

1 **The war of corals: patterns, drivers, and implications of changing coral competitive**  
2 **performances across reef environments**

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11 **Abstract**

12 Amidst global environmental changes, predicting species responses to future environments is a  
13 critical challenge for preserving biodiversity and associated human benefits. We explored the  
14 original idea that coral competitive performances, the ability of corals to preempt ecological  
15 space on the reef through territorial warfare, serve as indicators of species' ecological niches and  
16 environmental windows, and therefore, responses to future environments. Our surveys indicated  
17 that coral performances varied with taxonomic-identity, size, and position along environmental  
18 gradients, highlighting complex interplays between life-history, warfare-strategy, and niche  
19 segregation. Our results forewarn that growing alterations of coastal environments may trigger  
20 shifts in coral dominance, with decline of major reef-building taxa like acroporids, and  
21 underscore the importance of restraining human impacts for coastal resilience. Our empirical  
22 approach untangles the complexity of species' battle-like interactions and can help identify  
23 winners and losers in various communities caught in the interplay between ecological niches,  
24 environmental windows, and global changes.

25

26 **Keywords**

27 Coral reef, Competition, Territorial war, Niche segregation, Species coexistence, Global change.

## 28 **Introduction**

29           Predicting how global environmental changes will affect species performances in the  
30 future is crucial to anticipating biodiversity declines and defining sustainable management.  
31 However, large uncertainties blur current predictions of ecosystem trajectory in future  
32 environments [1,2]. Finding effective metrics of species responses to changing environments is  
33 key, particularly for vulnerable ecosystems in need of rapid intervention, and in developing and  
34 island nations where high reliance on natural resources exacerbates socio-ecosystem  
35 vulnerability [3–5]. This is particularly true with coral reefs, which support prolific marine life  
36 and coastal livelihoods yet stand at the frontline of declining ecosystems due to rapidly altering  
37 coastal environments [1,6–9]. Reef degradation from growing coastal development, pollution,  
38 fishing, and climate change predominantly involves a gradual decline in coral abundance,  
39 composition, and size, with the progressive loss of vulnerable species, particularly at sensitive  
40 life-stages, altering key ecosystem functions [7,10–13]. Recent demographic modeling  
41 approaches allow characterizing these dynamics on reefs with fine-scale monitoring data [2,14–  
42 16]. However, only a few eminent sites, representing an infinitesimal proportion of reefs, benefit  
43 from the necessary level of scientific knowledge, leaving out most coral reef ecosystems from  
44 such quantitative diagnosis.

45           As an alternative to using demographic modeling, we hypothesize that coral competitive  
46 performances, the ability of corals to preempt space on the reef substrate through territorial  
47 warfare, could be used as a proxy of species ecological success in different environments.  
48 Competition for space and other limiting vital resources is a key process shaping ecological  
49 communities in coral reefs, notorious for biodiversity and biotic interactions, and where  
50 competition warfare can drive community shifts and ecosystem collapse in altered environments

51 [17–19]. We stipulate that differences in competitive performances across environments can  
52 provide insights on species ecological niches, optimal environmental windows and, therefore,  
53 potential response to future conditions.

54         On reefs, direct competition for space is ubiquitous where neighboring organisms grow  
55 into physical contact, species inevitably engaging in warfare for survival and ecological  
56 dominance. On the front line (a.k.a. the battle-zone), corals have the capacity to invade opponent  
57 territories by killing enemy living tissues in their vicinity. This battle predominantly takes two  
58 forms with either smothering by growing over (a.k.a. overgrowth) or disintegrating using  
59 specialized nematocyst-rich attack tentacles (a.k.a. overreach), or a combination of the two  
60 (figure 1). In theory, the magnitude of killing varies with fixed characteristics of species life  
61 history such as attack mechanism, strength, and reach [14,20–24], but also with additional  
62 processes that vary in time, space, and across life-stages such as growth rates and metabolic  
63 states of corals [25–29]. As such, while a clear hierarchy of competitive dominance among coral  
64 species can be established in a given environment, competitive outcomes in fact appear spatio-  
65 temporally dynamic [30–34], and are therefore expected to differ in the future with changing reef  
66 environments. Because corals are slow growing, habitat-forming species at the foundation of reef  
67 ecosystems, even small differences in species abilities to preempt reef space can have strong  
68 implications for reef ecosystem structure and functions, and associated services to society.

69         We used observations of coral competitive interactions across the south-western reef  
70 system of New Caledonia as indicators of the capacity of coral species to prevail in different  
71 environments. The island nation is surrounded by large extents of biodiverse coral reefs,  
72 characterized by diverse habitats distributed along pronounced coast-to-ocean gradients  
73 associated with natural environmental variability amplified by human impacts [35,36] (figure

74 S1). The near shore is most exposed to terrigenous inputs of freshwater, nutrient, and sediment,  
75 as well as anthropogenic impacts such as pollution and fishing, and undergoes higher  
76 environmental variation with seasons and weather conditions [37–40]. Moving towards the  
77 ocean, marked increases in water quality and diminishing human pressure is observed. Portions  
78 of the reefs are classified as UNESCO World Heritage site due to their outstanding character for  
79 global coral reef conservation. Zonation in the relative abundance of coral species along the  
80 coast-to-ocean gradient indicates some degree of niche segregation among dominant taxa [36].  
81 However, the ecological mechanisms underlying such spatial patterns largely remain to be  
82 comprehended. Because coral species are expected to occupy delimited ecological niches  
83 distinguished by environmental preferences [7,29,41], we tested whether the spatial distribution  
84 of ecological windows would be reflected in coral competitive outcomes. In general, a deeper  
85 understanding of coral competition can help a better characterization of coral life-strategies,  
86 which at this stage predominantly relies on qualitative assumptions of species competitive  
87 abilities based on taxonomic traits and demographic performances [28,42]. A better  
88 understanding of coral competition can also inform on the ecological processes underlying  
89 species coexistence and the exceptional biodiversity of coral reefs. We illuminate our findings  
90 with analogies to warfare theory and lessons from human history to untangle the complexity of  
91 coral competitive interactions, and discuss implications for coral performances in changing reef  
92 environments.

