is represented by bubble size.

690

691 **S2 Fig. Representative photos of quadrats surveyed on Kiritimati (a, d) before, (b, e) at the**
692 **end, and (c, f) after the heatwave on reefs exposed to (a-c) very high levels of local human**
693 **disturbance and (d-f) very low levels.**

694

695 **S3 Fig. Widest width of juvenile corals (n=7732) on Kiritimati throughout the survey. Mean**
696 **width was 2.28 cm (\pm 0.01 SE). Bins are 0.5cm.**

697

698 **S4 Fig. Density of juvenile corals with different life history strategies across the human**
699 **disturbance gradient prior to the 2015-2016 marine heatwave modelled with a two-way**
700 **interaction.**

701

702 **S5 Fig. Generalized linear mixed model predictor coefficient effect size estimates and 95%**
703 **confidence intervals** for each tested life history strategy: **(a) stress-tolerant, (b) competitive, and**
704 **(c) weedy.** In models a and c, human disturbance was modelled as a quadratic (l = linear, q =
705 quadratic). Heat stress colors correspond with figure 4. X-axis scale varies among panels.

706

707 **S1 Table. Number of juvenile coral video assays conducted at each of 18 sites around**
708 **Kiritimati, by expedition before (July 2013, August 2014), during (May 2015, July 2015,**
709 **March 2016), and after (July 2017) the 2015-2016 El Niño.** Sites are ordered first by
710 decreasing levels of local chronic human disturbance then by exposure (Fig 1).

711
712 **S2 Table. Life history table of juvenile coral taxa identified from video assays processed**
713 **using Tracker.** Coral life history strategy retrieved from the Coral Traits Database
714 (<https://coraltraits.org/>), unless otherwise noted. Current taxonomy (and name synonymy)
715 retrieved from WoRMS (<http://www.marinespecies.org/>).

716
717 **S3 Table. Results for (a) pre-heatwave and (b) heatwave models.** Bolded values are
718 significantly different from baseline levels (i.e., before, stress-tolerant, leeward) at $\alpha = 0.05$,
719 asterisks indicate levels of significance ($\cdot p < 0.1$, $* p < 0.05$, $** p < 0.01$, $*** p < 0.001$). Red
720 shaded boxes correspond to variables with a negative parameter estimate.

721
722 **S4 Table. Results for the sensitivity analysis on the heatwave effect by controlling for sites**
723 **sampled.** The first model (a) was run using only the 9 sites that were sampled in all four heat
724 stress periods (S1 Fig). The second model (b) is run with the 10 sites that were sampled in both
725 the before and late heat stress periods. Bolded values are significantly different from baseline
726 levels (i.e., before, stress-tolerant, leeward) at $\alpha = 0.05$, asterisks indicate levels of significance (\cdot
727 $p < 0.1$, $* p < 0.05$, $** p < 0.01$, $*** p < 0.001$). Red shaded boxes correspond to variables with a
728 negative parameter estimate.

729

730 **S5 Table. Numbers of each species identified in the video assays during each time point and**
731 **overall.** Current taxonomy retrieved from WoRMS (<http://www.marinespecies.org/>).

732

733 **S5 Table. Percent bleaching for juvenile (JV) corals during three time points for top 16**
734 **coral species and two other species** of which there is adult data to compare to. Rank column
735 denotes level of common-ness before the heatwave; the 7th most common was unidentified and
736 thus not included on this table. Adult data was only available for seven species from Baum and
737 colleagues [31]. (n = total for that time period)

