

Title: Flexibility in coral-algal symbiosis is positively correlated with host geographic range.

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DZ and JL did study design; DZ and JG did data preparation and compilation; DZ, JG, and JL did analysis, interpretation of results and manuscript preparation. All authors reviewed the results and approved the final version of the manuscript.

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Data availability statement:

The data utilized towards the findings of this study are available at The Coral Trait Database at coraltraits.org, GeoSymbio Database at GeoSymbio.com/Home_Page.html, and from Hartman et al. 2017 at <https://doi.org/10.1016/j.cub.2017.10.036>. Should this manuscript be accepted, data compiled for this study will be openly available at a repository (Dryad or Figshare) and as supplemental.

Abstract

1
2 Generalists are thought to adapt to a broader breadth of ecological conditions compared
3 to less flexible specialists. However, few studies have systematically tested what ecological or
4 life-history traits are associated with organisms' ecological flexibility. Here, we used stony
5 corals to test the relative effects of host traits and ecological factors on corals' flexibility to form
6 photosymbioses with algae. We analyzed data from 211 stony coral species to test if coral's
7 geographic distribution, depth range, symbiont transmission mode, or colony morphology predict
8 coral-algal flexibility. We report a novel positive correlation between coral-algal flexibility and
9 coral species' geographic range. Symbiont transmission mode was also a predictor of flexibility,
10 albeit the result is less robust against sampling bias. Coral depth range and morphology did not
11 show significant effects. We discuss how host-symbiont dispersal abilities, interactions, and
12 evolutionary history could contribute to the observed patterns and how this finding could inform
13 conservation efforts.

14

Introduction

15 Biotic interactions are important yet underappreciated drivers of biodiversification (Liow
16 et al., 2011) and shape large-scale species distributions (Wisz et al., 2013; Anderson, 2017;
17 Lewis et al., 2017). A species' flexibility to interact with the changing biological environment
18 profoundly influences its fitness and adaptation (van Toor et al., 2016; Schratzberger et al.,
19 2019). Highly flexible species (generalists) tend to survive on a wider breadth of habitats, which
20 may contribute to their ability to overcome ecological barriers, colonize new niches, and become
21 invasive species (Wright et al., 2010; Gutiérrez et al., 2017). Species with limited flexibility
22 (specialists) may be restricted to narrow niches but exhibit higher relative fitness in local habitats
23 (Marvier et al., 2004).

24 Mutualistic symbiosis is an important source of evolutionary novelty and allows species
25 to adapt to challenging environments (Gilbert et al., 2010; Cavanaugh et al., 2013). Conversely,
26 symbiosis is sometimes considered an evolutionary constraint (Parker, 2001; Simonsen et al.,
27 2017; Delavaux et al., 2019) because compatible symbiotic partners cannot always be established
28 in a changing or new environment. Therefore, it can be advantageous for the partners to maintain
29 flexibility regarding symbiosis (i.e., they can work with diverse or novel partners). Despite the
30 prevalence of mutualistic symbiosis across a variety of ecosystems, our understanding of how
31 ecological factors produce varying degrees of symbiosis flexibility is limited (Baker, 2001;
32 Devictor et al., 2008; Ziegler et al., 2015; Chagnon et al., 2019). Therefore, this study uses the
33 vastly studied stony corals as a system to evaluate what host characteristics and ecological
34 factors impact flexibility in coral-algal symbiosis.

35 Stony corals (Scleractinia) rely on a mutualistic symbiosis with dinoflagellate algae
36 (Symbiodiniaceae) to thrive in nutrient-poor waters (Davy et al., 2012). The symbiosis involves a

37 nutritional exchange, wherein the photosynthetic algae provide organic carbon to the host, and in
38 return, the host provides inorganic nutrients, shelter, and better access to light (Kirk et al., 2016).
39 This symbiotic relationship is thought to drive the rise and evolutionary success of coral reefs
40 (LaJeunesse et al., 2018), and the radiation has resulted in high levels of taxonomic diversity for
41 both partners, as well as a high number of partner combinations (Baker, 2003; Fabina et al.,
42 2012). Most symbiotic coral species are associated with a single symbiont phylotype, whereas
43 some coral species can establish symbiosis with a variety of algal species (Baker, 2003; Goulet,
44 2006; Silverstein et al., 2012; Biquand et al., 2017). A host's ability to form symbioses with
45 multiple symbiont strains is referred to here as coral-algal flexibility, also known as host
46 specificity (Baker, 2003).

47 Certain coral life-history traits have been shown to impact coral-algal flexibility or
48 symbiont composition. For example, coral larvae and juveniles tend to be associated with a
49 greater variety of algal strains, and host flexibility decreases as they mature into adults (Little et
50 al., 2004; Cumbo et al., 2013; Reich et al., 2017; Ng et al., 2019). This is thought to be an
51 adaptation for obtaining locally beneficial symbionts when settling into a new location (Swain et
52 al., 2021). Coral flexibility is also influenced by its symbiont acquisition mode: coral offspring
53 may acquire symbionts directly from the environment (horizontal transmission) or maternally
54 from adults to egg or larvae (vertical transmission) (Quigley et al., 2017; Hartmann et al., 2017).
55 Within transmission mode, broadcast spawners tend to show higher symbiont diversity than
56 brooders, likely because spawners generally acquire symbionts horizontally (Bongaerts et al.,
57 2014a; Swain et al., 2021). In addition, coral colonies can exhibit highly diverse, genetically
58 determined morphologies, which are further influenced by environmental factors such as
59 currents, light, competition, and predation (Stocking et al., 2018). These different morphologies

60 can affect symbiont density and photosynthetic performance (Scheufen et al., 2017; McLachlan
61 et al., 2021), although it is currently unknown if colony morphology is related to coral-algal
62 flexibility.