93

## 94 **Methods**

95 We evaluated coral competitive performances by inspecting natural occurrences of direct  
96 physical interactions among corals, as well as with other sessile benthic species (figure S2).

97 Surveys were performed on 20 sites distributed along pronounced cross-shelf environmental  
98 gradients (figure S1), and over a five-month period to capture seasonal variability with a shift  
99 from the warm (January) to the cold (June) season (decreasing water temperature, 27-23°C). For  
100 each interaction haphazardly encountered, the taxonomic identities, morphotypes, and three-  
101 dimensional size (length, width, and height) of each organism (the focal coral plus all its direct  
102 competitors) were recorded, along with the contact perimeter characterizing the battle zone, and  
103 overreach and overgrowth distances as short- and long-term metrics of competitive outcomes  
104 (figure 1). Because coral demographic performances in survival, growth, and reproduction vary  
105 with size [28,43], changes in coral abilities to defend their territories were related to species  
106 fitness (i.e. chances of ecological success). We focused specifically on direct competition for  
107 space (a.k.a. territorial war), leaving aside indirect competition for light, food, and other  
108 resources.

109 As competitive interactions regularly consisted of bilateral attacks, net overreach and  
110 overgrowth performances were calculated as the difference between the observed maximum  
111 conquered and ceded distances along the frontline. These measurements of net performances  
112 differ from most studies on competition, which typically characterize species interactions as a  
113 simplistic binomial (win or loss) or trinomial (win or loss or standoff) outcome (e.g. [23,24,31–  
114 33]). Further characteristics of the interaction and environment that could also potentially  
115 influence competitive outcomes, such as distance to the coastal city Noumea, water depth,  
116 competitor abundance, total competing perimeter, and differences in height among competitors,  
117 were also recorded (figure 1I, table S1).

118 Because coral performances were expected to be influenced by various ecological factors  
119 acting at different scales and that in concert shape species responses (figure 1I), we used

120 generalized additive models to characterize changes in competitive outcome as a function of  
121 different candidate ecological descriptors (table S1) in a non-linear, multi-dimensional account  
122 [44]. Model parametrization was designed to capture a set of common ecological processes  
123 regulating coral performances, such as size- and density-dependence (e.g. covariates *Coral-size*  
124 and *Competitor-abundance*), as well as taxonomic deviations in such processes (e.g. interaction  
125 *Coral-size* × *Coral-taxon*) to account for evolutionary differences among species [28]. The  
126 degree of non-linearity of model terms was optimized based on semi-parametric spline-  
127 penalization (see [28,45] for details), and non-significant model terms were sequentially  
128 excluded during the model selection process [44] (figures S3 and S4). Among the multitude of  
129 possible models resulting from combinations of the explanatory variables, the models best  
130 describing competitive outcomes were identified using Akaike information criteria, a measure of  
131 trade-off between model performance and complexity [46]. The final models (tables S2 and S3)  
132 explained variability in coral competitive performances at 66.6% in terms of net overreach and  
133 79.0% in terms of net overgrowth (figures S3 and S4). This is relatively high compared to  
134 previous attempts (e.g. [23,24,32]) and considering the many additional biological and  
135 environmental factors that may influence competitive outcome between two living organisms  
136 (genotype, age, health, metabolic state, disturbance history, etc.), suggesting that our models  
137 accounted for key ecological gradients influencing coral competitive performances in our study  
138 system. Restricting data to the most abundant taxa resulted in similar patterns (figures S5 and  
139 S6), confirming the prevalence of the identified mechanisms among dominant species.

140 A total of 1073 competitive interactions were recorded encompassing 41 taxa and 8  
141 morphotypes (table S1). All surveys were performed by the same observer using SCUBA,  
142 occasionally assisted by another diver. Analyses and graphing were coded in R statistical

143 software complemented by the mgcv package [44]. Over-dispersed variables were log-  
144 transformed, and model residuals were systematically checked for normality and  
145 homoscedasticity.

146

## 147 **Results and Discussion**

### 148 *Identifying drivers of coral competitive performance*

149         Of the 1073 coral competitive interactions inspected, 84.3% (905) involved traces of  
150 tentacle deployment along the frontline, out of which 7.4% (67, or 6.2% of all interactions) were  
151 bilateral. In 8.9% (6) of these bilateral overreach attacks, net space intrusions were tied between  
152 competitors (i.e. net overreach = 0). Similarly, 69.8% (749) of all interactions involved  
153 overgrowth, out of which 2.0% (15, or 1.4% of all interactions) were bilateral. In 13.3% (2) of  
154 these bilateral overgrowth attacks, net space invasions were tied between competitors (i.e. net  
155 overgrowth = 0). Only 0.5% (5) of all interactions were characterized as standoffs for both  
156 overgrowth and overreach, demonstrating the complementary nature of these two metrics to  
157 assess competitive wars among corals.