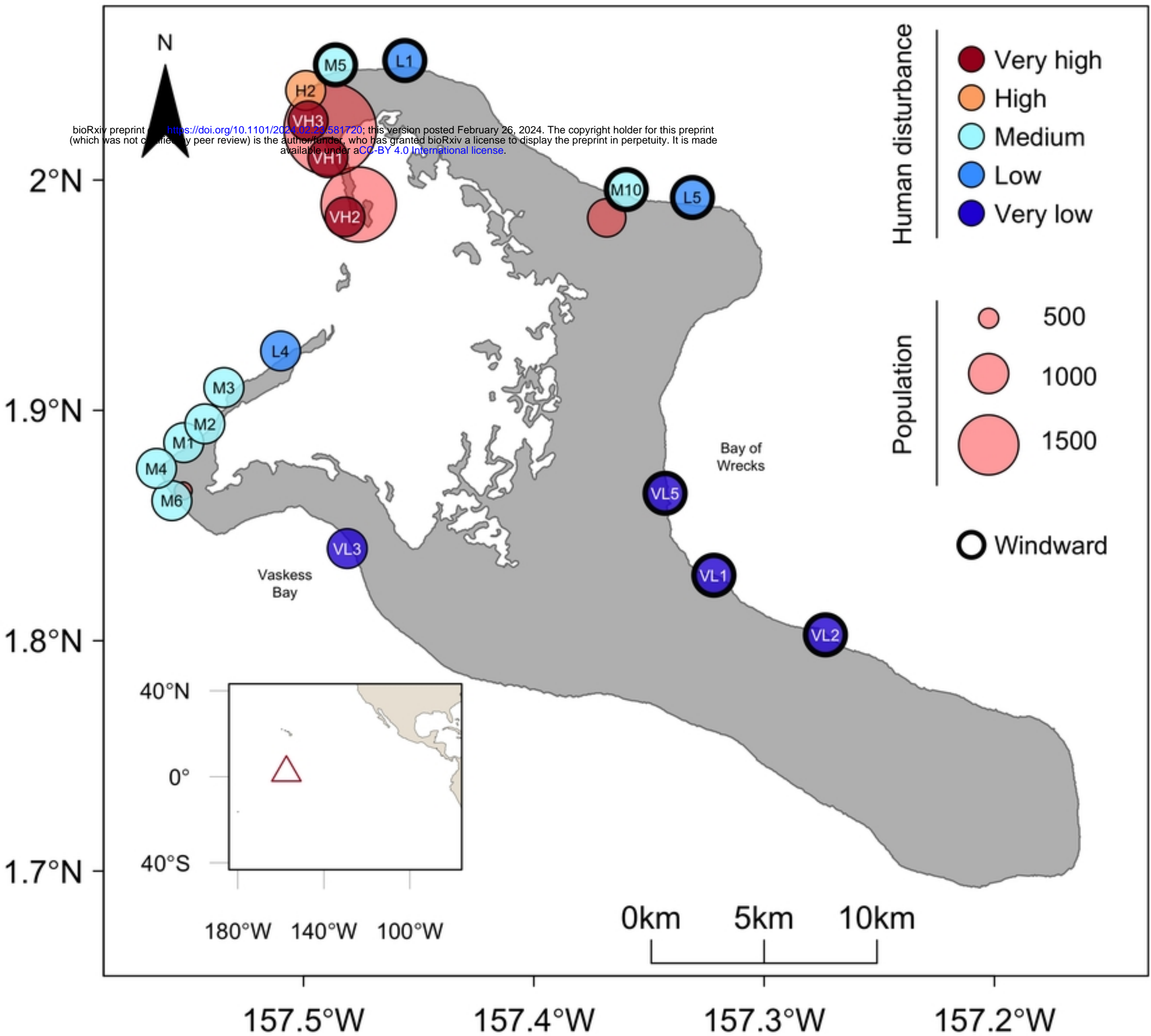