63 Symbiodiniaceae algae are known to exhibit habitat-specific adaptations and host
64 specializations (Davies et al., 2023). The algae usually form a coccoid state when associated with
65 a host, but can also resume a free-living motile stage when outside of the host, and may disperse
66 among hosts in this stage (Figueroa et al., 2021; Hata et al., 2017; Kirk & Weis, 2016).
67 Therefore, environmental factors such as thermal regimes, light availability, or current dynamics
68 can influence Symbiodiniaceae distribution and, consequently how hosts uptake, modify, or
69 switch their symbiotic compositions.

70 For example, habitat depth can affect symbiont composition within a host (Baker, 2001;
71 Finney et al., 2010; Bongaerts et al., 2014b; Eckert et al., 2020), as corals that occupy a wider
72 range of depths sometimes harbor multiple symbiont strains that prefer different light and
73 temperature regimes (Lampert-Karako et al., 2008; Cooper et al., 2011). A single coral colony
74 can be distributed along light and temperature gradients and possess different symbiont
75 compositions (Fay & Weber, 2012). Thus, it is possible that corals distributed in a wider depth
76 range exhibit higher symbiosis flexibility as compared to those restricted to narrow ranges.

77 Coral-algal flexibility may also be correlated with the host geographic range, which is
78 shaped not only by temperature, salinity ((Maginnis, 2020), and nutrient levels of the water
79 (Radice et al., 2019; Zheng et al., 2021) but also dispersal capabilities (Hata et al., 2017) and
80 evolutionary histories of the host (Roff, 2021). High coral-algal flexibility is important for corals
81 to endure environmental stressors and colonize novel habitats (Baker, 2001; Putnam et al., 2012;
82 Reich et al., 2017; Wee et al., 2021), so it follows that highly flexible coral species may be better

83 at range expansion. However, coral species that already have higher dispersal abilities may
84 encounter a greater diversity of algal lineages and gain mixed infections (Fay & Weber, 2012).
85 Both scenarios predict a positive correlation between coral-algal flexibility and coral species
86 range (Goulet et al., 2008; Cunning & Baker, 2014; Kennedy et al., 2016).

87 Despite case studies revealing different degrees of coral-algal flexibility, it is currently
88 unclear how coral traits—such as symbiont transmission mode or geographic range—are
89 correlated with this flexibility on a global scale. Therefore, we use a meta-analysis to investigate
90 associations between coral traits and coral-algal flexibility. We hypothesize that coral traits, such
91 as symbiont transmission mode, growth morphology, depth ranges, and geographical
92 distributions can influence coral-algal flexibility. To test these hypotheses, we first assessed the
93 number of different symbiont strains per coral species utilizing the GeoSymbio Database
94 (Franklin et al., 2012), providing a metric for coral-algal flexibility. We then used the Coral Trait
95 Database (Madin et al., 2016) and data from Hartman et al. 2017 to obtain coral geographical
96 ranges and biological traits. Lastly, we used generalized linear mixed models (GLMM) to test
97 which coral traits are associated with coral-algal flexibility.

98

99

Methods

100 *Coral algal flexibility assessment*

101 In this study, coral-algal flexibility is defined as the total number of distinct
102 Symbiodiniaceae lineages known to associate with a given coral species. The family
103 Symbiodiniaceae was formally divided into nine phylogenetically divergent clades (A-I), each
104 further divided into sub-clades. These clades were then re-classified as genera (LaJeunesse et al.,
105 2018). To date, only a few subclades have been formally characterized as species (LaJeunesse et

106 al., 2018; Tsang et al., 2022), with the rest still defined through subclade affiliations.
107 Morphological differences, host habitat, and other factors can distinguish some of the lineages.
108 However, genetic markers are still considered the most reliable identification method,
109 particularly when using the Internal Transcribed Spacer 2 marker (ITS2) (Thornhill et al., 2017).
110 Therefore, this study will adhere to the ITS2 symbiont identification designation.

111 Symbiont association data were obtained from the GeoSymbio Database (Franklin et al.,
112 2012). A total of 378 coral species (Anthozoa: Scleractinia) were initially obtained. We reviewed
113 study methods for all species in 54 references and excluded any data collected from only coral
114 juveniles or larvae, as they might not accurately represent the Symbiodiniaceae diversity in a
115 mature coral colony (Little et al., 2004; Cumbo et al., 2013; Reich et al., 2017; Ng et al., 2019).
116 Next, we filtered the dataset and included only studies wherein symbionts were identified by
117 denaturing gradient gel electrophoresis (DGGE) or amplicon sequencing methodologies using
118 the ITS2 marker. This resulted in a new dataset of 363 coral species from 36 references (S1). We
119 then calculated the total number of symbiont sub-clades identified for each coral species.