158         Coral competitive performances varied with attributes relative to individuals,  
159 interactions, and environments, highlighting the interactive importance of biological and  
160 environmental factors in defining competitive outcomes. Overgrowth and overreach  
161 performances were both contingent on taxonomic identity, morphology, size, competitor  
162 abundance, and shelf-position, whereas perimeter of contact and height differences only  
163 influenced overgrowth, and day of year only overreach (tables S2 and S3). As a metric of short-  
164 term competitive interactions, overreach reflects recently deployed battle strategies such as  
165 spontaneous attack-tentacle developments into opponent territories, brief skirmishes along the



166 frontline that were seasonally variable in several taxa (figure 2C) and may reveal transitory in  
167 long-running competitive battles [22,25,30,32,34]. In contrast, as a more integrated measure of  
168 competitive interactions over time, overgrowth accounts for additional ecological mechanisms  
169 that prevail across successive battles in war strategy. This includes the capacity to sustain siege  
170 and lead large battlefields, sometimes for long times and simultaneously on multiple fronts  
171 (figure 1), performances that rely heavily on resource provisions and differed across taxa.

172

### 173 *Individual-level attributes*

174 Coral overgrowth and overreach performances differed among taxa as expected for  
175 species exhibiting contrasting life history traits, with differences in growth form and rate, in  
176 tentacle size and reach, etc. [23,34,42]. Yet, contrasting responses to ecological gradients  
177 provided deeper insights into distinct life-strategies as reflected by different patterns of  
178 competitive performance across life-stages, as well as contrasting susceptibilities to  
179 environmental variation as reflected by segregated environmental optima. Larger corals  
180 generally exhibited higher net overgrowth, though many taxa deviated from a common size-  
181 dependent pattern in overgrowth and overreach (figures 2A and 3A). While evidence of size-  
182 dependent variability in coral competitive performance is not new [25,26], our comparative study  
183 indicates maximum competitive capacities occur at different stages among species, suggesting  
184 differences in size-specific investments in competition. Some taxa showed higher overgrowth  
185 and overreach at small sizes, potentially in a strategy to secure enough space early on, until  
186 reaching a size-refuge that guarantees survival and investment in other demographic processes  
187 such as reproduction [28,33,43]. This was the case for *Porites*, in which competitive  
188 performances declined with colony size (-0.3 cm in net overreach and -1.5 cm in net overgrowth

189 across the size-range), with an inflection point at a size of ~15 cm diameter (figures 2A and 3A).  
190 Other taxa performed better at intermediate or larger sizes, which corresponds with higher ability  
191 in allocating large energetic resources to competitive battles. A marked positive effect of colony  
192 size was detected in mean overreach of *Merulina* (+14 cm across the size-range), *Montastrea*  
193 (+12 cm), and the soft-coral *Sarcophyton* (+7 cm), as well as in mean overgrowth of *Goniastrea*  
194 (+11 cm), *Hydnophora* (+9 cm), *Merulina* (+10 cm), and the soft-coral *Nephthea* (+70 cm). The  
195 latter taxon reveals being a particularly fierce competitor of reef-building corals with an  
196 unmatched ability to overgrow them (figure 3A) [21].

197

#### 198 *Interaction-level attributes*

199 Coral competitive outcomes were influenced by several characteristics of species  
200 interactions, namely competitor abundance (a.k.a. number of enemies), contact perimeter (a.k.a.  
201 battlefield stretch), and height difference among competitors (a.k.a. unequal battlegrounds).  
202 Competitor abundance was associated with changes in overreach performances of four coral taxa  
203 (figure 2B), and generally influenced size-specific overgrowth, with larger corals showing higher  
204 capacities in leading multi-front wars (figure 3B). Larger battlefields were associated with higher  
205 overgrowth in some taxa, such as *Millepora* and *Montipora* (+2 cm in net overgrowth), showing  
206 high capacities in waging large-scale competitive endeavors to the detriment of others such as  
207 *Porites*, in which a threshold in the capacity to hold space against competitors was observed (-10  
208 cm in net overgrowth, with again a size-threshold at ~15 cm diameter, figure 3B). Overall,  
209 extended battlefield perimeters were associated with higher overgrowth performance in  
210 encrusting and columnar species and decreasing in branching and massive taxa, reflecting  
211 evolutionary differences in competitive abilities among morphological groups [24,42].

