Received: 26 April 2022 | Revised: 1 December 2022 | Accepted: 8 December 2022

DOI: 10.1111/jbi.14560

Journal of Biogeography WILEY

RESEARCH ARTICLE

Environmental and geographical factors structure cauliflower coral's algal symbioses across the Indo-Pacific

Victoria M. Glynn[1,2] | **Steven V. Vollmer**[2,3] | **David I. Kline**[2] | **Rowan D. H. Barrett**[1]

[1]Redpath Museum and Department of Biology, McGill University, Montréal, Québec, Canada

[2]Smithsonian Tropical Research Institute, Balboa, Republic of Panama

[3]Marine Science Center, Northeastern University, Nahant, Massachusetts, USA

Correspondence
Victoria M. Glynn, Redpath Museum and Department of Biology, McGill University, Montréal, Québec H3A 1B1, Canada.
Email: victoria.glynn@mail.mcgill.ca

Rowan D.H. Barrett, McGill University, 859 Sherbrooke Street West, Montréal, Québec H3A 0C4, Canada.
Email: rowan.barrett@mcgill.ca

Funding information
Canada Research Chairs; Natural Sciences and Engineering Research Council of Canada (NSERC) Collaborative Research and Training Experience (CREATE) in Biodiversity, Ecosystem Services and Sustainability (BESS); Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant; Vanier Canada Graduate Scholarship

Handling Editor: Jonathan Waters

Abstract

Aim: The symbioses between corals and endosymbiotic dinoflagellates have been described as a flexible relationship whose dynamics could serve as a source of resilience for coral reef ecosystems. However, the factors that drive the establishment and maintenance of this co-evolutionary relationship remain unclear. We examined the environmental and geographical factors structuring dinoflagellate communities in a wide-ranging Indo-Pacific coral to begin to address this gap.

Location: Djibouti, Oman, Taiwan and French Polynesia.

Taxon: Cauliflower corals (*Pocillopora* spp.), dinoflagellates (family Symbiodiniaceae).

Methods: We analysed publicly available amplicon sequence data from the nuclear ribosomal DNA internal transcribed spacer 2, originating from *Pocillopora* spp. We also compiled environmental data such as sea surface temperature (SST) and time since the last local mass bleaching event. We ran generalized least squares models, PERMANOVAs and indicator species analyses, to understand how thermal regimes and geographical distances impacted *Pocillopora* spp.'s Symbiodiniaceae community composition.

Results: Sea surface temperature was the most important factor driving Symbiodiniaceae community differences, with the largest effect size of the statistically significant factors. When focusing on individual Symbiodiniaceae genera, SST was likewise the most important factor. Our indicator species analyses revealed that specimens that had recently bleached were characterized by roughly equal proportions of *Cladocopium* spp. and *Durusdinium* spp., while specimens that had not recently bleached had a similar proportion of *Durusdinium* spp. as those that had recently bleached, but also showed a reduction in *Cladocopium* spp., with this deficiency made up by the presence of *Symbiodinium* spp.

Main Conclusions: We provide further support for the hypothesis that coral's Symbiodiniaceae communities could facilitate host resilience to thermal stress. Our work is in direct conversation with a larger body of biogeography literature that highlights how local environmental regimes can impact contemporary population structure, even in marine taxa with widespread distributions.

Rowan D.H. Barrett and David I. Kline are joint senior authors.

KEYWORDS
biogeography, cauliflower corals, corals, environment, geography, Indo-Pacific, *Pocillopora*, Symbiodiniaceae, Symbiosis, thermal stress

1 | INTRODUCTION

Host–symbiont relationships are increasingly recognized as being important for contributing to host tolerance of environmental stress (Ainsworth et al., 2010; Dastogeer et al., 2022; Iltis et al., 2022). A classic example are reef-building corals (Order Scleractinia), which thrive in nutrient-poor, tropical and sub-tropical marine ecosystems due to an ancient, co-evolutionary relationship with photosynthetic dinoflagellates from the family Symbiodiniaceae (Campoy et al., 2020; Frankowiak et al., 2016; Liu et al., 2018). As atmospheric CO_2 levels increase due to anthropogenic climate change, corals face increasing extinction risk due to rising sea water temperatures driving mass coral bleaching events (Carpenter et al., 2008; Hughes et al., 2018), which destabilizes the coral–algal symbiosis (Hoegh-Guldberg, 1999). Changes in the symbiont communities associated with coral have been connected to ecological and performance shifts in the host–symbiont relationship, potentially assisting these corals in coping with repeat thermal stress events (Cunning et al., 2015; Glynn et al., 2001; Rodríguez-Román et al., 2006; Rowan et al., 1997). However, the specific environmental and geographical factors that structure the distribution of symbiont communities are not fully understood. Prior studies on the factors structuring marine invertebrate communities suggest that despite high potential for long-distance dispersal with oceanic currents, regional differentiation can often arise in response to local environmental conditions (e.g. Cineas & Dolédec, 2022; Coppard et al., 2021; Hirschfeld et al., 2021; Lessios et al., 2003; Lim et al., 2021; Lopes da Silva Ferrette et al., 2021; Pappalardo et al., 2015; van der Ven et al., 2021; Wepfer et al., 2020). In particular, the Indo-Pacific has served as a key area of study for understanding how current species distributions can be structured by the complex interplay between contemporary environmental pressures and historical patterns of gene flow (see Benzie, 1999; Crandall et al., 2019; Lessios et al., 2001). However, there remains a knowledge gap concerning where and why particular Symbiodiniaceae taxa are associated with particular coral genera. To date, coral studies have typically focused on the factors structuring these symbioses in either a single geographical location (Johnston, Cunning, & Burgess, 2022; O'Brien et al., 2020; Osman et al., 2020; Pollock et al., 2018; Ricci et al., 2022) or for a single Symbiodiniaceae genus at the regional level (Turnham et al., 2021). It is important to consider how environmental and geographical factors together are driving the establishment and maintenance of this symbiotic relationship, as the diversity, distribution and stability of Symbiodiniaceae communities is central to coral's future in an increasingly warmer, high CO_2 world.

Generally, host specificity results in an individual coral being in symbiosis with a single Symbiodiniaceae taxon (see LaJeunesse et al., 2004; Smith et al., 2017; van Oppen et al., 2001). Given the evolutionary distance between taxa, LaJeunesse et al. (2018) recently reclassified each as its own genus. While many coral species often associate with a single Symbiodiniaceae genus, two coral genera—*Orbicella* (Western Atlantic) and *Pocillopora* (Indo-Pacific)—regularly host multiple genera, suggesting more labile and potentially adaptive coral–symbiont associations (Cunning et al., 2013; Kemp et al., 2015; Kennedy et al., 2016; Toller et al., 2001; Ziegler et al., 2017). For example, *O. faveolata* has been shown to be most resistant to bleaching when harbouring phylotype A3 (now *Symbiodinium* spp.), and during bleaching events there was an increased presence of this phylotype alongside the D1a phylotype (now *Durusdinium* spp.; Kemp et al., 2014). Within *Orbicella* spp., the length of thermal stress events can also dictate longer-term dynamics of *Durusdinium*, with D1a phylotypes being most retained after 14 days versus 7 or 10 days of experimentally induced heat stress (Cunning, Bay, et al., 2018). Likewise, cauliflower coral (*Pocillopora* spp.) colonies in Panama (the easternmost part of this genus's range) were shown to shift their communities from *Cladocopium* spp. to *Durusdinium* spp. during the 1997–1998 El Niño–Southern Oscillation (ENSO) event (Glynn et al., 2001). *Pocillopora* colonies dominated by *Durusdinium* experienced less bleaching and mortality during the 1997–1998 ENSO thermal bleaching event compared to the 1982–1983 ENSO event (Glynn et al., 2001). *Pocillopora* has also been observed to be less susceptible to bleaching during cold-water events when associated with *Durusdinium* spp. (LaJeunesse et al., 2010). More recently, *Pocillopora* spp. has been reported to acquire novel *Durusdinium* and *Cladocopium* species from the environment and maintain stable associations for up to 18 months after two subsequent bleaching events, suggesting that symbiont community changes could be an adaptive and flexible response to environmental stressors (Boulotte et al., 2016).

Together, data from *Orbicella* and *Pocillopora* corals present that changes in coral symbiont genera can be linked to environmental stress, and that these changes to Symbiodiniaceae communities could provide benefits to the coral host. Although there is a considerable body of work that underscores the dynamic nature of coral–Symbiodiniaceae partnerships in the face of bleaching (Baker et al., 2004; Quigley et al., 2019; Rowan et al., 1997), other studies have highlighted the stability of Symbiodiniaceae communities or have suggested that many changes cannot be conclusively linked to environmental stressors (Epstein et al., 2019; Hoegh-Guldberg et al., 2002; Manzello et al., 2019; McGinley et al., 2012; Rouzé et al., 2019), urging us to consider additional factors that structure coral host–symbiont interactions.

In addition to thermal stress and bleaching events, Symbiodiniaceae communities can be structured by other abiotic and geographical factors, such as dispersal potential and adaptation to local abiotic regimes. Previous research has shown that different oceanic basins possess divergent Symbiodiniaceae communities, both free living and in-hospite (LaJeunesse, 2005; Manning & Gates, 2008). For example, *O. annularis* in the Caribbean and Bahamas is predominantly associated with the genera *Breviolum*, *Cladocopium* and *Durusdinium* (Kennedy et al., 2016), while *Pocillopora* in the Red Sea and Tropical Eastern Pacific is predominantly associated with the genera *Symbiodinium*, *Cladocopium* and *Durusdinium* (Baker et al., 2017; LaJeunesse et al., 2004; Ziegler et al., 2017). Some Symbiodiniaceae taxa like *Cladocopium latusorum* are found in association with corals across the entire Indo-Pacific (Turnham et al., 2021). In addition, host and local environmental regimes, such as sea surface temperature (SST), appear to influence coral–Symbiodiniaceae partnerships (Cooper et al., 2011; Osman et al., 2020; Tonk et al., 2013), with particular genetic lineages more likely to associate with particular Symbiodiniaceae genera (Cunning et al., 2013). It has also been noted that *Symbiodinium* spp. and *Breviolum* spp. are most common at higher latitudes, while *Cladocopium* spp. is more common in tropical latitudes (Baker, 2003). The complex interplay between genera specificity, dispersal and environmental conditions represents a challenge for elucidating the factors that structure coral–algal symbioses across broad species ranges, particularly because most studies focus on local patterns at a single geographical location.

Pocillopora is a genus of reef-building corals that is widely distributed across the Indo-Pacific—ranging from the Red Sea to the Tropical Eastern Pacific (TEP) in Central and South America—and thus provides an excellent system to explore the factors that drive patterns of host–Symbiodiniaceae associations across large spatial scales and environmental regimes. *Pocillopora* corals are capable of withstanding considerable environmental heterogeneity compared to other coral taxa (Hoegh-Guldberg, 2011). For example, *Pocillopora* corals in the Red Sea are found at extreme salinities up to 41 ppt (Paldor & Anati, 1979) and at temperatures above 30°C (Fine et al., 2013). In the TEP, *Pocillopora* corals experience seasonal upwelling conditions that trigger drastic annual fluctuations in abiotic conditions (D'Croz & O'Dea, 2007; O'Dea et al., 2012); for instance, corals in the Gulf of Panama experience a 10-degree shift in temperature across the non-upwelling and upwelling seasons, and as much as a 5-point drop in salinity, among other parameters (Manzello et al., 2008). To date, there has not been a study systematically exploring *Pocillopora*'s Symbiodiniaceae communities across its range. Given this taxon's symbiont flexibility during thermal stress events and the environment heterogeneity encompassed by its range, it represents an ideal system to address larger questions regarding the factors structuring coral–Symbiodiniaceae establishment and maintenance.

In this study, we analysed publicly available Symbiodiniaceae nuclear ribosomal DNA internal transcribed spacer 2 (ITS2) sequences that spanned study locations across *Pocillopora*'s range to investigate the environmental and geographical factors structuring the Symbiodiniaceae communities in this wide-ranging Indo-Pacific coral. Given the evidence that bleaching disrupts symbiosis (Ainsworth et al., 2016; Brown, 1997; Carpenter et al., 2008; Douglas, 2003; Glynn, 1996; Hoegh-Guldberg, 1999; Hughes et al., 2018; Weis, 2008) and that migrant establishment may be lower in thermally unsuitable locations relative to locally adapted populations (Fitzpatrick et al., 2015; Kelly et al., 2014; Lessios et al., 2001; Nosil et al., 2009; Osman et al., 2020), we predicted that a region's thermal history, followed by geography, would most strongly drive host–symbiont associations. By focusing on a single cosmopolitan genus and its algal symbionts, we aim to identify and disentangle the various interconnected factors responsible for the establishment and diversity of coral–Symbiodiniaceae symbioses, thus providing insights into how corals' symbiotic partnerships are structured and potentially impacted by environmental change.