Figure 1

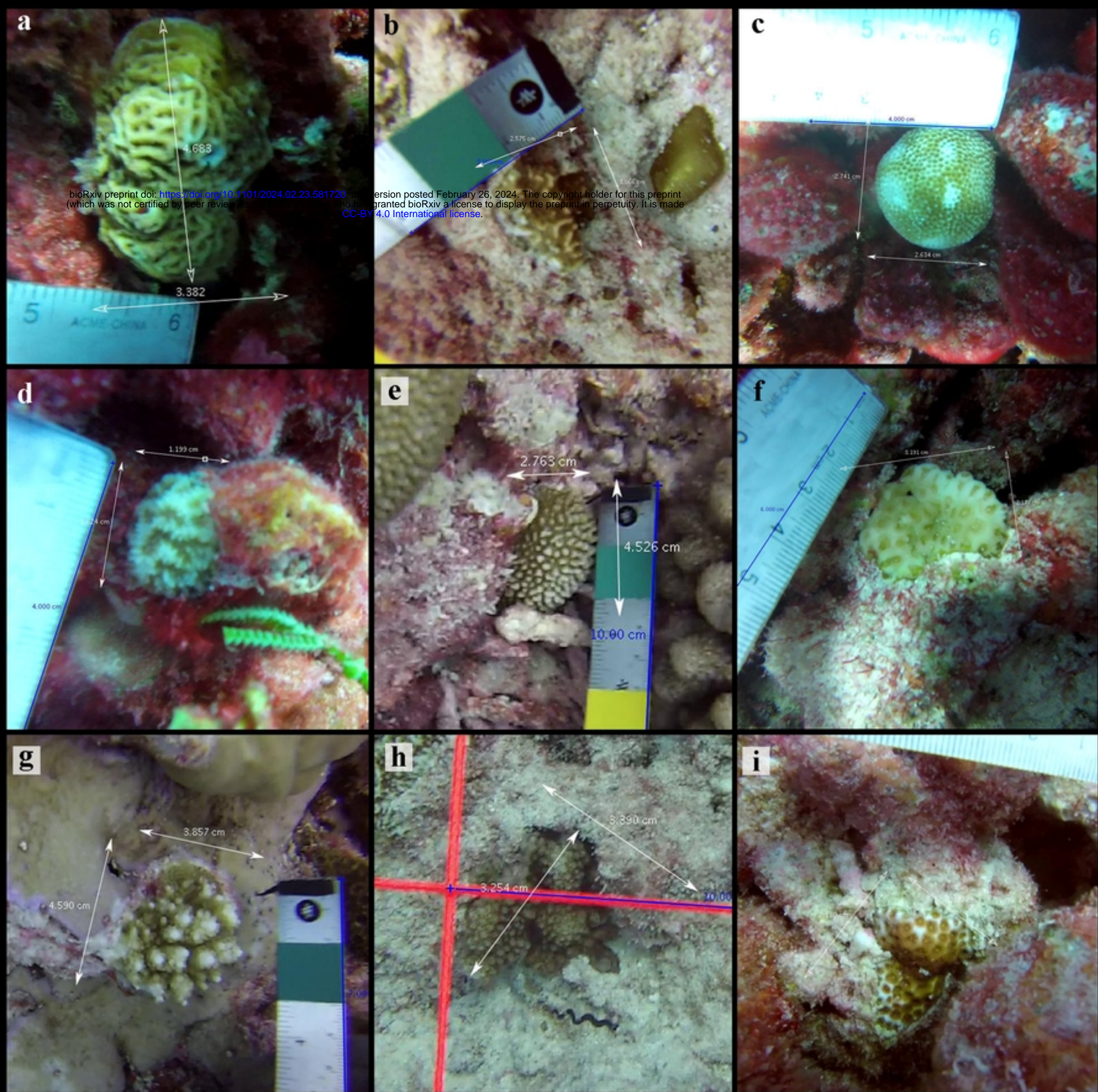