212

213 *Environmental attributes*

214       Battlefield environments also influenced coral competitive performances as reflected by  
215 the effects of shelf position, depth, and time, revealing differing environmental preferences  
216 among taxa (tables S2 and S3). Cross-shelf variability in coral performances was detected in five  
217 taxa, among which peak overgrowth and/or overreach performances were spatially segregated.  
218 *Pocillopora* showed higher net overreach (+1 cm) near the coast, whereas *Acropora* (+0.6 cm)  
219 and *Favia* (+4 cm) peaked in mid-lagoon, *Porites* exhibited highest overgrowth (+2.0 cm)  
220 towards the barrier-reef, and *Echinopora* showed contrasting spatial patterns between  
221 overgrowth and overreach metrics (figures 2C and 3C). Similarly, overreach performances  
222 varied seasonally in six taxa with a marked temporal segregation (figure 2C). *Acropora* (+0.4  
223 cm) and *Montipora* (+0.2 cm) showed higher performance in warm season, *Pocillopora* (+0.7  
224 cm) in cool season, *Isopora* (+1.5 cm) and *Porites* (+0.3 cm) during the inter-season, whereas  
225 *Galaxea* (+3.5 cm) peaked in each season. While the spatial differences in competitive  
226 performances among taxa confirm contrasting environmental optima along the coast-to-ocean  
227 gradient, the temporal patterns identified may reflect differences in environmental preferences  
228 *per se* (e.g. differing temperature optima) or different timings of investments in other  
229 demographic processes such as growth and reproduction (i.e. differing temporal windows).  
230 Indeed, territorial wars as well as growth and reproduction are energetically costly processes, and  
231 some corals may show temporal tradeoffs in their investment in these endeavors [22,26,28,32].  
232 For example, in New Caledonia as in the neighboring Great Barrier Reef, acroporids including  
233 *Acropora* and *Montipora* reproduce at the onset of the warm season following a 6-month period  
234 of gametogenesis, whereas other species such as *Pocillopora* reproduce throughout the year [47–

235 50]. In addition, portions of the temporal trends identified may be attributable to response to  
236 external stimuli, which may explain the higher overreach observed in *Porites* during the inter-  
237 season between the performance peaks of acroporids and *Pocillopora*, and conversely high  
238 overreach in *Galaxea* during both seasons potentially as retaliation to attacks from these  
239 dominant taxa [32,36].

240

#### 241 *Species baseline attributes*

242 When the effects of ecological gradients were isolated, species with encrusting and  
243 massive morphologies were associated with higher overreach (figure 2A), whereas encrusting,  
244 columnar, and foliaceous species exhibited higher overgrowth (figure 3A). These differences  
245 may reflect differing evolutionary pathways among species. In contrast to other growth forms  
246 that enable refuging via vertical ascension, encrusting species are fully exposed to competition  
247 and their survival relies fundamentally on their capacity to preempt space on a two-dimensional  
248 substrate [14,22,33]. Similarly, several coral species with massive growth forms exhibit large  
249 polyps able to rebuff competitors on longer distances by developing long-range tentacles (figure  
250 1) [20,23,24,34]. A maximum overreach distance of 5.7 cm performed by a massive *Galaxea* on  
251 a branching *Pocillopora* was recorded in this study, and the three massive taxa *Euphyllia*,  
252 *Lobophyllia*, and *Montastrea* exhibited high baseline overreach (figure 2A). Noticeably, marked  
253 negative effects of competitors on coral overreach and overgrowth were only detected from hard-  
254 and soft- corals, whereas interactions with ascidians, sponges, and algae were characterized  
255 solely by positive deviations from the average patterns (figures 2A and 3A). This suggests a less  
256 substantial effect of chemical wars alone as employed by these later taxa, compared to additional

257 uses of physical wars involving tentacle-attacks as deployed by cnidarians, in direct competitive  
258 interactions [27,51,52].

259

### 260 *Comprehending coral competitive interactions*

261 Our study shows that coral competitive performances are governed by a complex  
262 interplay between who is involved and how, where, and when the interactions occur, with  
263 outcomes in terms of net overreach and overgrowth that are largely predictable (figures 2 and 3).  
264 Species baseline performances associated with inherited taxonomic traits (e.g. tentacle reach) are  
265 modulated by a set of ecological gradients related to intrinsic characteristics of organisms (e.g.  
266 size, evolutionary life-strategy) as well as extrinsic features of their interactions and  
267 environments that vary in time and space (e.g. competitor abundance, contact perimeter,  
268 seasonality). The mechanisms governing coral competitive performances are therefore  
269 fundamentally analogous to those prevailing in human warfare where concerted military power  
270 (weapon abundance, deadliness, and reach), war strategy (attack, defense, skirmish tactics),  
271 battle characteristics (stretch of battlefronts, duration of conflicts, number of enemies and allies),  
272 and battlefield features (battleground evenness, weather conditions) influence outcomes [53,54].  
273 Notorious instances when battle characteristics and environmental condition influenced war  
274 outcome and sealed the fate of human history include the deleterious effects of multi-front wars  
275 for Napoleon's endeavor to expand the French empire across Europe between 1805 and 1815  
276 [55], and the contribution of wintery weather conditions to Hitler's army's defeat at the Soviet  
277 frontline in 1941 [56]. Another historical example relates to the Battle of Agincourt in 1415, a  
278 turn in the Hundred Years' War for the dominion of France and England, where muddy terrain

279 following rainfall severely handicapped the heavily armored knights of the numerically superior  
280 French army to the advantage of Henri V [57].