120

121 *Host ecological and life-history traits information*

122 We further narrowed down the list to 211 coral species for whom biogeographical
123 information is available. Biogeographical information and ecological traits for each coral species
124 were obtained from the Coral Trait Database (Madin et al., 2016) based on 57 references (S1),
125 including geographic range, observed depth range, and typical growth morphologies. Host
126 geographic distribution (area) was calculated using the GIS shapefiles in km². Depth range (m)
127 was calculated as the difference between a host's average minimum (shallowest) observed depth
128 and the average maximum (deepest) observed depth (Madin et al., 2016). For morphology, we

129 included all 12 growth form categories: encrusting, encrusting long uprights, massive,
130 submassive, branching open, branching closed, corymbose, tables or plates, digitate, hispidose,
131 laminar, and columnar (Madin et al., 2016). The taxonomical family for each coral species was
132 also documented.

133 Coral data on symbiont transmission (characterized as horizontal or vertical) were
134 obtained from Hartman et al. 2017 for all 211 coral species. We also attempted to assess the
135 impact of coral reproductive modality (spawner or brooder), but there were only eight brooder
136 species in our dataset. Therefore, reproductive mode was not included as a predictor for the
137 statistical models.

138

139 *Statistical analysis*

140 We used generalized linear mixed models (GLMM) with a negative binomial distribution
141 to evaluate coral-algal flexibility as a function of the fixed effects, including coral geographic
142 range, depth range, growth morphology, and symbiont transmission mode. We chose a
143 generalized linear model because our coral-algal flexibility data is highly right-skewed and non-
144 transformable. The taxonomic family was used as a random effect to account for a proxy of
145 phylogenetic signal and not used as a fixed effect due to the high number of categories (i.e., 15
146 families). All statistical analyses were conducted in R 4.2.3 (R Core Team, 2018). Coral
147 geographic range as a continuous predictor was scaled using the scale function in R before
148 inclusion to obtain comparable coefficients in model outputs. We used the lme4 package (Bates
149 et al., 2015) for all GLMM analyses. AICc (Akaike's Information Criterion for small sample
150 size) was used for model comparison using the Aicmodavg package (Mazerolle, 2020).

151 Research intensity can also influence the number of symbiont types associated with a
152 coral species. That is, the more studies being done on a coral species, the more symbiont types
153 might be revealed from that species. To assess such sampling bias, we first tested how the
154 number of references per coral species predicts coral-algal flexibility. References ranged from 1
155 to 16 (median of 2) per coral species and were significantly correlated with our estimates of
156 coral-algal flexibility ($\beta \approx 0.20$ in most models, $P < 0.001$). Therefore, we included it as a
157 nuisance fixed effect in all models.

158 The complete model of all fixed and random effects is shown below, with coral-algal
159 flexibility as a function of the host species' geographic range (Area), depth range (Depth),
160 growth morphology (Growth), symbiont transmission mode (Transmission), number of
161 references (References), and the taxonomic family as a mixed effect (1|Family):

162 Coral-algal flexibility = $\beta_0 + \beta_1(\text{Area}) + \beta_2(\text{Depth}) + \beta_3(\text{Growth}) + \beta_4(\text{Transmission}) +$
163 $\beta_5(\text{References}) + \beta_6(1|\text{Family})$. Glm, Family=Negative Binomial.

164 A set of initial analyses assessed host range, depth, growth, and symbiont transmission
165 mode as a single effect, respectively. Results indicated that the host range was the strongest and
166 most consistent predictor of host flexibility, even when the number of references was accounted
167 for. Therefore, an additional seven models (Table 1, S2) combining host range with the other
168 three effects were evaluated and included in the model comparisons.

169 To assess the impact of outlier species, we ran the analyses on a subset of data that
170 excluded three coral species that had associations over 20 symbiont types (i.e., *Montipora*
171 *capitata* with 21, and *Stylophora pistillata* and *Pocillopora damicornis* both with 28 symbiont
172 associations). This subset resulted in 208 coral species with 1-16 symbiont types and 1-8
173 references per coral. Note that the three outliers also had the highest number of studies

174 performed on them (8, 11, and 16, respectively), and all three species exhibit vertical
175 transmission mode.

176 To further account for researcher bias or differences in symbiont identification across
177 research teams, we ran the same analyses on a subset of coral species whose data were obtained
178 from papers published by Dr. T.C. LaJeunesse as a primary author or a co-author only. This
179 resulted in 15 references from the GeoSymbio database and a total of 210 coral species, with 1-
180 16 symbiont types and 1-10 references per coral.

181 Lastly, to validate results from the GLMM analyses and to investigate any possible non-
182 linear, interacting relationships among the main effects, we employed a random forest method to
183 test their relative importance. The R package “gradientForest” (Ellis et al., 2012) was used to
184 assess the relative importance of number of references, host geographic range, depth, and
185 symbiont transmission mode in predicting host-symbiont flexibility. The analyses were done on
186 datasets with and without the outlier species.

187

188 **Results**

189 *Coral algal flexibility assessment*

190 Coral-algal flexibility (sum of Symbiodiniaceae lineages per species) was low for most
191 coral species reviewed here (Fig. 1a). It ranged from 1 to 28 symbiont lineages per host: 41.2%
192 of corals are associated with only 1 to 2 different symbiont lineages; 52.6% of corals harbor
193 between 3 and 8 lineages; 4.7% of corals harbor 10 to 16 lineages; and three coral species (1.4%)
194 are associated with more than 20 symbiont lineages (21, 28 and 28 respectively).