Figure 2

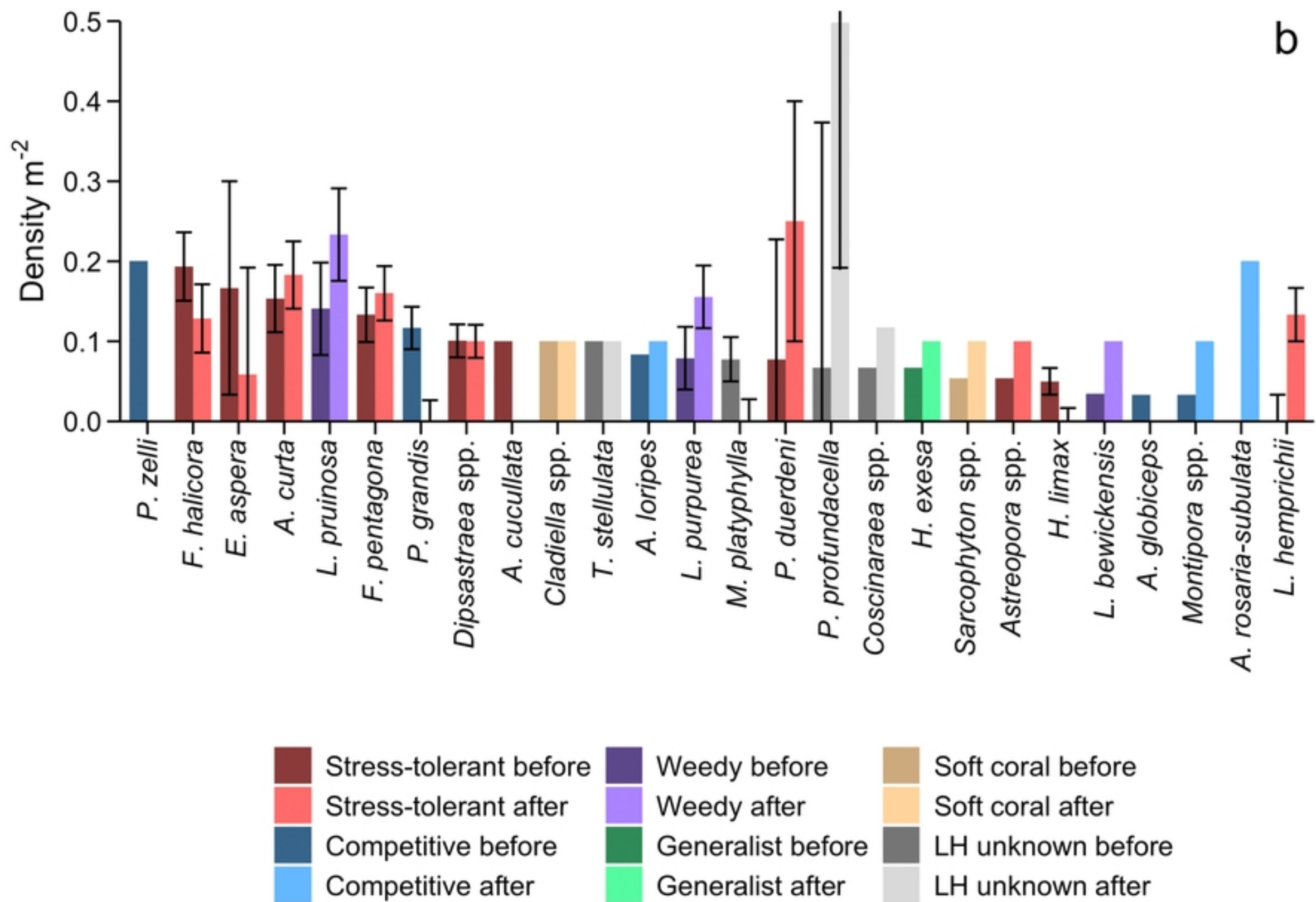