281

282 *Niche segregations and implications in changing environments*

283         The contrasted responses of coral taxa as identified across multiple ecological gradients  
284 provide new insights into the variety of mechanisms underlying niche segregation in biodiverse  
285 species assemblages. Indeed, the diversity of ecological windows occupied by species is  
286 reflected in the contrasting environmental preferences revealed by differing performances in time  
287 and space, as well as the divergent evolutionary pathways as indicated by different responses to  
288 individual and interaction level attributes (figure 4). These differences may explain how the  
289 species coexist as a result of distinct demographic life-strategies, environmental heterogeneity,  
290 and competitive interactions, resulting in the exceptional biodiversity observed on reefs  
291 [17,23,28,42]. Nevertheless, several key coral taxa were sensitive to environmental variability as  
292 reflected by distance to the coast and seasonality, indicating that their competitive success, and  
293 perhaps overall fitness, may be affected by alterations of coastal environments. Our findings  
294 suggest that warmer oceanic conditions, similar to those presently observed in summer, may  
295 advantage higher competitive performances of acroporids to the detriment of pocilloporids,  
296 although further anthropization of coastal habitats, currently restricted to the coastline, benefits  
297 pocilloporids over acroporids (figure 4). In New Caledonia and globally, acroporids contribute  
298 exceptionally to coral reef structural complexity, biodiversity, and calcification [13,36,58–60].  
299 Despite high capabilities to dominate reefs in peri-optimal environments, acroporids are  
300 particularly sensitive to environmental stressors such as warming and declining water quality,  
301 with community shifts from acroporid dominance to pocilloporids or poritids often observed in

302 sub-optimal conditions [7,10,11,29,41]. Widespread acroporid declines have been associated  
303 with reef environment degradation in various regions including the Caribbean, Persian Gulf,  
304 Great Barrier Reef, and French Polynesia [12,15,16,61]. In contrast to other regions where  
305 acroporids appear to face their upper temperature limits [11,29], our study suggests acroporid  
306 performances may actually increase in a warmer climate in the sub-tropical reef system of New  
307 Caledonia where few large-scale bleaching events have been recorded. Nevertheless, restraining  
308 anthropization of coastal environments appears key to preserving near-shore acroporid  
309 populations and their unique contributions to reef accretion and resilience.

310

### 311 *Conclusions*

312 As global changes increasingly alter coastal marine environments, some ecosystems are  
313 inexorably expected to collapse while others may transform to new community compositions,  
314 structures, and functions, changes that remain hard to predict [1,3,4,11,]. Nevertheless, present  
315 trajectories of coastal degradation indicate future reef environments may increasingly resemble  
316 those found near dense human concentrations today [6–8]. Our study suggests that such  
317 anthropization results in lower abilities of some major coral taxa in preempting reef space via  
318 direct competition. Because corals are slow growing habitat-forming species at the basis of reef  
319 ecosystems, such differences in competitive performances may result in extirpations of  
320 vulnerable populations, with implications for reef ecosystem biodiversity and services to society.

321 Overall, competitive performance appears as an effective, widespread, and accessible  
322 indicator of species performances across ecological gradients. It can help identify the biological  
323 and environmental constraints underlying ecological niches and environmental windows that  
324 define species distributions, coexistence, and therefore biodiversity patterns. Given the many

325 ecological pathways that link species performances to their environment, we encourage similar  
326 quantitative investigations to further understanding of determinants of species interactions at the  
327 interplay between evolutionary traits, life-strategies, and global changes, and implications for the  
328 dynamics of ecosystems in a changing environment.

329

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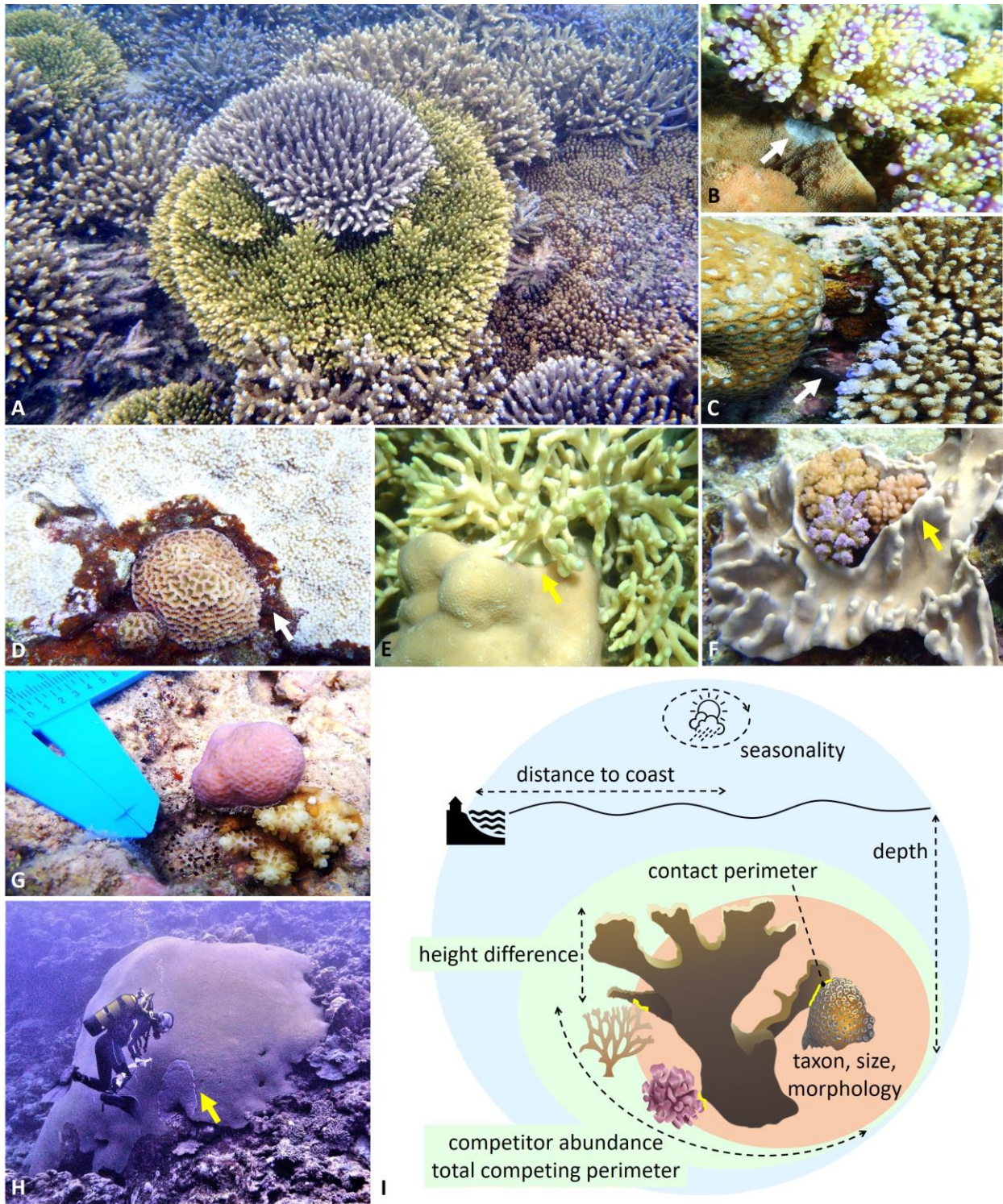
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496 **Figures**