2 | MATERIALS AND METHODS

2.1 | Downloading data

We downloaded all available Symbiodiniaceae ITS2 FASTQ sequence files in July 2021 from *Pocillopora* corals from NCBI's Sequence Read Archive (SRA) via the SRA Toolkit on Compute Canada (Baldwin, 2012). We also downloaded their associated metadata (i.e. publication source, species sampled, location sampled, coordinates of sampling location, time of year sampled, ITS2 primers used). We used NOAA's Coral Reef Watch Operational Daily Near-Real-Time Global 5-km Satellite Coral Bleaching Monitoring Products (NOAA Coral Reef Watch, 2000) to extrapolate SST from the study locations, if this data was not already provided in the associated publication. Finally, we ascertained the time since the last local bleaching event (TSB) by referencing government monitoring program reports and scientific publications.

2.2 | Sequence quality control and amplicon sequence variant (ASV) detection

Given the heterogeneous nature of the downloaded files, we used the R package 'DADA2' version 1.20 (Callahan et al., 2016; https://github.com/benjjneb/dada2) to filter and trim the downloaded ITS2 sequences and detect amplicon sequence variants (ASVs). We used an ASV approach rather than detecting and constructing operational taxonomic units (OTUs), because ASVs represent sequences that are stand-alone, reproducible and informative, as a detected ASV is a sequence in and of itself and is not contingent on the nature of the clustering approach used (see Callahan et al., 2017). We followed a standard DADA2 workflow: we trimmed and de-replicated sequences, removed chimeras and generated a FASTA file with our detected ASVs. For sample inference, we took a pseudo-pooling approach as a compromise between processing time and improving the detection of low-frequency Symbiodiniaceae ASVs (cf. Silverman et al., 2018). We ran our DADA2 R Script on the Compute Canada Cedar server.

2.3 | Phylogenetic tree

We used FastTree 2 version 2.1.11 (Price et al., 2010) to construct a ITS2 phylogenetic tree, which implements a heuristic variant of neighbour joining and the Shimodaira–Hasegawa (SH) test to compare alternative topologies with 1000 resamples. For our tree, we first used Clustal Omega (Sievers & Higgins, 2021) on the Compute Canada Cedar server with default parameters to align our DADA2-generated FASTA sequences. We then used these aligned sequences to build our phylogenetic tree with FastTree 2, using a generalized time-reversible model. The support values are SH-like local supports (see Price et al., 2010).

2.4 | Taxonomic assignment

We took two approaches to assign taxonomy to our ASVs using (1) the SymPortal database (Hume et al., 2019) and (2) NCBI BLAST (Altschul et al., 1990; see details below). We selected the taxonomic assignment that most closely matched the phylogenetic tree presented in LaJeunesse et al. (2018), which is the most widely accepted phylogeny of Symbiodiniaceae, where each Symbiodiniaceae phylotype is its own clade on the tree; other recent Symbiodiniaceae phylogenetic trees have shown concordance with this tree (see Teschima et al., 2019; Turnham et al., 2021).

The SymPortal database (Hume et al., 2019) is a community-driven Symbiodiniaceae-specific database that uses the ITS2 marker and provides ITS 'clade' and 'type' assignments as it was built before this family's taxonomic reorganization. Yet, these assignments represent ITS2-type profiles and will be referred to as such hereon. We downloaded the database and then used vsearch version 2.4.3 (Rognes et al., 2016; https://github.com/torognes/vsearch) and usearch version 11.0 (Edgar, 2010; http://www.drive5.com/usearch) to assign taxonomy to our ASV FASTA file generated in DADA2, requiring a pairwise identity of at least 0.6. As SymPortal is optimized for the SYM_VAR_5.8S2/SYM_VAR_REV primer pair (Hume et al., 2018, 2019) and our dataset included sequences generated using different primers, namely the ITSIntFor2 (LaJeunesse, 2002) and ITS2 pair (Coleman et al., 1994), or the ITS-DINO (Pochon et al., 2001) and ITS2Rev2 (Stat et al., 2009) pair, we also assigned taxonomy with NCBI BLAST. For NCBI BLAST, we set an *E*-value cut-off of 1×10^{-5} and a maximum of 5 target sequences. We manually annotated non-Symbiodiniaceae hits as no hits ('N') and established ITS2-type profiles based on the NCBI output reference entries, mirroring the SymPortal output. For ASVs that had multiple ITS2-type profiles as hits, we selected the one with the smallest E-value, least number of mismatches and/or greatest percent alignment. If an ASV had two different ITS2-type profiles with the same E-value, number of mismatches and percent alignment, we only assigned taxonomic resolution down to the genus level. Furthermore, as not all Symbiodiniaceae form symbioses with corals (cf. Baker, 2003), if an ASV hit did not provide further taxonomic resolution past Symbiodiniaceae, it was also denoted as 'N'. We removed these uninformative ASVs before downstream analyses. The SymPortal taxonomic assignment is found in Table S4, and the NCBI taxonomic assignment in Table S5.

2.5 | ASV quality control and cumulative sum square transformation

All statistical analyses were performed in R version 4.1.2 (R Core Team, 2021). Using the R package 'phyloseq' version 1.39.1 (McMurdie & Holmes, 2013; https://github.com/joey711/phyloseq), we integrated ASVs, taxonomy and sample information into a single object. We then performed quality control, including removing taxa that had less than 1000 reads, those that were observed less than once in at least 5% of the specimens, and removing any singleton ASVs. We performed a cumulative sum square (CSS) transformation, as opposed to rarefying Symbiodiniaceae reads, to avoid omitting data whose differences in library size and presence/absence of particular ASVs may be of biological importance (McMurdie & Holmes, 2014). CSS corrects for differences in library size by standardizing to the quartile where lower abundance taxa are well represented (Paulson et al., 2013).

Given that the majority of our sequences (64% of downloaded SRA entries) were identified on NCBI as being from *P. damicornis*, we only analysed this subset for downstream applications. We recognize that these sequences are not necessarily from *P. damicornis* sensu lato, as although some of the data originated from studies that employed marker-based taxonomic assessment of the host, none implemented whole-genome sequencing. With increasing genetic resources, recent studies have come to highlight the complex genetics within this genus that often contradict marker-based approaches (see Oury et al., 2022 using ultra-conserved elements). Therefore, in taking a more conservative approach, we have decided to refer to our analysed sequences as coming from *Pocillopora* spp. In addition, in generating diagnostic standardized residual and QQ-plots, some of our variables showed a multimodal distribution, even after log and square-root transformations, and thus we removed these outlier sequences to meet normality assumptions. These removed sequences included specimens from the locations of Heron Island (Great Barrier Reef, Australia; $n = 153$ SRA entries) and New Caledonia ($n = 70$ SRA entries), specimens collected during the summer ($n = 10$ SRA entries), and specimens experiencing bleaching ($n = 19$ SRA entries). This pruned dataset was used for all subsequent analyses, which comprised a total of 101 SRA sample entries (see Table S2 for the entries used in downstream analyses and their associated data; the metadata is found in Table S3).

2.6 | ASV richness across abiotic parameters

To understand how Symbiodiniaceae diversity varied across abiotic parameters, we plotted taxa richness, the Shannon diversity index and the inverse Simpson index across locations (categorized by region) and TSB. For SST, we created scatterplots with 'ggplot2' package version 3.3.5 (Wickham, 2016). Given that there was heteroscedasticity in our residuals, even after transformation of the alpha diversity metrics, we fit linear models using generalized least squares (GLS) using the 'nlme' package version 3.1-153 (Pinheiro et al., 2021), where we allowed each level within our explanatory variable 'location' to have different variances. For our GLS models, we nested locations within regions, and set SST and TSB as fixed effects. We performed post-hoc comparisons using the 'emmeans' package version 1.7.0 as this uses estimated marginal means to compare the effects of factors (Lenth, 2021), with effective degrees of freedom calculated with the Welch Satterthwaite approximation and implements the Benjamini and Hochberg *p*-value correction for multiple comparisons. All comparisons were tested at a 95% confidence level.

2.7 | Symbiodiniaceae community composition

We created pie charts for each location's Symbiodiniaceae community using the 'plot_bar' argument from 'phyloseq' (McMurdie & Holmes, 2013) to further visualize differences across the Indo-Pacific; these pie charts were placed over a map of our study region. We also plotted Symbiodiniaceae ASV networks to ascertain how Symbiodiniaceae partnerships were structured across locations. We created connectivity networks via the 'plot_net' argument in 'phyloseq' (McMurdie & Holmes, 2013) using only the top 20 taxa by abundance, implementing the Fruchterman-Reingold layout algorithm (Fruchterman & Reingold, 1991) and using Bray–Curtis dissimilarity to calculate distances (Bray & Curtis, 1957).

We performed non-metric multidimensional scaling (nMDS) ordination with Bray–Curtis dissimilarities to visualize how Symbiodiniaceae community composition varied across our geographical parameters. We performed an nMDS with Bray–Curtis dissimilarities because this is a robust ordination approach that is able to handle missing ASVs (Buttigieg & Ramette, 2014). Bray–Curtis distances focus on compositional dissimilarity without making assumptions about the phylogenetic relationships between samples and can also process missing values. We created our ordination plots via 'ordinate' in the 'phyloseq' package (McMurdie & Holmes, 2013) and plotted 95% confidence ellipses. We performed a PERMANOVA with 999 permutations and Bray–Curtis distances via the *adonis2* function in the R package 'vegan' version 2.5 (Oksanen et al., 2020) to determine which variables were driving significant differences in Symbiodiniaceae communities; post-hoc pairwise comparisons were performed with the *pairwise.adonis2* function (Martinez Arbizu, 2020), implementing the Benjamini and Hochberg *p*-value correction for multiple comparisons. In the PERMANOVA, we nested locations within regions, and set SST and TSB as fixed effects. We detected statistically significant heterogeneity of dispersions based on 'betadisper' in 'vegan' (Oksanen et al., 2020), and thus used PERMANOVA, which is more robust to heteroscedasticity than ANOSIM (see Anderson & Walsh, 2013).

We further explored how different Symbiodiniaceae ITS2-type profiles varied across our locations and environmental parameters by running each genus in its own PERMANOVA model, with 999 permutations and Bray–Curtis distances via the *adonis2* function (Oksanen et al., 2020). Here, we nested locations within regions, and set SST and TSB as fixed effects in the model.

2.8 | Mantel tests and indicator species analyses

We ran Mantel tests using the package 'vegan' (Oksanen et al., 2020) to determine if geographical distances and temperature differences could explain Symbiodiniaceae community dissimilarity. We calculated geographical distances from our sample location's coordinates using Haversine distances in the package 'geosphere' version 1.5 (Hijmans, 2019), as this takes into account the Earth's spherical shape. We used these calculated geographical distances for our Mantel tests, which we ran with 999 permutations and used Spearman correlation coefficients. For our temperature Mantel tests, we used the same parameters as for geographical distances, with the exception that we calculated differences across temperatures using Euclidean distances.

We performed an indicator species analysis (Dufrêne & Legendre, 1997) using the 'indicspecies' package's version 1.7.9 (Cáceres & Legendre, 2009) 'multipatt' command with 999 permutations and implementing the Benjamini and Hochberg *p*-value correction for multiple comparisons, to ascertain if certain Symbiodiniaceae taxa were significantly associated with certain locations or TSB.

3 | RESULTS

3.1 | Overview of the downloaded data

From NCBI's SRA, we downloaded 839 FASTQ files representing Symbiodiniaceae ITS2 sequences from *Pocillopora* corals. Our FASTQ files encompassed three different ITS2 primer pairs, 27 locations, and were referenced on NCBI as representing 4 *Pocillopora* species: *Pocillopora acuta*, *P. damicornis*, *P. meandrina* and *P. verrucosa*. The majority of the sequences (79%) used one of two primer sets: the ITSIntFor2 (LaJeunesse, 2002) and ITS2 pair (Coleman et al., 1994), or the ITS-DINO (Pochon et al., 2001) and ITS2Rev2 (Stat et al., 2009) pair. As each primer set amplifies a slightly different length of the ITS2 region, combining these datasets could potentially cause the differences in length to be interpreted as mismatches by DADA2, and thus we only analysed sequences amplified with the ITS-DINO and ITS2Rev2 primer pair (referred to as the 'DINO' dataset hereon) because it represented the greatest geographical distribution and number of independent studies. We focused solely on entries identified as being from *P. damicornis* on NCBI for all our downstream analyses, as this was also the most abundant species present in the DINO primer set dataset, representing 63% of DINO sequences (see Table S1 to see all the downloaded DINO sequences' SRA numbers and associated data; the metadata are found in Table S3). However, given the genetic delineation of species boundaries within of this genus is still being resolved (see Combosch & Vollmer, 2015; Johnston, Wyatt, et al., 2022; Johnston et al., 2017; Oury et al., 2021, 2022; Pinzón & LaJeunesse, 2011), we will refer to these sequences as originating from *Pocillopora* spp. Furthermore, for downstream analyses, we used a subset of 101 SRA entries that met normality assumptions (see Table S2 for the entries used in downstream analyses and their associated data; the metadata are found in Table S3).