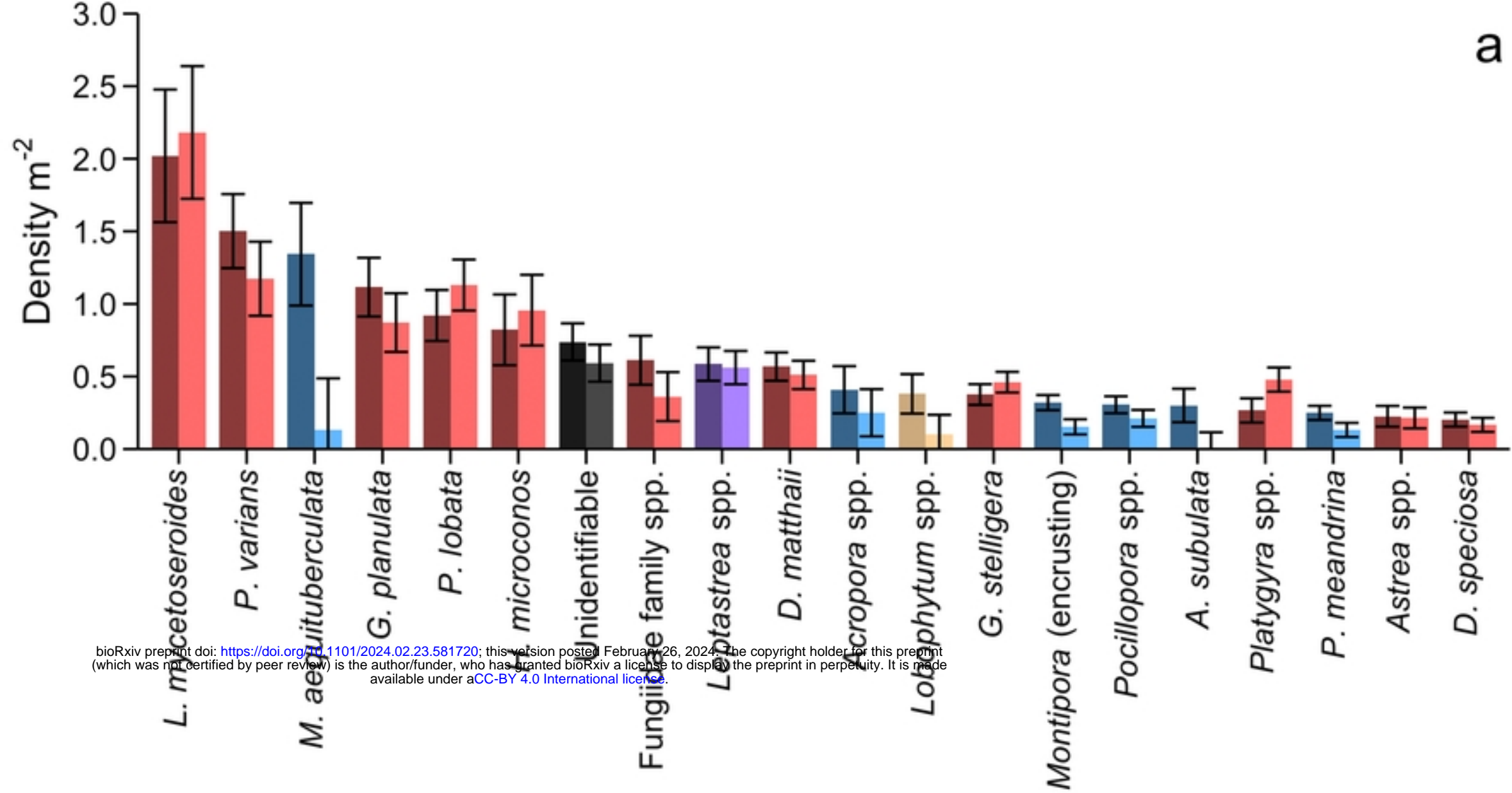