497

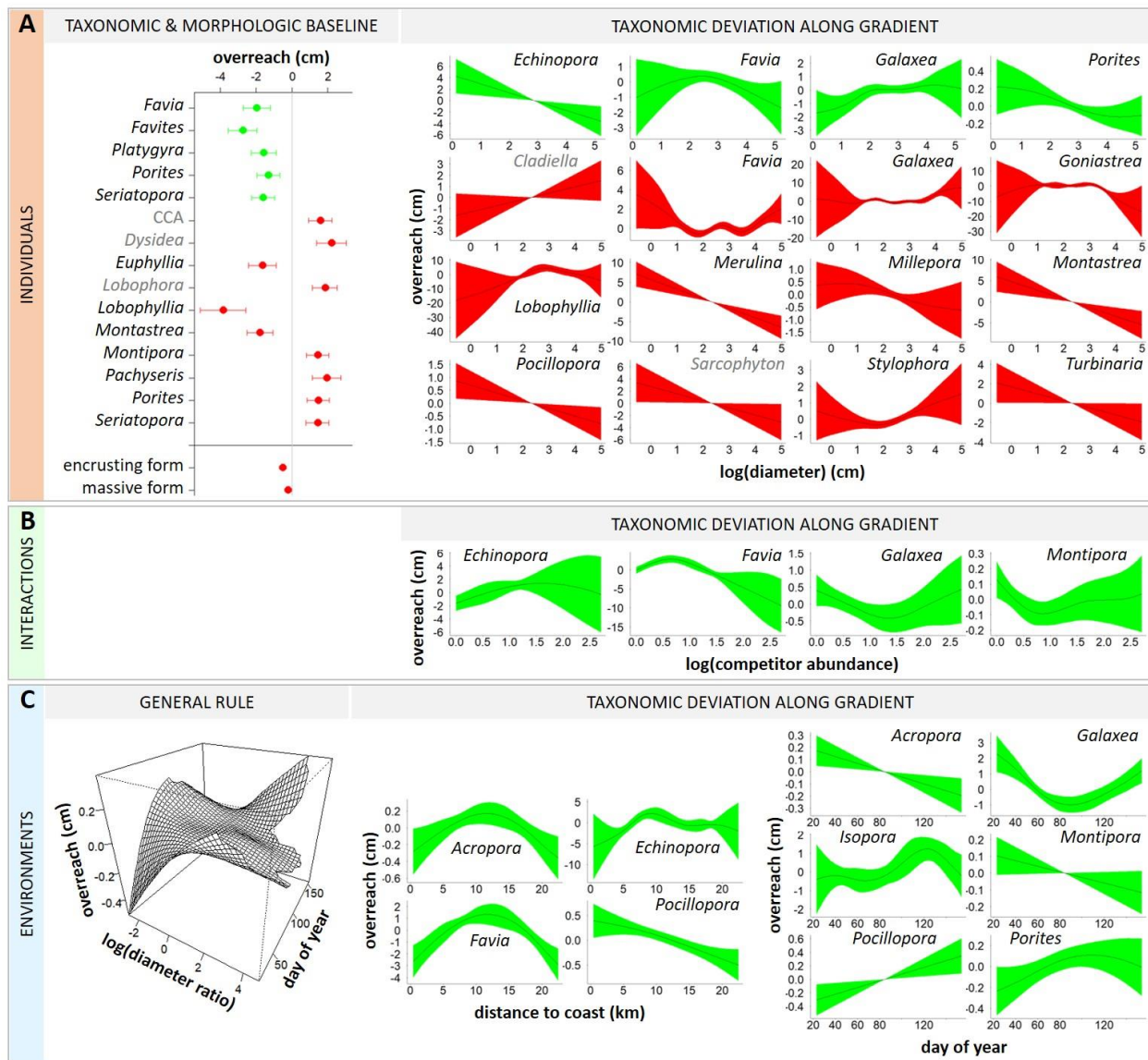


498

499 **Figure 1.** Photographs illustrating encountered coral competitive interactions (A-H), and  
500 schematic (I) indicating how they were characterized by taking into account a set of factors

501 relating to individual organisms (beige), interactions (green), and environments (blue). By  
502 quantifying the dead-zones left by sweeper attack-tentacles on opponent coral skeletons in the  
503 aftermath of competitive battles, overreach distances (white arrows) reflect short-term  
504 competitive outcomes resulting from recently deployed assaults (hours to months preceding  
505 observations). In contrast, given the slow growth of corals, overgrowth distances (yellow arrows)  
506 often integrate competitive interactions over several years. See appendix 1 for further  
507 information, and figure S2 for visualizations of the raw data.