195

196 ***Host ecological and life-history traits information***

197 For all 211 corals, the host geographic distribution ranged from 29,848 km² to
198 135,900,979 km², with a mean of 67,805,686 km² and a median of 71,677,606 km² (Fig 1b). The
199 upper depth spanned from 0 to 32.33 m (median = 2 m, mean = 3.7 m). The lower depth spanned
200 from 5 to 62 m (median = 27.5 m, mean = 28.1 m). The depth range per species (Fig. 1c) was
201 between 4 and 60.5 m (median = 23.0 m, mean = 24.4 m). For host symbiont transmission, 168
202 corals represented horizontal transmission, and 43 corals represented vertical transmission (Fig.
203 1d). Additionally, the average number of associated symbiont types for horizontal transmission
204 was lower than that of vertical transmission (3.8 and 5.4 symbiont types, respectively), which
205 was mainly driven by several outlier vertical transmission species who were associated with
206 exceptionally high numbers of symbiont types. Corals of both transmission modes shared the
207 same median symbiont types (3 and 3, respectively).

208 Growth morphologies included 12 different main types (Fig. 1e), with the majority
209 belonging to massive (n= 63) and laminar forms (n= 32), followed by branching (closed, n=19),
210 encrusting (n=16), branching (open, n=14), corymbose (n=14), digitate (n=13), submassive
211 (n=13), tables or plates (n=10), columnar (n=7), encrusting (long uprights, n=7), and hispidose
212 (n=3).

213 The corals in this study belonged to 15 different taxonomic families (Fig. 1f), the
214 majority belonging to the families Acroporidae (n=76), specifically within the genera *Acropora*
215 (n=50) and *Montipora* (n=24). The rest of the corals belonged to the families Faviidae (n=38),
216 Poritidae (n=19), and Agariciidae (n=18), followed by Pectiniidae (n=11), Siderastreidae (n=9),
217 Pocilloporidae (n=8), Mussidae (n=7), Fungiidae (n=7), Merulinidae (n=5), Dendrophylliidae
218 (n=5), Cayophylliidae (n=3), Oculinidae (n=2), Euphylliidae (n=2), and Astrocoeniidae (n=1).

219 Host-symbiont flexibility varied within each family; each family contained coral species with
220 both high and low flexibility, except for families with very small sample sizes. Coral-algal
221 flexibility doesn't appear to be conserved at the family level.

222

223 *Statistical analysis*

224 Our models showed a significant positive correlation between a coral's geographic range
225 and its host-algal flexibility (Table 1, Fig. 1b). The best-fit model included geographic range
226 (area) and symbiont transmission mode as the main predictors, which carried 64% of the
227 cumulative model weight (AICc=821.53). Within this model, geographic range was a significant
228 predictor ($\beta = 0.15$, $P = 0.001$), where for every 97.8 million km² (or one unit of scaled area) a
229 coral can occupy, host flexibility increases by 16%. Horizontal transmission also showed a
230 positive correlation with host-algal flexibility ($\beta = 0.18$). It was not a significant predictor in this
231 top model ($P = 0.09$), albeit being significant in some of the lower ranked models.

232 All models that utilized host geographic range and symbiont transmission mode as
233 predictors had much lower AICc values than models without (Table 1, S2). The host depth range
234 showed no significant effect in any model. For all models using growth morphology, there were
235 multiple observed significant differences between branching (closed) morphology and other
236 morphologies ($P < 0.05$). Still, variations between colony morphology did not appear consistently
237 within models and all produced much higher (and thus less significant) AICc scores. All models
238 included the number of references as a nuisance factor, as it was a significant predictor of host-
239 algal flexibility.

240 Our analyses removing three outlier species resulted in an identical model rank compared
241 to the full analyses (S3). This time, however, symbiont transmission mode was a significant

242 predictor ($\beta = 0.26$, $P = 0.007$) in the top mode. This indicated that the impact of symbiont
243 transmission mode on coral flexibility was sensitive to outliers.

244 The analyses that utilized data authored by Dr. T.C. LaJeunesse also showed similar
245 trends as the full analyses, in which geographic range remained consistently a significant
246 predictor of coral-algal flexibility (S4). Within this set of models, the same top model retained
247 geographic range ($\beta = 0.11$) and symbiont transmission mode ($\beta = 0.25$) as predictors, both were
248 significant ($P = 0.01$).

249 For the random forest model analyses, the weighted importance of number of references,
250 coral geographic range, depth, and symbiont transmission mode was 0.42, 0.08, 0, and 0,
251 respectively. Removing outliers did not significantly impact the result - the weighted importance
252 for the above four factors became 0.37, 0.09, 0.009, and 0. Geographic range was again a
253 consistent ecological factor that predicted host-symbiont flexibility, and there were no complex
254 interactions among different predictors.

255

256 **Discussion**

257 *Effects of coral geographic distribution on coral-algal flexibility*

258 Our GLMM results suggest a significant positive correlation between coral-algal
259 flexibility and coral geographic range. Geographic distribution was the most significant
260 ecological predictor for coral-algal flexibility in all models and in the random forest analyses,
261 and the result is robust against outliers and research intensity bias. This correlation between
262 generalist hosts and greater geographic distributions has been observed in other symbiotic
263 systems. For example, plant species with facultative mycorrhizal associations (i.e., more flexible)
264 exhibit wider geographic distributions and inhabit a greater diversity of ecological niches

265 compared to obligatorily mycorrhizal plants (Hempel et al., 2013; Gerz et al., 2018). Similarly,
266 flexible photobiont associations in some lichen-forming fungi species are thought to contribute to
267 the lichen's broad ranges (Muggia et al., 2014). Although these studies often suggest that high
268 host flexibility drives the range expansion of the symbiotic system, a true causal relationship
269 between high host flexibility and wide species distribution is challenging to establish based on
270 correlations only. In the coral-Symbiodiniaceae system, a symbiont-generalist may indeed have
271 greater distribution due to its ability to adapt to novel habitats. Yet it is also possible that a host
272 with good dispersal ability naturally encounters a greater diversity of symbionts, resulting in
273 association with more symbiont types. Below we discuss these mechanisms in detail.