3.2 | Phylogenetic tree

The SymPortal-based taxonomic assignment did not group Symbiodiniaceae ITS2-type profiles into clades on our phylogenetic tree (Figure 1a; see Table S4). By comparison, the NCBI-based ITS2 taxonomic assignment resulted in a tree whose relationships best-represented the accepted phylogeny of Symbiodiniaceae (see LaJeunesse et al., 2018), whose most important feature is that each Symbiodiniaceae genus is a distinct phylogenetic clade on the tree (Figure 1b; see Table S5). By comparison, the SymPortal-based taxonomic assignment did not group Symbiodiniaceae ITS2-type profiles into clades on our phylogenetic tree (Figure 1a; see Table S4). Therefore, we decided to use the NCBI-based taxonomic assignment to assign Symbiodiniaceae genera ITS2-type profiles as we were interested in how environmental and geographical parameters impacted the entire Symbiodiniaceae community at the ASV level with no additional classification. However, we also needed classification to the level of Symbiodiniaceae genera, which required us to classify the ASVs into generic groupings.

3.3 | Patterns of diversity within Symbiodiniaceae communities

Symbiodiniaceae from Djibouti corals had the lowest median alpha diversity scores across richness, Shannon diversity and inverse Simpson metrics, while Symbiodiniaceae from Oman corals had the highest median scores across all indices (Figure 2a). Corals from French Polynesia (four islands in our dataset) had a Symbiodiniaceae community with a narrow spread around the median for all metrics, except for Tahiti's Shannon and inverse Simpson indices (Figure 2a). There was no apparent difference in the median scores for sequences originating from corals that had recently versus those that had not recently bleached, but across all alpha diversity metrics the range of diversity values was greatest for sequences originating from corals that had not bleached recently (Figure 2b, category 'Long'). For SST, our scatterplots did not reveal a clear association between our three alpha diversity metrics and temperature (Figure 2c). Overall, our GLS models did not detect significant variation in median scores between sequences collected from corals representing distinct locations, regions, SST regimes or TSB, except for the interaction between the Indian Ocean (region) and Oman (location) for Shannon diversity and inverse Simpson scores (Tables S6–S8).

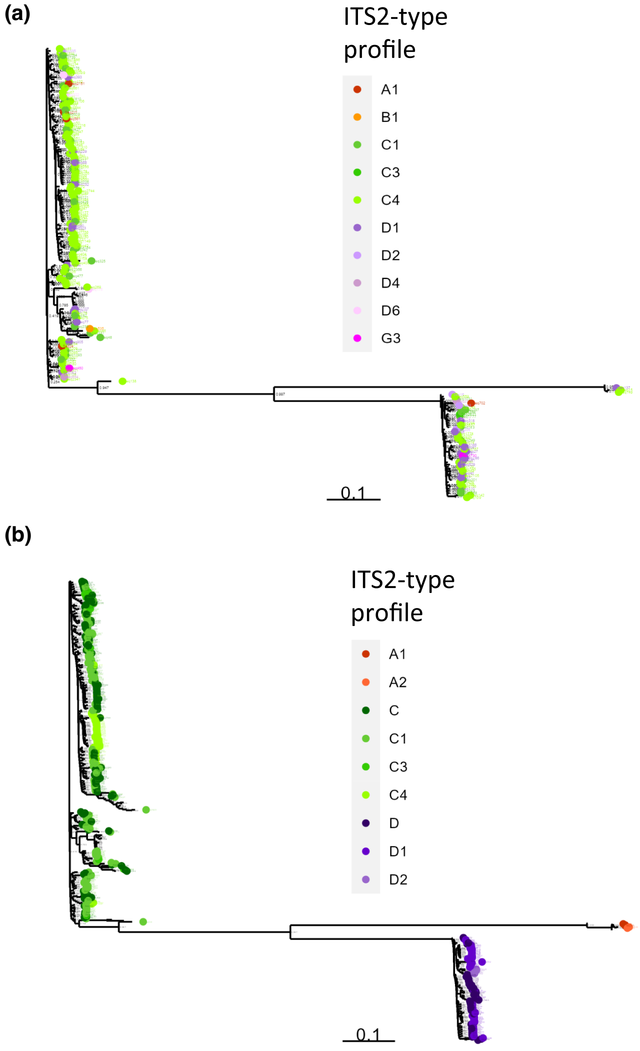

FIGURE 1 Symbiodiniaceae phylogenetic tree using internal transcribed spacer 2 (ITS2) sequences derived from *Pocillopora* spp. The tree is a heuristic variant of a neighbour-joining tree made using FastTree 2 with 1000 resamples and a generalized time-reversible model. The scale bar represents substitutions per site and support values are Shimodaira–Hasegawa-like local supports. Symbiodiniaceae taxonomy is shown on the basis of ITS2-type profiles mirroring the SymPortal database's output. Yet, based on recent taxonomic revision of the Symbiodiniaceae family, these profiles represent different genera and species. Briefly, ITS2-type A profiles correspond to *Symbiodinium* spp., ITS2-type B profiles correspond to *Breviolum* spp., ITS2-type C profiles correspond to *Cladocopium* spp., ITS2-type D profiles correspond to *Durusdinium* spp. and ITS2-type G profiles to *Gerakladium* spp. (a) Phylogenetic tree with the taxonomy assigned using SymPortal. (b) Phylogenetic tree with the taxonomy assigned using NCBI BLAST.

3.4 | Regional differences in Symbiodiniaceae communities

We observed broad differences in Symbiodiniaceae communities across regions (Figure 3). The farthest west location, Djibouti, was the only location with *Symbiodinium* spp. taxa (ITS2-type profiles A1 and A2) and was overall dominated by *Durusdinium* spp., ITS2 type

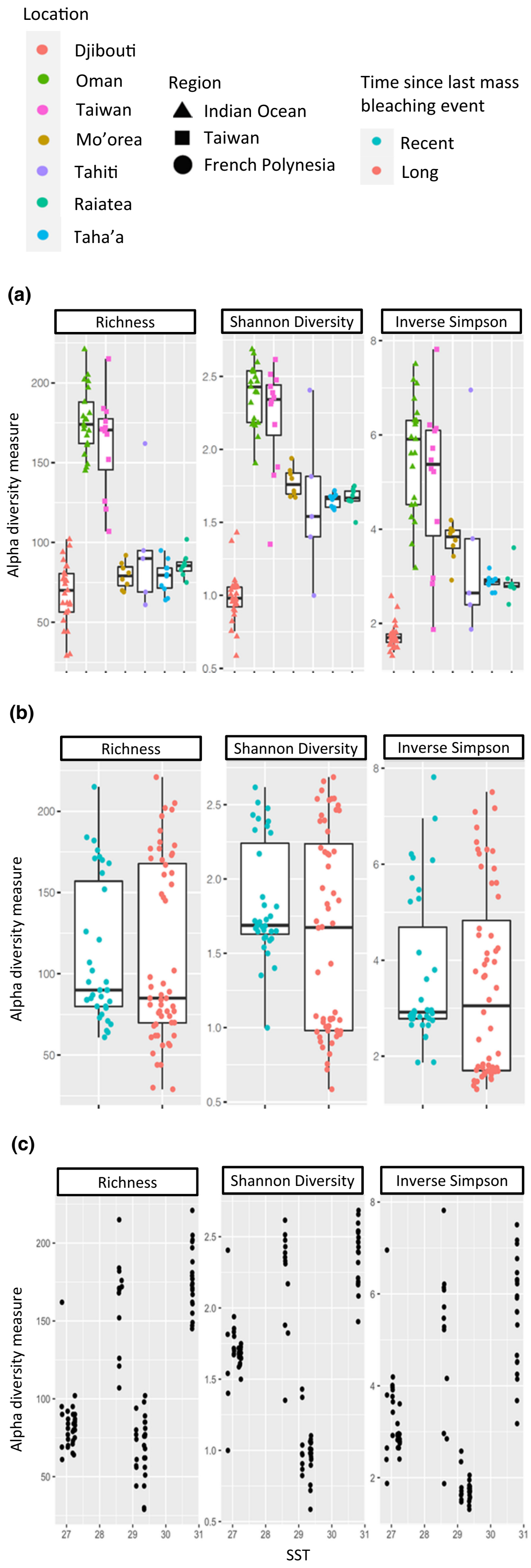

FIGURE 2 Symbiodiniaceae community diversity across locations, regions, time since last mass bleaching event (TSB) and sea surface temperature (SST). The locations are (from west to east): Djibouti, Oman, Taiwan, Taha'a, Raiatea, Mo'orea and Tahiti. The three regions (from west to east) are: the Indian Ocean, Taiwan and French Polynesia. Three alpha diversity indices are shown: richness, Shannon diversity index and inverse Simpson index (left to right on each plot). Differences across locations (as colours) and regions (as symbols) are shown in (a), (b) shows differences across TSB. (c) Scatterplots of SST and richness, Shannon index and inverse Simpson indices.

profile D1 (Figure 3, location 1). Moving from west to east, specimens from Oman and Taiwan had Symbiodiniaceae communities predominantly composed of *Cladocopium* spp. (ITS2-type profiles C; Figure 3, locations 2–3, respectively). Specimens from French Polynesia, which were the furthest east (Figure 3, locations 4–7), were dominated by *Durusdinium* spp. (ITS2-type profile D). Network analysis supported these findings, as sequences from corals originating from Taiwan and Oman, which are in different oceanic basins, clustered with one another, although there was an isolated group of sequences from Oman which formed a separate cluster (Figure 4a). Likewise, all sequences from French Polynesia (Mo'orea, Raiatea, Tahiti and Taha'a), clustered with one another, and sequences from Djibouti did not cluster with other locations and instead formed two independent clusters (Figure 4a). nMDS plots also revealed concordant regional clustering of Symbiodiniaceae communities, where there was an overlap in the ellipses for sequences from Oman and Taiwan, while sequences from Djibouti formed their own separate, 95% confidence ellipse (Figure 4b). Sequences from French Polynesia also clustered with one another in ordination space (Figure 4b).

3.5 | Geographical and environmental factors structuring Symbiodiniaceae communities

Our PERMANOVA analyses revealed that three variables were significantly associated with differences ($p < 0.05$) in ASVs across locations: SST ($p = 0.001$, pseudo-F-statistic$_{1,83}$ = 61.384, $R^2 = 0.238$), region ($p = 0.001$, pseudo-F-statistic$_{2,83}$ = 51.626, $R^2 = 0.401$) and TSB ($p = 0.031$, pseudo-F-statistic$_{1,83}$ = 2.474, $R^2 = 0.01$), as well as the interaction between region and location ($p = 0.003$, pseudo-F-statistic$_{3,83}$ = 2.499, $R^2 = 0.029$; Table S9). Pairwise comparisons revealed that all locations significantly differed from each other except Taha'a versus Raiatea; all regions also significantly differed from one another (all $p < 0.05$; see Tables S10 and S11). Mantel tests revealed that more distant specimens had more distinct Symbiodiniaceae communities (Mantel r statistic = 0.371, $p = 1 \times 10^{-4}$, 9999 permutations). We found the same trend for SST, with specimens collected from regions with more distinct SST values possessing more divergent Symbiodiniaceae communities (Mantel r

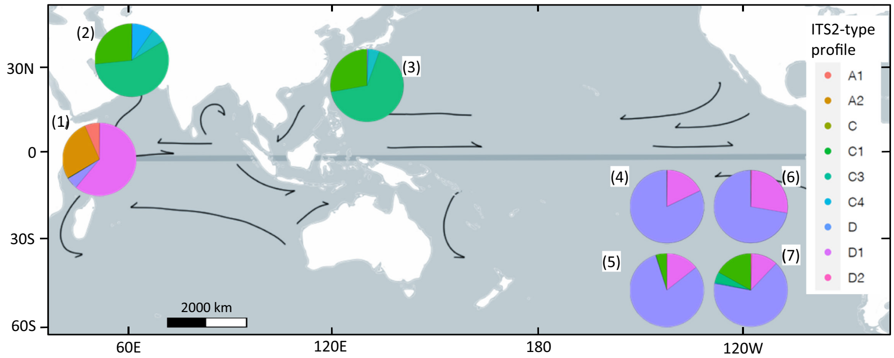

FIGURE 3 Symbiodiniaceae communities from *Pocillopora* spp. across the Indo-Pacific. Pie charts represent community composition on the basis of internal transcribed spacer 2 (ITS2)-type profiles. Symbiodiniaceae taxonomy is shown on the basis of ITS2-type profiles mirroring the SymPortal database's output. Yet, based on recent taxonomic revision of the Symbiodiniaceae family, these profiles represent different genera and species. Briefly, ITS2-type A profiles correspond to *Symbiodinium* spp., ITS2-type B profiles correspond to *Breviolum* spp., ITS2-type C profiles correspond to *Cladocopium* spp. and TS2-type D profiles correspond to *Durusdinium* spp. Major oceanic currents are shown as black arrows, with the equator shown as a thick dark grey line across the map. The map uses an equirectangular projection to best represent distances across studied locations. Locations are as follows (from west to east): (1) Djibouti, (2) Oman, (3) Taiwan, (4) Taha'a, (5) Raiatea, (6) Mo'orea and (7) Tahiti.

statistic = 0.409, $p = 1 \times 10^{-4}$, 9999 permutations). The Mantel r statistic for SST comparisons was marginally larger than for geographical distances, 0.409 versus 0.371, respectively. In comparing effect sizes from our PERMANOVA, SST emerged as the strongest driver of Symbiodiniaceae community composition across all statistically significant factors, followed by region (Table S9).