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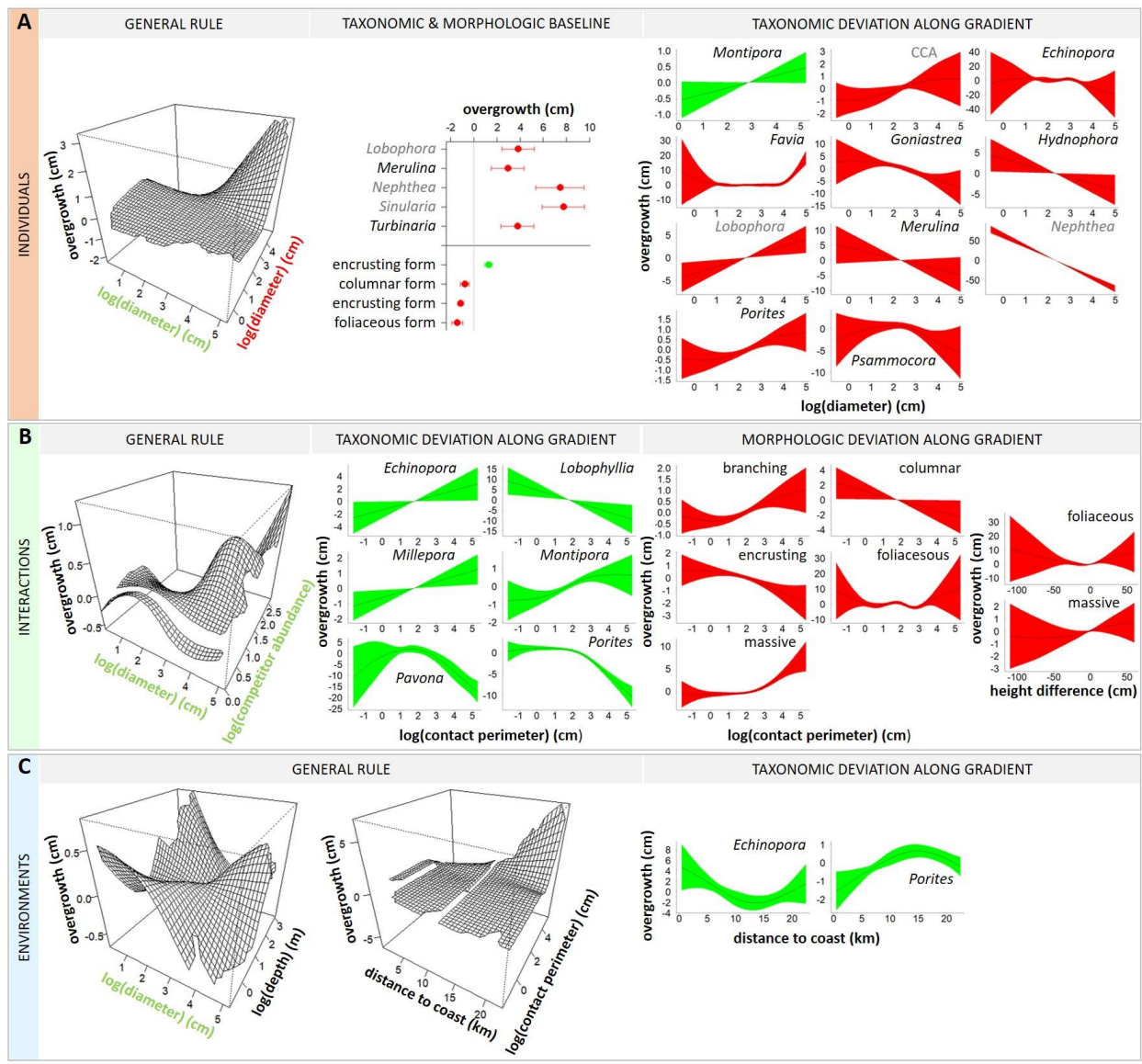


510

511 **Figure 2.** Changes in coral competitive performance as measured by net overreach distance  
 512 along multiple ecological gradients. Plots illustrate partial contributions of different covariables  
 513 to variation in net overreach of focal corals (mean  $\pm$  standard error). Covariables are organized  
 514 by scale, characterizing which organisms are involved (A, individuals), and how (B, interactions)  
 515 and where/when (C, environments) the interactions occur. Covariables measured on focal corals  
 516 are displayed in green (e.g. a positive effect of focal coral diameter on focal coral performance)  
 517 and those on competing organisms in red (e.g. a negative effect of competitor diameter on focal