Figure 3

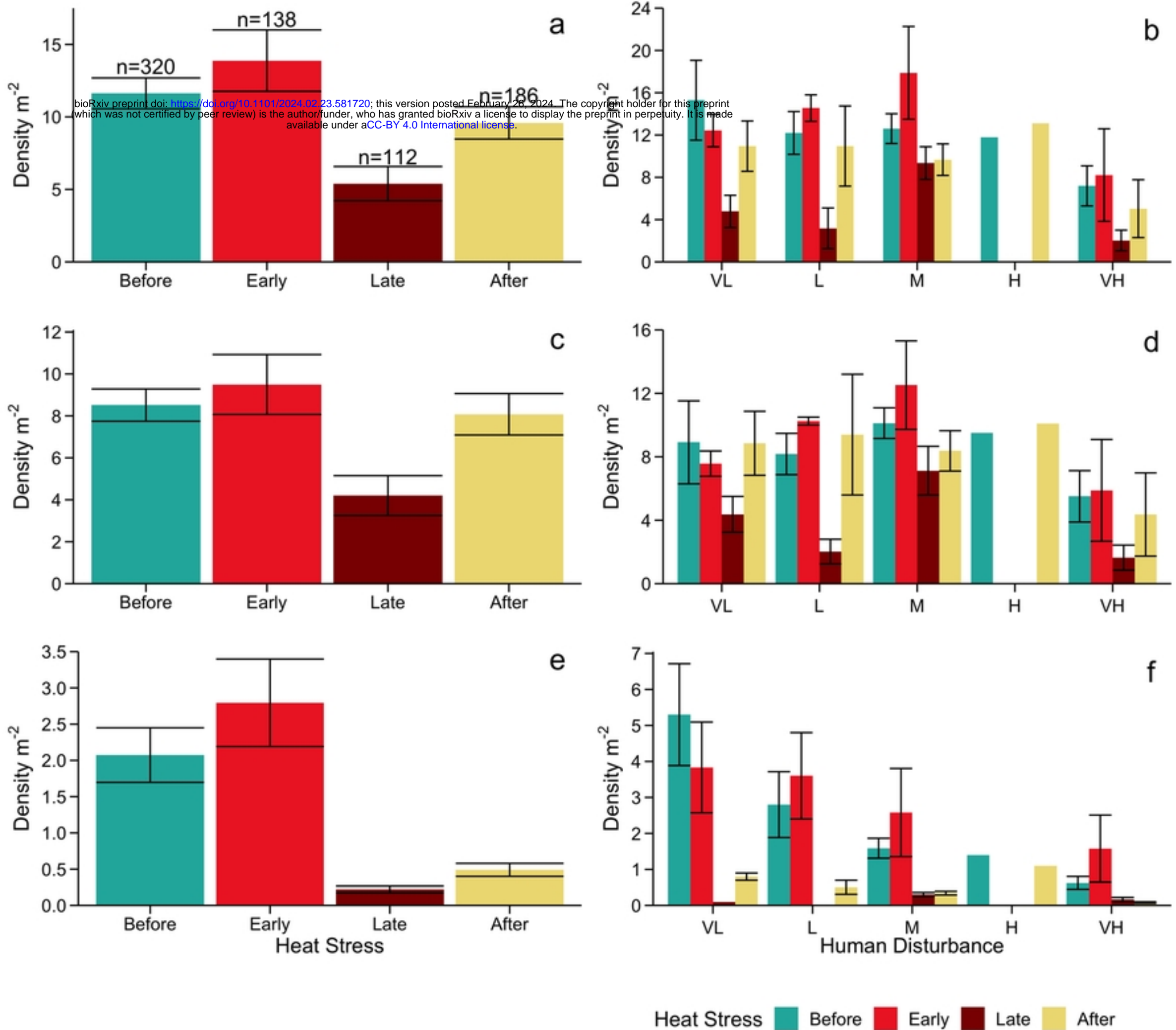


Figure 4

