

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

**Authors and affiliations:**

Daniel Zarate<sup>1</sup>. Email: Daniel.Zarate@Colorado.edu

Jaclyn Gary<sup>1</sup>. Email: Jaclyn.Gary@Colorado.edu

Jingchun Li<sup>1,2</sup>. Email: Jingchun.Li@Colorado.edu

1. Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, Colorado, USA

2. Museum of Natural History, University of Colorado Boulder, Boulder, Colorado, USA.

**Author contributions:**

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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**Corresponding author:**

Daniel Zarate. [Daniel.Zarate@colorado.edu](mailto:Daniel.Zarate@colorado.edu) and [Danezarate@gmail.com](mailto:Danezarate@gmail.com). Mail to 66 Ocean View Ave. Apt. 24. Santa Barbara. California. 93103

**Data availability statement:**

The data utilized towards the findings of this study are available at The Coral Trait Database at [coraltraits.org](http://coraltraits.org), GeoSymbio Database at [GeoSymbio.com/Home\\_Page.html](http://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

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

## Introduction

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

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

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

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

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

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

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

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

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

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

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

## Methods

### *Coral algal flexibility assessment*

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

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

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

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

We further narrowed down the list to 211 coral species for whom biogeographical information is available. Biogeographical information and ecological traits for each coral species were obtained from the Coral Trait Database (Madin et al., 2016) based on 57 references (S1), including geographic range, observed depth range, and typical growth morphologies. Host geographic distribution (area) was calculated using the GIS shapefiles in km<sup>2</sup>. Depth range (m) was calculated as the difference between a host's average minimum (shallowest) observed depth and the average maximum (deepest) observed depth (Madin et al., 2016). For morphology, we



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

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

### *Statistical analysis*

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

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

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

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

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

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

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

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

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

## Results

### *Coral algal flexibility assessment*

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

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

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

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

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

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

### *Statistical analysis*

Our models showed a significant positive correlation between a coral's geographic range and its host-algal flexibility (Table 1, Fig. 1b). The best-fit model included geographic range (area) and symbiont transmission mode as the main predictors, which carried 64% of the cumulative model weight (AICc=821.53). Within this model, geographic range was a significant predictor ( $\beta = 0.15$ ,  $P = 0.001$ ), where for every 97.8 million km<sup>2</sup> (or one unit of scaled area) a coral can occupy, host flexibility increases by 16%. Horizontal transmission also showed a positive correlation with host-algal flexibility ( $\beta = 0.18$ ). It was not a significant predictor in this top model ( $P = 0.09$ ), albeit being significant in some of the lower ranked models.

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

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

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

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

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

## Discussion

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

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

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

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

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

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

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



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

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

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

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

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

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

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

### ***Limitations and future directions***

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

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

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

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

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

### ***Ecological and conservation implications***

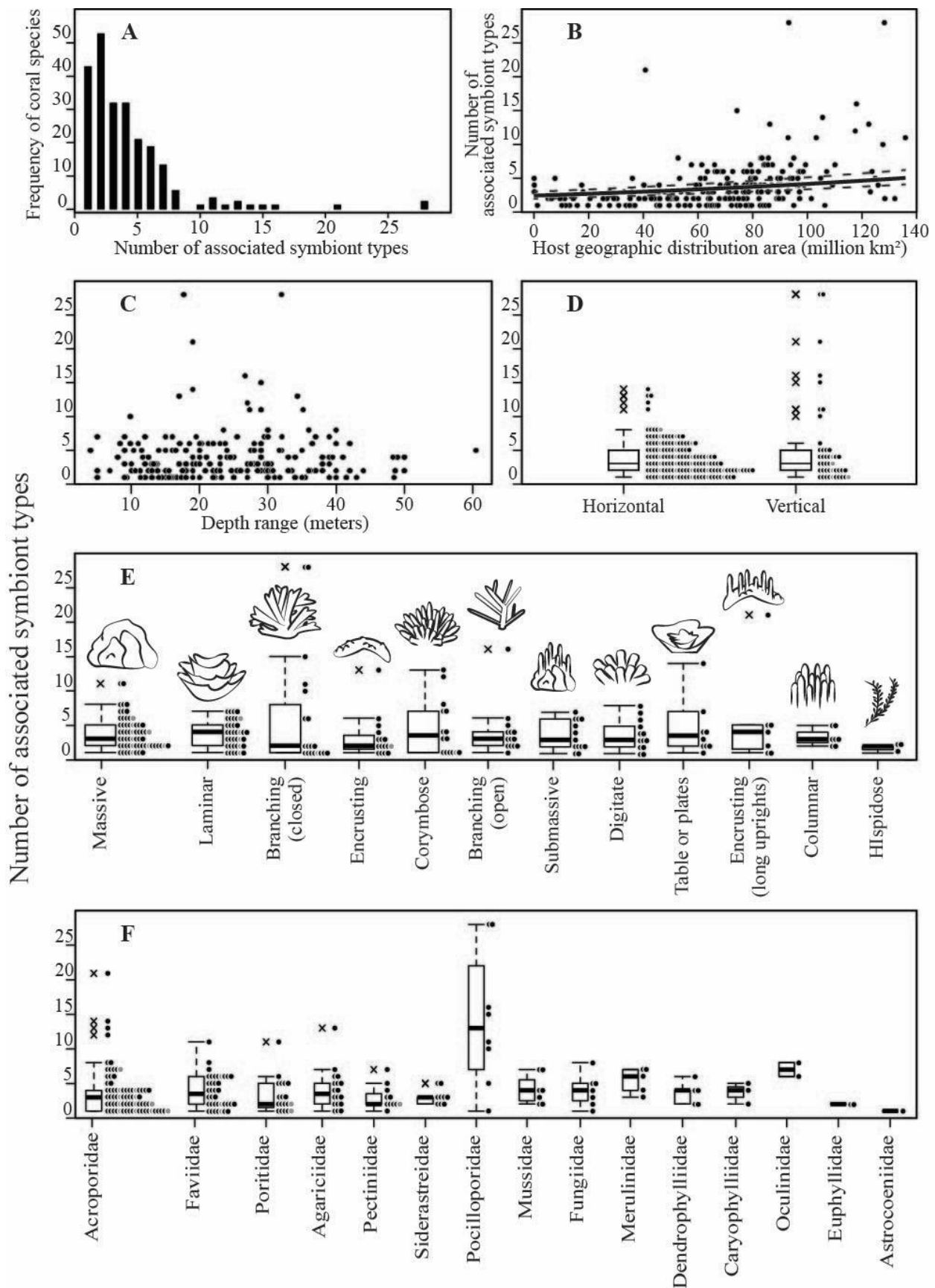
Climate change and anthropogenic disturbances may be selecting generalist species. This has been seen in some reef fish, wherein generalists show higher survival rates, and specialists experience greater rates of extinction (Wilson et al., 2008; Begger, 2021). This pattern has also been observed in other non-reef ecosystems (Dharmarajan et al., 2021). The same effects may be occurring in corals, but more research is needed to fully understand the differential survival of coral generalists and specialists under disturbances. As reefs face mass bleaching events (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.