274 Within a contemporary timescale, a flexible (generalist) coral host can rely on its
275 symbionts to expand its range in two major ways. Firstly, the host may already harbor diverse
276 symbiont lineages tolerant to different environmental conditions, therefore giving the entire
277 holobiont broader environmental tolerance (Fig. 2a). When entering a new habitat, some of the
278 host's existing symbiont lineages can thrive in the new environment and allow the host to
279 survive in the new range. This type of symbiont facilitation might be more common in corals that
280 transmit symbionts vertically, as the dispersing larvae already possess diverse symbiont
281 communities passed down by the parents before encountering novel environments. Secondly, a
282 flexible coral host may easily uptake novel symbionts from the new habitat. These locally
283 adapted novel symbionts can then facilitate the host's establishment (Fig. 2b). This is supported
284 by empirical evidence that some coral symbiont distribution is strongly structured according to
285 geographic regions (Ziegler et al., 2017), indicating that many symbiont communities are locally
286 adapted to certain geographic ranges and are therefore restricted to these areas. This second type
287 of facilitation is likely to occur in coral species that acquire symbionts horizontally. Our analyses

288 partially support this scenario, as horizontal transmission was positively correlated with host-
289 symbiont flexibility. However, the significance of the impact may be influenced by sampling
290 bias and outliers (See discussion in the next section).

291 Despite the ecological importance of coral-algal flexibility, high flexibility may not be
292 the cause for greater host distribution but instead the result of it. Host-level characteristics may
293 drive some coral species to be better at dispersal or survival in novel habitats. This will lead to
294 exposure to novel symbionts and result in more diverse symbiont associations (Fig. 2c). Corals
295 with limited ability to become established in new habitats may appear to be symbiont specialists,
296 not because they cannot uptake new symbionts but because they don't encounter them. Some
297 studies have shown that coral animals play important roles in adapting to novel environmental
298 conditions. For example, differential temperature and light regimes often represent ecological
299 barriers to coral dispersal. One study showed that optical morphology in different coral species
300 has variable effects on light absorption and symbiont performance (Scheufen et al., 2017),
301 impacting how holobionts react to light shifts. Another study showed that host identity has an
302 influence on holobiont survival during heat stress independent of symbiont types (Bowden-
303 Kerby & Carne, 2012). Coral hosts also have varied abilities to switch between autotrophy and
304 heterotrophy (Sturaro et al., 2021), therefore a mixotrophic host has a greater opportunity to
305 expand its range in unfavorable environments. Overall, more ecological comparative
306 experiments are needed to test how hosts and symbionts contribute to coral range expansion and
307 to understand the ecological implications of coral-algal flexibility further.

308 Lastly, the observed wider geographic distribution in flexible coral species could be a
309 byproduct of Scleractinia's evolutionary history, which may not be related to coral dispersal
310 abilities. For example, it's possible that generalist and specialist corals previously shared similar

311 geographic distributions, but in the face of environmental disturbances, the generalists were
312 better at responding due to their diverse symbiont communities, resulting in lower extinction
313 rates as compared to specialists (Fig. 2d). In other words, the currently restricted distribution of
314 specialist corals may be a result of frequent extinction instead of low dispersal. Another
315 possibility is that a generalist strategy is ancestral to Scleractinia corals. Symbiont-specialists are
316 derived and simply have had less time to expand their ranges compared to the generalists (Fig.
317 2e). To tease apart these possible mechanisms, further macroevolutionary studies on coral
318 flexibility are needed. For example, coral-algal flexibility traits can be mapped to existing
319 phylogenies (Kitahara et al., 2016) and used to assess the ancestral flexibility state. Fossil
320 records can be used to estimate range shifts of modern host species. Given that coral-algal
321 flexibility data may not be readily available for a large proportion of coral species, it is possible
322 to test our hypotheses with well-studied subgroups [such as Acroporidae (Rosser et al., 2017)],
323 as our data indicated high levels of variation on coral-algal flexibility within individual coral
324 families.

325

326 *Effects of other factors on coral-algal flexibility*

327 A positive correlation between horizontal symbiont transmission and coral-symbiont flexibility
328 was found in all top GLMM models. However, this predictor was only significant when highly
329 flexible outlier species were removed or when research authorship was controlled. Notably, the
330 top three most flexible species were *Stylophora pistillata*, *Pocillopora damicornis*, and
331 *Montipora capitata*, all exhibiting vertical transmission mode. Not surprisingly, removing them
332 shifted the positive correlation between horizontal transmission and flexibility from non-
333 significant to significant. The rationale for removing the outliers is driven by them being

334 associated with the highest number of references. It is likely that their high symbiont type counts
335 are a result of high research intensity. However, this research intensity bias should also apply to
336 species with horizontal symbiont transmission, and the full GLMM already controlled for
337 number of references. Therefore, the fact that transmission mode is still sensitive to the impact of
338 references makes biological interpretations less reliable. It is still highly possible that coral
339 species with horizontal symbiont transmission are more flexible in symbiont uptake, but more in-
340 depth research is needed to validate if this is a global trend. This result also highlights the
341 importance of diversifying study systems in coral ecology research, as uneven research efforts on
342 different taxa may bias meta-analyses.