Our PERMANOVAs for each major ITS2-type profile (A, C and D) further revealed the factors structuring these symbioses. For all genera, on the basis of pseudo-*F*-statistics, SST most strongly impacted the presence/absence of specific ASVs, followed by region and then the interaction of region and location (all $p < 0.05$; see Tables S12–S14). Pairwise post-hoc analyses revealed that for *Symbiodinium* spp., detected ASVs were statistically distinct between the Indian Ocean and French Polynesia, and the Indian Ocean and Taiwan, while for *Cladocopium* spp. and *Durusdinium* spp., pairwise comparisons between all regions were statistically significant (all $p < 0.05$; see Tables S15–S20 pairwise comparisons between locations and regions).

Indicator species analysis identified 79 ASVs that were differentially associated with TSB, while 328 and 267 ASVs were differentially associated with a given location and region, respectively (Tables S21–S23). When focusing on specific locations, all but one ASV (99.45%) from Taiwan were from *Cladocopium* spp., predominantly ITS2-type profile C1 (48.62%), with the sole remaining ASV being *Durusdinium* spp. ITS2-type profile D1 (Table S21). For French Polynesia, all ASVs were *Durusdinium* spp., however the majority of the sequences could not be identified down to a specific ITS2-type profile, for example, D1 (62.5%; Table S22). For specimens from the Indian Ocean (Oman, Djibouti), the associations were more heterogeneous, with 5% of ASVs being *Symbiodinium* spp., 24% *Durusdinium* spp. and 71% *Cladocopium* spp. (Table S22). In comparing these two locations, Djibouti mostly had ASVs from *Durusdinium* spp. (81.82%), while Oman only had *Cladocopium* spp. (Table S21). In recently bleached specimens, 48.84% of the ASVs were *Cladocopium* spp. and 51.16% were *Durusdinium* spp. For specimens that had not recently bleached, 13.89% of ASVs were *Symbiodinium* spp., 30.56% were *Cladocopium* spp. and 55.56% were *Durusdinium* spp. (Table S23).

4 | DISCUSSION

This study represents the only meta-analysis to date that explicitly considers how geographical and environmental parameters structure the Symbiodiniaceae communities associated with a coral genus across its range. Our dataset captures the considerable diversity of thermal parameters, such as SST and TSB, which are found across *Pocillopora*'s range. We find support for our prediction that thermal regimes, here SST, most strongly structured *Pocillopora*–Symbiodiniaceae associations, and yet to a lesser extent, geographical isolation also explained community similarity patterns. Overall, our work underscores previous studies on *Pocillopora*'s diverse Symbiodiniaceae assemblages, while also placing potential mechanisms and consequences of this symbiont flexibility in conversation with previous work on the biogeographical factors impacting the distribution of Indo-Pacific marine taxa.

4.1 | Patterns of diversity in Symbiodiniaceae communities

Although alpha diversity metrics varied across locations, regions, SST and TSB, based on our GLS models only the interaction between Oman and the Indian Ocean was significant for Shannon diversity and inverse Simpson indices; all other associations were not significant. This is in line with the most notable pattern in the alpha diversity data, which was the strong difference between Oman and Djibouti within the Indian Ocean. Oman was the location with the

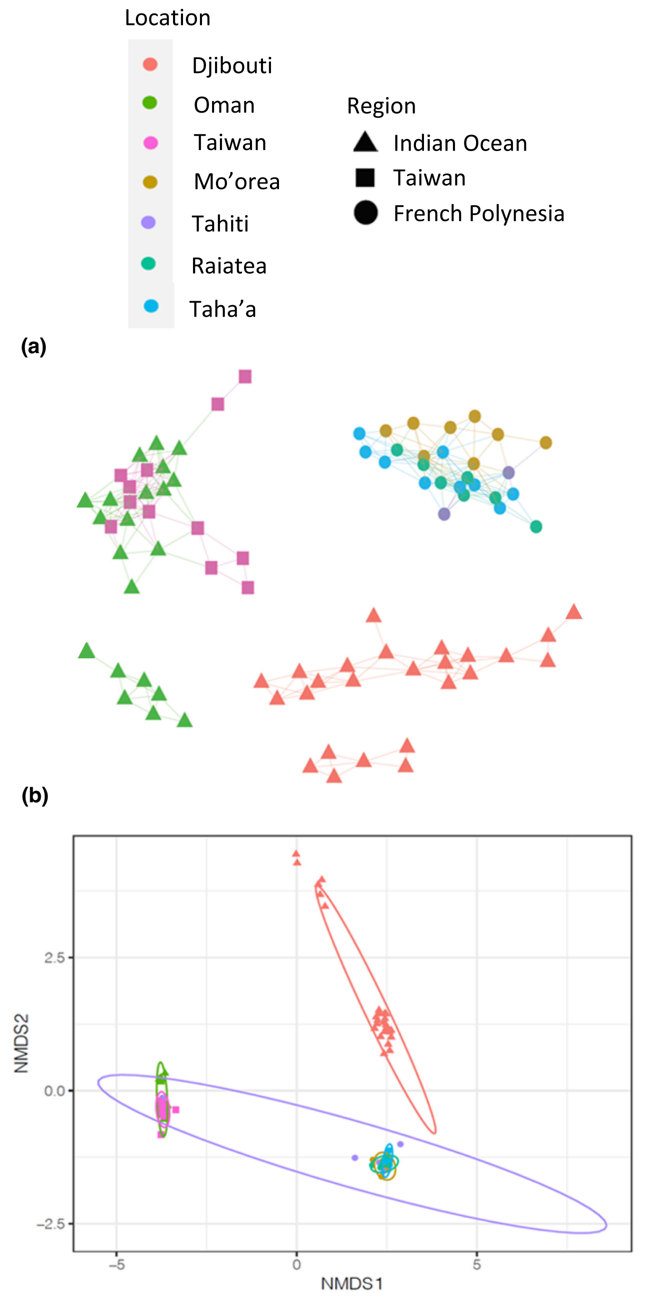

FIGURE 4 Regional differences in Symbiodiniaceae communities from *Pocillopora* spp. across the Indo-Pacific. (a) Symbiodiniaceae networks across locations, where colours represent different locations and shapes are different regions. The locations are as follows (from west to east): Djibouti, Oman, Taiwan, Taha'a, Raiatea, Mo'orea and Tahiti. The regions shown are (from west to east): the Indian Ocean, Taiwan and French Polynesia. The network was created via the Fruchterman–Reingold layout algorithm with Bray–Curtis dissimilarities used as distances. (b) Non-metric multidimensional scaling (nMDS) ordination plots of Symbiodiniaceae across locations and regions, where colours represent different locations and shapes are different regions. Locations and regions are the same as in (a). The nMDS plot implements Bray–Curtis dissimilarities and shows 95% confidence ellipses.

largest values for Shannon diversity and inverse Simpson metrics in the dataset and also experienced the highest SST (30.8°C).

4.2 | Symbiodiniaceae communities are structured by geography and thermal regimes

Our results highlight the diverse Symbiodiniaceae community that is associated with *Pocillopora* spp. and reveal how these symbioses are structured across space and impacted by environmental parameters. *Cladocopium* spp., *Durusdinium* spp. and *Symbiodinium* spp. were most commonly associated with *Pocillopora* spp. within our dataset, in concordance with previous studies (Baker et al., 2017; Brener-Raffalli et al., 2022; LaJeunesse et al., 2004; Ziegler et al., 2017). At the ASV level, both geographical and environmental (SST and TSB) factors significantly influenced Symbiodiniaceae community dissimilarity, as revealed by our Mantel tests and PERMANOVA results. These findings suggest that local thermal regimes represent a key mechanism structuring Symbiodiniaceae communities.

While this study represents the first to investigate Symbiodiniaceae community composition across broad geographical scales for *Pocillopora* spp., previous work has revealed that differences in temperature, light availability, depth and geographical separation can result in location-specific Symbiodiniaceae communities (cf. Cooper et al., 2011; Frade et al., 2008; Wicks et al., 2010). Together, these results may reflect the dual processes of isolation by distance and isolation by adaptation (Nosil et al., 2009; Spurgin et al., 2014; Wang & Bradburd, 2014). For instance, prior studies with *Pocillopora* in the Arabian Peninsula have posited that Symbiodiniaceae communities exhibit high host specificity and site fidelity due to local adaptation to the region's high salinity and temperature regimes (Ziegler et al., 2017); other genera in this region exhibit similar host–symbiont interactions (Howells et al., 2020). Our results indicate that these patterns could be relatively widespread, with Symbiodiniaceae communities strongly associated with local SST, which was the variable with the largest effect size of the statistically significant factors in our PERMANOVAs. For example, despite being in distant regions of the Indo-Pacific, the communities found in Oman and Taiwan, which have similar SSTs (mean of 30.8 and 28.63°C, respectively), were most similar to one another.

However, environmental conditions are not the only factor structuring these symbioses—our analyses also revealed a general pattern of isolation by distance across the Symbiodiniaceae communities. A recent *Pocillopora*-wide study in the Indo-Pacific proposed two newly defined Symbiodiniaceae taxa, *Cladocopium latusorum* and *C. pacificum*. These two taxa are genetically connected across their range but show greater genetic differentiation between populations from distant regions (Turnham et al., 2021). Symbiodiniaceae can disperse over long distances via sea surface currents (Chen et al., 2020; Pettay & LaJeunesse, 2013), and yet currents may also create hydrographic barriers preventing their movement (LaJeunesse et al., 2008). Our results suggest that long-distance dispersal does have limits, and that geographical distance and local SST regimes could act synergistically as a filter that determines the connectivity of Symbiodiniaceae communities across the disparate regions of *Pocillopora*'s range in the Indo-Pacific.

4.3 | Bleaching events as a driver of Symbiodiniaceae community change

A switch from *Cladocopium* spp. to *Durusdinium* spp. has been reported to assist coral colonies experiencing thermal stress by significantly reducing bleaching-induced mortality (Baker et al., 2004; Glynn et al., 2001; Stat & Gates, 2010). Experimental work suggests that both *Symbiodinium* spp. and *Cladocopium* spp. show variable thermotolerance, with strain/species-level differences revealing thermotolerant and sensitive members alike (Díaz-Almeyda et al., 2017; Fisher et al., 2012). Long-term acclimation, or adaptation, of *Symbiodinium* spp. in the Red Sea has also been proposed, given this genus predominates under conditions that encompass a 6.0°C temperature gradient across seasons (Sawall et al., 2014). Our indicator species analyses present a community shift in relation to TSB, with *Symbiodinium* spp. no longer detected in recently bleached specimens, alongside a concordant increase in *Cladocopium* spp. The prevalence of *Durusdinium* spp. and *Cladocopium* spp. was comparable between specimens that had and had not recently bleached, albeit there was marginally less *Cladocopium* spp. found in specimens that had not recently bleached, purporting that perhaps the relative abundance of *Symbiodinium* spp. and *Cladocopium* spp. may be more indicative of responses to thermal stress within our system.