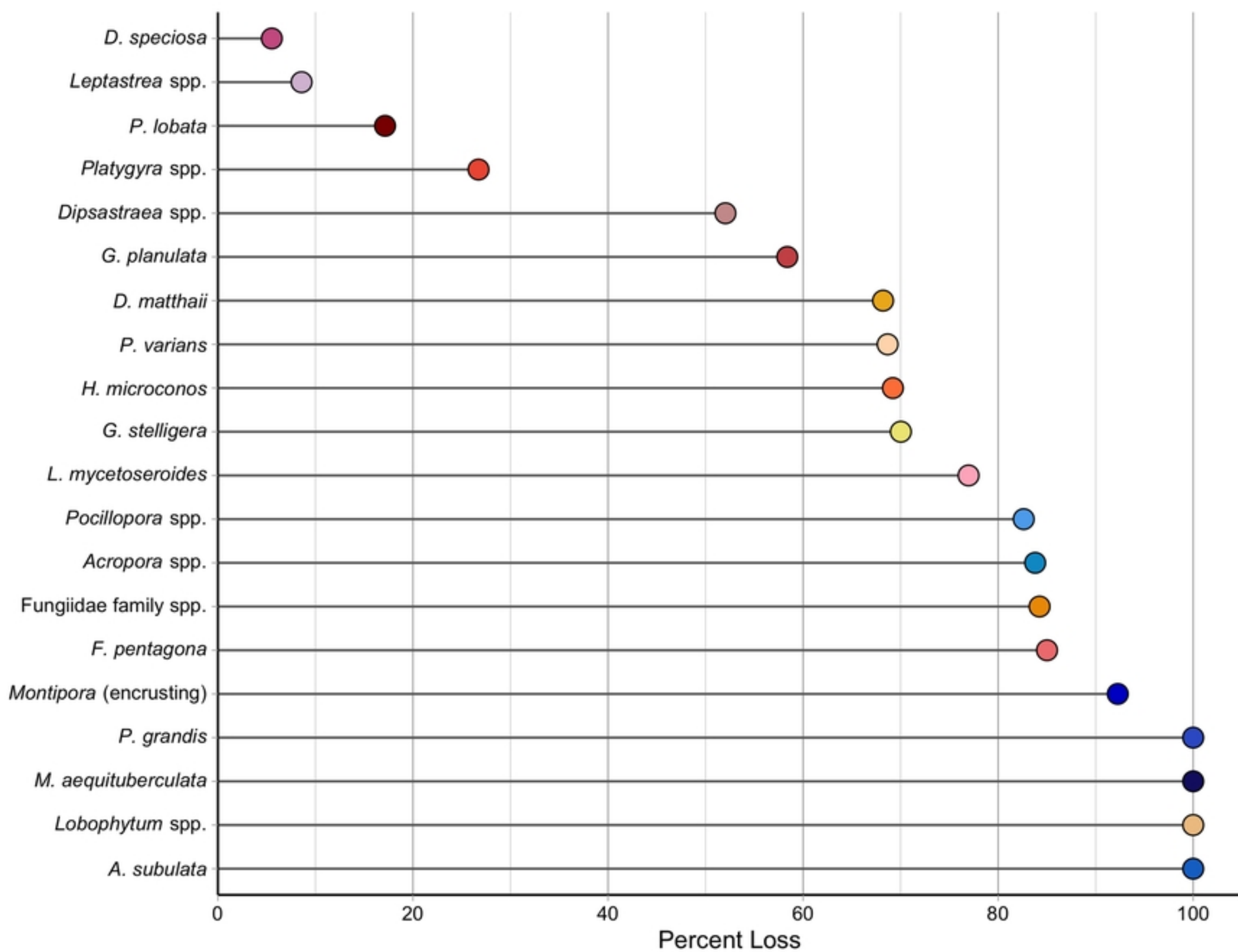


Figure 5

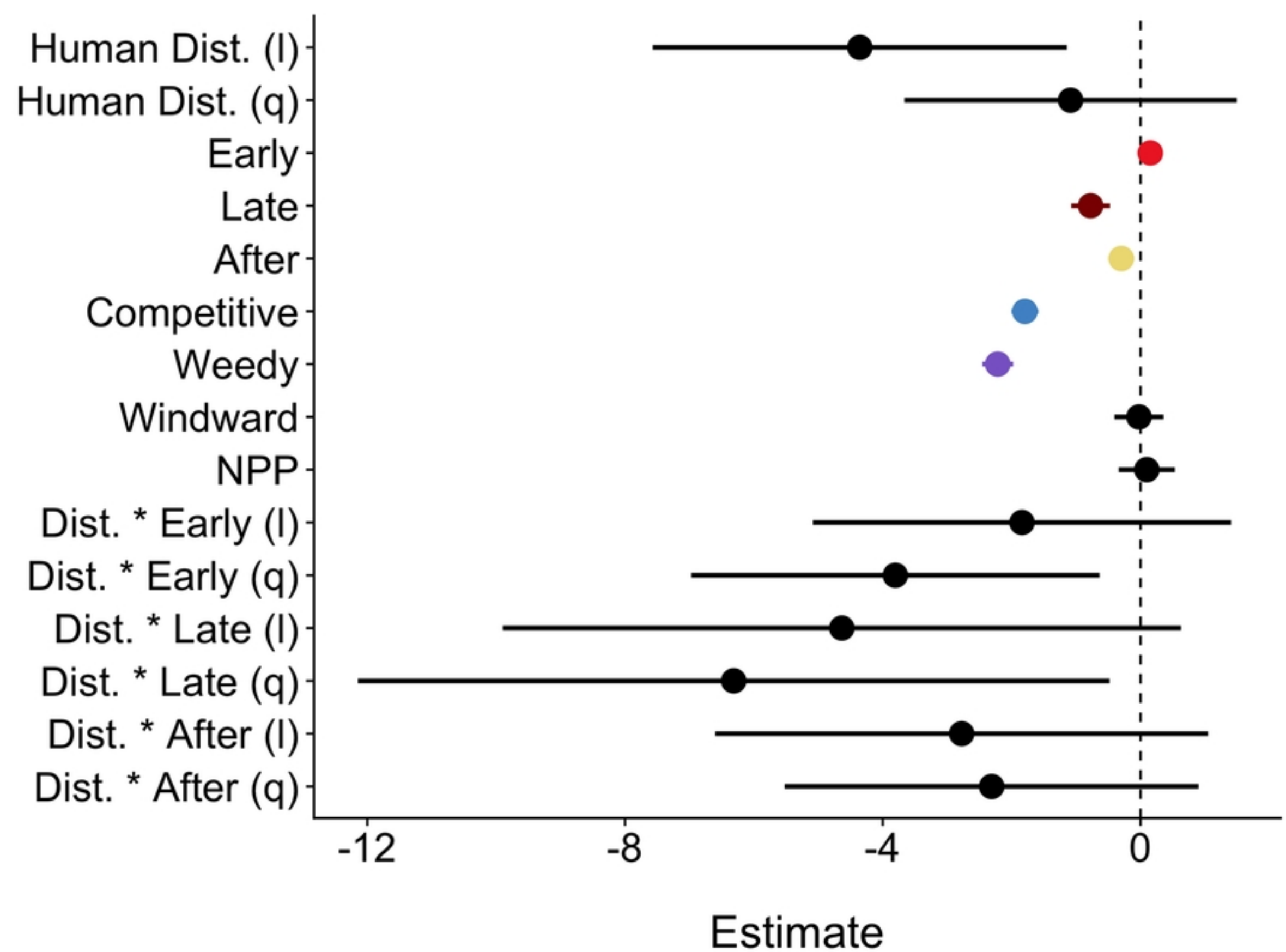