343 We did not record any significant effects of depth range on coral-algal flexibility, and this
344 may have several causes. Firstly, host physiology may play a more important role than symbiont
345 diversity in adaption to wider depth gradients (Tamir et al., 2019). Secondly, the depth range was
346 calculated as the difference between maximum and minimum observed depths, yet this range
347 may not reflect where most host individuals are established and might result in a range
348 overestimation for some species. Thirdly, studies have shown that light (Tamir et al., 2019) and
349 turbidity (Morgan et al., 2020) likely have more influence on coral distributions than depth per
350 se, but our data did not have the resolution to capture such habitat heterogeneity across depths.
351 Furthermore, in many coral habitats, light gradients may not have significant effects on coral
352 assemblages until depths of 40 meters or greater (Tamir et al., 2019). Most corals included in this
353 study had averaged maximum depths of less than 40 meters. Therefore, our samples did not
354 capture any strong light/environmental gradients.

355 Coral growth morphology also had little effect on coral-algal flexibility. This is
356 consistent with other studies indicating that coral size and shape variations are associated with

357 abiotic gradients more so than biotic ones (Soto et al., 2018; Tamir et al., 2019; Kramer et al.,
358 2020).

359

360 *Limitations and future directions*

361 Our metrics provide a rapid assessment of coral-algal flexibility and are consistent with
362 previous studies that show most corals are in association with limited numbers of
363 Symbiodiniaceae lineages (Goulet, 2006, 2007; Silverstein et al., 2012; Thornhill et al., 2017).
364 However, our method did not have the resolution to include certain aspects of the symbiont
365 identity. For example, a coral may host three symbiont species from the same or different genera,
366 and while the latter might be considered to have higher flexibility, our current metrics cannot
367 capture this. In addition, as the species-level diversity of Symbiodiniaceae becomes better
368 resolved along with new genetic classification regimes, the flexibility status of many coral
369 species will likely change. For example, some symbiont strains previously considered different
370 are being grouped into single species (e.g., LaJeunesse et al., 2018; Turnham et al., 2021), while
371 certain ITS2 variations are possibly intraspecific (Correa & Baker, 2008). As our understanding
372 of Symbiodiniaceae diversity improves, more accurate flexibility metrics can be developed.

373 Additional studies are required to understand better the mechanisms behind the
374 association of high coral-algal flexibility and wide geographic distribution. Long-term symbiont
375 sampling is needed to measure the temporal flexibility of hosts more accurately, as some corals
376 can switch symbionts over time and hosts differ in their abilities to exchange or shuffle
377 symbionts (Fay & Weber, 2012; Ziegler et al., 2015; Abbott et al., 2021). Similarly, symbiont
378 diversity assessments are needed across different geographic scales so we can test whether a
379 generalist host can harbor multiple symbionts all at once or if the host harbors different

380 symbionts in different localities. This could also provide a better understanding of why some
381 geographic areas have a higher ratio of specialists to generalists or vice versa (Freeman &
382 Hannan, 1983; Kassen, 2002).

383 Our study did not focus on the role of symbionts, even though Symbiodiniaceae also
384 includes generalists and specialists (Baker, 2003). For example, a coral host harboring a
385 generalist symbiont may show higher niche acclimatization due to the symbiont's greater
386 physiological tolerances (Ziegler et al., 2015; Butler et al., 2023), and therefore can occupy
387 wider ranges and large habitat gradients, but remains a symbiont specialist (Osvatic et al., 2021).
388 Future systematic assessment of Symbiodiniaceae flexibility and its impact on coral ecology is
389 essential.

390 Lastly, an important aspect yet to be fully resolved is assessing the influence of the
391 holobiont on coral-symbiont interactions and selectivity, which includes bacteria, archaea, and
392 other microbes (Rohwer et al., 2002; Ainsworth et al., 2010; Thompson et al., 2014; Blackall et
393 al., 2015; Peixoto et al., 2017; Pollock et al., 2018; Kwong et al., 2019).

394

395 *Ecological and conservation implications*

396 Climate change and anthropogenic disturbances may be selecting generalist species. This
397 has been seen in some reef fish, wherein generalists show higher survival rates, and specialists
398 experience greater rates of extinction (Wilson et al., 2008; Begger, 2021). This pattern has also
399 been observed in other non-reef ecosystems (Dharmarajan et al., 2021). The same effects may be
400 occurring in corals, but more research is needed to fully understand the differential survival of
401 coral generalists and specialists under disturbances. As reefs face mass bleaching events
402 (Graham et al., 2015), we need to prioritize conservation efforts on coral species that are crucial

403 for the maintenance of reef functional diversity, as this may include coral species with lower
404 flexibility. Understanding the distribution and ecology of generalist and specialist coral, the
405 different roles they play, and how they interact with each other will be vital for efficient and
406 effective conservation efforts.