Our indicator species analysis findings are potentially consistent with the notion of coral symbiont shuffling as an adaptive response to thermal stress (see Baker et al., 2004; Buddemeier & Fautin, 1993; Cunning et al., 2015; Glynn et al., 2001; Jones et al., 2008). For instance, in the coral genus *Acropora*, there are trade-offs in hosting *Durusdinium* spp. versus *Cladocopium* spp., with corals associated with *Durusdinium* spp. showing reduced growth rates but reduced temperature-induced bleaching (Jones & Berkelmans, 2010; Jones et al., 2008; Little, 2004). It is thought that this explains the pattern of Symbiodiniaceae communities reverting to their original composition once SSTs return to pre-bleaching conditions, which can take from several months to years (Lewis et al., 2019; Sampayo et al., 2008; Thornhill et al., 2006). We additionally present that the dynamics between *Cladocopium* spp. and *Symbiodinium* spp. may be another critical microbial interaction for *Pocillopora* corals under thermal stress, which has received much less attention to date (but see Sawall et al., 2014).

An important caveat is that none of the *Pocillopora* colonies in our analysed dataset were sampled during a bleaching event, so it is also possible that the stress induced by recent periods of elevated SST were not sufficient to cause a shift in Symbiodiniaceae communities towards more thermotolerant strains/species, or that communities did shift but had reverted back under more benign conditions. It is also possible that the documented elevated SST was not sufficient to trigger thermal stress, perhaps because the Symbiodiniaceae communities were already locally adapted to conditions that would otherwise be denoted as stressful (Howells et al., 2020; Ziegler et al., 2017). Our results suggest that the traditional conceptualization of the benefits of switching to *Durusdinium* spp. may not accurately capture the potential of microorganisms to adapt to thermal stress events (see Abrego et al., 2008). Characterizing the thermotolerance of different Symbiodiniaceae species and strains will be greatly aided by further molecular analyses, with recent genome assemblies providing insights into genomic adaptations to thermal stress and symbiosis establishment (e.g. Liu et al., 2018; Shoguchi et al., 2021).

4.4 | *Pocillopora*–Symbiodiniaceae associations complement previous work on the biogeographical factors structuring marine taxa

The influence of geographical and local environmental factors structuring *Pocillopora*–Symbiodiniaceae associations that we have reported here shows similarities with patterns that have been documented in a diversity of Indo-Pacific marine taxa (i.e. Benzie, 1999; Crandall et al., 2019; DeBoer et al., 2014; Hirschfeld et al., 2021; Lessios et al., 1999; van der Ven et al., 2021). In particular, there is consensus that current-assisted dispersal fails to fully explain contemporary species distributions, with regional environmental regimes being an important factor to consider. Our study adds new understanding by explicitly investigating the distribution of a core member of a microbiome within the context of its host range. In addition, we investigate the role of thermal regimes as a key environmental driver, whereas prior work has focused on factors such as salinity, habitat type (e.g. oceanic vs. benthopelagic), upwelling, or in some cases did not define specific factors but instead tested for 'regional differences' (e.g. Crandall et al., 2019; Hirschfeld et al., 2021; Lessios et al., 2001; but see Keith et al., 2013 where SST is explicitly considered). Although past studies of Symbiodiniaceae distributions have not explicitly considered thermal regimes, temperature has been hypothesized as being highly important in structuring marine host–microbiome interactions (see DeBoer et al., 2014 for *Tridacna* clams; Turnham et al., 2021 for *Pocillopora* corals). Given that climate change is causing SST to approach the thermal limits for many species, and the thermal sensitivity of many marine taxa (particularly corals), it is crucial to understand the influence of this factor for both the host and their microbiome.

4.5 | Further work is needed to improve species delimitations within the *Pocillopora* genus

Although all sequences used for downstream analyses were identified on NCBI as being from '*Pocillopora damicornis*', we recognize that sequences on public repositories are heterogeneous, and that species delineations within this genera are actively evolving (see Johnston, Wyatt, et al., 2022; Oury et al., 2021, 2022; Schmidt-Roach et al., 2013). None of the studies analysed employed whole-genome sequencing to verify the identity of the host, with most implementing only single-marker data, most notably the mitochondrial open reading frame (mtORF), which is the most commonly used to distinguish between *Pocillopora* species given there is concordance between this marker and nuclear and morphometric datasets (Johnston et al., 2017; Pinzón & LaJeunesse, 2011; Pinzón et al., 2013). A few studies have implemented reduced representation sequencing approaches (microsatellites, restriction-site associated DNA sequencing) to further improve genetic delineation of species within this genus, but the findings have yielded complex patterns of genetic differentiation and hybridization at both local and global scales (e.g. Aurelle et al., 2022; Combosch & Vollmer, 2011, 2015; Oury et al., 2021, 2022; van Oppen et al., 2018). With whole-genome approaches becoming more affordable, and the availability of many *Pocillopora* species' reference genomes (*P. acuta*: Vidal-Dupiol et al., 2020; *P. damicornis*: Cunning, Silverstein, et al., 2018; *P. verrucosa*: Buitrago-López et al., 2020), we expect significant advances in our understanding of the genetic basis of thermal stress tolerance within *Pocillopora* (see Fuller et al., 2020 for this work in *Acropora*).

5 | CONCLUSIONS

Our meta-analysis demonstrates the diversity of Symbiodiniaceae assemblages associated with cosmopolitan *Pocillopora* spp. and posits thermal regimes as a key factor driving variation in community composition across this genus' range. Our work suggests that although isolation by adaptation to thermal regimes may be driving some differences across locations, there is also a signal of isolation by distance, indicating limits to connectivity across the Indo-Pacific. In addition, time since the last mass bleaching event emerged as an important factor structuring Symbiodiniaceae communities, supporting previous work presenting Symbiodiniaceae community composition as a potentially adaptive response to local thermal regimes. Our work places coral–Symbiodiniaceae interactions in conversation with a robust corpus on the biogeographical factors structuring marine taxa's distributions, providing a framework for future Symbiodiniaceae community studies in *Pocillopora* corals that aim to characterize how the spatiotemporal patterns of diversity impact resilience to environmental stress.

ACKNOWLEDGEMENTS

Support was provided by a Vanier Canada Graduate Scholarship and NSERC Collaborative Research and Training Experience (CREATE) in Biodiversity, Ecosystem Services and Sustainability (BESS) (V.M.G.), and an NSERC Discovery Grant and Canada Research Chair (R.D.H.B.). We thank Dr. Sean R. Connolly, Savannah Bissegger O'Connor, Frida-Cecilia Acosta-Parenteau and Ninoska Adam for help with the data analyses. No permits were needed to carry out this work, as we used existing data.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Commands and scripts used to execute analyses and generate figures can be found on Zenodo at: https://doi.org/10.5281/zenodo.7297070. Downloaded ITS2 sequences' corresponding NCBI Sequence Read Archive (SRA) accession numbers, and associated metadata, are found in Tables S1–S3.

ORCID

Victoria M. Glynn https://orcid.org/0000-0003-2402-5002
Steven V. Vollmer https://orcid.org/0000-0002-1123-8706
David I. Kline https://orcid.org/0000-0001-5128-9439
Rowan D. H. Barrett https://orcid.org/0000-0003-3044-2531

REFERENCES

Abrego, D., Ulstrup, K. E., Willis, B. L., & van Oppen, M. J. H. (2008). Species–specific interactions between algal endosymbionts and coral hosts define their bleaching response to heat and light stress. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1648), 2273–2282. https://doi.org/10.1098/rspb.2008.0180

Ainsworth, T. D., Heron, S. F., Ortiz, J. C., Mumby, P. J., Grech, A., Ogawa, D., Eakin, C. M., & Leggat, W. (2016). Climate change disables coral bleaching protection on the Great Barrier Reef. *Science*, *352*(6283), 338–342. https://doi.org/10.1126/science.aac7125

Ainsworth, T. D., Thurber, R. V., & Gates, R. D. (2010). The future of coral reefs: A microbial perspective. *Trends in Ecology & Evolution*, *25*(4), 233–240. https://doi.org/10.1016/j.tree.2009.11.001

Altschul, S. F., Gish, W., Miller, W., Myers, E. W., & Lipman, D. J. (1990). Basic local alignment search tool. *Journal of Molecular Biology*, *215*(3), 403–410. https://doi.org/10.1016/S0022-2836(05)80360-2

Anderson, M. J., & Walsh, D. C. I. (2013). PERMANOVA, ANOSIM, and the mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs*, *83*(4), 557–574. https://doi.org/10.1890/12-2010.1

Aurelle, D., Pratlong, M., Oury, N., Haguenauer, A., Gélin, P., Magalon, H., Adjeroud, M., Romans, P., Vidal-Dupiol, J., Claereboudt, M., Noûs, C., Reynes, L., Toulza, E., Bonhomme, F., Mitta, G., & Pontarotti, P. (2022). Species and population genomic differentiation in *Pocillopora* corals (Cnidaria, Hexacorallia). *Genetica*. https://doi.org/10.1007/s10709-022-00165-7

Baker, A. C. (2003). Flexibility and specificity in coral-algal symbiosis: Diversity, ecology, and biogeography of *Symbiodinium*. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 661–689. https://doi.org/10.1146/annurev.ecolsys.34.011802.132417

Baker, A. C., Correa, A. M. S., & Cunning, R. (2017). Diversity, distribution and stability of *Symbiodinium* in Reef corals of the eastern tropical Pacific. In P. W. Glynn, D. P. Manzello, & I. C. Enochs (Eds.), *Coral reefs of the eastern tropical pacific: Persistence and loss in a dynamic environment* (pp. 405–420). Springer. https://doi.org/10.1007/978-94-017-7499-4_13

Baker, A. C., Starger, C. J., McClanahan, T. R., & Glynn, P. W. (2004). Corals' adaptive response to climate change. *Nature*, *430*(7001), 741. https://doi.org/10.1038/430741a

Baldwin, S. (2012). Compute Canada: Advancing computational research. *Journal of Physics: Conference Series*, *341*, 012001. https://doi.org/10.1088/1742-6596/341/1/012001

Benzie, J. A. H. (1999). Genetic structure of coral reef organisms: Ghosts of dispersal past. *American Zoologist*, *39*(1), 131–145. https://doi.org/10.1093/icb/39.1.131

Boulotte, N. M., Dalton, S. J., Carroll, A. G., Harrison, P. L., Putnam, H. M., Peplow, L. M., & van Oppen, M. J. (2016). Exploring the Symbiodinium rare biosphere provides evidence for symbiont switching in reef-building corals. *The ISME Journal*, *10*(11), 2693–2701. https://doi.org/10.1038/ismej.2016.54

Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs*, *27*(4), 326–349. https://doi.org/10.2307/1942268

Brener-Raffalli, K., Vidal-Dupiol, J., Adjeroud, M., Rey, O., Romans, P., Bonhomme, F., Pratlong, M., Haguenauer, A., Pillot, R., Feuillassier, L., Claereboudt, M., Magalon, H., Gélin, P., Pontarotti, P., Aurelle, D., Mitta, G., & Toulza, E. (2022). Gene expression plasticity and frontloading promote thermotolerance in *Pocillopora* corals. *Peer Community Journal*, 2. https://doi.org/10.24072/pcjournal.79

Brown, B. E. (1997). Coral bleaching: Causes and consequences. *Coral Reefs*, *16*(1), S129–S138. https://doi.org/10.1007/s003380050249

Buddemeier, R. W., & Fautin, D. G. (1993). Coral bleaching as an adaptive mechanism. *Bioscience*, *43*(5), 320–326. https://doi.org/10.2307/1312064

Buitrago-López, C., Mariappan, K. G., Cárdenas, A., Gegner, H. M., & Voolstra, C. R. (2020). The genome of the cauliflower coral *Pocillopora verrucosa*. *Genome Biology and Evolution*, *12*(10), 1911–1917. https://doi.org/10.1093/gbe/evaa184

Buttigieg, P. L., & Ramette, A. (2014). A guide to statistical analysis in microbial ecology: A community-focused, living review of multivariate data analyses. *FEMS Microbiology Ecology*, *90*(3), 543–550. https://doi.org/10.1111/1574-6941.12437

Cáceres, M. D., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, *90*(12), 3566–3574. https://doi.org/10.1890/08-1823.1

Callahan, B. J., McMurdie, P. J., & Holmes, S. P. (2017). Exact sequence variants should replace operational taxonomic units in marker-gene data analysis. *The ISME Journal*, *11*(12), 2639–2643. https://doi.org/10.1038/ismej.2017.119

Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A., & Holmes, S. P. (2016). DADA2: High-resolution sample inference from Illumina amplicon data. *Nature Methods*, *13*(7), 581–583. https://doi.org/10.1038/nmeth.3869

Campoy, A. N., Addamo, A. M., Machordom, A., Meade, A., Rivadeneira, M. M., Hernández, C. E., & Venditti, C. (2020). The origin and correlated evolution of symbiosis and coloniality in scleractinian corals. *Frontiers in Marine Science*, *7*. https://doi.org/10.3389/fmars.2020.00461