Figure 6

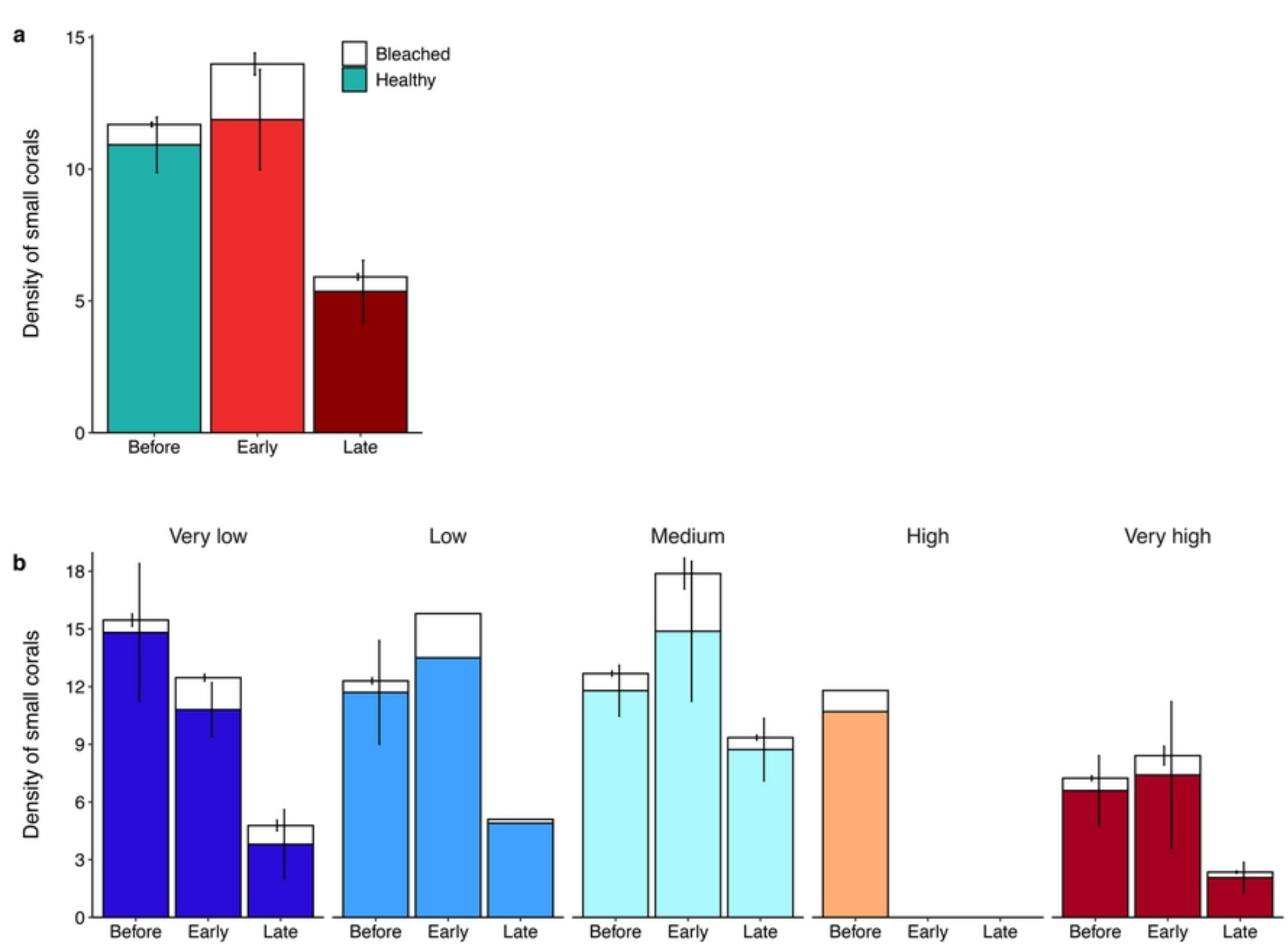


Figure 7