Model's fixed effects on host flexibility	K	AICc	Delt a AIC c	AICc Weight	Cumu- lative Weight	Log Like- lihood	Coefficient Name	Coef. Value	
Area + Transmission	6	821.53	0	0.64	0.64	-404.55	Area	0.148	*
							Transmission	0.177	
Area + Depth + Transmission	7	822.72	1.19	0.35	0.99	-404.07	Area	0.148	*
							Depth	0.004	
							Transmission	0.180	*
Transmission	5	829.87	8.34	0.01	1	-409.78	Transmission	0.230	*
Area + Growth + Transmission	17	838.24	16.71	0	1	-400.46	Area	0.151	*
							Transmission	0.168	
Area + Depth + Growth + Transmission	18	839.49	17.96	0	1	-399.89	Area	0.153	*
							Depth	0.004	
							Transmission	0.160	
Area	5	848.71	27.18	0	1	-419.21	Area	0.160	*
Area + Depth	6	850.52	28.99	0	1	-419.05	Area	0.161	*
							Depth	0.241	
References Only (Reference null)	4	860.01	38.48	0	1	-425.91	References	0.24	*
Depth	5	861.93	40.4	0	1	-425.82	Depth	0.002	
Area + Growth	16	863.87	42.34	0	1	-414.54	Area	0.15	*

Area + Depth + Growth	17	865.65	44.12	0	1	-414.24	Area	0.15	*
							Depth	0.003	
Growth	15	871.87	50.34	0	1	-419.7	Intercept	0.34	
Area (References removed)	4	953.27	131.74	0	1	-472.54	Area	0.32	*
Null (No fixed effects)	3	992.04	170.51	0	1	-492.96	Intercept	1.41	*

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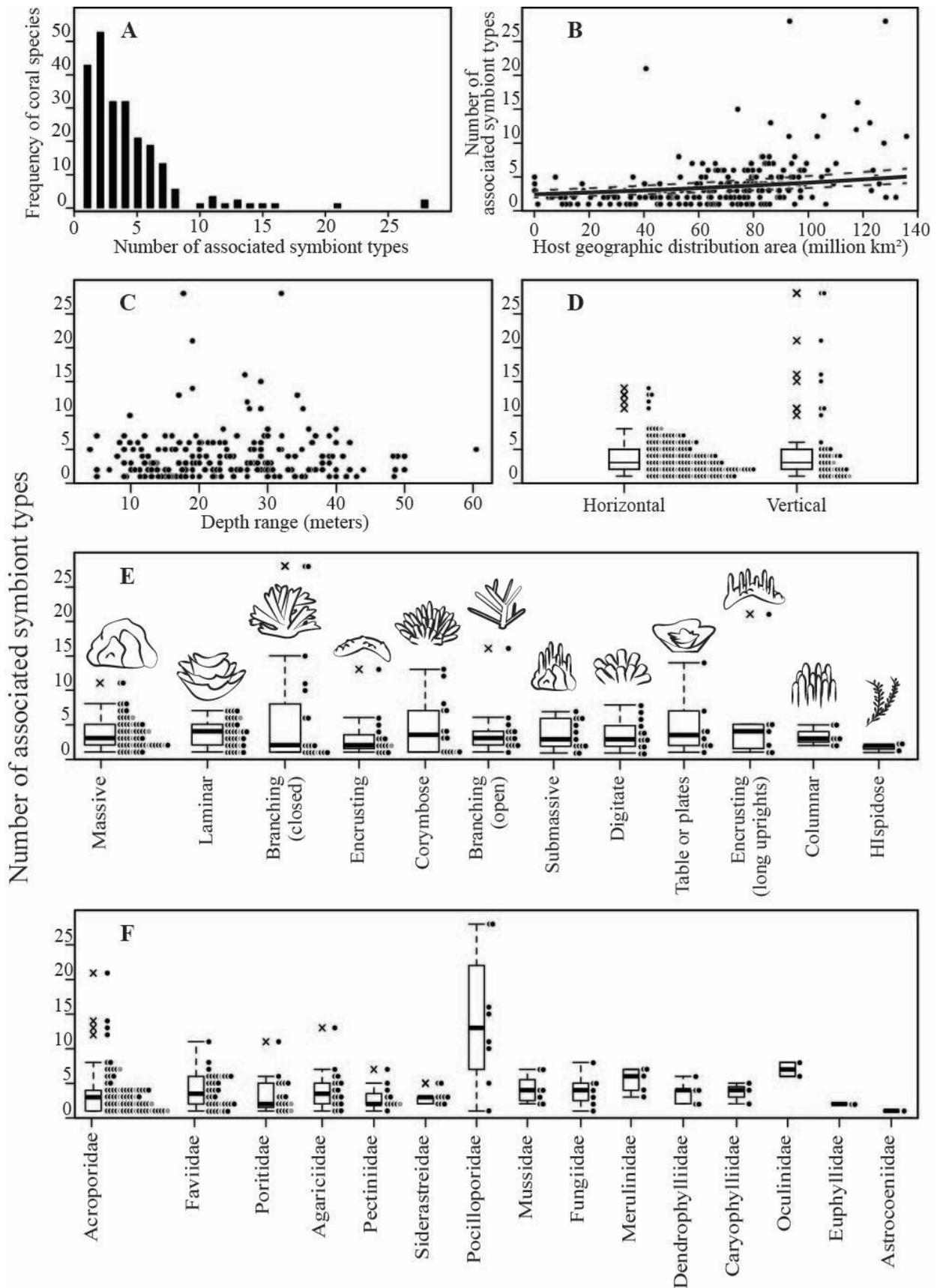
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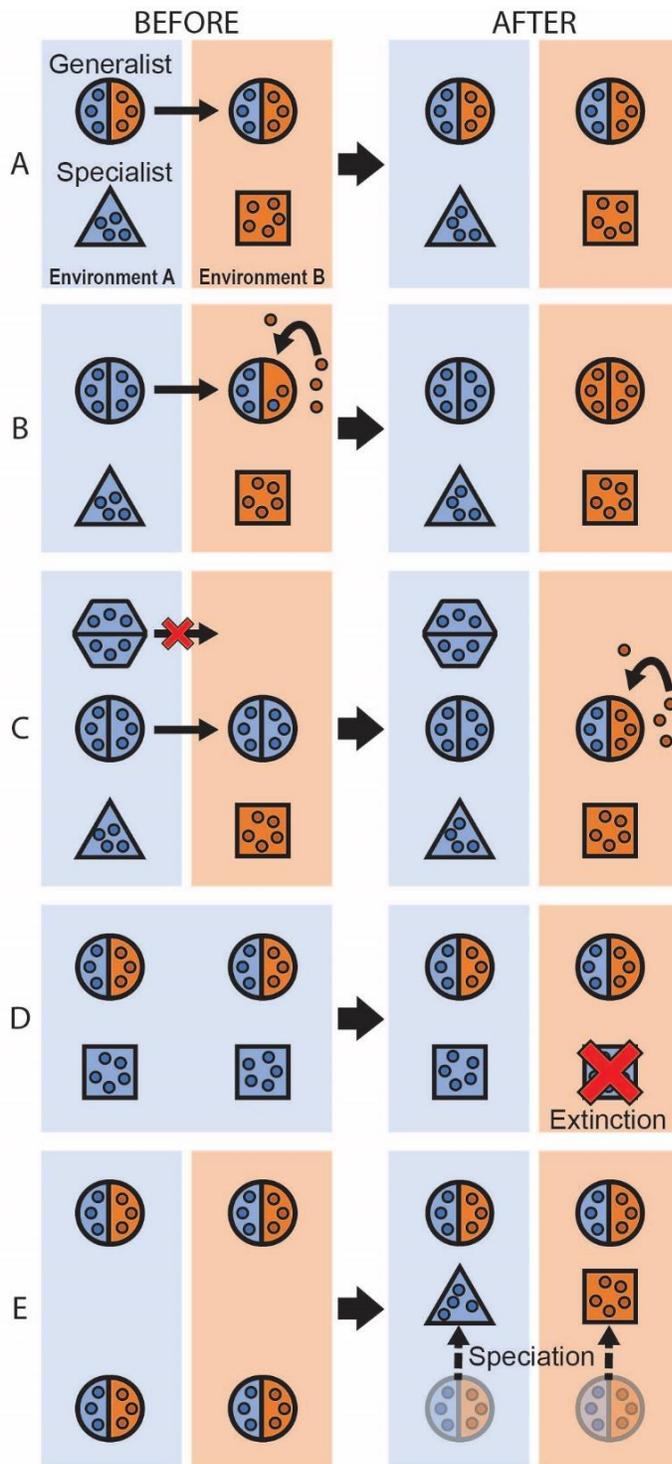
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Table 1. Model comparison results and coefficients. Coral-algal flexibility is a function of a combination of the host species' geographic distribution area (Area), depth range (Depth), main growth morphology (Growth), and symbiont transmission mode (Transmission). All models included coral's taxonomic family as a random effect. Models included number of references (References) except the Null model. Of all biological traits, geographic distribution (Area) is the only effect that consistently showed a significant effect. Coefficients for each growth morphology are shown in S2. Asterisk indicates coefficient with a significant effect ($P < 0.05$).