Carpenter, K. E., Abrar, M., Aeby, G., Aronson, R. B., Banks, S., Bruckner, A., Chiriboga, A., Cortes, J., Delbeek, J. C., DeVantier, L., Edgar, G. J., Edwards, A. J., Fenner, D., Guzman, H. M., Hoeksema, B. W., Hodgson, G., Johan, O., Licuanan, W. Y., Livingstone, S. R., … Wood, E. (2008). One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science*, *321*(5888), 560–563. https://doi.org/10.1126/science.1159196

Chen, B., Yu, K., Qin, Z., Liang, J., Wang, G., Huang, X., Wu, Q., & Jiang, L. (2020). Dispersal, genetic variation, and symbiont interaction network of heat-tolerant endosymbiont *Durusdinium trenchii*: Insights into the adaptive potential of coral to climate change. *Science of the Total Environment*, *723*, 138026. https://doi.org/10.1016/j.scitotenv.2020.138026

Cineas, C., & Dolédec, S. (2022). Species richness and composition of Caribbean aquatic entomofauna: Role of climate, Island area, and distance to mainland. *Frontiers of Biogeography*, *14*(3). https://doi.org/10.21425/F5FBG54479

Coleman, A. W., Suarez, A., & Goff, L. J. (1994). Molecular delineation of species and syngens in volvocacean green algae (Chlorophyta). *Journal of Phycology*, *30*(1), 80–90. https://doi.org/10.1111/j.0022-3646.1994.00080.x

Combosch, D. J., & Vollmer, S. V. (2011). Population genetics of an ecosystem-defining reef coral *Pocillopora damicornis* in the Tropical Eastern Pacific. *PLoS One*, *6*(8), e21200. https://doi.org/10.1371/journal.pone.0021200

Combosch, D. J., & Vollmer, S. V. (2015). Trans-Pacific RAD-Seq population genomics confirms introgressive hybridization in eastern Pacific *Pocillopora* corals. *Molecular Phylogenetics and Evolution*, *88*, 154–162. https://doi.org/10.1016/j.ympev.2015.03.022

Cooper, T. F., Berkelmans, R., Ulstrup, K. E., Weeks, S., Radford, B., Jones, A. M., Doyle, J., Canto, M., O'Leary, R. A., & Van Oppen, M. J. H. (2011). Environmental factors controlling the distribution of *Symbiodinium* harboured by the coral *Acropora millepora* on the Great Barrier Reef. *PLoS One*, *6*(10), e25536. https://doi.org/10.1371/journal.pone.0025536

Coppard, S. E., Jessop, H., & Lessios, H. A. (2021). Phylogeography, colouration, and cryptic speciation across the Indo-Pacific in the sea urchin genus *Echinothrix*. *Scientific Reports*, *11*(1), 1. https://doi.org/10.1038/s41598-021-95872-0

Crandall, E. D., Riginos, C., Bird, C. E., Liggins, L., Treml, E., Beger, M., Barber, P. H., Connolly, S. R., Cowman, P. F., DiBattista, J. D., Eble, J. A., Magnuson, S. F., Horne, J. B., Kochzius, M., Lessios, H. A., Liu, S. Y. V., Ludt, W. B., Madduppa, H., Pandolfi, J. M., … Gaither, M. R. (2019). The molecular biogeography of the Indo-Pacific: Testing hypotheses with multispecies genetic patterns. *Global Ecology and Biogeography*, *28*(7), 943–960. https://doi.org/10.1111/geb.12905

Cunning, R., Bay, R. A., Gillette, P., Baker, A. C., & Traylor-Knowles, N. (2018). Comparative analysis of the *Pocillopora damicornis* genome highlights role of immune system in coral evolution. *Scientific Reports*, *8*(1), 16134. https://doi.org/10.1038/s41598-018-34459-8

Cunning, R., Gillette, P., Capo, T., Galvez, K., & Baker, A. C. (2015). Growth tradeoffs associated with thermotolerant symbionts in the coral *Pocillopora damicornis* are lost in warmer oceans. *Coral Reefs*, *34*(1), 155–160. https://doi.org/10.1007/s00338-014-1216-4

Cunning, R., Glynn, P. W., & Baker, A. C. (2013). Flexible associations between *Pocillopora* corals and *Symbiodinium* limit utility of symbiosis ecology in defining species. *Coral Reefs*, *32*(3), 795–801. https://doi.org/10.1007/s00338-013-1036-y

Cunning, R., Silverstein, R. N., & Baker, A. C. (2018). Symbiont shuffling linked to differential photochemical dynamics of *Symbiodinium* in three Caribbean reef corals. *Coral Reefs*, *37*(1), 145–152. https://doi.org/10.1007/s00338-017-1640-3

Dastogeer, K. M. G., Zahan, M. I., Rhaman, M. S., Sarker, M. S. A., & Chakraborty, A. (2022). Microbe-mediated thermotolerance in plants and pertinent mechanisms- a meta-analysis and review. *Frontiers in Microbiology*, *13*, 833566. https://doi.org/10.3389/fmicb.2022.833566

D'Croz, L., & O'Dea, A. (2007). Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll. *Estuarine, Coastal and Shelf Science*, *73*(1), 325–340. https://doi.org/10.1016/j.ecss.2007.01.013

DeBoer, T. S., Naguit, M. R. A., Erdmann, M. V., Ablan-Lagman, M. C. A., Carpenter, K. E., Toha, A. H. A., & Barber, P. H. (2014). Concordance between phylogeographic and biogeographic boundaries in the coral triangle: Conservation implications based on comparative analyses of multiple giant clam species. *Bulletin of Marine Science*, *90*(1), 277–300. https://doi.org/10.5343/bms.2013.1003

Díaz-Almeyda, E. M., Prada, C., Ohdera, A. H., Moran, H., Civitello, D. J., Iglesias-Prieto, R., Carlo, T. A., LaJeunesse, T. C., & Medina, M. (2017). Intraspecific and interspecific variation in thermotolerance and photoacclimation in *Symbiodinium* dinoflagellates. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1868), 20171767. https://doi.org/10.1098/rspb.2017.1767

Douglas, A. E. (2003). Coral bleaching––How and why? *Marine Pollution Bulletin*, *46*(4), 385–392. https://doi.org/10.1016/S0025-326X(03)00037-7

Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, *67*(3), 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2

Edgar, R. C. (2010). Search and clustering orders of magnitude faster than BLAST. *Bioinformatics*, *26*(19), 2460–2461. https://doi.org/10.1093/bioinformatics/btq461

Epstein, H. E., Torda, G., & van Oppen, M. J. H. (2019). Relative stability of the *Pocillopora acuta* microbiome throughout a thermal stress event. *Coral Reefs*, *38*(2), 373–386. https://doi.org/10.1007/s00338-019-01783-y

Fine, M., Gildor, H., & Genin, A. (2013). A coral reef refuge in the Red Sea. *Global Change Biology*, *19*(12), 3640–3647. https://doi.org/10.1111/gcb.12356

Fisher, P. L., Malme, M. K., & Dove, S. (2012). The effect of temperature stress on coral–*Symbiodinium* associations containing distinct symbiont types. *Coral Reefs*, *31*(2), 473–485. https://doi.org/10.1007/s00338-011-0853-0

Fitzpatrick, S. W., Gerberich, J. C., Kronenberger, J. A., Angeloni, L. M., & Funk, W. C. (2015). Locally adapted traits maintained in the face of high gene flow. *Ecology Letters*, *18*(1), 37–47. https://doi.org/10.1111/ele.12388

Frade, P. R., Bongaerts, P., Winkelhagen, A. J. S., Tonk, L., & Bak, R. P. M. (2008). In situ photobiology of corals over large depth ranges: A multivariate analysis on the roles of environment, host, and algal symbiont. *Limnology and Oceanography*, *53*(6), 2711–2723. https://doi.org/10.4319/lo.2008.53.6.2711

Frankowiak, K., Wang, X. T., Sigman, D. M., Gothmann, A. M., Kitahara, M. V., Mazur, M., Meibom, A., & Stolarski, J. (2016). Photosymbiosis and the expansion of shallow-water corals. *Science Advances*, *2*(11), e1601122. https://doi.org/10.1126/sciadv.1601122

Fruchterman, T. M. J., & Reingold, E. M. (1991). Graph drawing by force-directed placement. *Software: Practice and Experience*, *21*(11), 1129–1164. https://doi.org/10.1002/spe.4380211102

Fuller, Z. L., Mocellin, V. J. L., Morris, L. A., Cantin, N., Shepherd, J., Sarre, L., Peng, J., Liao, Y., Pickrell, J., Andolfatto, P., Matz, M., Bay, L. K., & Przeworski, M. (2020). Population genetics of the coral *Acropora millepora*: Toward genomic prediction of bleaching. *Science*, *369*(6501), eaba4674. https://doi.org/10.1126/science.aba4674

Glynn, P. W. (1996). Coral reef bleaching: Facts, hypotheses and implications. *Global Change Biology*, *2*(6), 495–509. https://doi.org/10.1111/j.1365-2486.1996.tb00063.x

Glynn, P. W., Maté, J. L., Baker, A. C., & Calderón, M. O. (2001). Coral bleaching and mortality in Panama and Ecuador during the 1997–1998 El Nino-Southern Oscillation event: Spatial/temporal patterns and comparisons with the 1982–1983 event. *Bulletin of Marine Science*, *69*(1), 31.

Hijmans, R. J. (2019). *geosphere: Spherical trigonometry*. R package version 1.5-10. https://CRAN.R-project.org/package=geosphere

Hirschfeld, M., Dudgeon, C., Sheaves, M., & Barnett, A. (2021). Barriers in a sea of elasmobranchs: From fishing for populations to testing hypotheses in population genetics. *Global Ecology and Biogeography*, *30*(11), 2147–2163. https://doi.org/10.1111/geb.13379

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research*, *50*(8), 839–866. https://doi.org/10.1071/mf99078

Hoegh-Guldberg, O. (2011). The impact of climate change on coral reef ecosystems. In *Coral reefs: An ecosystem in transition* (pp. 391–403). https://doi.org/10.1007/978-94-007-0114-4_22

Hoegh-Guldberg, O., Jones, R. J., Ward, S., & Loh, W. K. (2002). Is coral bleaching really adaptive? *Nature*, *415*(6872), 601–602. https://doi.org/10.1038/415601a

Howells, E. J., Bauman, A. G., Vaughan, G. O., Hume, B. C. C., Voolstra, C. R., & Burt, J. A. (2020). Corals in the hottest reefs in the world exhibit symbiont fidelity not flexibility. *Molecular Ecology*, *29*(5), 899–911. https://doi.org/10.1111/mec.15372

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., Baird, A. H., Baum, J. K., Berumen, M. L., Bridge, T. C., Claar, D. C., Eakin, C. M., Gilmour, J. P., Graham, N. A. J., Harrison, H., Hobbs, J.-P. A., Hoey, A. S., Hoogenboom, M., Lowe, R. J., … Wilson, S. K. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, *359*(6371), 80–83. https://doi.org/10.1126/science.aan8048

Hume, B. C. C., Smith, E. G., Ziegler, M., Warrington, H. J. M., Burt, J. A., LaJeunesse, T. C., Wiedenmann, J., & Voolstra, C. R. (2019). SymPortal: A novel analytical framework and platform for coral algal symbiont next-generation sequencing ITS2 profiling. *Molecular Ecology Resources*, *19*(4), 1063–1080. https://doi.org/10.1111/1755-0998.13004

Hume, B. C. C., Ziegler, M., Poulain, J., Pochon, X., Romac, S., Boissin, E., de Vargas, C., Planes, S., Wincker, P., & Voolstra, C. R. (2018). An improved primer set and amplification protocol with increased specificity and sensitivity targeting the *Symbiodinium* ITS2 region. *PeerJ*, *6*. https://doi.org/10.7717/peerj.4816

Iltis, C., Tougeron, K., Hance, T., Louâpre, P., & Foray, V. (2022). A perspective on insect—Microbe holobionts facing thermal fluctuations in a climate-change context. *Environmental Microbiology*, *24*(1), 18–29. https://doi.org/10.1111/1462-2920.15826

Johnston, E. C., Cunning, R., & Burgess, S. C. (2022). Cophylogeny and specificity between cryptic coral species (*Pocillopora* spp.) at Mo'orea and their symbionts (Symbiodiniaceae). *Molecular Ecology*, *31*(20), 5368–5385. https://doi.org/10.1111/mec.16654