518 coral performance). Taxonomic and morphologic baselines identify differences in performance  
519 among species and growth-forms once the effects of other ecological gradients are accounted for.  
520 Three-dimensional plot illustrates the interactive effects of two ecological gradients on the  
521 response of all species, while other plots indicate deviations specific to some taxa and growth  
522 forms. Note differences in axes ranges. Texts in grey distinguish non hard-coral species (CCA  
523 for crustose coralline algae). Only significant effects are illustrated (table S2).  
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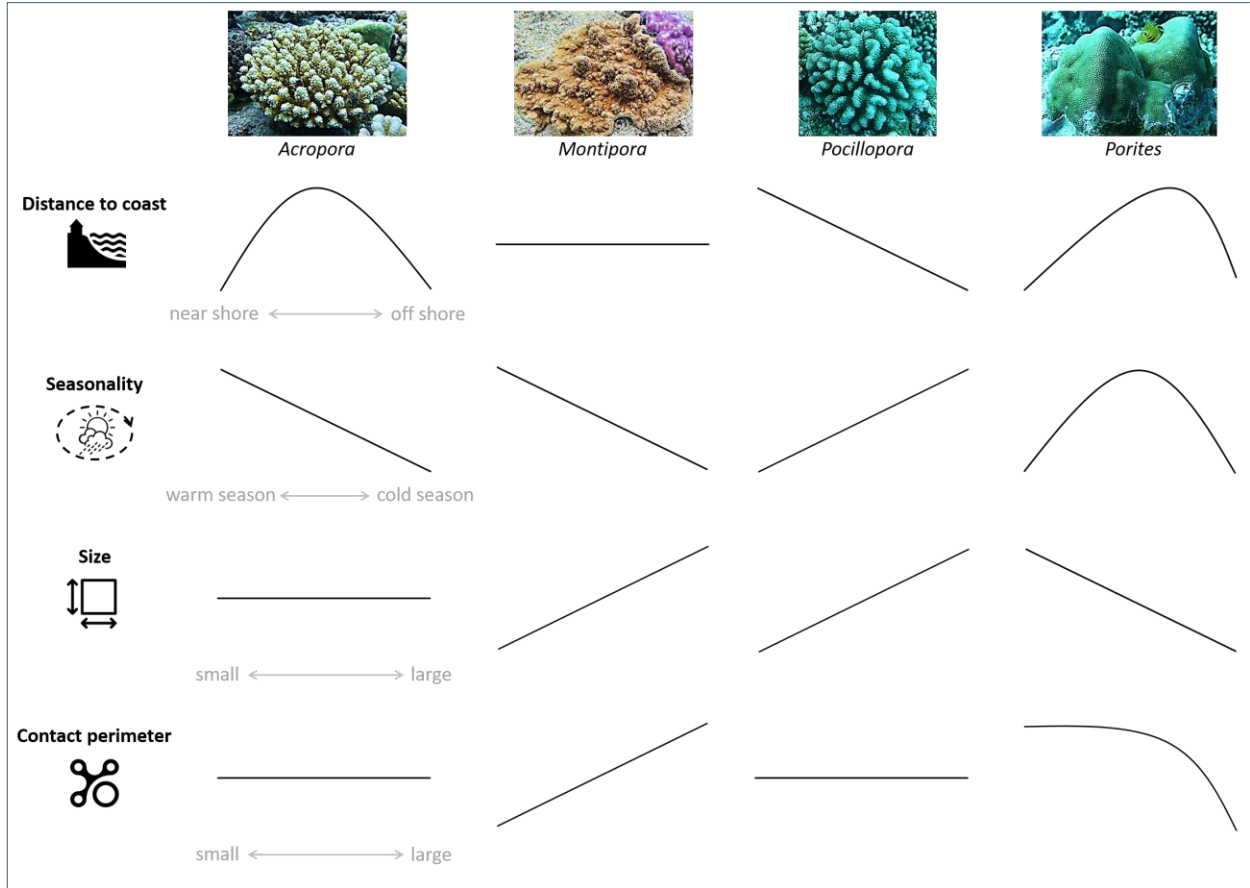


528

529 **Figure 3.** Changes in coral competitive performance as measured by net overgrowth distance  
 530 along multiple ecological gradients. Plots illustrate partial contributions of different covariables  
 531 to variation in net overgrowth of focal corals (mean  $\pm$  standard error). Covariables are organized  
 532 by scale, characterizing which organisms are involved (A, individuals), and how (B, interactions)  
 533 and where/when (C, environments) the interactions occur. Covariables measured on focal corals  
 534 are displayed in green (e.g. a positive effect of focal coral diameter on focal coral performance)  
 535 and those on competing organisms in red (e.g. a negative effect of competitor diameter on focal

536 coral performance). Taxonomic and morphologic baselines identify differences in performance  
537 among species and growth-forms once the effects of other ecological gradients are accounted for.  
538 Three-dimensional plots illustrate the interactive effects of two ecological gradients on the  
539 response of all species, while other plots indicate deviations specific to some taxa and growth  
540 forms. Note differences in axes ranges. Texts in grey distinguish non hard-coral species (CCA  
541 for crustose coralline algae). Only significant effects are illustrated (table S3).

543



544

545 **Figure 4.** Multi-dimensional niche segregation among the four major reef-building coral taxa as  
546 revealed by variability in their competitive performances. The response patterns (summarized  
547 from figures 2 and 3) indicate segregation in time and space (different environmental  
548 preferences) as well as in life-strategies (different optimal sizes and warfare capacities).