417 **Figure 1.** Relationship between number of associated symbiont types (coral-symbiont flexibility)
418 and coral host ecological/life-history traits. A) Frequency distribution of 211 coral species
419 associated with different numbers of symbiont types. Symbiont types were calculated based on
420 algal strains identified within an adult coral species using the ITS2 genetic marker. B)
421 Relationship between coral geographic range and coral-algal flexibility. A significant positive
422 correlation ($P=0.001$) is revealed by a generalized linear mixed model (GLMM), with the host
423 taxonomical family as a mixed effect. Continuous line indicates model with median number of
424 references as a fixed effect ($n=2$), dashed lines indicate both high and low quartile for number of
425 references ($n=3$ and 1 respectively). C-F) Coral-algal flexibility distribution is based on hosts'
426 depth range (C), symbiont transmission mode (D), growth morphology (E), and family (F). For
427 all boxplots, an "x" represents an outlier (i.e. data outside the interquartile range by 1.5 times).
428 The number of dots near each box plot represents the sample size of coral species. Box plots in
429 all categories are ordered by decreasing sample size.



430

431 **Figure 2.** Ecological and evolutionary mechanisms may contribute to the positive correlation
 432 between coral-algal flexibility and coral geographic range. Circle and hexagon shapes represent
 433 generalist hosts. Square and triangle shapes represent specialists. Blue and orange dots represent

434 different symbiont lineages. Blue and orange backgrounds represent different environments. A)
435 Generalist corals disperse further because of the diverse symbiont communities they carry. B)
436 Generalist corals expand their ranges because of the ability to uptake locally beneficial algae. C)
437 Generalist corals expand ranges thanks to innate dispersal mechanisms not related to their ability
438 to uptake or change symbionts. Instead, the increased coral-algal flexibility is a byproduct of
439 exposure to diverse symbiont communities over time. D) Generalists show greater geographic
440 distribution as they are more resilient to habitat change and have lower rates of extinction than
441 specialists. E) Being a generalist is the ancestral state among corals. Specialists are recently
442 evolved and therefore did not have enough time to expand their ranges.
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