Johnston, E. C., Forsman, Z. H., Flot, J.-F., Schmidt-Roach, S., Pinzón, J. H., Knapp, I. S. S., & Toonen, R. J. (2017). A genomic glance through the fog of plasticity and diversification in *Pocillopora*. *Scientific Reports*, *7*(1), 5991. https://doi.org/10.1038/s41598-017-06085-3

Johnston, E. C., Wyatt, A. S. J., Leichter, J. J., & Burgess, S. C. (2022). Niche differences in co-occurring cryptic coral species (*Pocillopora* spp.). *Coral Reefs*, *41*(3), 767–778. https://doi.org/10.1007/s00338-021-02107-9

Jones, A., & Berkelmans, R. (2010). Potential costs of acclimatization to a warmer climate: Growth of a reef coral with heat tolerant vs. sensitive symbiont types. *PLoS One*, *5*(5), e10437. https://doi.org/10.1371/journal.pone.0010437

Jones, A. M., Berkelmans, R., van Oppen, M. J. H., Mieog, J. C., & Sinclair, W. (2008). A community change in the algal endosymbionts of a scleractinian coral following a natural bleaching event: Field evidence of acclimatization. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1641), 1359–1365. https://doi.org/10.1098/rspb.2008.0069

Keith, S. A., Baird, A. H., Hughes, T. P., Madin, J. S., & Connolly, S. R. (2013). Faunal breaks and species composition of Indo-Pacific corals: The role of plate tectonics, environment and habitat distribution. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1763), 20130818. https://doi.org/10.1098/rspb.2013.0818

Kelly, L. W., Williams, G. J., Barott, K. L., Carlson, C. A., Dinsdale, E. A., Edwards, R. A., Haas, A. F., Haynes, M., Lim, Y. W., McDole, T., Nelson, C. E., Sala, E., Sandin, S. A., Smith, J. E., Vermeij, M. J. A., Youle, M., & Rohwer, F. (2014). Local genomic adaptation of coral reef-associated microbiomes to gradients of natural variability and anthropogenic stressors. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(28), 10227–10232. https://doi.org/10.1073/pnas.1403319111

Kemp, D. W., Hernandez-Pech, X., Iglesias-Prieto, R., Fitt, W. K., & Schmidt, G. W. (2014). Community dynamics and physiology of *Symbiodinium* spp. before, during, and after a coral bleaching event. *Limnology and Oceanography*, *59*(3), 788–797. https://doi.org/10.4319/lo.2014.59.3.0788

Kemp, D. W., Thornhill, D. J., Rotjan, R. D., Iglesias-Prieto, R., Fitt, W. K., & Schmidt, G. W. (2015). Spatially distinct and regionally endemic *Symbiodinium* assemblages in the threatened Caribbean reef-building coral *Orbicella faveolata*. *Coral Reefs*, *34*(2), 535–547. https://doi.org/10.1007/s00338-015-1277-z

Kennedy, E. V., Tonk, L., Foster, N. L., Chollett, I., Ortiz, J.-C., Dove, S., Hoegh-Guldberg, O., Mumby, P. J., & Stevens, J. R. (2016). *Symbiodinium* biogeography tracks environmental patterns rather than host genetics in a key Caribbean reef-builder, *Orbicella annularis*. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1842), 20161938. https://doi.org/10.1098/rspb.2016.1938

LaJeunesse, T., Bhagooli, R., Hidaka, M., deVantier, L., Done, T., Schmidt, G., Fitt, W., & Hoegh-Guldberg, O. (2004). Closely related *Symbiodinium* spp. differ in relative dominance in coral reef host communities across environmental, latitudinal and biogeographic gradients. *Marine Ecology Progress Series*, *284*, 147–161. https://doi.org/10.3354/meps284147

LaJeunesse, T. C. (2002). Diversity and community structure of symbiotic dinoflagellates from Caribbean coral reefs. *Marine Biology*, *141*(2), 387–400. https://doi.org/10.1007/s00227-002-0829-2

LaJeunesse, T. C. (2005). "Species" radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition. *Molecular Biology and Evolution*, *22*(3), 570–581. https://doi.org/10.1093/molbev/msi042

LaJeunesse, T. C., Bonilla, H. R., Warner, M. E., Wills, M., Schmidt, G. W., & Fitt, W. K. (2008). Specificity and stability in high latitude eastern Pacific coral-algal symbioses. *Limnology and Oceanography*, *53*(2), 719–727. https://doi.org/10.4319/lo.2008.53.2.0719

LaJeunesse, T. C., Parkinson, J. E., Gabrielson, P. W., Jeong, H. J., Reimer, J. D., Voolstra, C. R., & Santos, S. R. (2018). Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of Coral endosymbionts. *Current Biology*, *28*(16), 2570–2580.e6. https://doi.org/10.1016/j.cub.2018.07.008

LaJeunesse, T. C., Smith, R., Walther, M., Pinzón, J., Pettay, D. T., McGinley, M., Aschaffenburg, M., Medina-Rosas, P., Cupul-Magaña, A. L., Pérez, A. L., Reyes-Bonilla, H., & Warner, M. E. (2010). Host–symbiont recombination versus natural selection in the response of coral–dinoflagellate symbioses to environmental disturbance. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1696), 2925–2934. https://doi.org/10.1098/rspb.2010.0385

Lenth, R. V. (2021). *emmeans: Estimated marginal means, aka least-squares means*. R package version 1.6.3. https://CRAN.R-project.org/package=emmeans

Lessios, H. A., Kane, J., & Robertson, D. R. (2003). Phylogeography of the Pantropical Sea urchin *Tripneustes*: Contrasting patterns of population structure between oceans. *Evolution*, *57*(9), 2026–2036. https://doi.org/10.1111/j.0014-3820.2003.tb00382.x

Lessios, H. A., Kessing, B. D., & Pearse, J. S. (2001). Population structure and speciation in tropical seas: Global phylogeography of the sea urchin *Diadema*. *Evolution*, *55*(5), 955–975. https://doi.org/10.1111/j.0014-3820.2001.tb00613.x

Lessios, H. A., Kessing, B. D., Robertson, D. R., & Paulay, G. (1999). Phylogeography of the pantropical sea urchin *Eucidaris* in relation to land barriers and ocean currents. *Evolution*, *53*(3), 806–817. https://doi.org/10.1111/j.1558-5646.1999.tb05374.x

Lewis, C., Neely, K., & Rodriguez-Lanetty, M. (2019). Recurring episodes of thermal stress shift the balance from a dominant host-specialist to a background host-generalist zooxanthella in the threatened pillar Coral. *Dendrogyra cylindrus*. *Frontiers in Marine Science*, *6*, 5. https://doi.org/10.3389/fmars.2019.00005

Lim, K. C., Then, A. Y.-H., Wee, A. K. S., Sade, A., Rumpet, R., & Loh, K.-H. (2021). Brown banded bamboo shark (*Chiloscyllium punctatum*) shows high genetic diversity and differentiation in Malaysian waters. *Scientific Reports*, *11*(1), 1. https://doi.org/10.1038/s41598-021-94257-7

Little, A. F. (2004). Flexibility in algal endosymbioses shapes growth in reef corals. *Science*, *304*(5676), 1492–1494. https://doi.org/10.1126/science.1095733

Liu, H., Stephens, T. G., González-Pech, R. A., Beltran, V. H., Lapeyre, B., Bongaerts, P., Cooke, I., Aranda, M., Bourne, D. G., Forêt, S., Miller, D. J., van Oppen, M. J. H., Voolstra, C. R., Ragan, M. A., & Chan, C. X. (2018). *Symbiodinium* genomes reveal adaptive evolution of functions related to coral-dinoflagellate symbiosis. *Communications Biology*, *1*(1), 1–11. https://doi.org/10.1038/s42003-018-0098-3

Lopes da Silva Ferrette, B., Coelho, R., Peddemors, V. M., Ovenden, J. R., De Franco, B. A., Oliveira, C., Foresti, F., & Mendonça, F. F. (2021). Global phylogeography of the smooth hammerhead shark: Glacial refugia and historical migration patterns. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*(9), 2348–2368. https://doi.org/10.1002/aqc.3629

Manning, M. M., & Gates, R. D. (2008). Diversity in populations of free-living *Symbiodinium* from a Caribbean and Pacific reef. *Limnology and Oceanography*, *53*(5), 1853–1861. https://doi.org/10.4319/lo.2008.53.5.1853

Manzello, D. P., Kleypas, J. A., Budd, D. A., Eakin, C. M., Glynn, P. W., & Langdon, C. (2008). Poorly cemented coral reefs of the eastern tropical Pacific: Possible insights into reef development in a high-CO_2 world. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(30), 10450–10455. https://doi.org/10.1073/pnas.0712167105

Manzello, D. P., Matz, M. V., Enochs, I. C., Valentino, L., Carlton, R. D., Kolodziej, G., Serrano, X., Towle, E. K., & Jankulak, M. (2019). Role of host genetics and heat-tolerant algal symbionts in sustaining populations of the endangered coral *Orbicella faveolata* in the Florida keys with ocean warming. *Global Change Biology*, *25*(3), 1016–1031. https://doi.org/10.1111/gcb.14545

Martinez Arbizu, P. (2020). *pairwiseAdonis: Pairwise multilevel comparison using adonis*. R package version 0.4. https://github.com/pmartinezarbizu/pairwiseAdonis

McGinley, M., Aschaffenburg, M., Pettay, D., Smith, R., LaJeunesse, T., & Warner, M. (2012). *Symbiodinium* spp. in colonies of eastern Pacific *Pocillopora* spp. are highly stable despite the prevalence of low-abundance background populations. *Marine Ecology Progress Series*, *462*, 1–7. https://doi.org/10.3354/meps09914

McMurdie, P. J., & Holmes, S. (2013). Phyloseq: An R package for reproducible interactive analysis and graphics of microbiome census data. *PLoS One*, *8*(4), e61217. https://doi.org/10.1371/journal.pone.0061217

McMurdie, P. J., & Holmes, S. (2014). Waste not, want not: Why rarefying microbiome data is inadmissible. *PLoS Computational Biology*, *10*(4), e1003531. https://doi.org/10.1371/journal.pcbi.1003531

NOAA Coral Reef Watch. (2000). *NOAA Coral Reef Watch operational daily near-real-time global 5-km satellite Coral bleaching monitoring products (June 1, 2008–Nov. 31, 2014) [data set]*. NOAA Coral Reef Watch. Data set. https://pae-paha.pacioos.hawaii.edu/erddap/griddap/dhw_5km.graph

Nosil, P., Funk, D. J., & Ortiz-Barrientos, D. (2009). Divergent selection and heterogeneous genomic divergence. *Molecular Ecology*, *18*(3), 375–402. https://doi.org/10.1111/j.1365-294X.2008.03946.x

O'Brien, P. A., Tan, S., Yang, C., Frade, P. R., Andreakis, N., Smith, H. A., Miller, D. J., Webster, N. S., Zhang, G., & Bourne, D. G. (2020). Diverse coral reef invertebrates exhibit patterns of phylosymbiosis. *The ISME Journal*, *14*(9), 9. https://doi.org/10.1038/s41396-020-0671-x

O'Dea, A., Hoyos, N., Rodríguez, F., Degracia, B., & De Gracia, C. (2012). History of upwelling in the tropical eastern Pacific and the paleogeography of the isthmus of Panama. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *348–349*, 59–66. https://doi.org/10.1016/j.palaeo.2012.06.007

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M., Szoecs, E. H., & Wagner, H. (2020). *vegan: Community Ecology Package*. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Osman, E. O., Suggett, D. J., Voolstra, C. R., Pettay, D. T., Clark, D. R., Pogoreutz, C., Sampayo, E. M., Warner, M. E., & Smith, D. J. (2020). Coral microbiome composition along the northern Red Sea suggests high plasticity of bacterial and specificity of endosymbiotic dinoflagellate communities. *Microbiome*, *8*. https://doi.org/10.1186/s40168-019-0776-5

Oury, N., Gélin, P., Rajaonarivelo, M., & Magalon, H. (2021). Exploring the *Pocillopora* cryptic diversity: A new genetic lineage in the Western Indian Ocean or remnants from an ancient one? *Marine Biodiversity*, *52*(1), 5. https://doi.org/10.1007/s12526-021-01246-0

Oury, N., Noël, C., Mona, S., Aurelle, D., & Magalon, H. (2022). From genomics to integrative taxonomy? The case study of *Pocillopora* corals. *bioRxiv*, 22.10.04.510617. https://doi.org/10.1101/2022.10.04.510617

Paldor, N., & Anati, D. A. (1979). Seasonal variations of temperature and salinity in the Gulf of Elat (Aqaba). *Deep Sea Research Part A. Oceanographic Research Papers*, *26*(6), 661–672. https://doi.org/10.1016/0198-0149(79)90039-6