<b>Model's fixed effects on host flexibility</b>	<b>K</b>	<b>AICc</b>	<b>Delt a AIC c</b>	<b>AICc Weight</b>	<b>Cumu- lative Weight</b>	<b>Log Like- lihood</b>	<b>Coefficient Name</b>	<b>Coef. Value</b>	
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	*

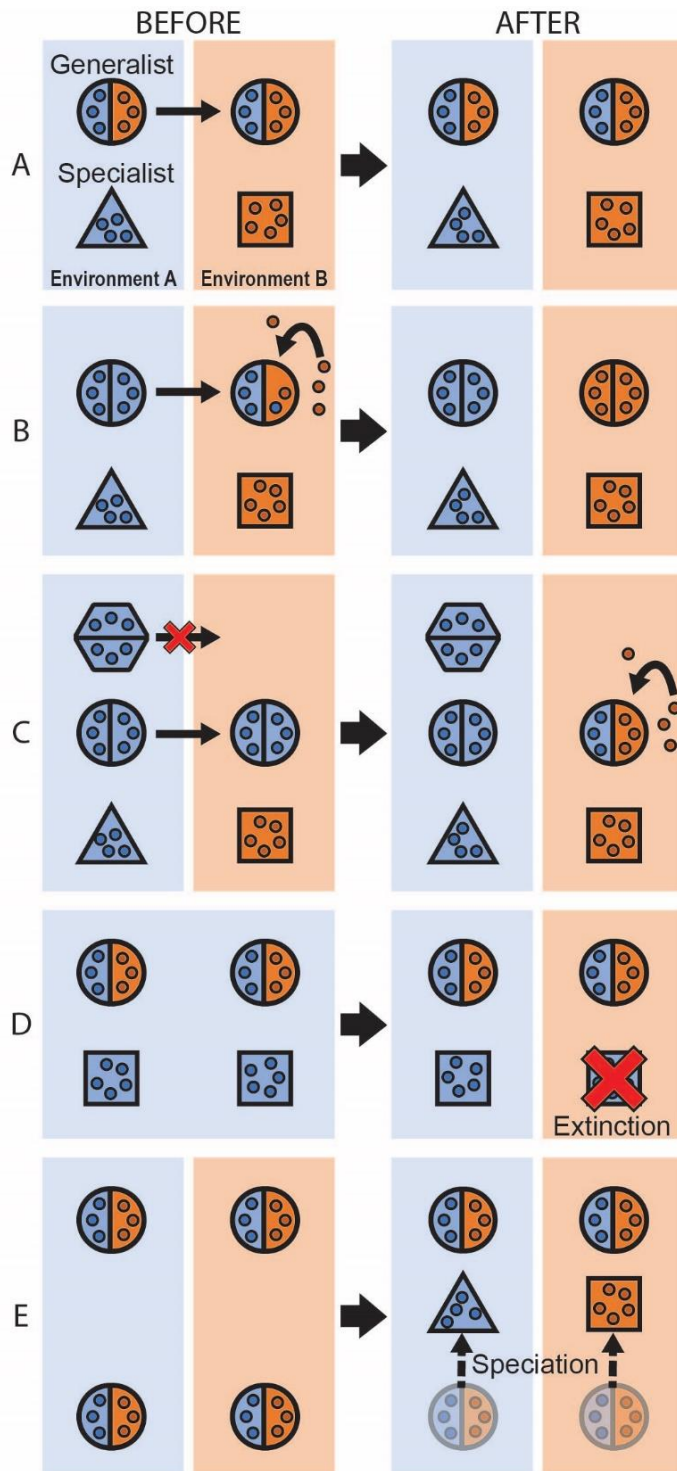
Area + Depth + Growth	17	865.65	44.12	0	1	-414.24	Area	0.15	*
							Depth	0.003	
Growth	15	871.87	50.34	0	1	-419.7	Intercept	0.34	
Area (References removed)	4	953.27	131.74	0	1	-472.54	Area	0.32	*
Null (No fixed effects)	3	992.04	170.51	0	1	-492.96	Intercept	1.41	*

**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 ( $P < 0.05$ ).





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



**Figure 2.** Ecological and evolutionary mechanisms may contribute to the positive correlation between coral-algal flexibility and coral geographic range. Circle and hexagon shapes represent 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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