Pappalardo, P., Pringle, J. M., Wares, J. P., & Byers, J. E. (2015). The location, strength, and mechanisms behind marine biogeographic boundaries of the east coast of North America. *Ecography*, *38*(7), 722–731. https://doi.org/10.1111/ecog.01135

Paulson, J. N., Stine, O. C., Bravo, H. C., & Pop, M. (2013). Differential abundance analysis for microbial marker-gene surveys. *Nature Methods*, *10*(12), 1200–1202. https://doi.org/10.1038/nmeth.2658

Pettay, D. T., & LaJeunesse, T. C. (2013). Long-range dispersal and high-latitude environments influence the population structure of a "stress-tolerant" dinoflagellate endosymbiont. *PLoS One*, *8*(11), e79208. https://doi.org/10.1371/journal.pone.0079208

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2021). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-153. https://CRAN.R-project.org/package=nlme

Pinzón, J. H., & LaJeunesse, T. C. (2011). Species delimitation of common reef corals in the genus *Pocillopora* using nucleotide sequence phylogenies, population genetics and symbiosis ecology. *Molecular Ecology*, *20*(2), 311–325. https://doi.org/10.1111/j.1365-294X.2010.04939.x

Pinzón, J. H., Sampayo, E., Cox, E., Chauka, L. J., Chen, C. A., Voolstra, C. R., & LaJeunesse, T. C. (2013). Blind to morphology: Genetics identifies several widespread ecologically common species and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). *Journal of Biogeography*, *40*(8), 1595–1608. https://doi.org/10.1111/jbi.12110

Pochon, X., Pawlowski, J., Zaninetti, L., & Rowan, R. (2001). High genetic diversity and relative specificity among *Symbiodinium*-like endosymbiotic dinoflagellates in soritid foraminiferans. *Marine Biology*, *139*(6), 1069–1078. https://doi.org/10.1007/s002270100674

Pollock, F. J., McMinds, R., Smith, S., Bourne, D. G., Willis, B. L., Medina, M., Thurber, R. V., & Zaneveld, J. R. (2018). Coral-associated bacteria demonstrate phylosymbiosis and cophylogeny. *Nature Communications*, *9*(1), 1. https://doi.org/10.1038/s41467-018-07275-x

Price, M. N., Dehal, P. S., & Arkin, A. P. (2010). FastTree 2—Approximately maximum-likelihood trees for large alignments. *PLoS One*, *5*(3), e9490. https://doi.org/10.1371/journal.pone.0009490

Quigley, K. M., Willis, B. L., & Kenkel, C. D. (2019). Transgenerational inheritance of shuffled symbiont communities in the coral *Montipora digitata*. *Scientific Reports*, *9*(1), 13328. https://doi.org/10.1038/s41598-019-50045-y

R Core Team. (2021). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. https://www.R-project.org/

Ricci, F., Tandon, K., Black, J. R., Lê Cao, K.-A., Blackall, L. L., & Verbruggen, H. (2022). Host traits and phylogeny contribute to shaping coral-bacterial symbioses. *MSystems*, *7*(2), e00044-22. https://doi.org/10.1128/msystems.00044-22

Rodríguez-Román, A., Hernández-Pech, X., Thome, P. E., Enríquez, S., & Iglesias-Prieto, R. (2006). Photosynthesis and light utilization in the Caribbean coral *Montastraea faveolata* recovering from a bleaching event. *Limnology and Oceanography*, *51*(6), 2702–2710. https://doi.org/10.4319/lo.2006.51.6.2702

Rognes, T., Flouri, T., Nichols, B., Quince, C., & Mahé, F. (2016). VSEARCH: A versatile open source tool for metagenomics. *PeerJ*, *4*, e2584. https://doi.org/10.7717/peerj.2584

Rouzé, H., Lecellier, G., Pochon, X., Torda, G., & Berteaux-Lecellier, V. (2019). Unique quantitative Symbiodiniaceae signature of coral colonies revealed through spatio-temporal survey in Mo'orea. *Scientific Reports*, *9*(1), 7921. https://doi.org/10.1038/s41598-019-44017-5

Rowan, R., Knowlton, N., Baker, A., & Jara, J. (1997). Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature*, *388*(6639), 265–269. https://doi.org/10.1038/40843

Sampayo, E. M., Ridgway, T., Bongaerts, P., & Hoegh-Guldberg, O. (2008). Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(30), 10444–10449. https://doi.org/10.1073/pnas.0708049105

Sawall, Y., Al-Sofyani, A., Banguera-Hinestroza, E., & Voolstra, C. R. (2014). Spatio-temporal analyses of *Symbiodinium* physiology of the coral *Pocillopora verrucosa* along large-scale nutrient and temperature gradients in the Red Sea. *PLoS One*, *9*(8), e103179. https://doi.org/10.1371/journal.pone.0103179

Schmidt-Roach, S., Lundgren, P., Miller, K. J., Gerlach, G., Noreen, A. M. E., & Andreakis, N. (2013). Assessing hidden species diversity in the coral *Pocillopora damicornis* from eastern Australia. *Coral Reefs*, *32*(1), 161–172. https://doi.org/10.1007/s00338-012-0959-z

Shoguchi, E., Beedessee, G., Hisata, K., Tada, I., Narisoko, H., Satoh, N., Kawachi, M., & Shinzato, C. (2021). A new dinoflagellate genome illuminates a conserved gene cluster involved in sunscreen biosynthesis. *Genome Biology and Evolution*, *13*(2). https://doi.org/10.1093/gbe/evaa235

Sievers, F., & Higgins, D. G. (2021). The clustal omega multiple alignment package. In K. Katoh (Ed.), *Multiple sequence alignment: Methods and protocols* (pp. 3–16). Springer. https://doi.org/10.1007/978-1-0716-1036-7_1

Silverman, J. D., Shenhav, L., Halperin, E., Mukherjee, S., & David, L. A. (2018). Statistical considerations in the design and analysis of longitudinal microbiome studies. *bioRxiv*, 448332. https://doi.org/10.1101/448332

Smith, H., Epstein, H., & Torda, G. (2017). The molecular basis of differential morphology and bleaching thresholds in two morphs of the coral *Pocillopora acuta*. *Scientific Reports*, *7*(1), 10066. https://doi.org/10.1038/s41598-017-10560-2

Spurgin, L. G., Illera, J. C., Jorgensen, T. H., Dawson, D. A., & Richardson, D. S. (2014). Genetic and phenotypic divergence in an Island bird: Isolation by distance, by colonization or by adaptation? *Molecular Ecology*, *23*(5), 1028–1039. https://doi.org/10.1111/mec.12672

Stat, M., & Gates, R. D. (2010). Clade D *Symbiodinium* in Scleractinian corals: A "nugget" of hope, a selfish opportunist, an ominous sign, or all of the above? *Journal of Marine Biology*, *2011*, e730715. https://doi.org/10.1155/2011/730715

Stat, M., Pochon, X., Cowie, R., & Gates, R. (2009). Specificity in communities of *Symbiodinium* in corals from Johnston Atoll. *Marine Ecology Progress Series*, *386*, 83–96. https://doi.org/10.3354/meps08080

Teschima, M. M., Garrido, A., Paris, A., Nunes, F. L. D., & Zilberberg, C. (2019). Biogeography of the endosymbiotic dinoflagellates (Symbiodiniaceae) community associated with the brooding coral *Favia gravida* in the Atlantic Ocean. *PLoS One*, *14*(3), e0213519. https://doi.org/10.1371/journal.pone.0213519

Thornhill, D. J., LaJeunesse, T. C., Kemp, D. W., Fitt, W. K., & Schmidt, G. W. (2006). Multi-year, seasonal genotypic surveys of coral-algal symbioses reveal prevalent stability or post-bleaching reversion. *Marine Biology*, *148*(4), 711–722. https://doi.org/10.1007/s00227-005-0114-2

Toller, W. W., Rowan, R., & Knowlton, N. (2001). Zooxanthellae of the *Montastraea annularis* species complex: Patterns of distribution of four taxa of *Symbiodinium* on different reefs and across depths. *The Biological Bulletin*, *201*(3), 348–359. https://doi.org/10.2307/1543613

Tonk, L., Sampayo, E. M., Weeks, S., Magno-Canto, M., & Hoegh-Guldberg, O. (2013). Host-specific interactions with environmental factors shape the distribution of *Symbiodinium* across the Great Barrier Reef. *PLoS One*, *8*(7), e68533. https://doi.org/10.1371/journal.pone.0068533

Turnham, K. E., Wham, D. C., Sampayo, E., & LaJeunesse, T. C. (2021). Mutualistic microalgae co-diversify with reef corals that acquire symbionts during egg development. *The ISME Journal*, *1–15*. https://doi.org/10.1038/s41396-021-01007-8

van der Ven, R. M., Flot, J.-F., Buitrago-López, C., & Kochzius, M. (2021). Population genetics of the brooding coral *Seriatopora hystrix* reveals patterns of strong genetic differentiation in the Western Indian Ocean. *Heredity*, *126*(2), 2. https://doi.org/10.1038/s41437-020-00379-5

van Oppen, M. J. H., Bongaerts, P., Frade, P., Peplow, L. M., Boyd, S. E., Nim, H. T., & Bay, L. K. (2018). Adaptation to reef habitats through selection on the coral animal and its associated microbiome. *Molecular Ecology*, *27*(14), 2956–2971. https://doi.org/10.1111/mec.14763

van Oppen, M. J. H., Palstra, F. P., Piquet, A. M.-T., & Miller, D. J. (2001). Patterns of coral-dinoflagellate associations in Acropora: Significance of local availability and physiology of Symbiodinium strains and host-symbiont selectivity. *Proceedings: Biological Sciences*, *268*(1478), 1759–1767.

Vidal-Dupiol, J., Chaparro, C., Pratlong, M., Pontarotti, P., Grunau, C., & Mitta, G. (2020). Sequencing, de novo assembly and annotation of the genome of the scleractinian coral, *Pocillopora acuta*. *bioRxiv*, 698688. https://doi.org/10.1101/698688

Wang, I. J., & Bradburd, G. S. (2014). Isolation by environment. *Molecular Ecology*, *23*(23), 5649–5662. https://doi.org/10.1111/mec.12938

Weis, V. M. (2008). Cellular mechanisms of cnidarian bleaching: Stress causes the collapse of symbiosis. *Journal of Experimental Biology*, *211*(19), 3059–3066. https://doi.org/10.1242/jeb.009597

Wepfer, P. H., Nakajima, Y., Sutthacheep, M., Radice, V. Z., Richards, Z., Ang, P., Terraneo, T., Sudek, M., Fujimura, A., Toonen, R. J., Mikheyev, A. S., Economo, E. P., & Mitarai, S. (2020). Evolutionary biogeography of the reef-building coral genus *Galaxea* across the Indo-Pacific ocean. *Molecular Phylogenetics and Evolution*, *151*, 106905. https://doi.org/10.1016/j.ympev.2020.106905

Wickham, H. (2016). Programming with ggplot2. In H. Wickham (Ed.), *Ggplot2: Elegant graphics for data analysis* (pp. 241–253). Springer International Publishing. https://doi.org/10.1007/978-3-319-24277-4_12

Wicks, L. C., Sampayo, E., Gardner, J. P. A., & Davy, S. K. (2010). Local endemicity and high diversity characterise high-latitude coral–Symbiodinium partnerships. *Coral Reefs*, *29*(4), 989–1003. https://doi.org/10.1007/s00338-010-0649-7

Ziegler, M., Arif, C., Burt, J. A., Dobretsov, S., Roder, C., LaJeunesse, T. C., & Voolstra, C. R. (2017). Biogeography and molecular diversity of coral symbionts in the genus *Symbiodinium* around the Arabian peninsula. *Journal of Biogeography*, *44*(3), 674–686. https://doi.org/10.1111/jbi.12913

BIOSKETCH

Victoria M. Glynn is broadly interested in how the interactions between corals and their microorganisms may serve as a critical response mechanism to environmental stress. This work represents part of her PhD research at McGill University (Montréal, Québec) and the Smithsonian Tropical Research Institute (Panama City, Panama).

Author Contributions: Victoria M. Glynn, Steven V. Vollmer, David I. Kline and Rowan D.H. Barrett conceived the ideas, Victoria M. Glynn downloaded and analysed the data, Victoria M. Glynn led the writing with assistance of Steven V. Vollmer, David I. Kline and Rowan D. H. Barrett.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Glynn, V. M., Vollmer, S. V., Kline, D. I., & Barrett, R. D. H. (2023). Environmental and geographical factors structure cauliflower coral's algal symbioses across the Indo-Pacific. *Journal of Biogeography*, *50*, 669–684. https://doi.org/10.1111/jbi.14560